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Physiological adaptations of ruminants and their potential relevance for production systems

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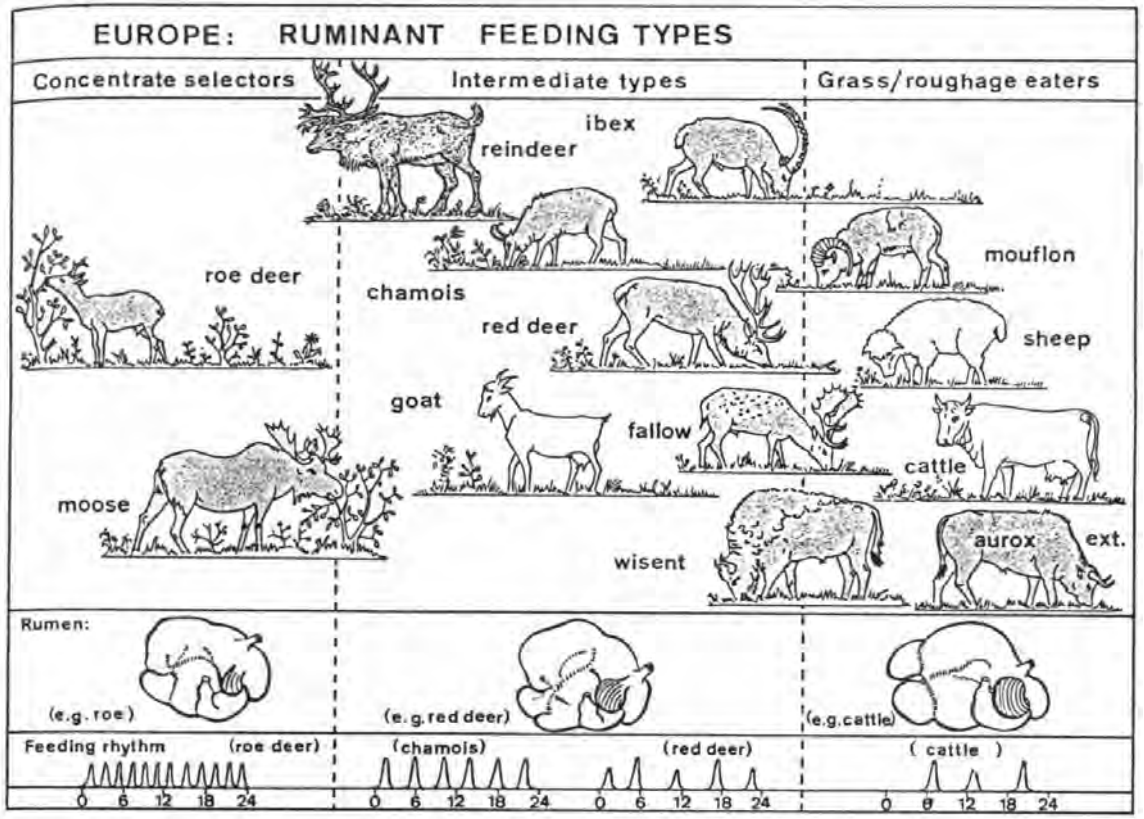
Clinic of Zoo Animals, Exotic Pets and Wildlife

Comparative physiology

- Understanding adaptations by the comparative method



from Hofmann (1989)

Digestive adaptations

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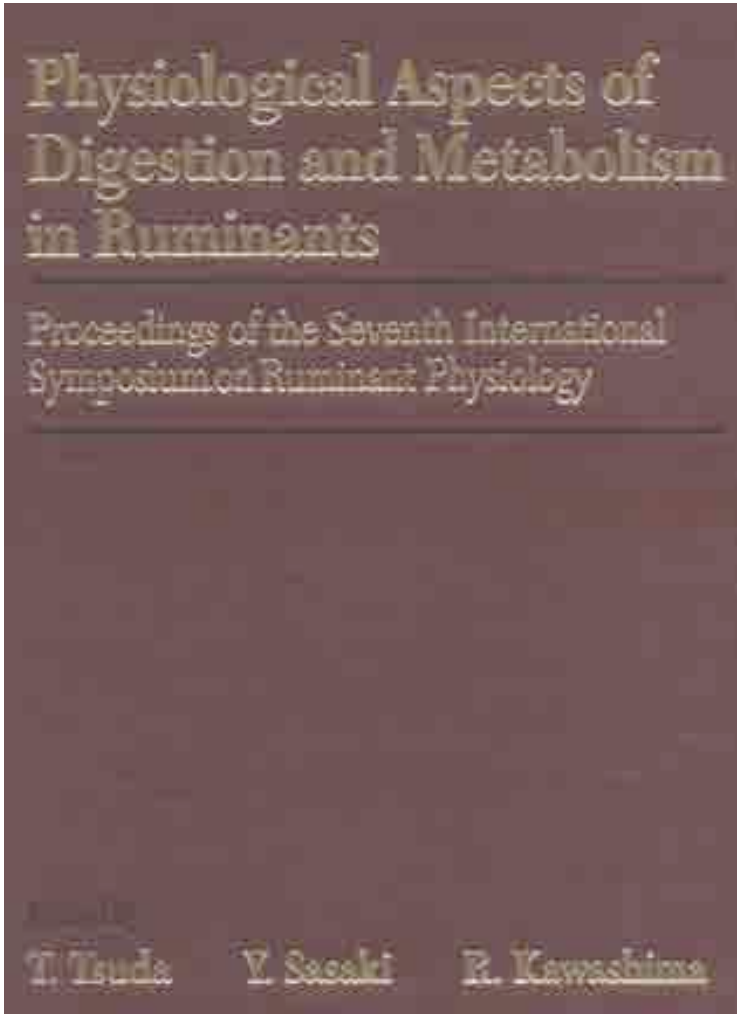

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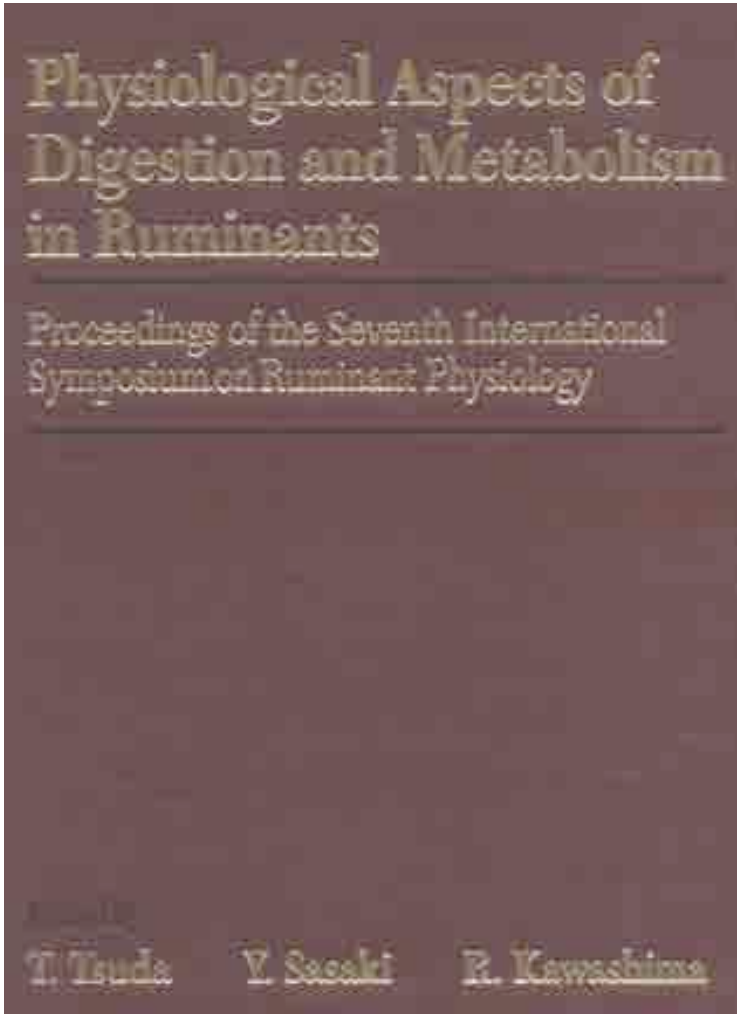

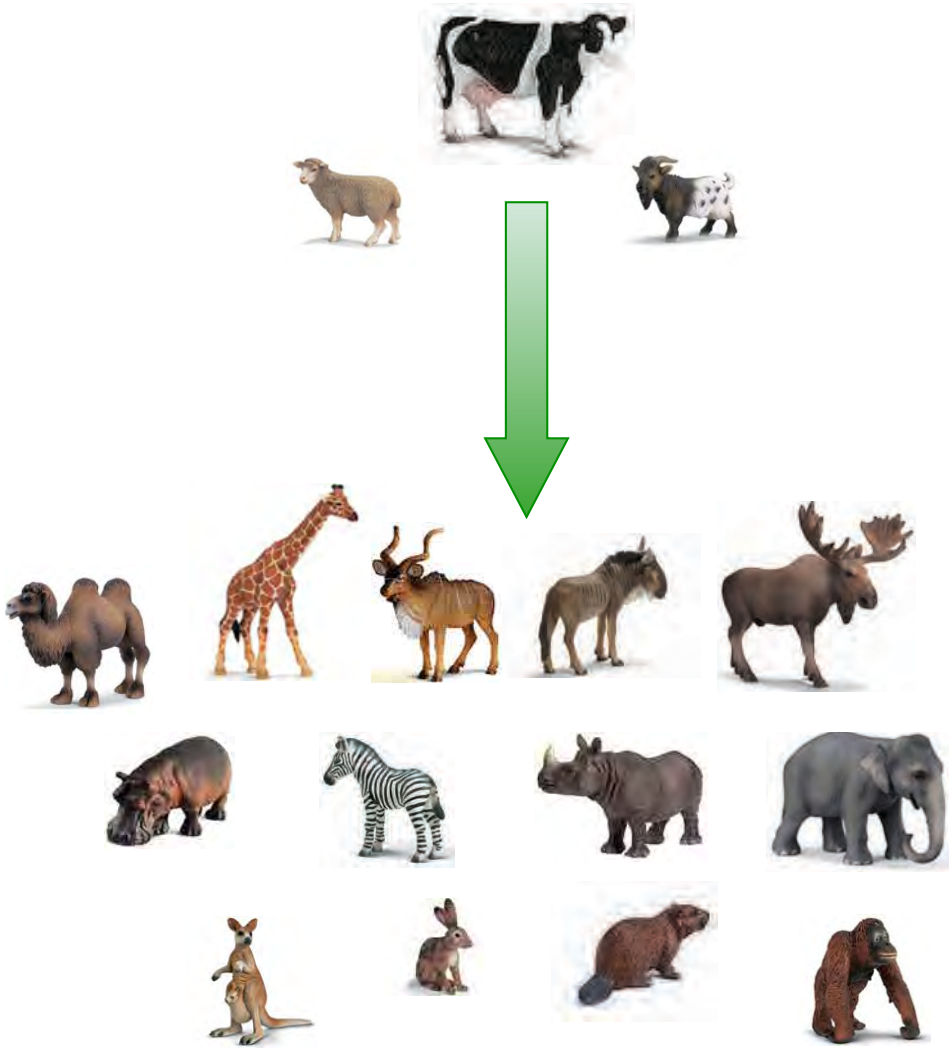

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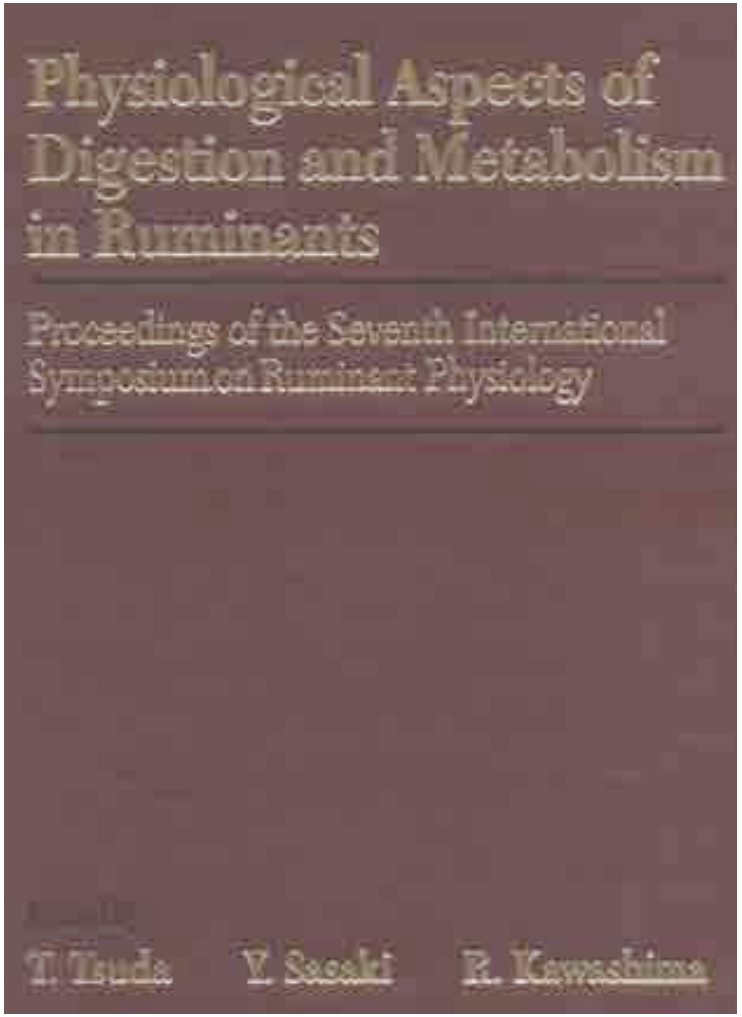

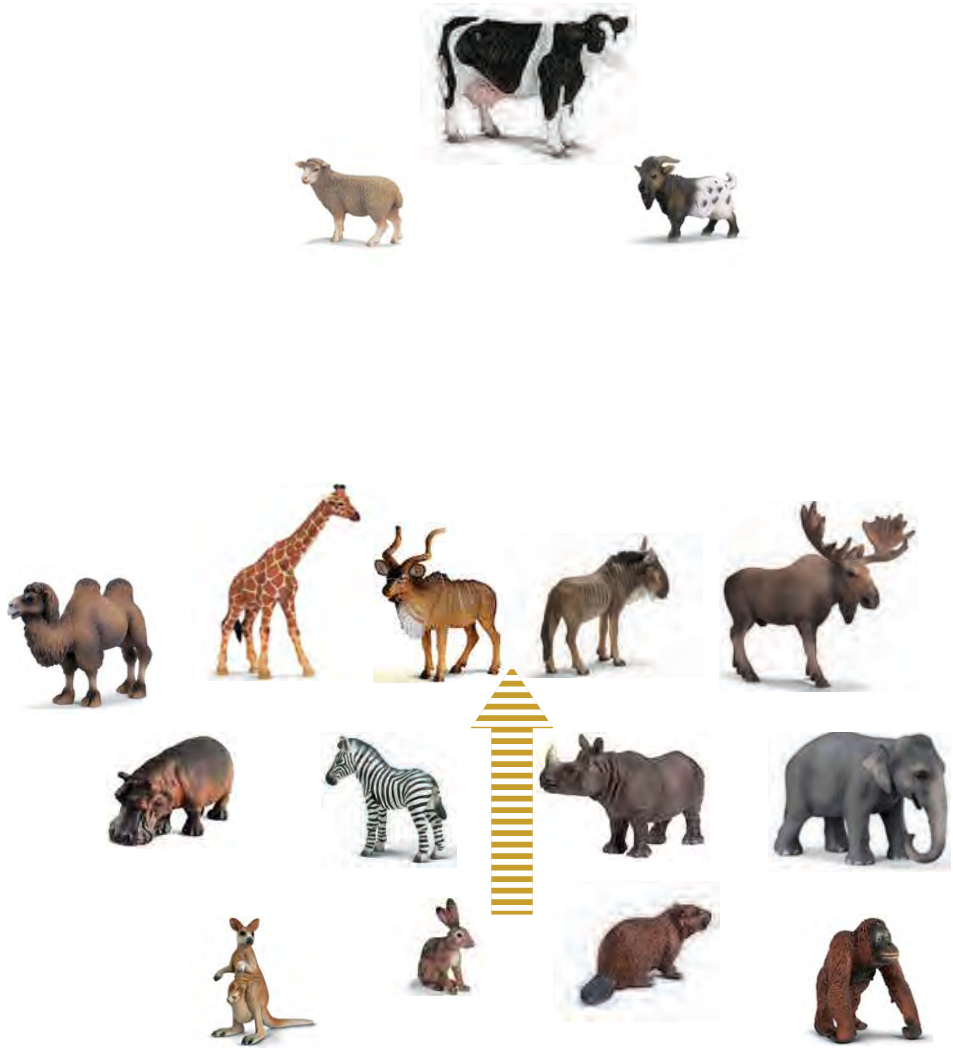

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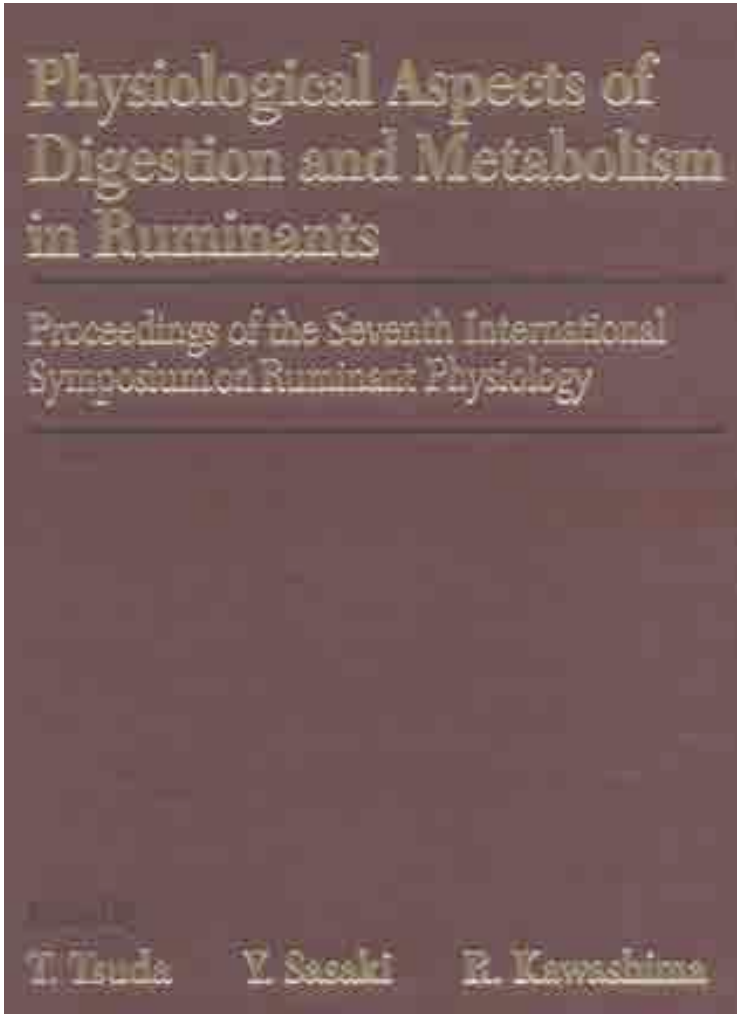

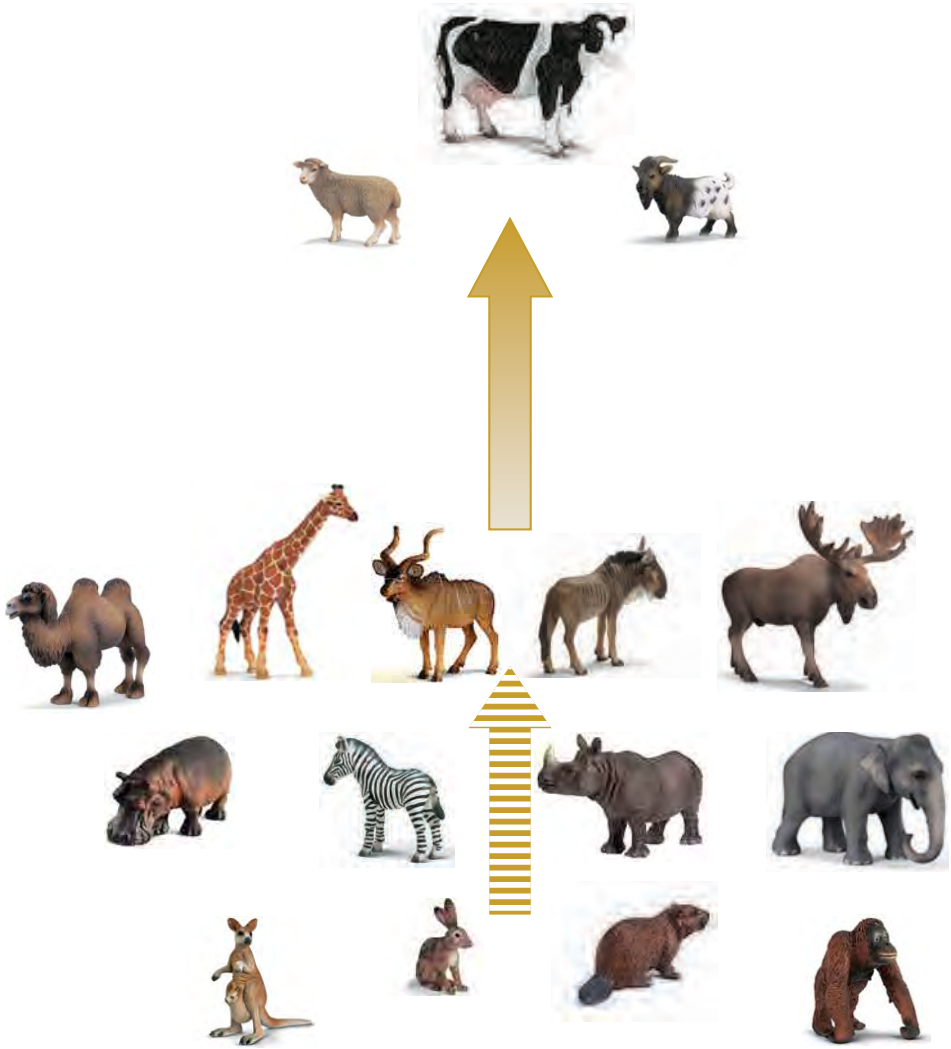

What comparative digestive physiology can offer to domestic ruminant research

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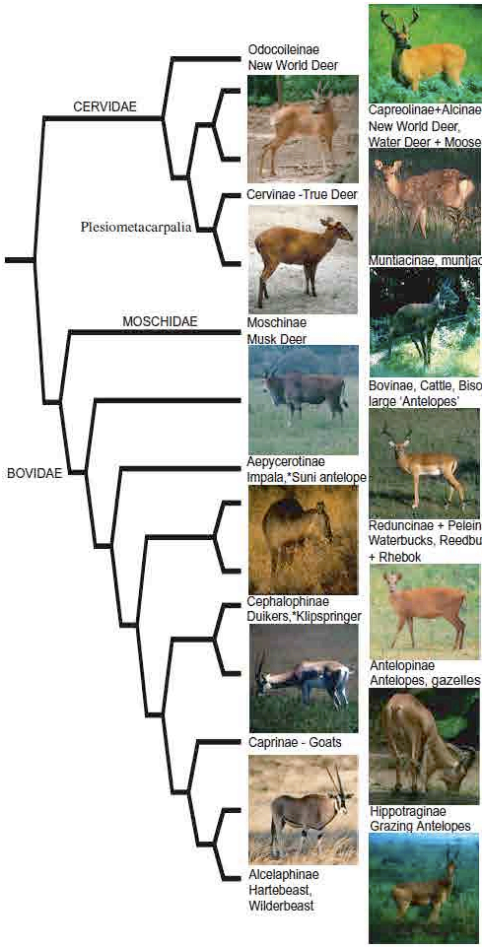
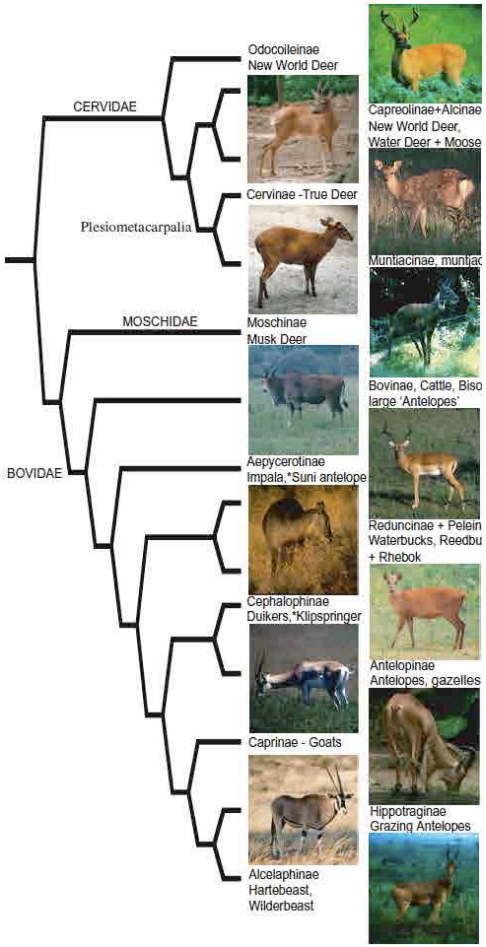
- Understanding where domestic ruminants ‘came from’ among the ruminants



from Agnarsson et al. (2008)

What comparative digestive physiology can offer to domestic ruminant research

- Understanding where domestic ruminants ‘came from’ among the ruminants ...



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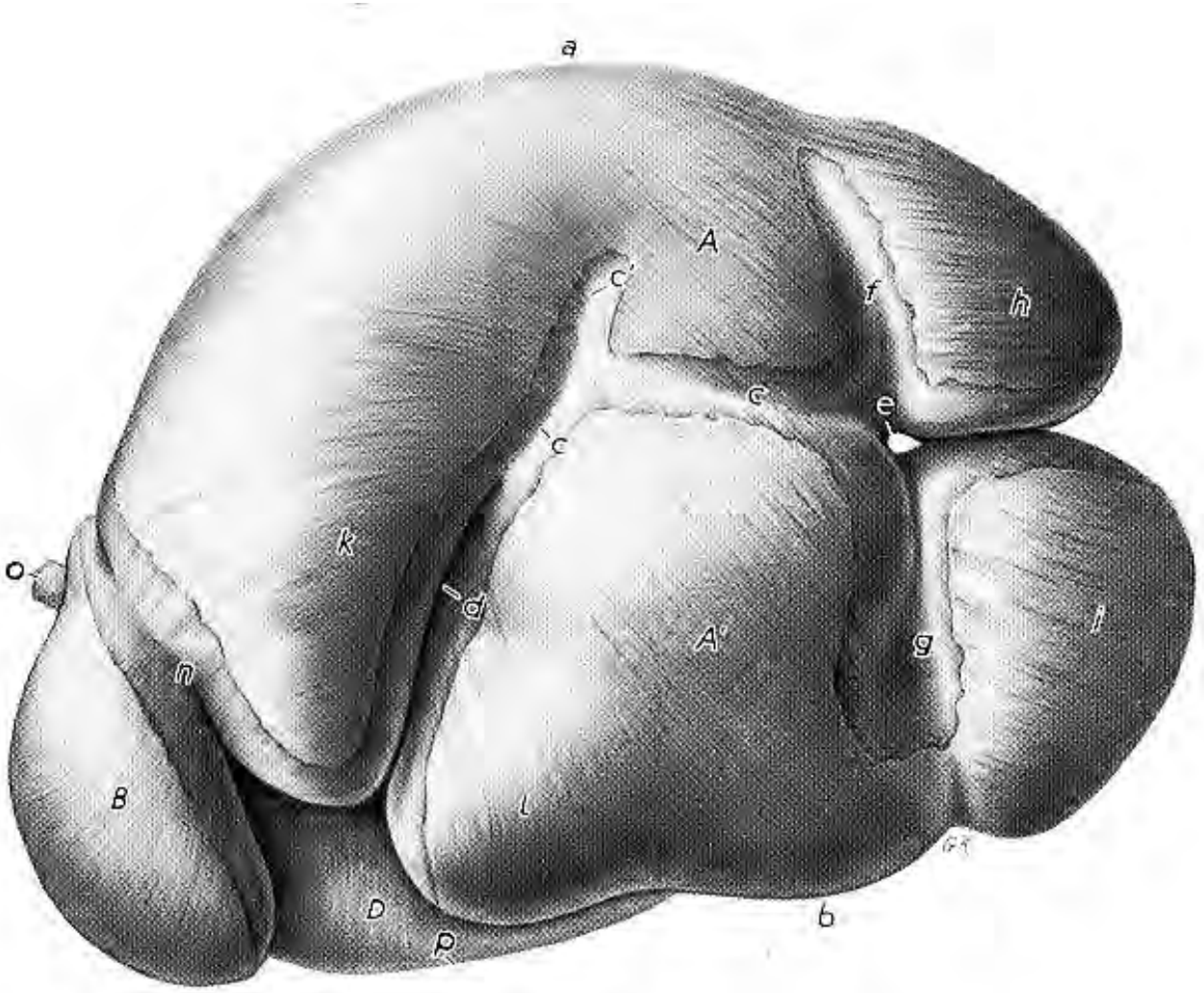
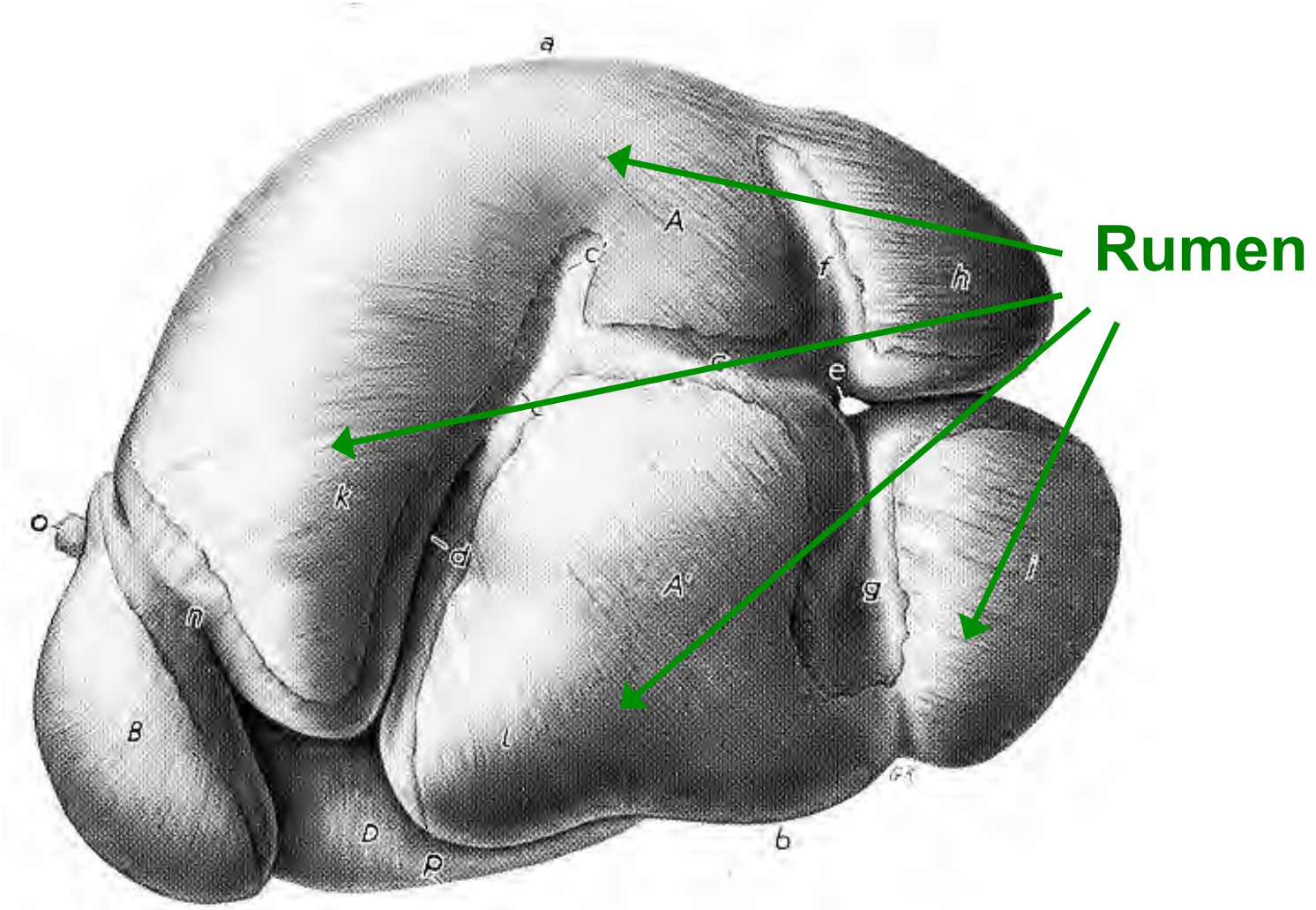
... and where they might be taken to in the future



(from Nickel-Schummer-Seiferle 1967)



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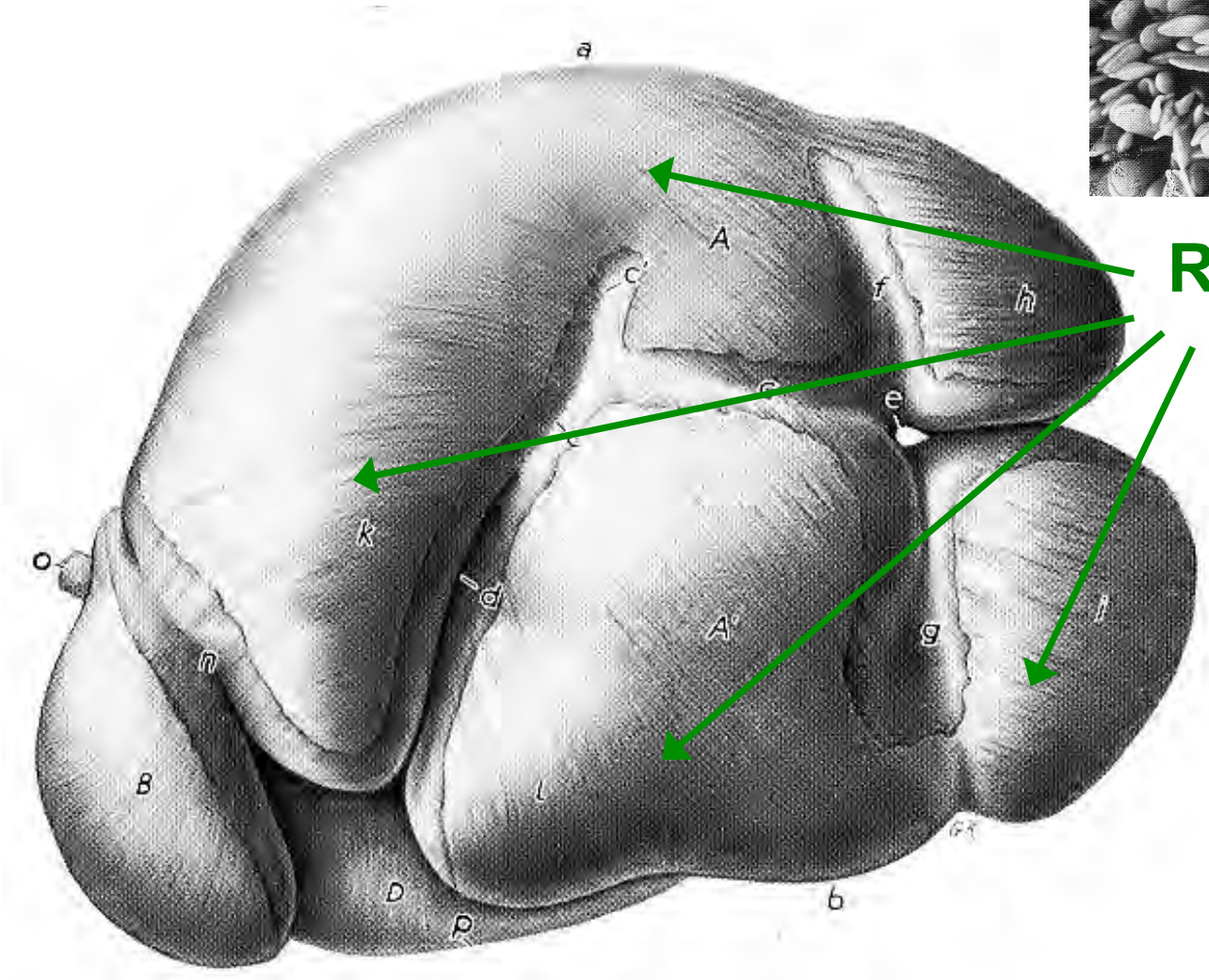
Rumen



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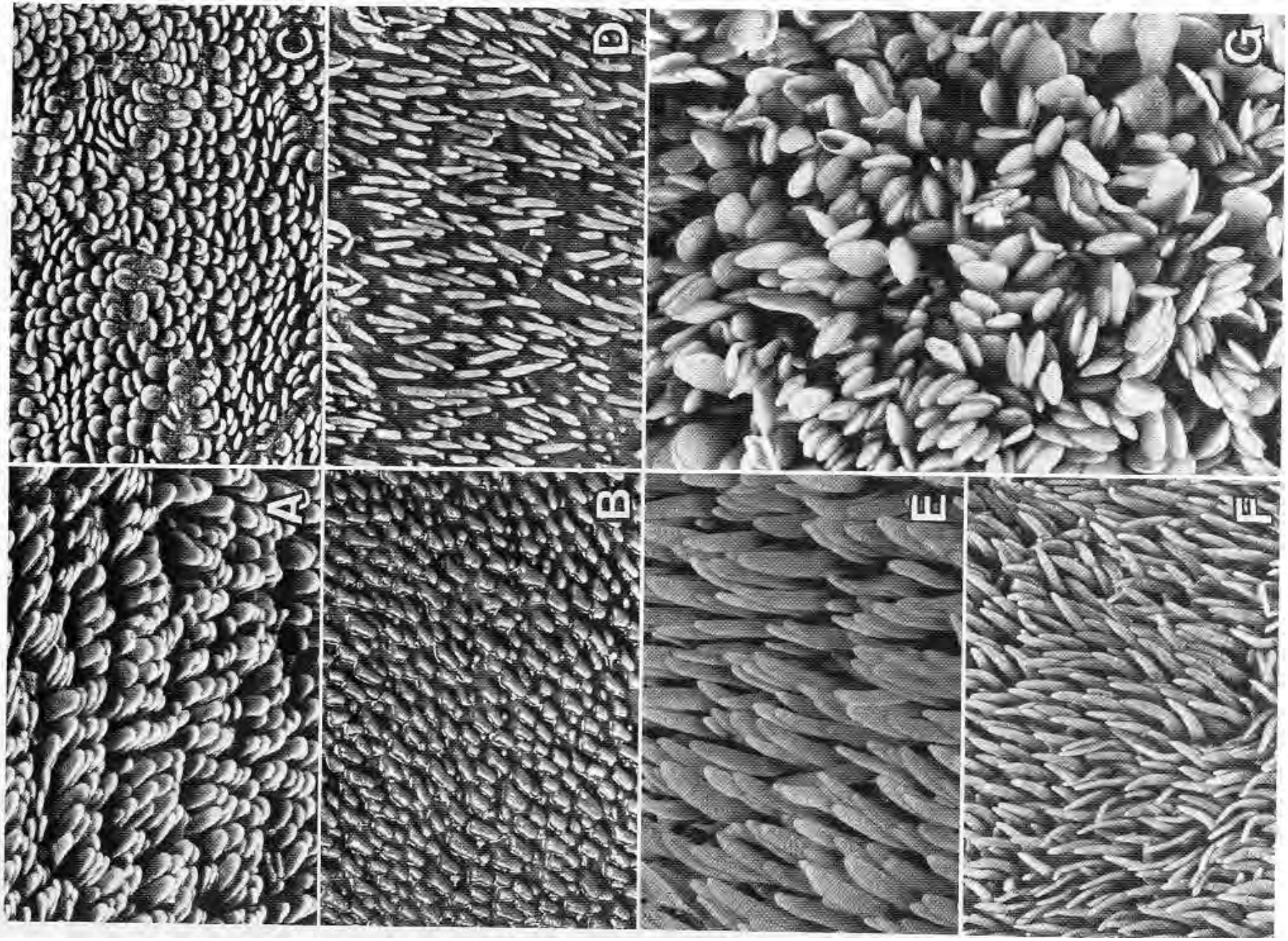
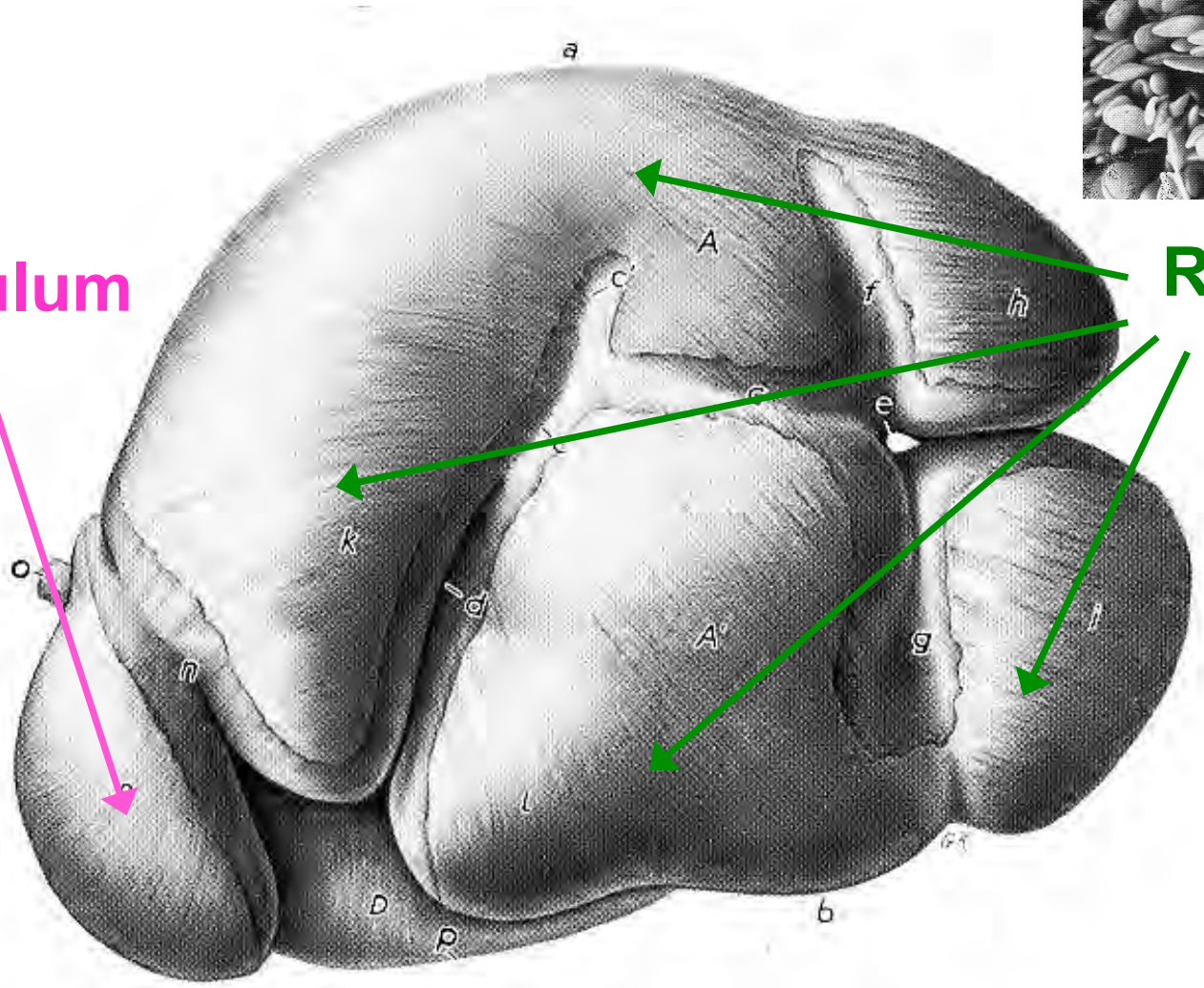


(from Hofmann & Schnorr1982)

Reticulum

Rumen



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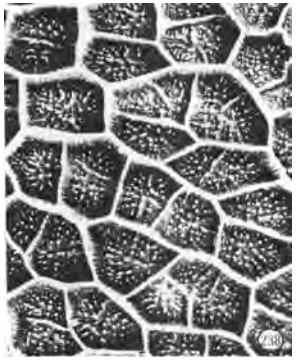

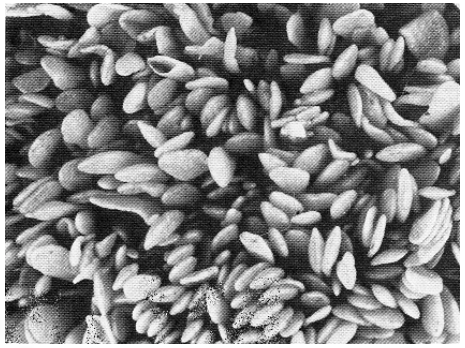

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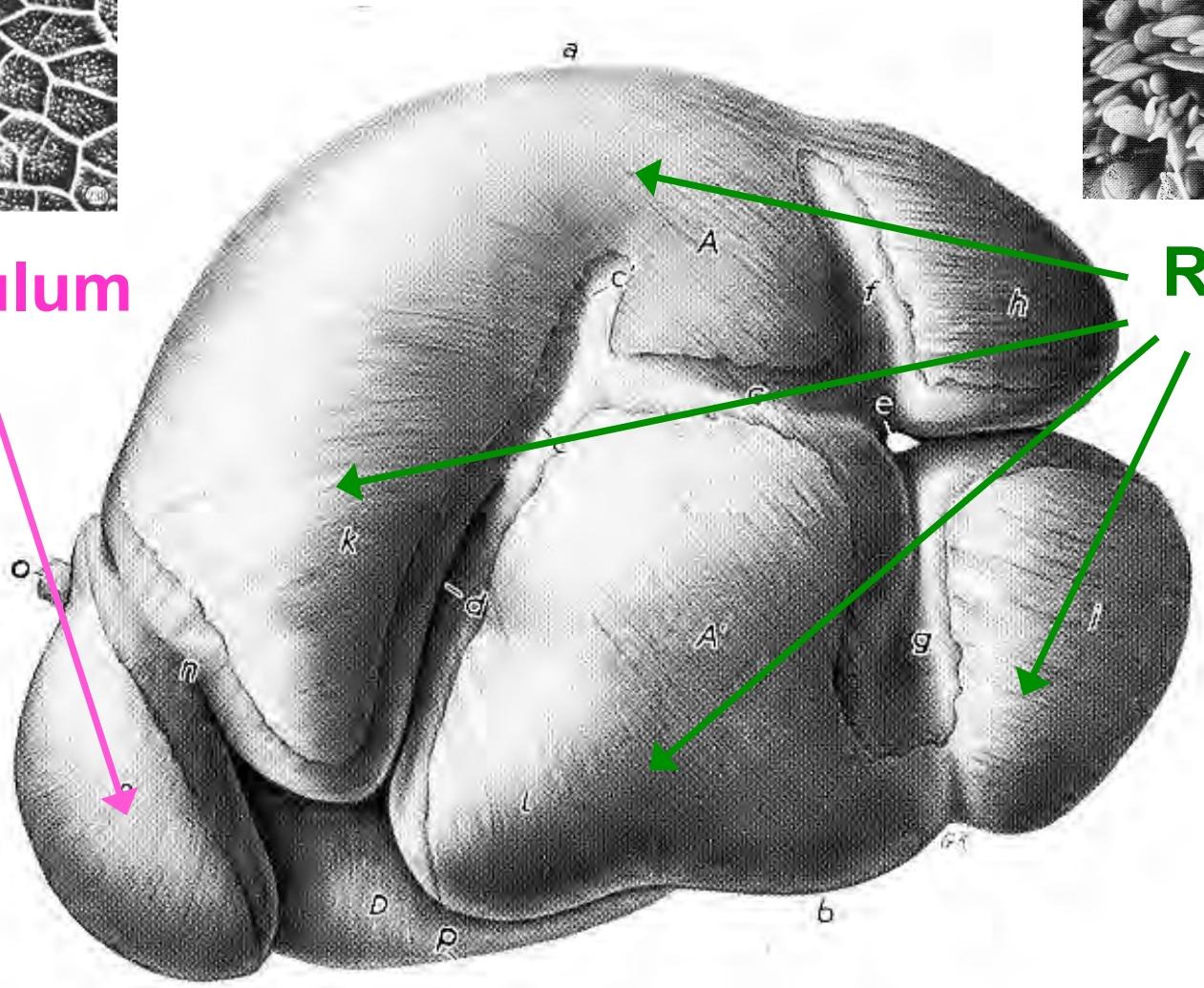

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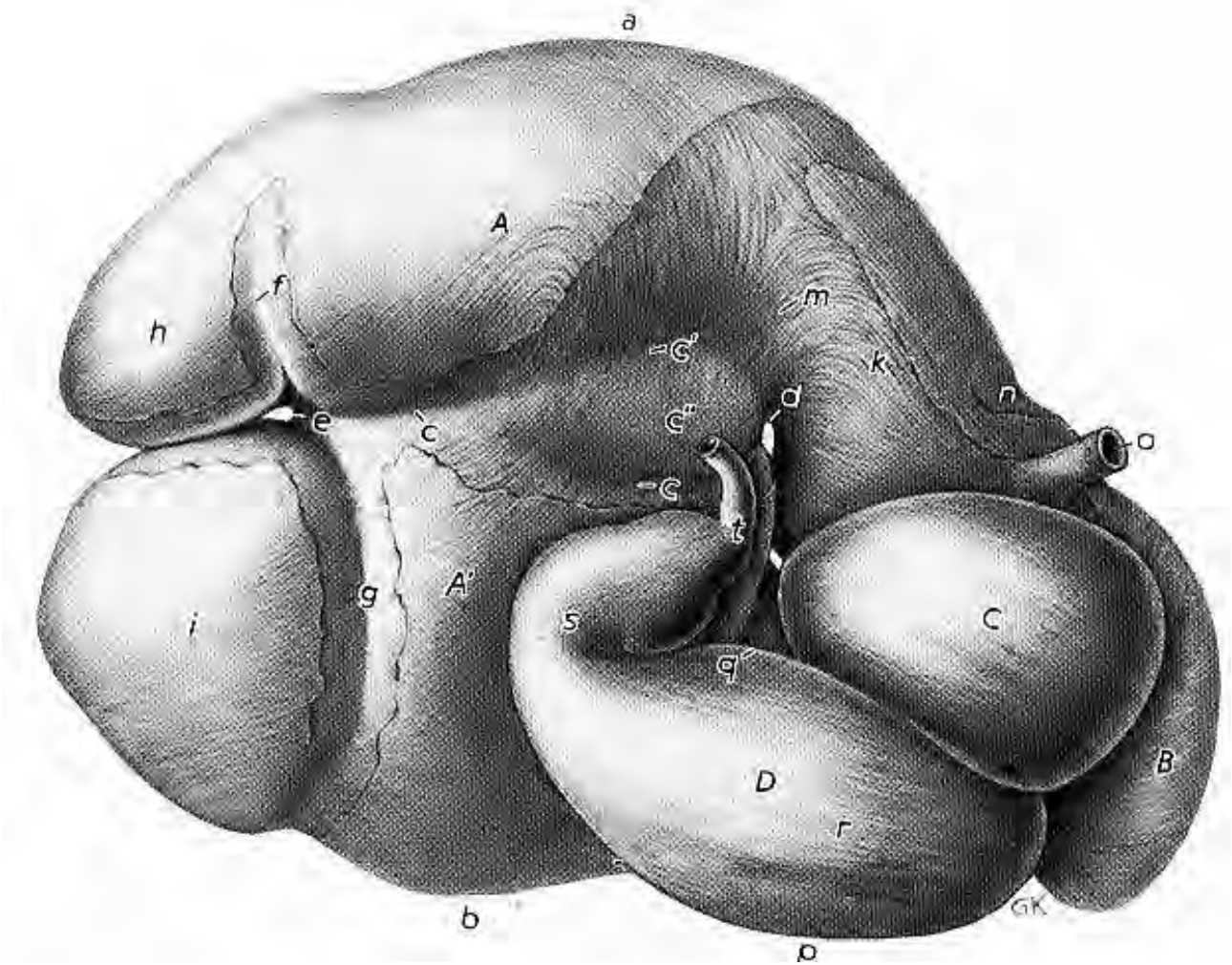

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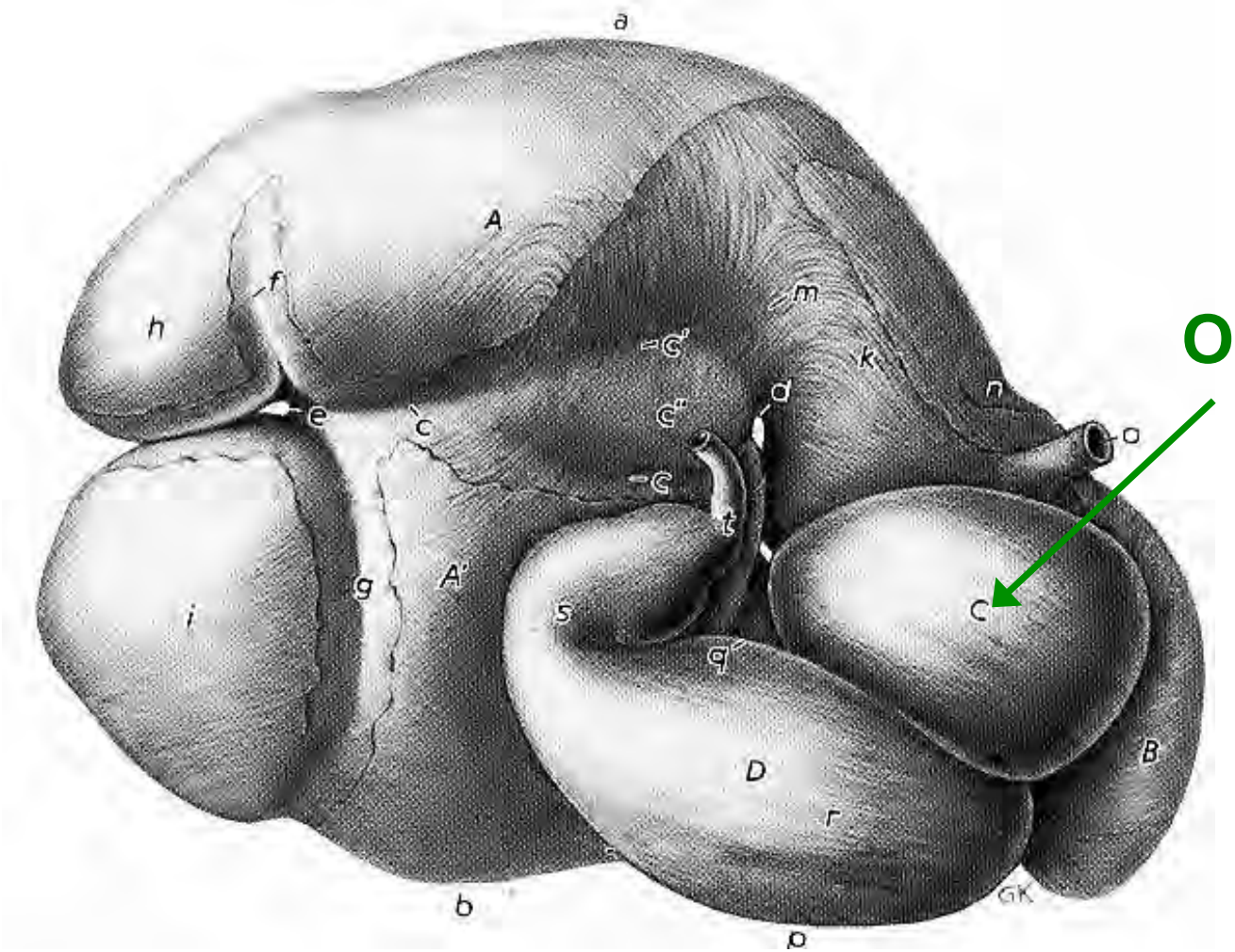
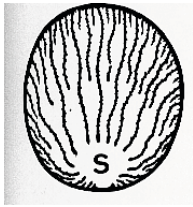


Omasum

(from Nickel-Schummer-Seiferle 1967)



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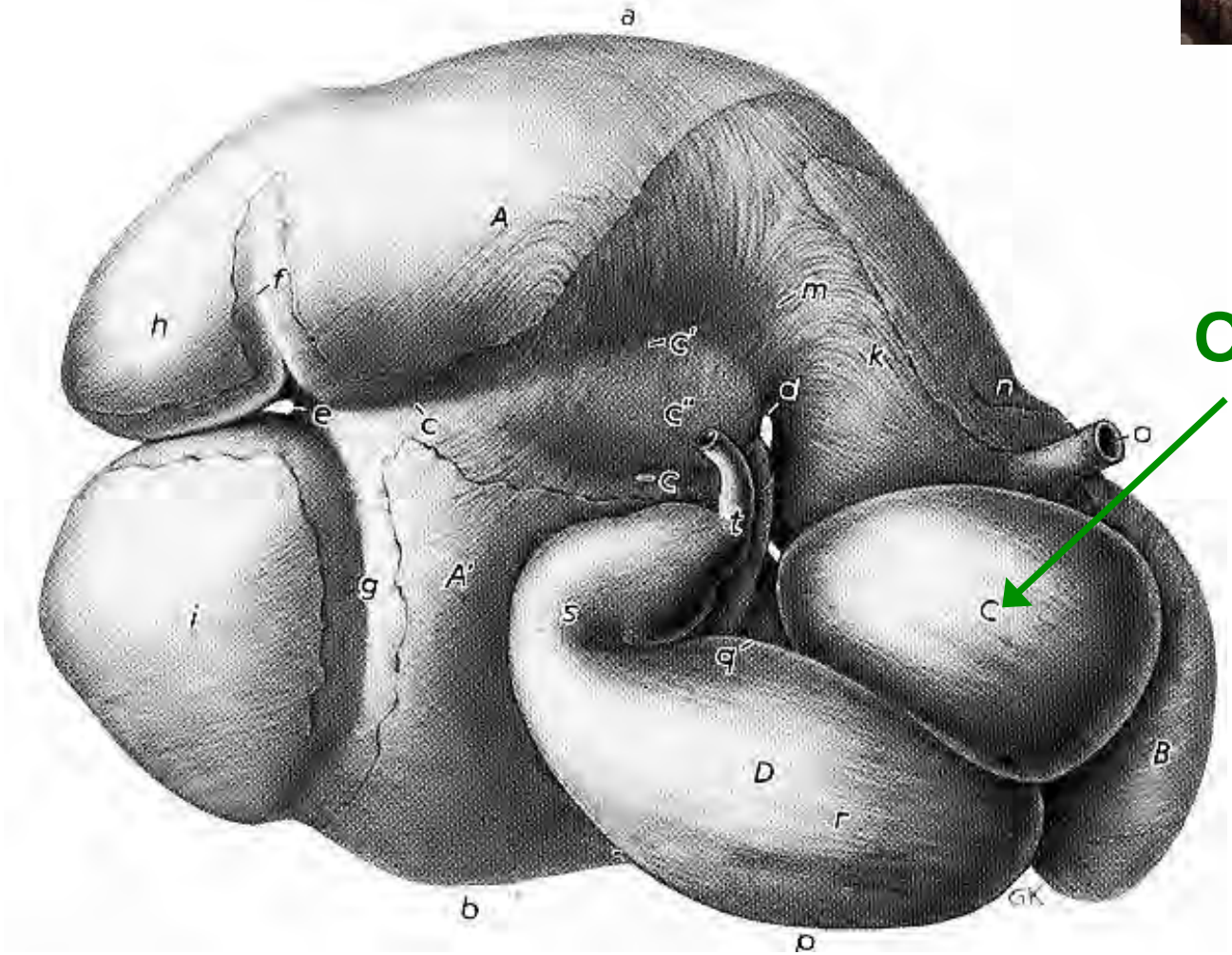

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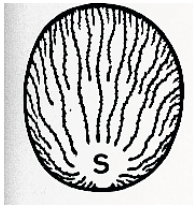
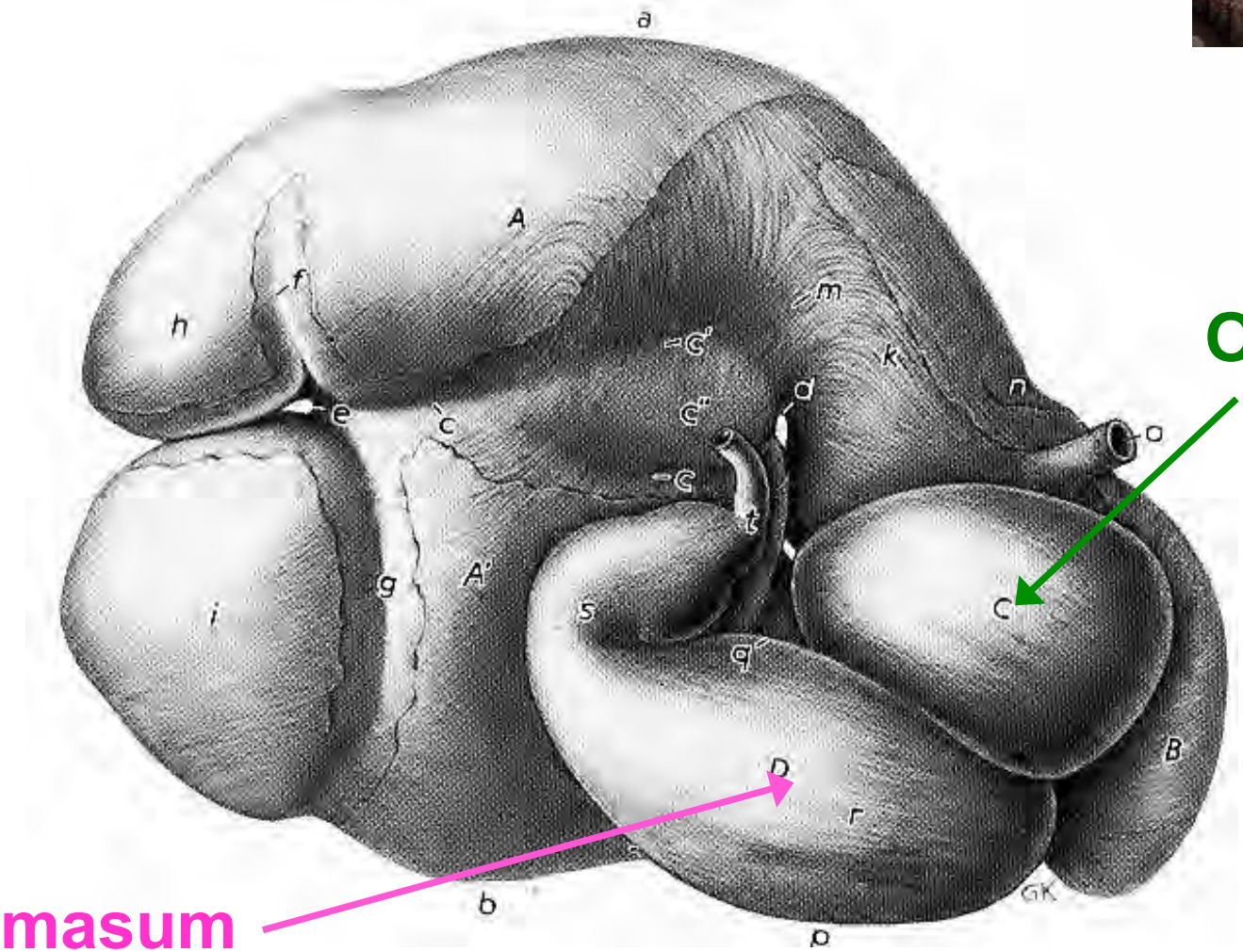


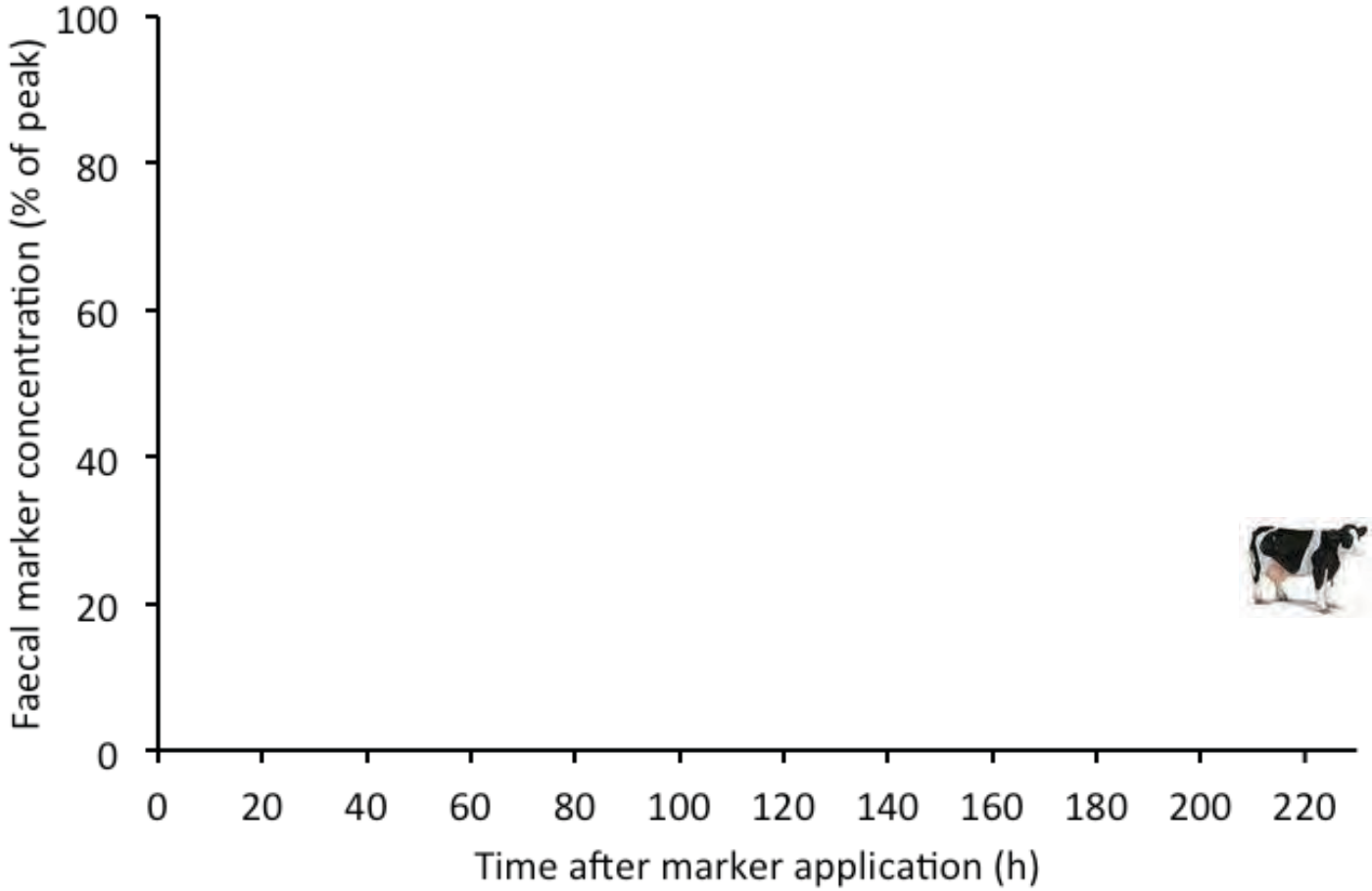


Omasum

Abomasum

(from Nickel-Schummer-Seiferle 1967)

Passage kinetics of markers: ‘cattle-type’



from Lechner et al. (2010)

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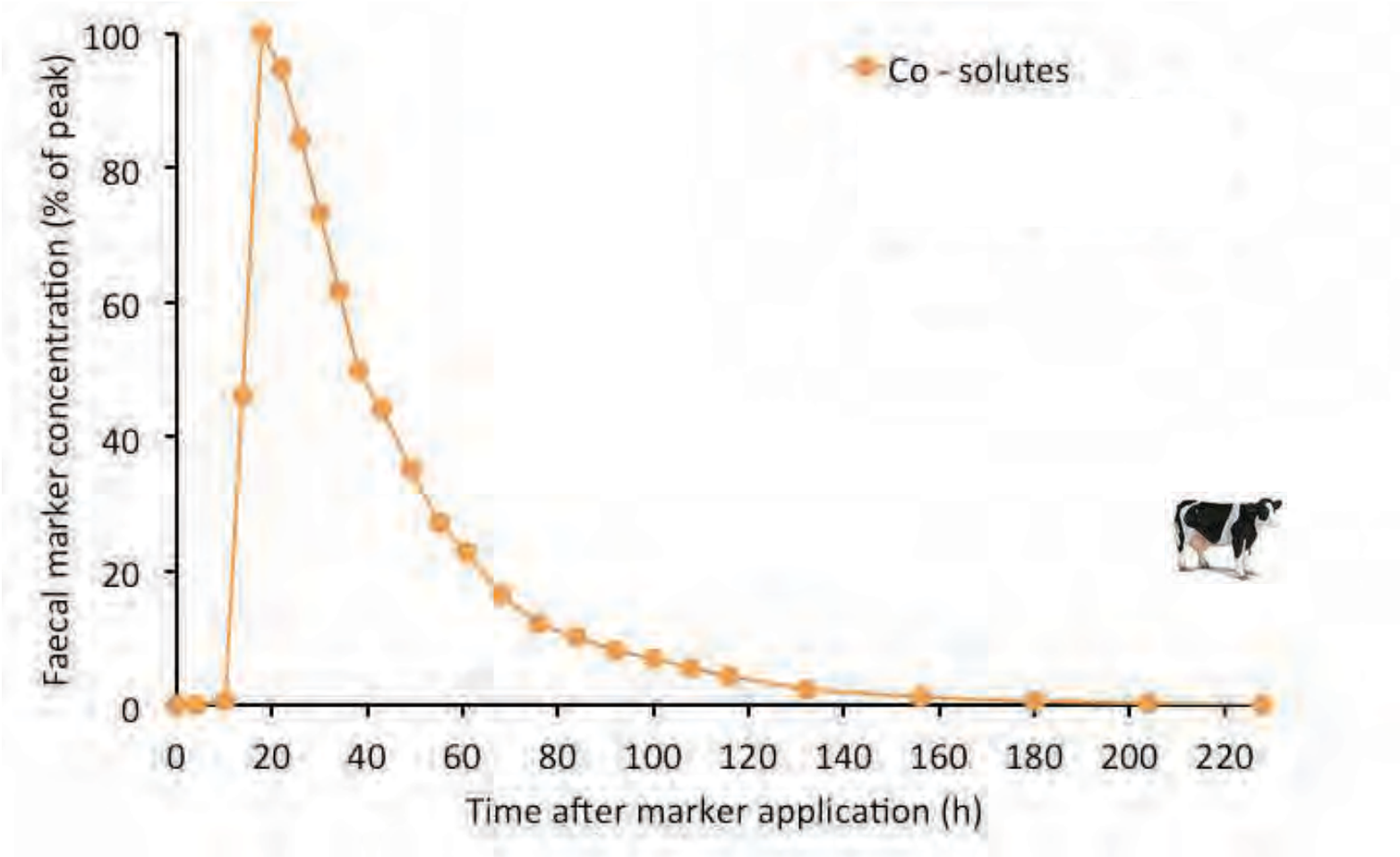

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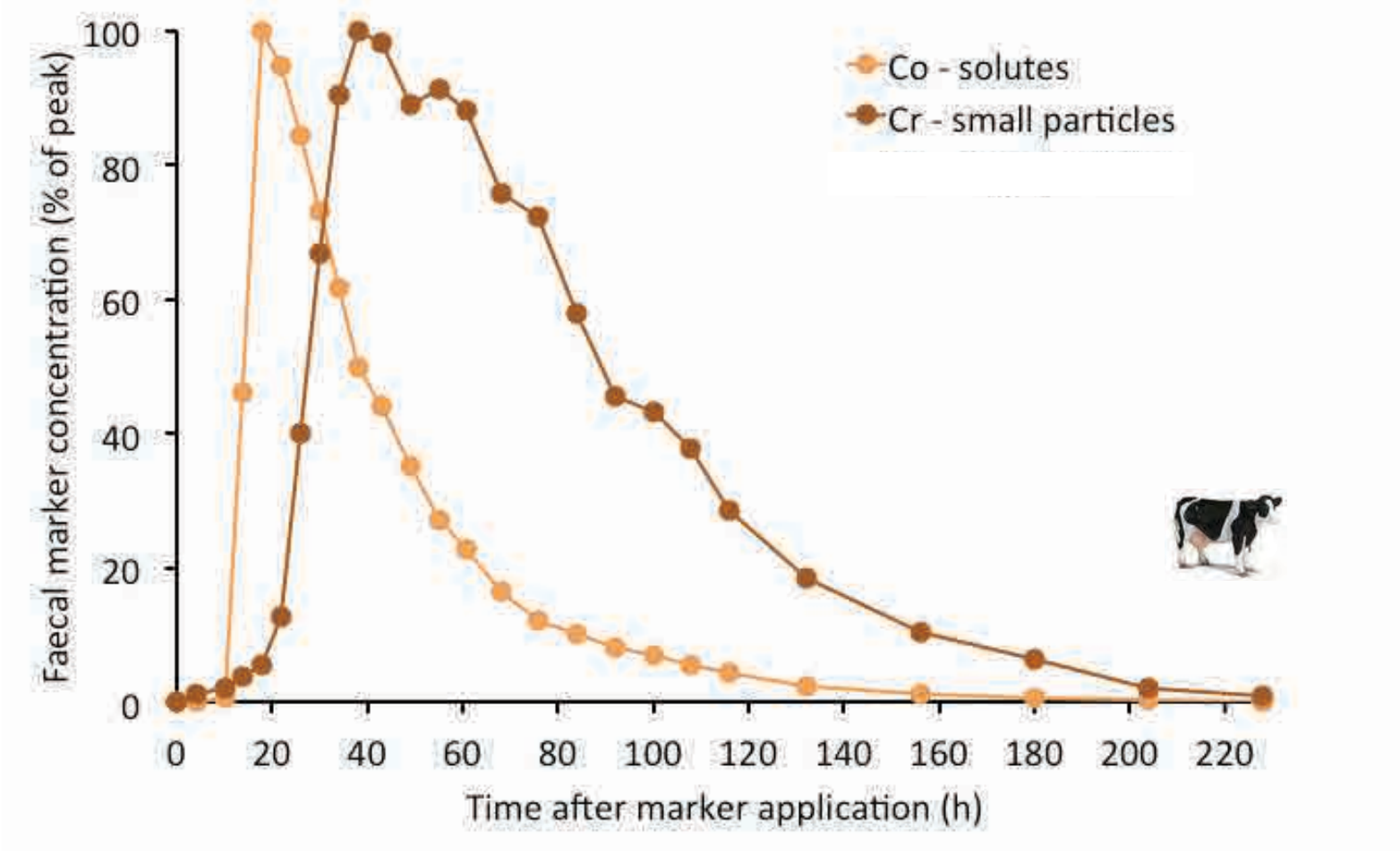

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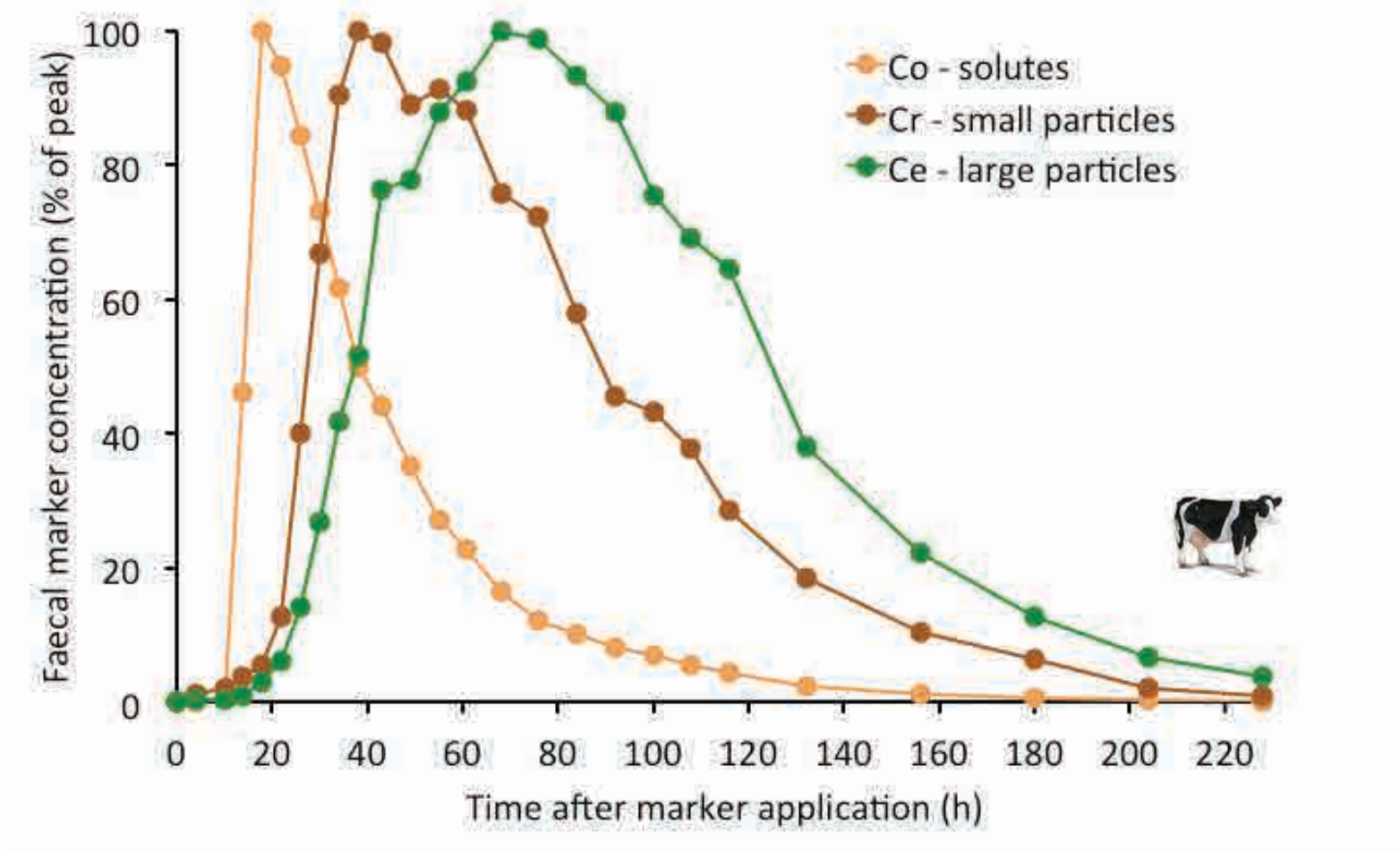

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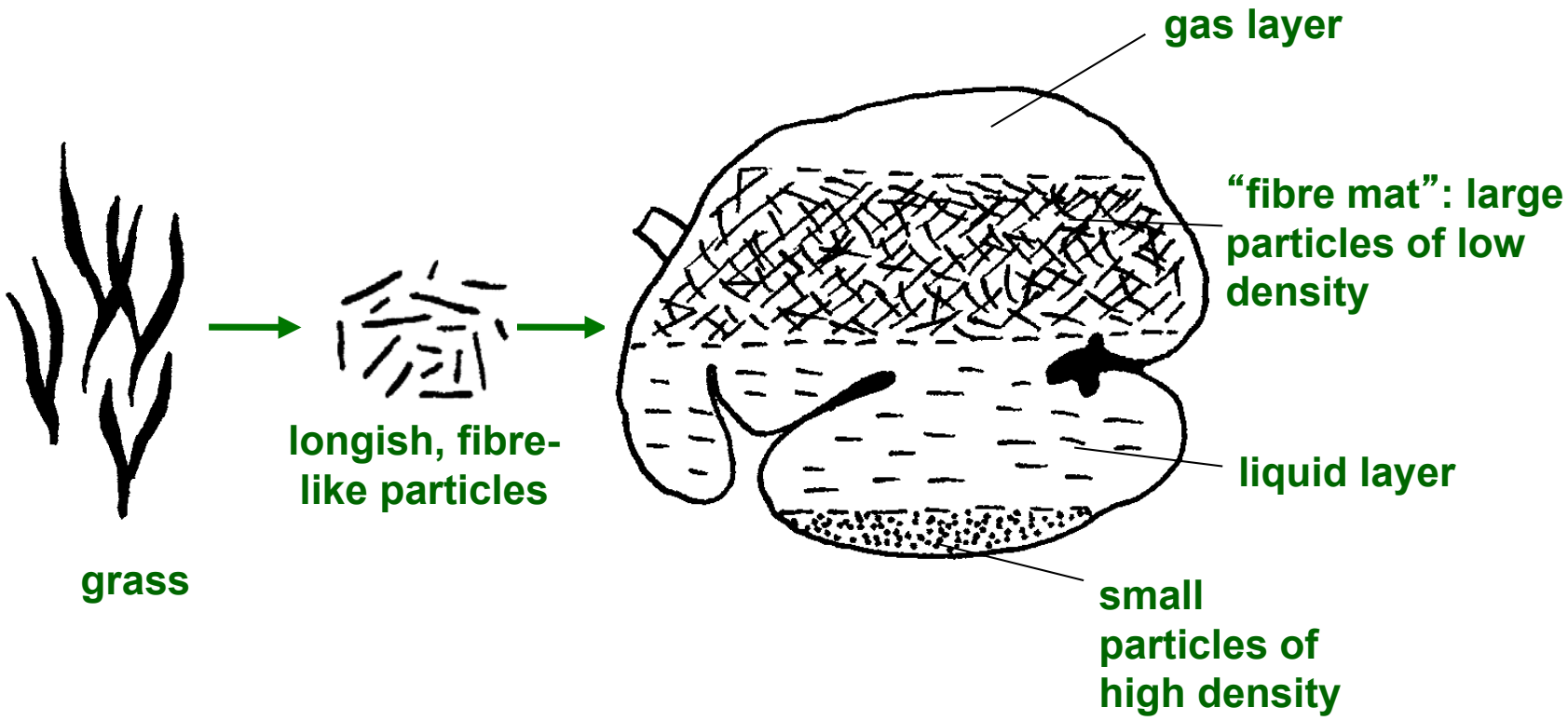
Stratification of rumen contents: ‘cattle-type’



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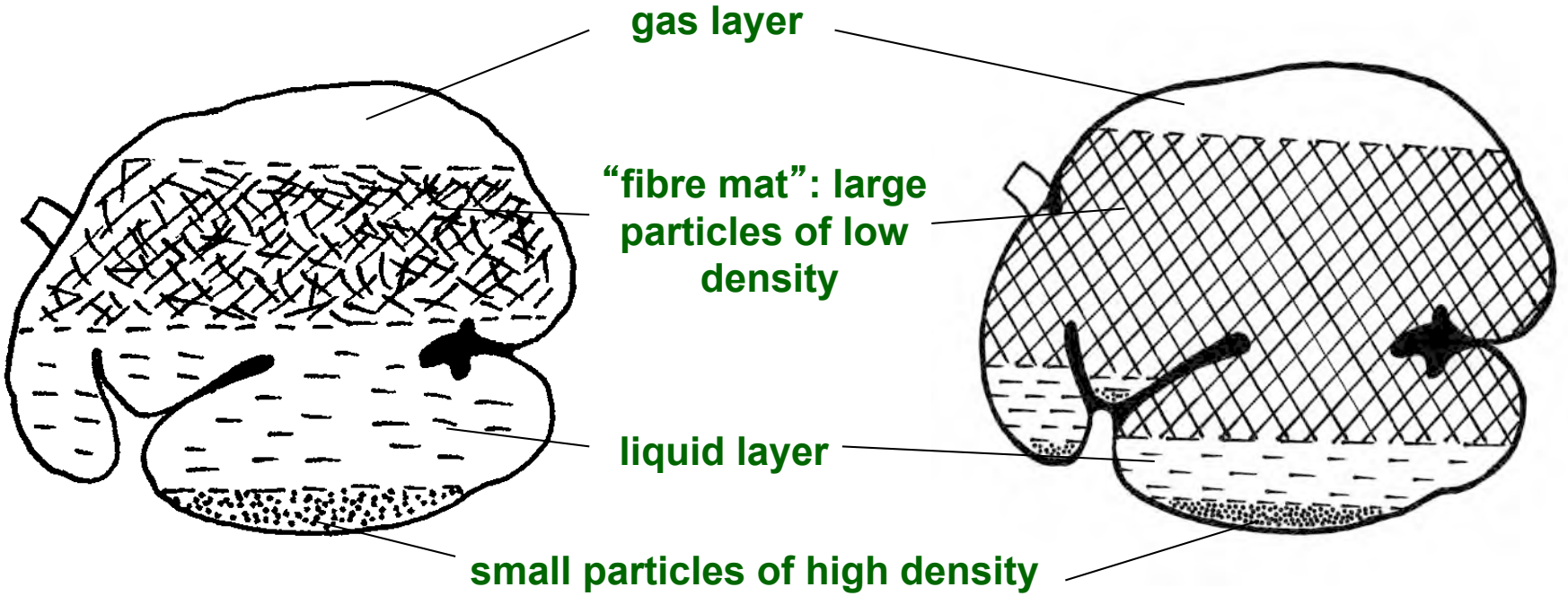
Stratification of rumen contents: ‘cattle-type’



from Hummel et al. (2009)

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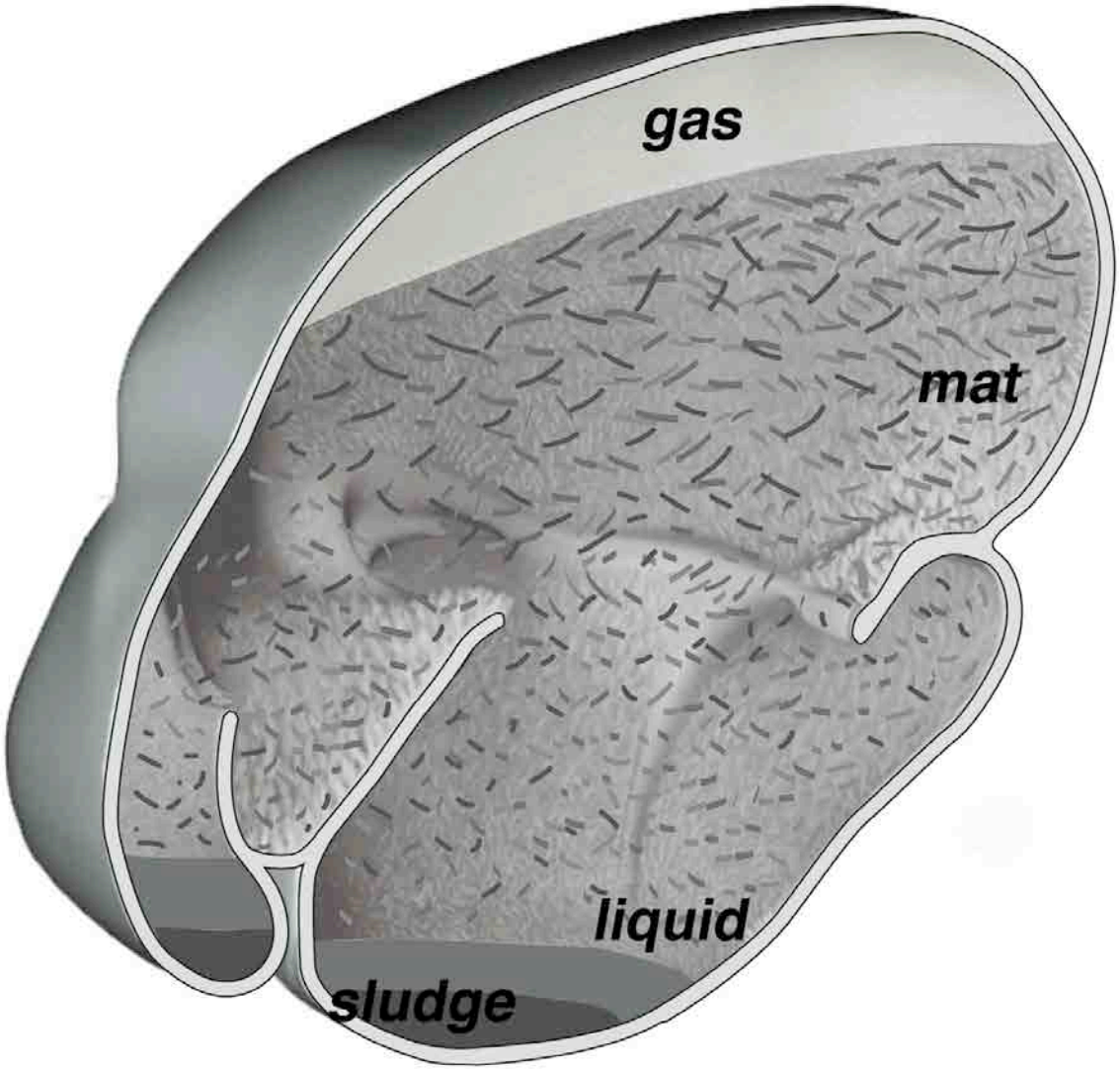
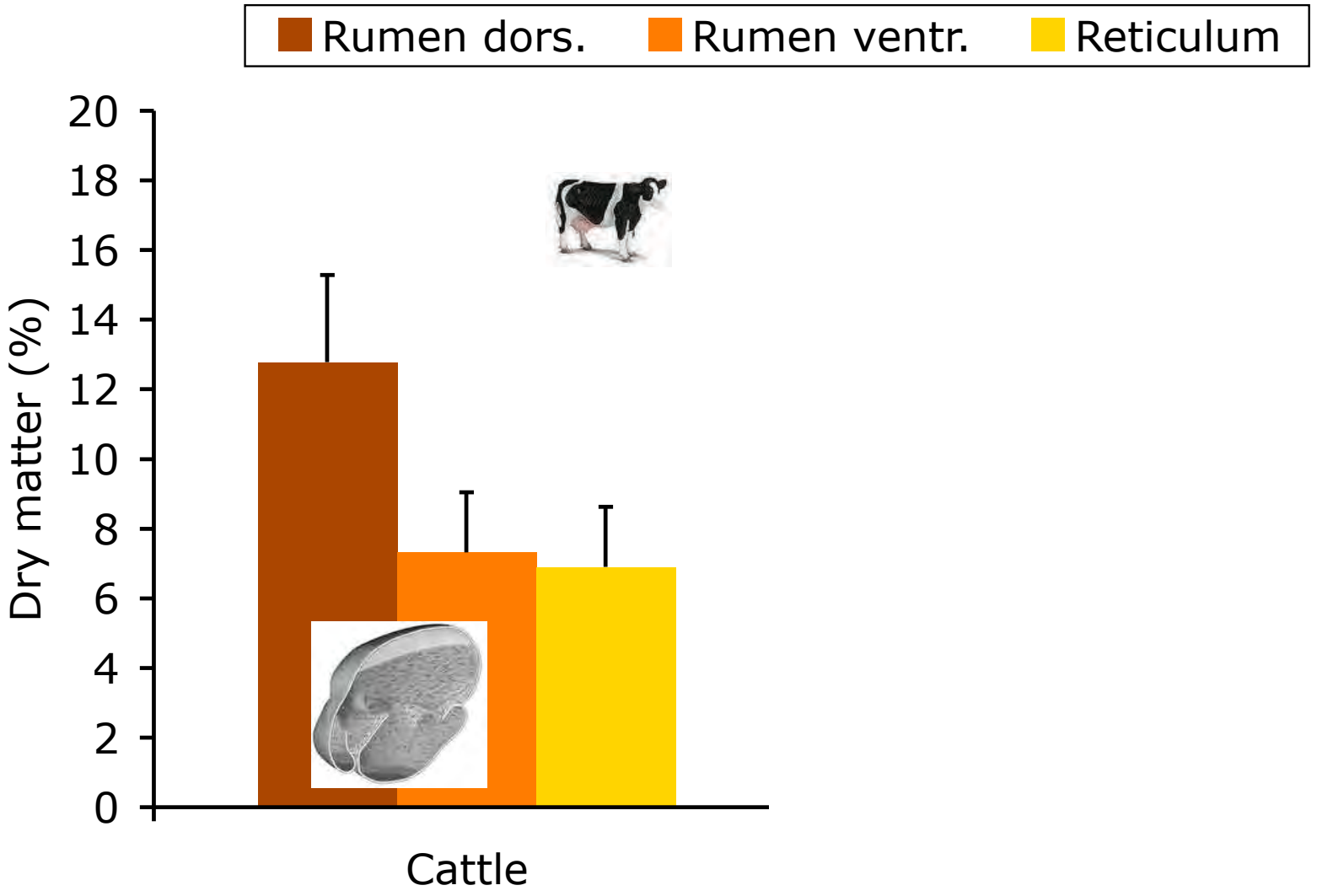


from Clauss et al. (2010)

Rumen of addax - a grazer

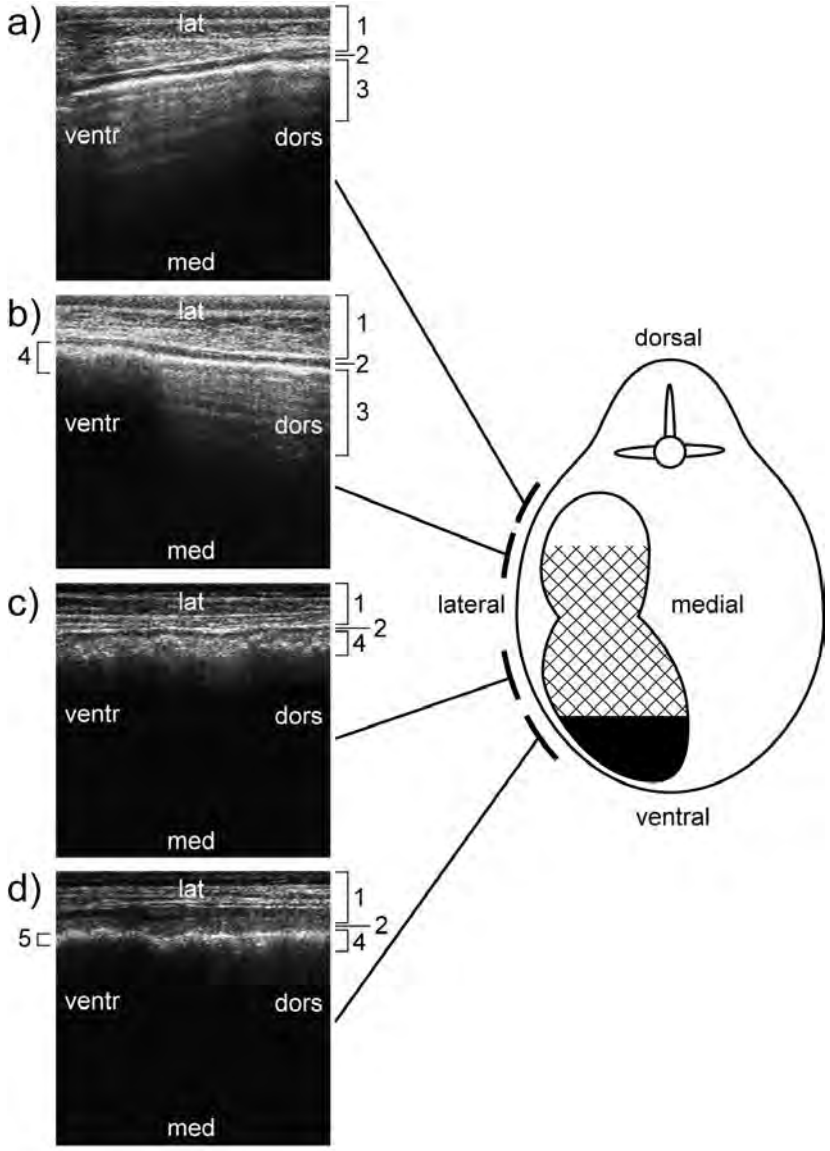
from Clauss et al. (2009)

Stratification of rumen contents



from Clauss et al. (2010)

Testing stratification by ultrasound - cattle

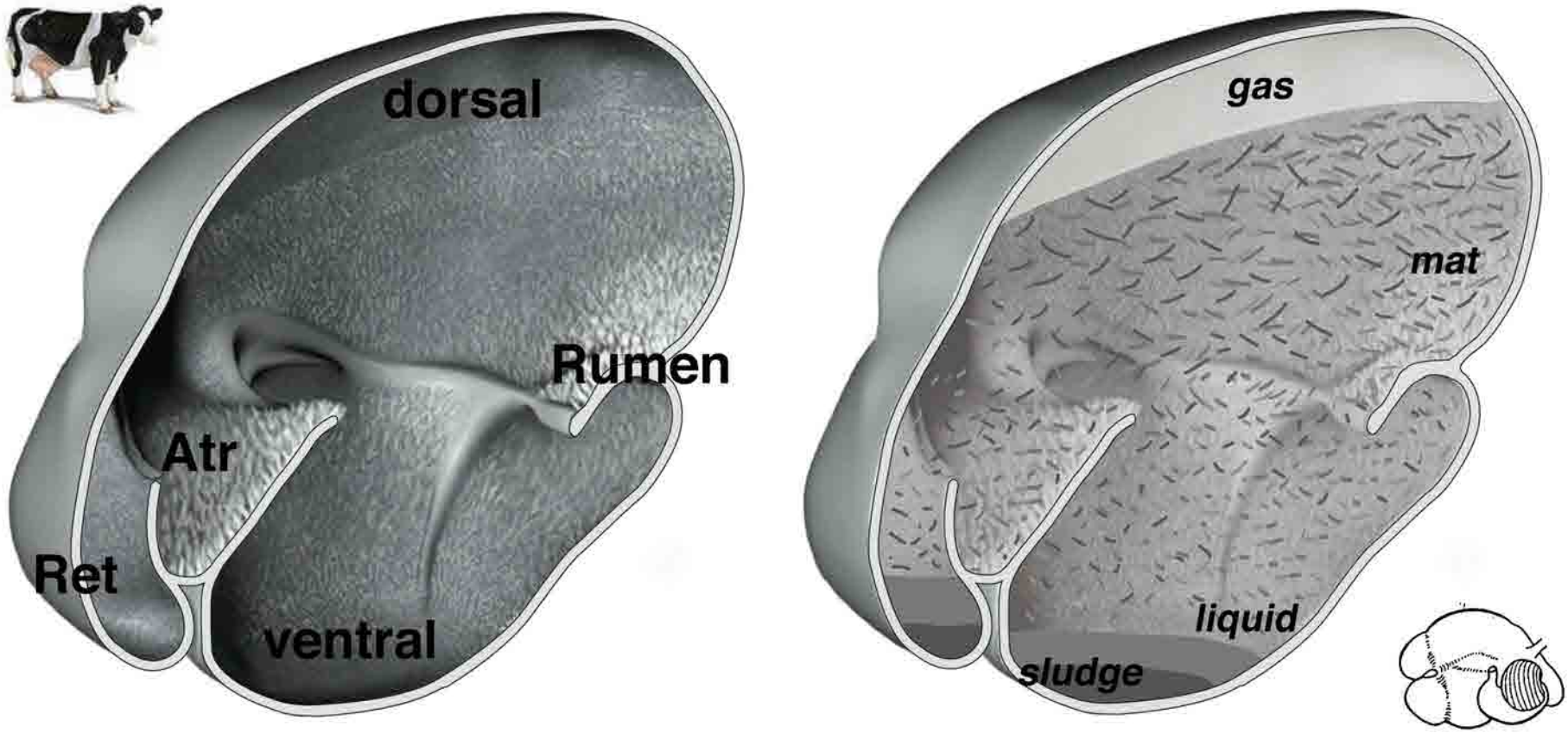


from Tschuor & Clauss (2008)

Stratification and rumen papillation

from Clauss, Hofmann et al. (2009)

Stratification and rumen papillation



from Clauss et al. (2010)

Stratification and rumen papillation

from Clauss, Hofmann et al. (2009)

until 1970:

All ruminants are similar and function as cattle and sheep.

The Ruminant Stomach

EAST AFRICAN MONOGRAPHS IN BIOLOGY

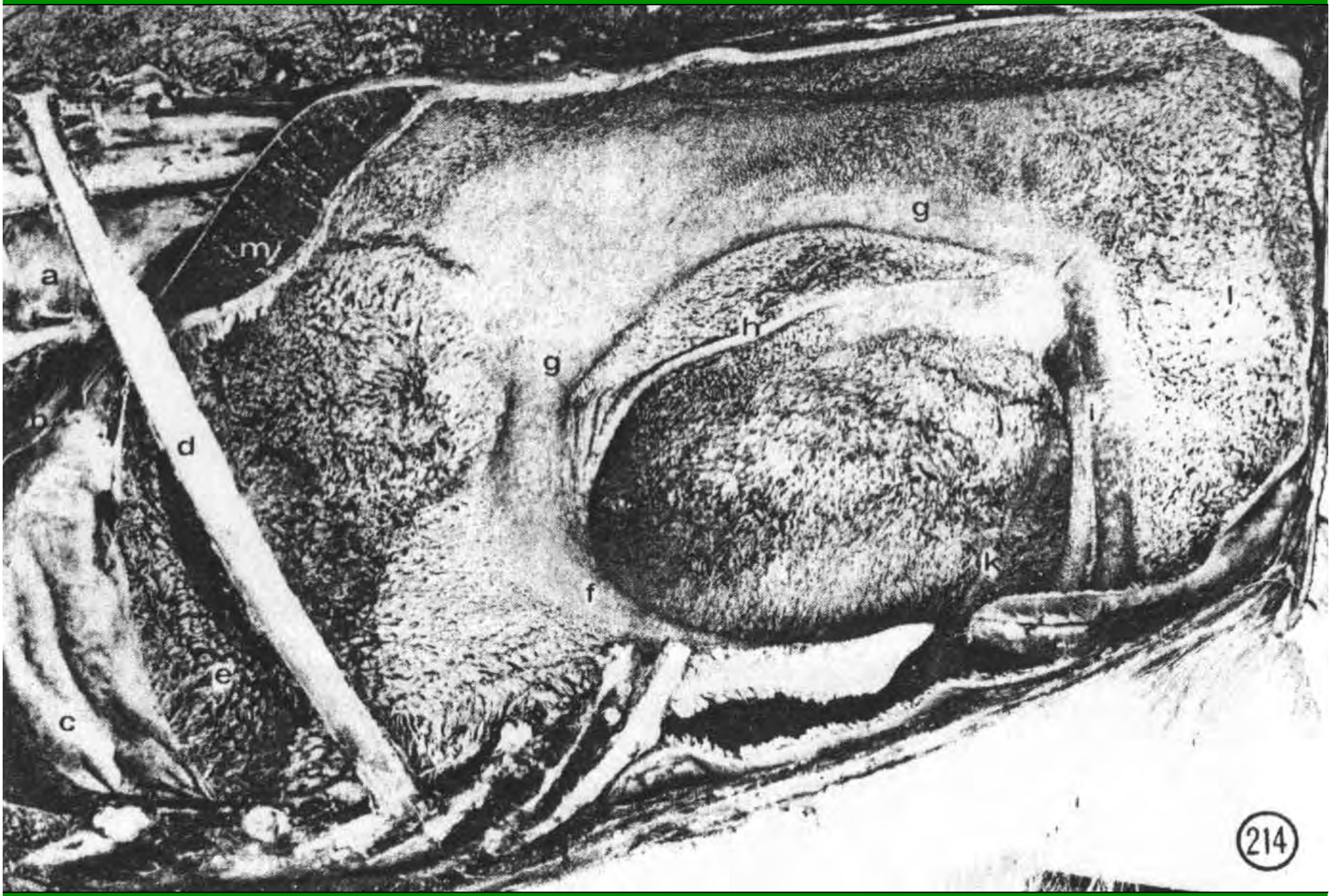
VOLUME 2

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

from Hofmann (1973)



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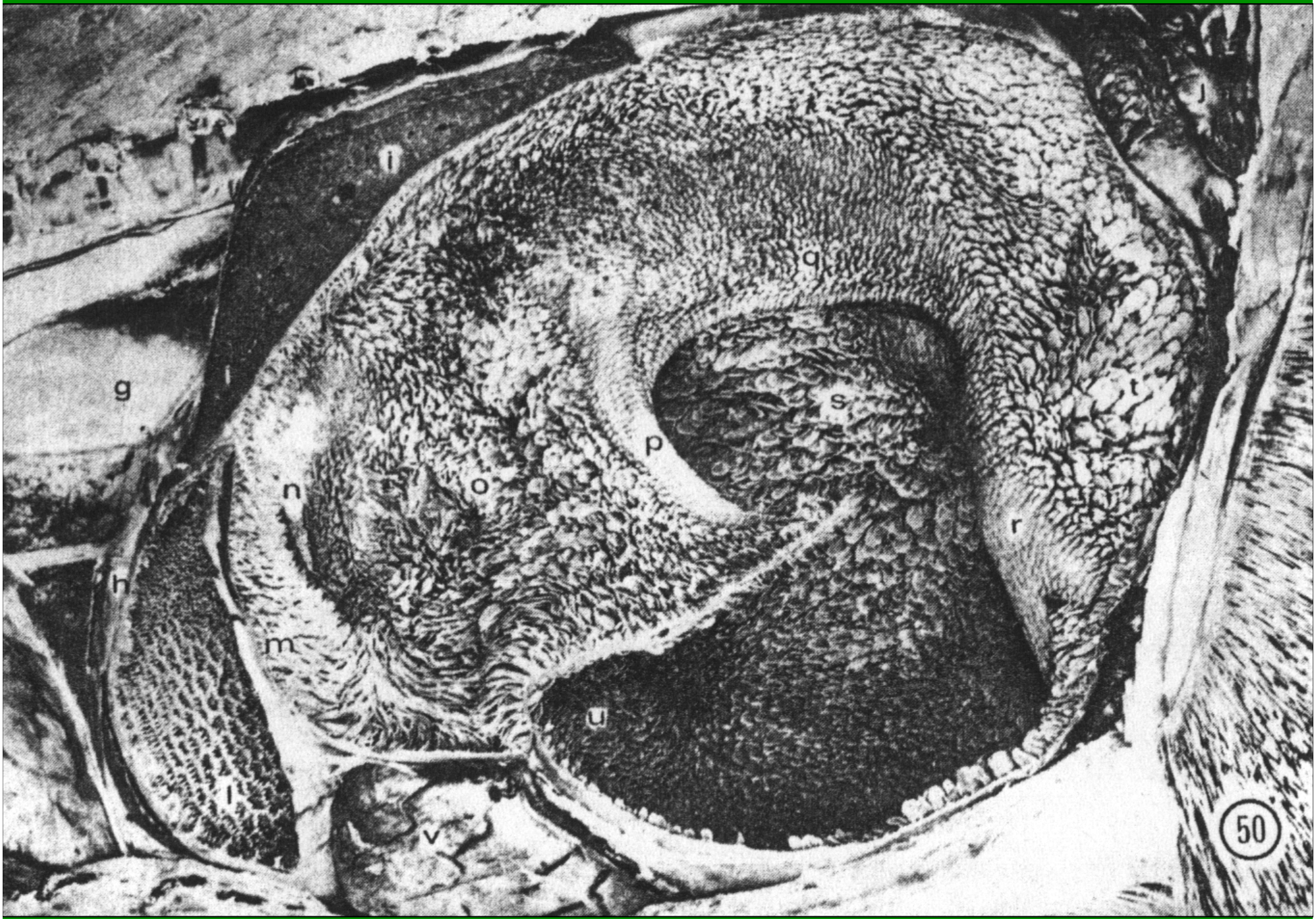

from Hofmann (1973)

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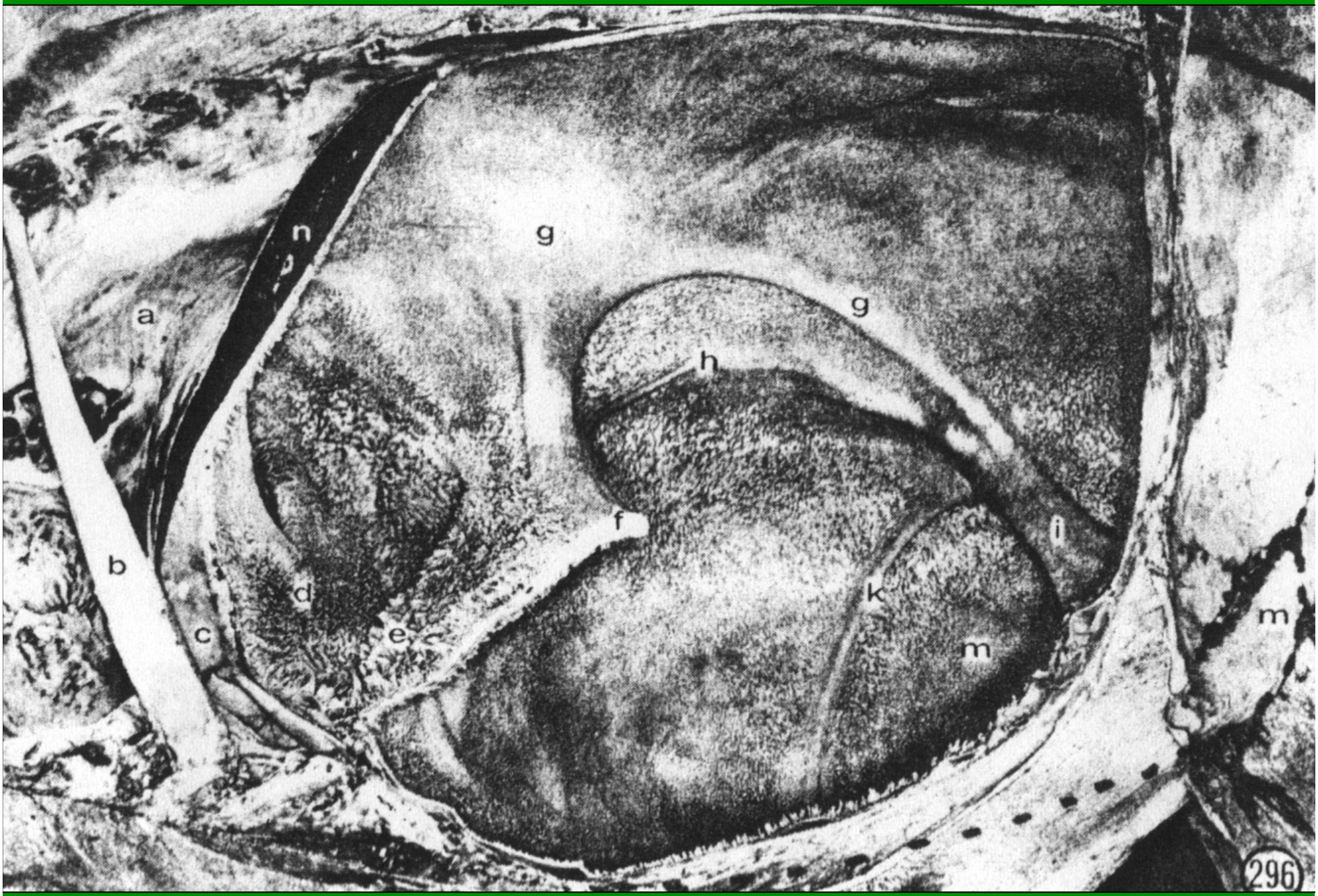

from Hofmann (1973)

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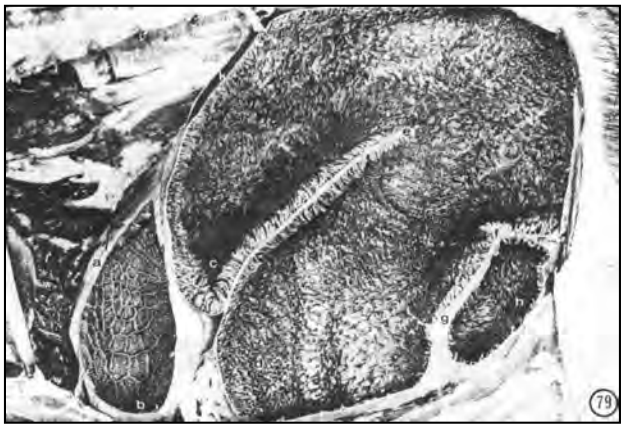
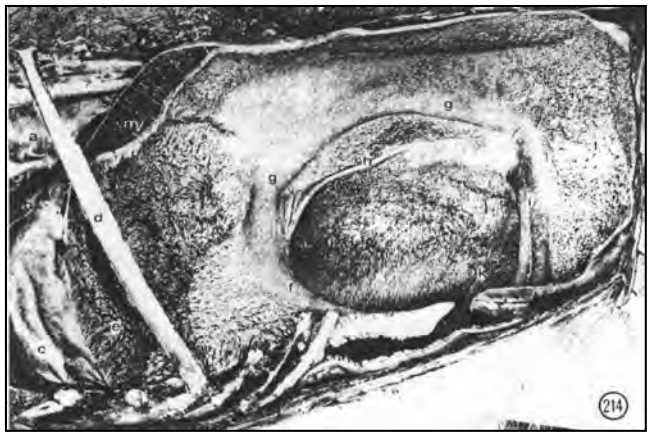
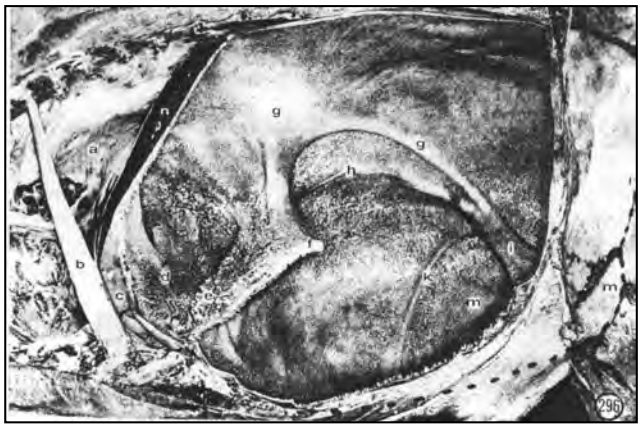
BROWSER



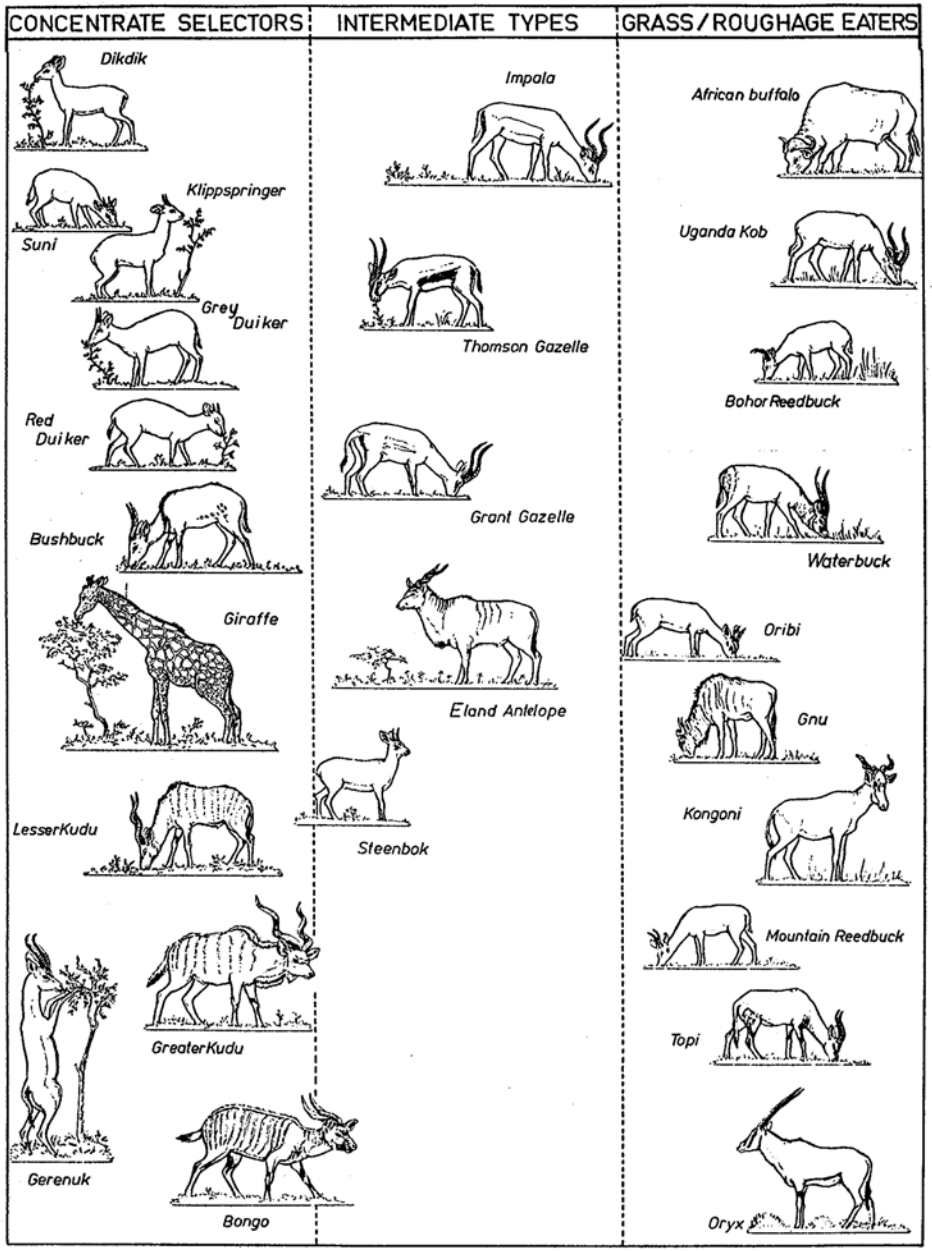
GRAZER





from Hofmann (1973)

Ruminant feeding types (Hofmann)



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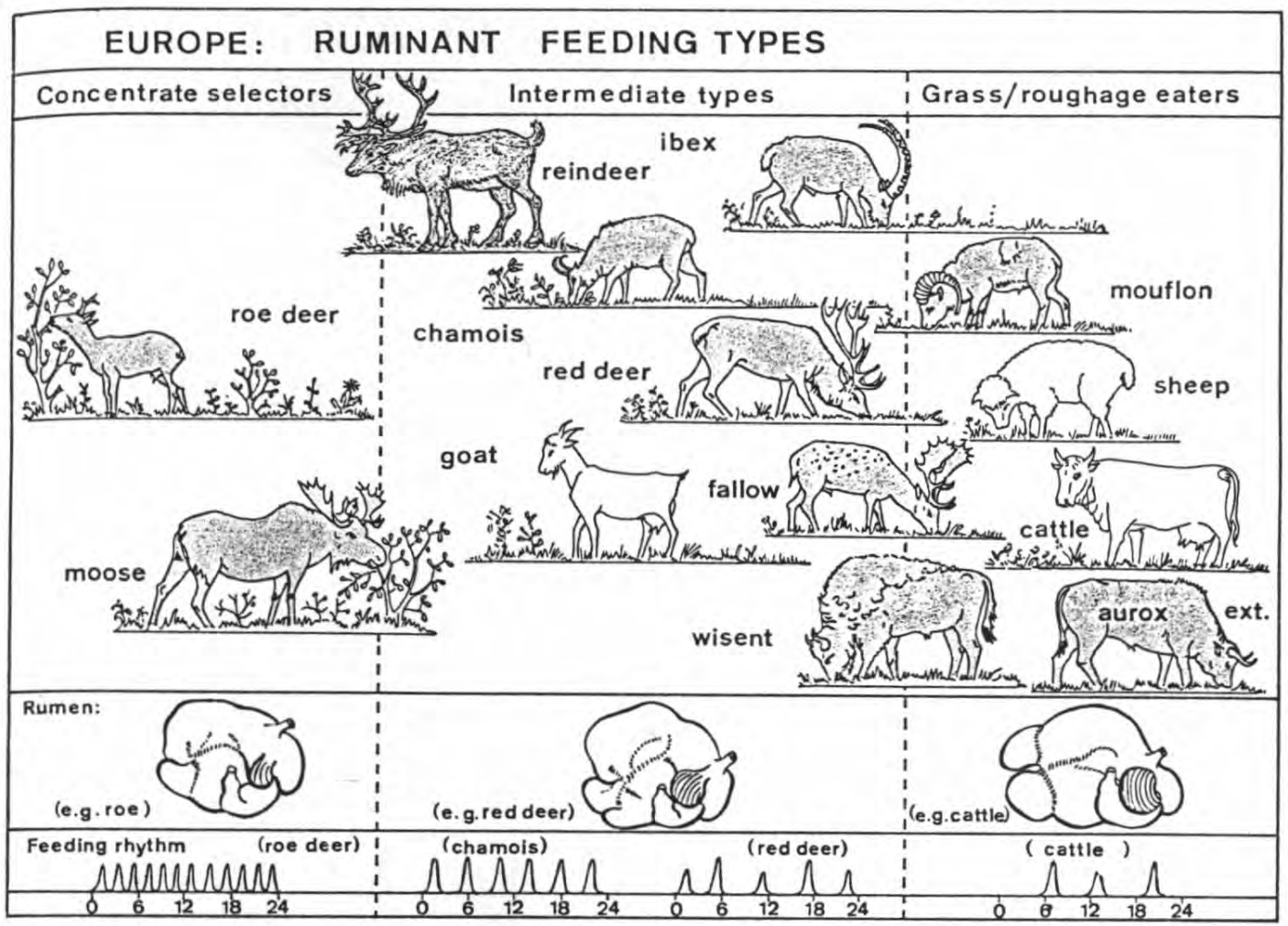

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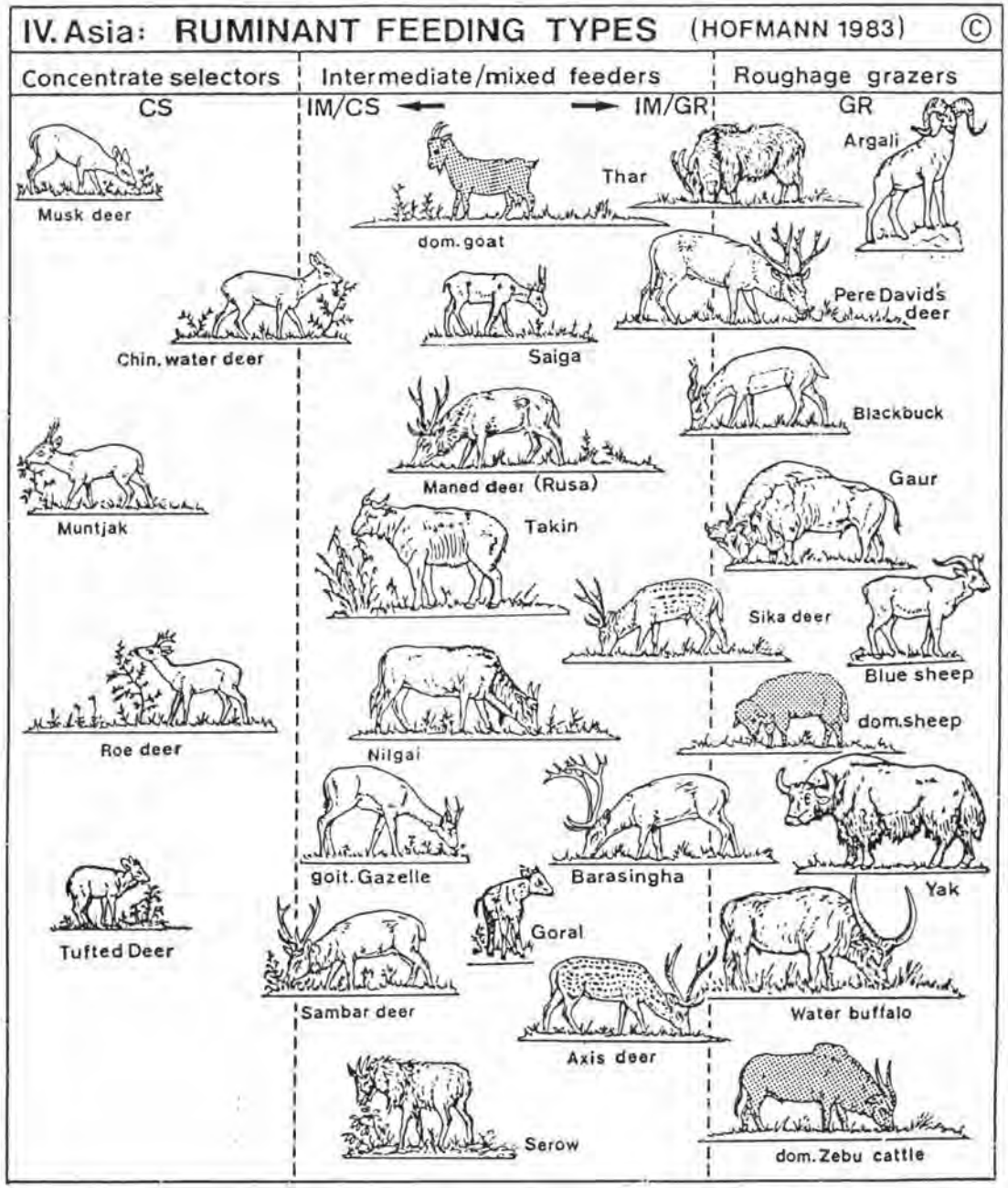
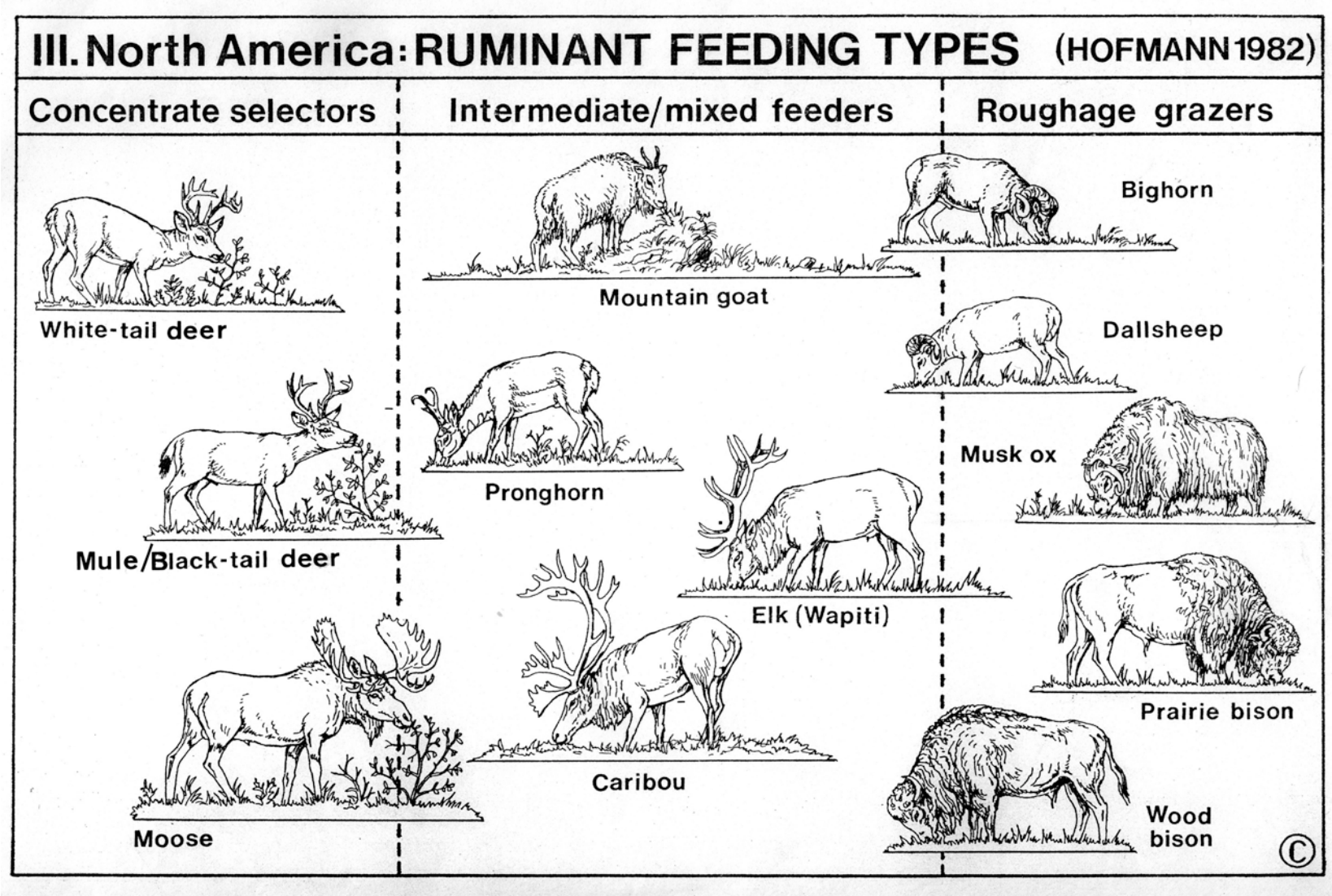


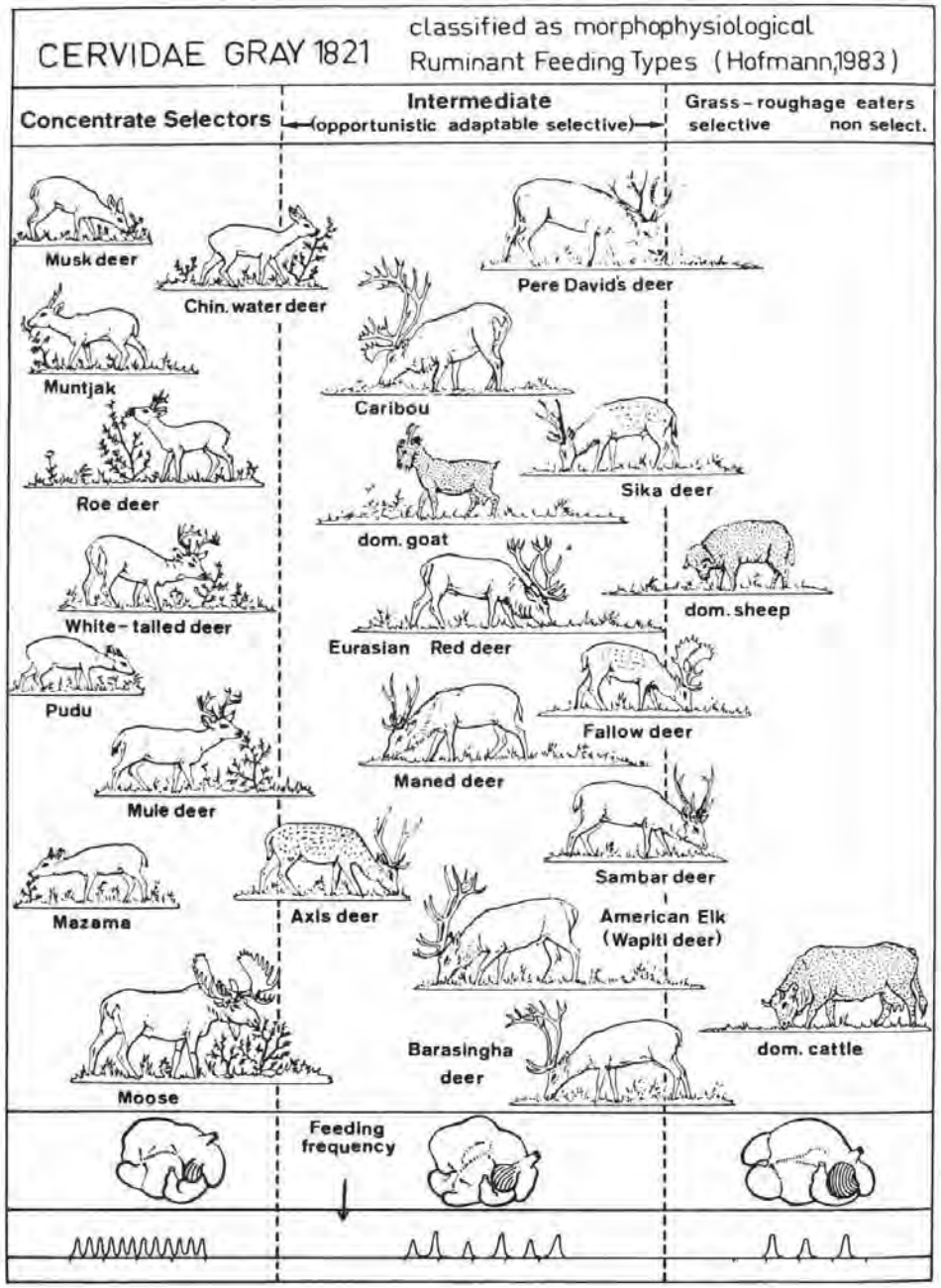
from Hofmann (1991)

Ruminant feeding types (Hofmann)



from Hofmann (unpubl.)

Ruminant feeding types (Hofmann)



from Hofmann (1985)

Oecologia (1989) 78:443–457

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.

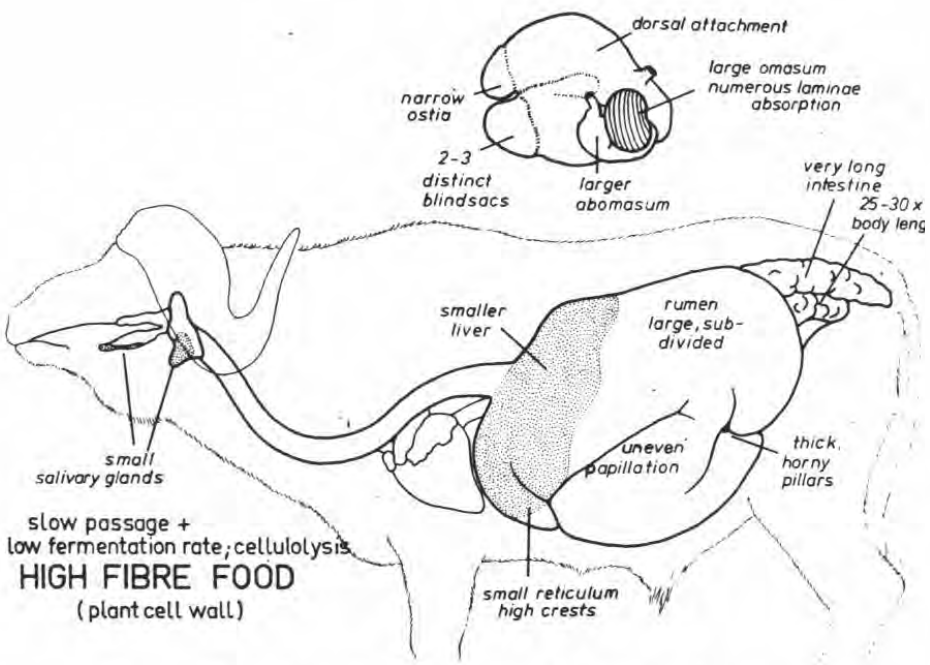
Because they convert apparently indigestible carbohydrates and chemically trapped or protected proteins into nutritious and useful products, they deserve more than *one* approach. Ruminants are late-comers in evolution. Their stomach is a phylogenetic peak of complexity, not only compared with our own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

> 750 citations (and counting)

Differences between the feeding types



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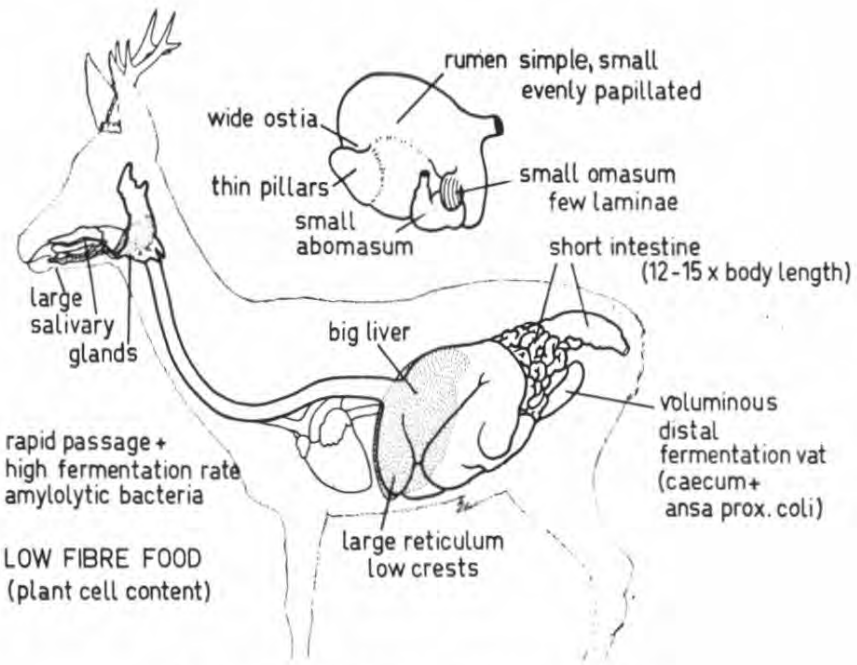


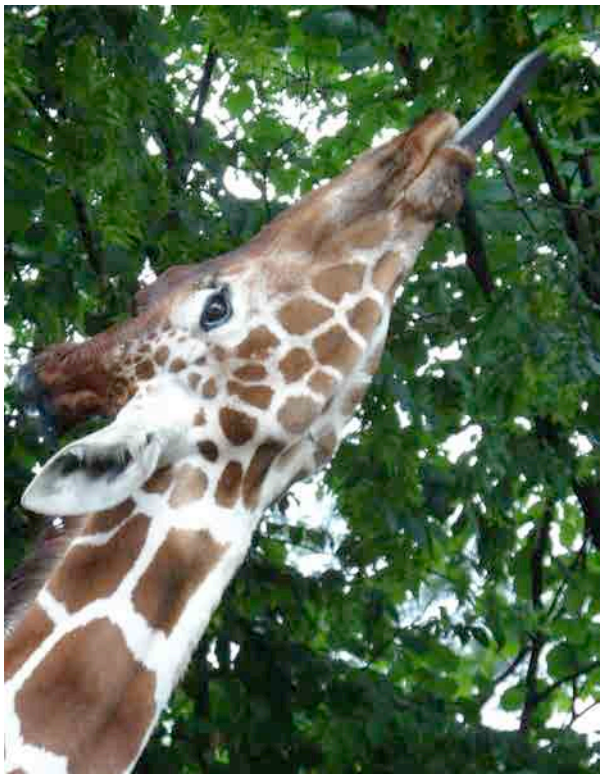
Fig. 2: The roe deer, a concentrate selector.

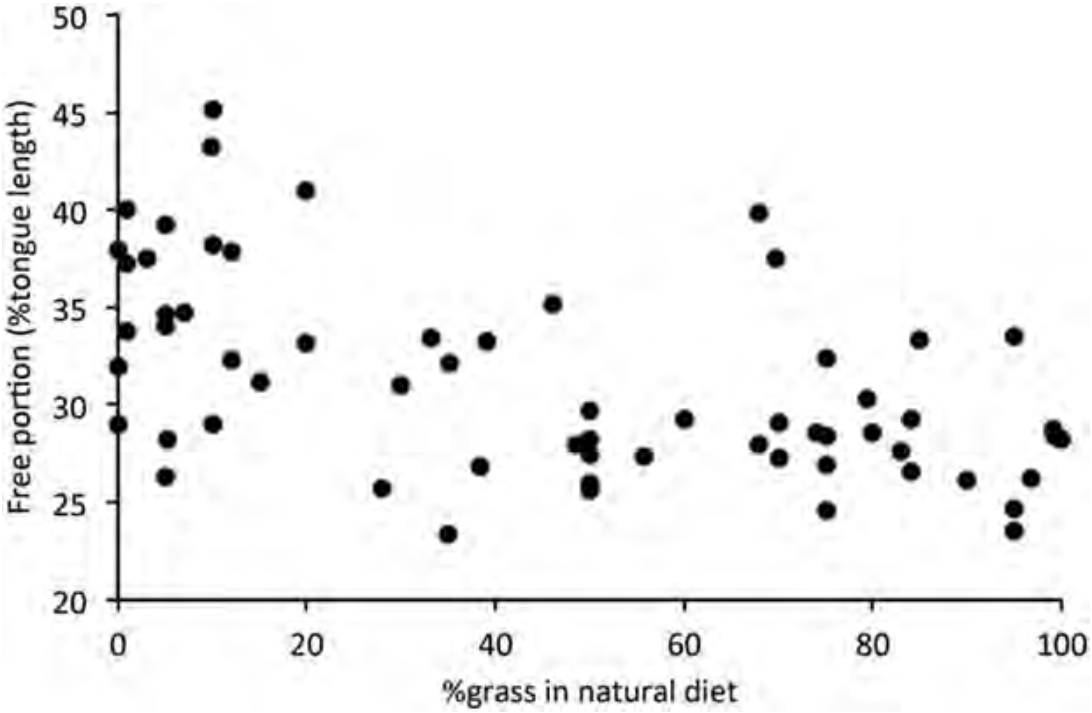
from Hofmann (1989)

JOURNAL OF MORPHOLOGY 277:351–362 (2016)

Convergence of Macroscopic Tongue Anatomy in Ruminants and Scaling Relationships with Body Mass or Tongue Length

Andrea R. Meier,[1] Ute Schmuck,[2] Carlo Meloro,[3] Marcus Clauss,[1]* and Reinhold R. Hofmann[4]





Journal of Zoology

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Journal of Zoology. Print ISSN 0952-8369

Enamel ridge alignment in upper molars of ruminants in relation to their natural diet

T. M. Kaiser[1], J. Fickel[2], W. J. Streich[2], J. Hummel[3] & M. Clauss[4]

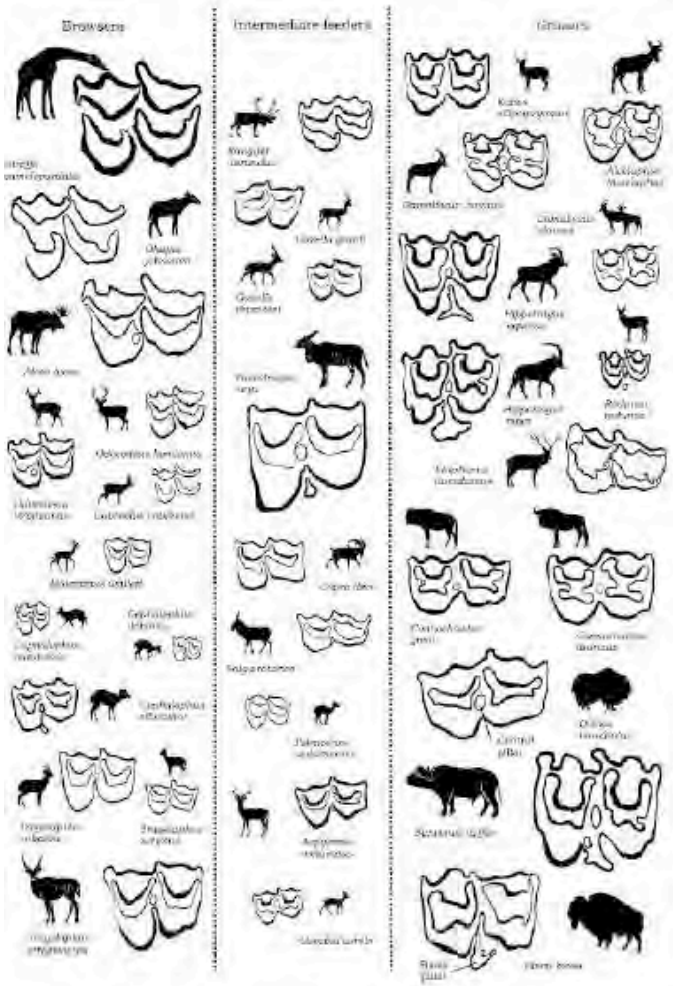


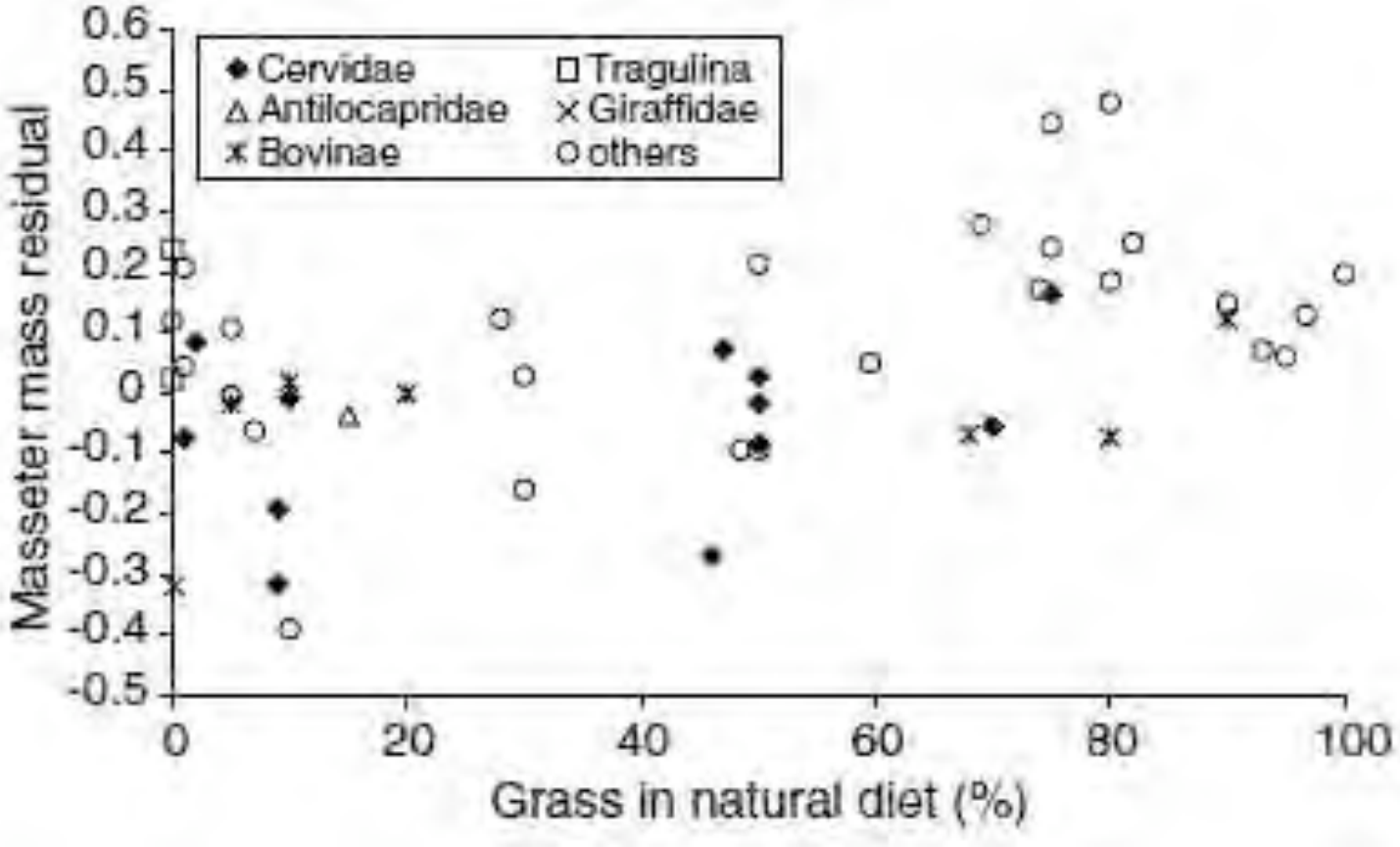
Figure 2 Upper second molar occlusal surfaces of some of the species included in this study. The occlusal enamel ridge pattern of a typical specimen is shown in original size. The buccal side of the molar is directed towards the top of the page, and the lingual side towards the bottom. Note the presence of central and basal pillars in some species. Animal pictograms are partly adapted from Mason & Carter (1971).

Oecologia (2008) 157:377–385
DOI 10.1007/s00442-008-1093-z

PHYSIOLOGICAL PHYSIOLOGY - ORIGINAL PAPER

Higher masseter muscle mass in grazing than in browsing ruminants

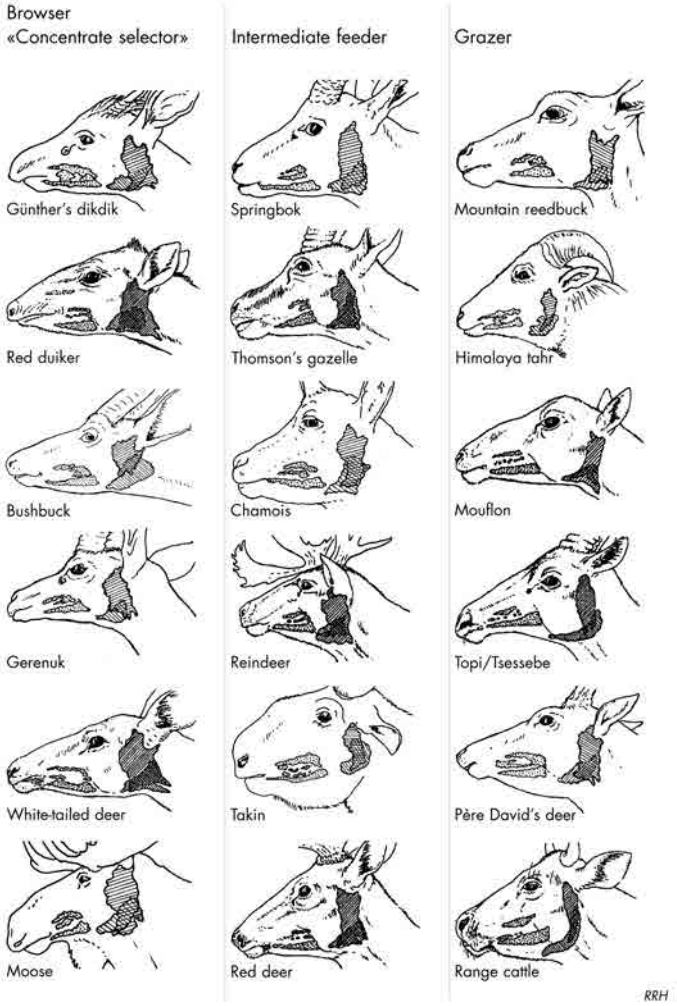
Marcus Clauss · Reinold R. Hofmann ·
W. Jürgen Streich · Jörns Fickel · Jürgen Hummel

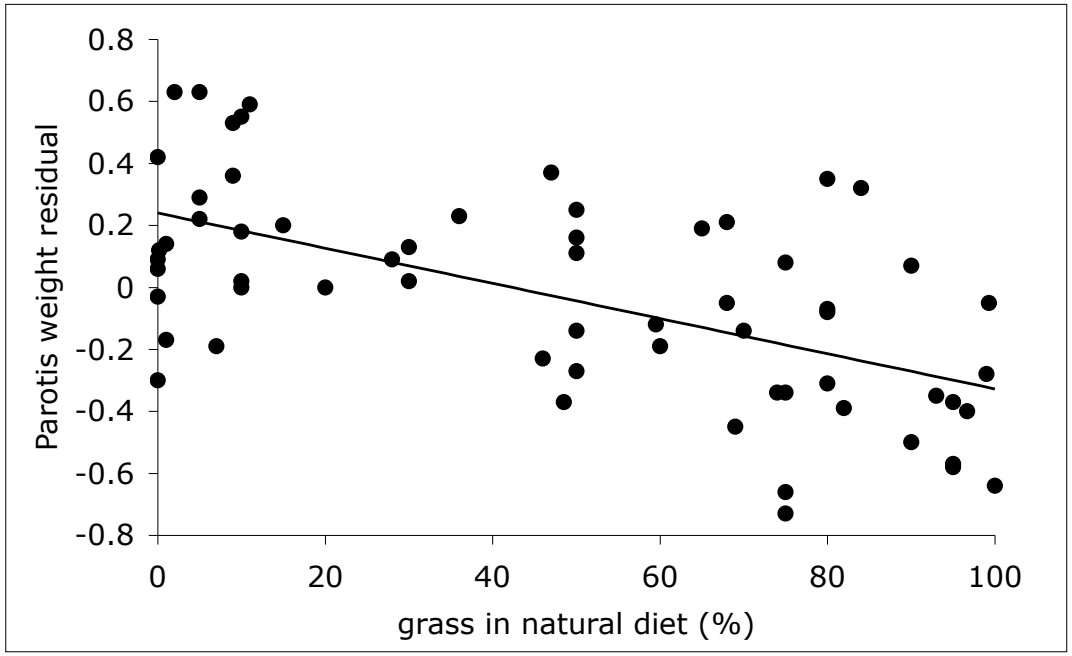


JOURNAL OF MORPHOLOGY 269:240–257 (2008)

Convergent Evolution in Feeding Types: Salivary Gland Mass Differences in Wild Ruminant Species

Reinold R. Hofmann,[1] W. Jürgen Streich,[1] Jörns Fickel,[1] Jürgen Hummel,[2] and Marcus Clauss[3]*

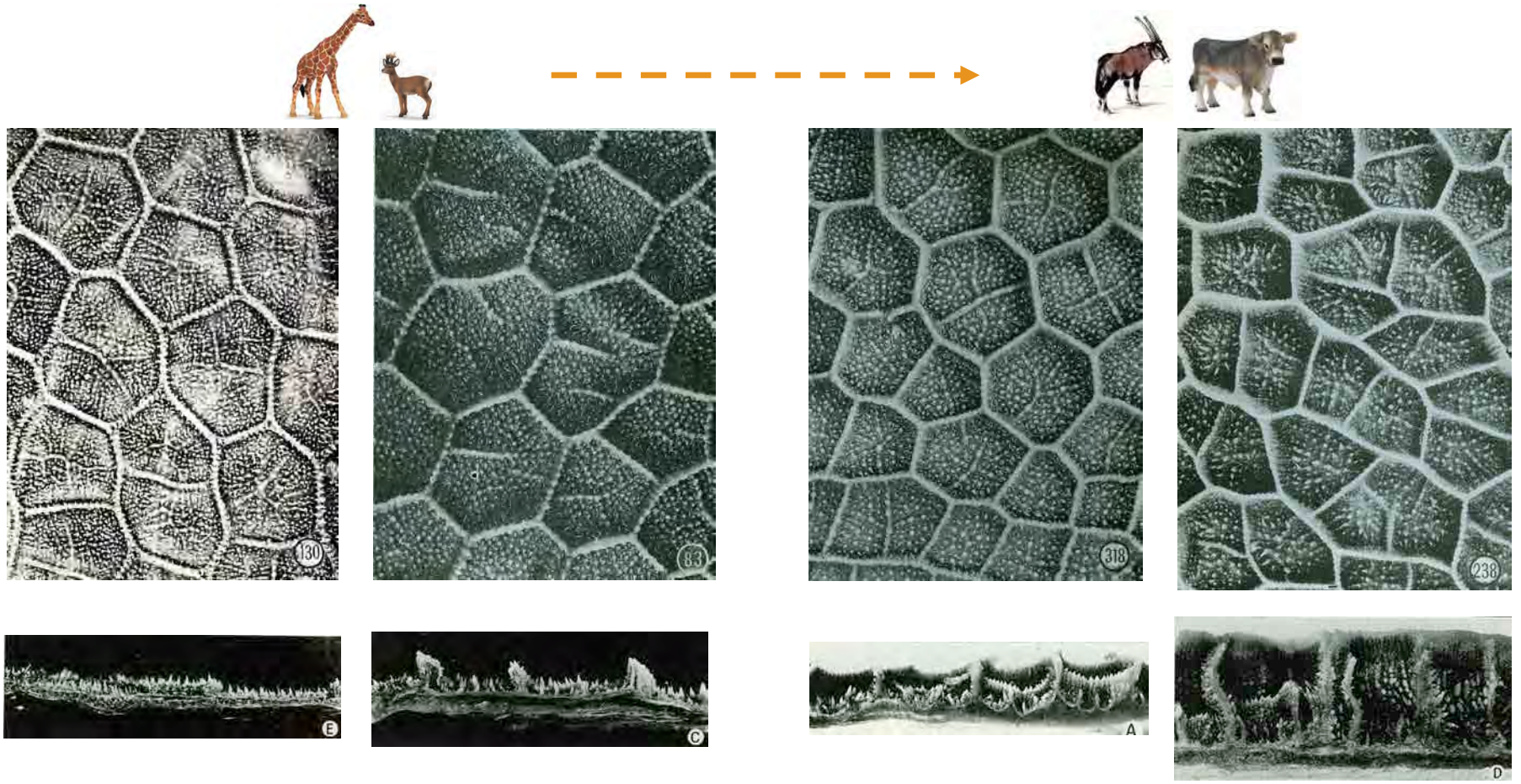




Journal of Zoology. Print ISSN 0952-8369

Convergence in the macroscopic anatomy of the reticulum in wild ruminant species of different feeding types and a new resulting hypothesis on reticular function

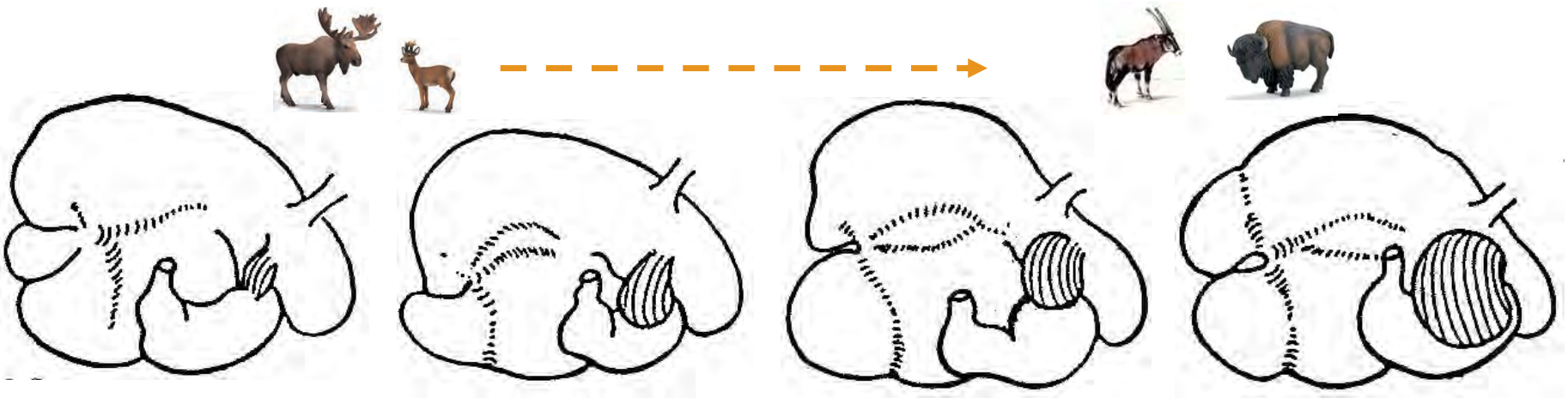
M. Clauss[1], R. R. Hofmann[2*], W. J. Streich[3], J. Fickel[3] & J. Hummel[4]

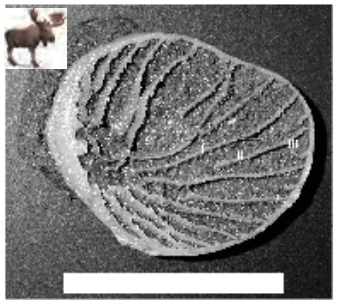


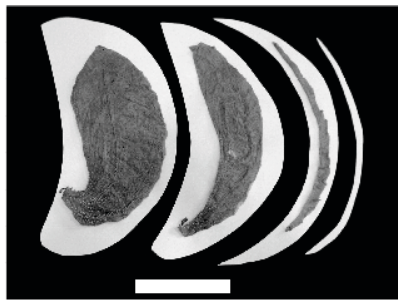
Journal of Zoology **270** (2006) 346–358

Macroscopic anatomy of the omasum of free-ranging moose (*Alces alces*) and muskoxen (*Ovibos moschatus*) and a comparison of the omasal laminal surface area in 34 ruminant species

M. Clauss[1], R. R. Hofmann[2], J. Hummel[3], J. Adamczewski[4], K. Nygren[5], C. Pitra[2], W. J. Streich[2] & S. Reese[6]







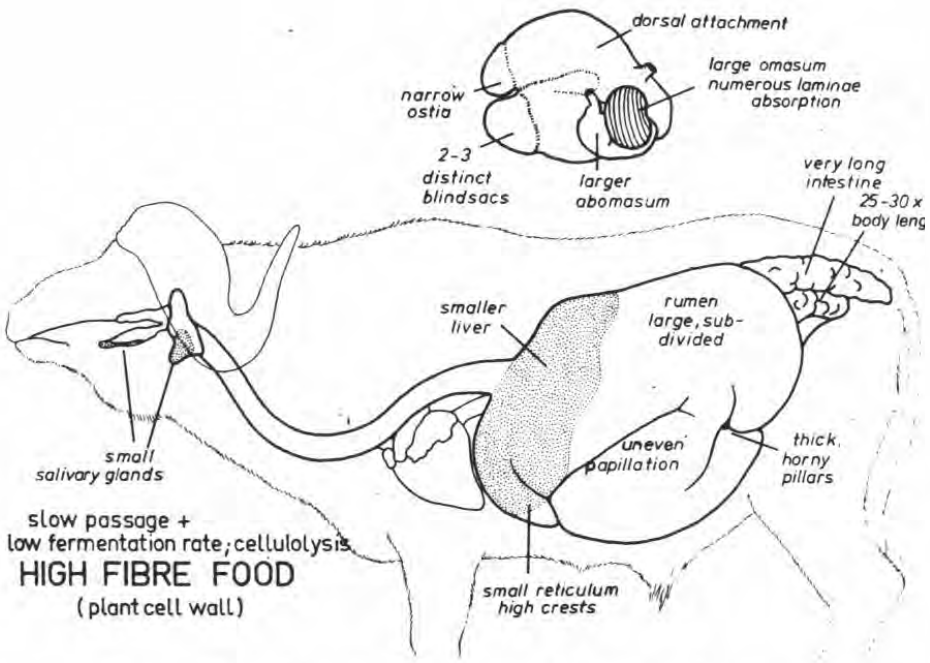
Sequence of hypotheses

Soft tissue variation and forestomach physiology is linked to

diet fibre content ?

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

R.R. Hofmann



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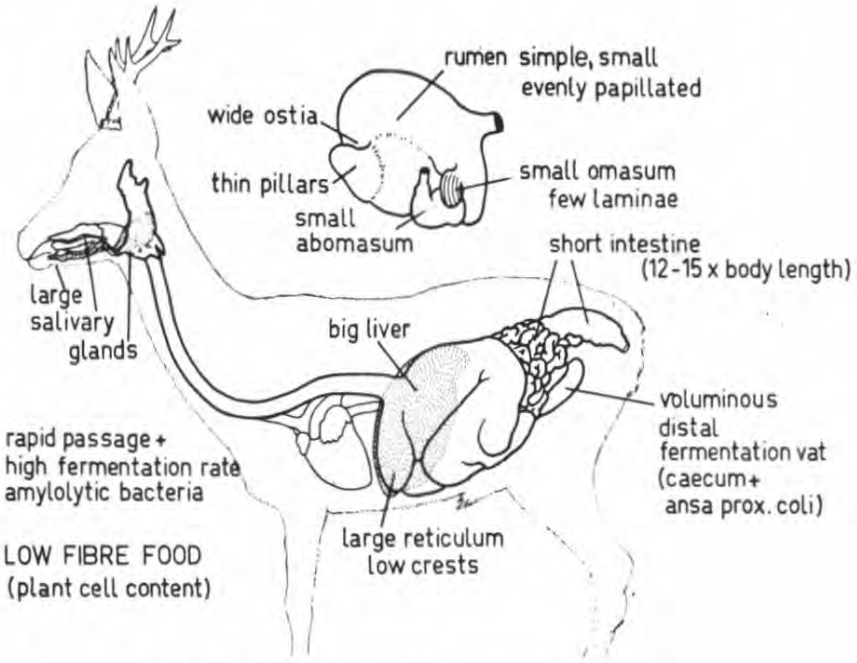

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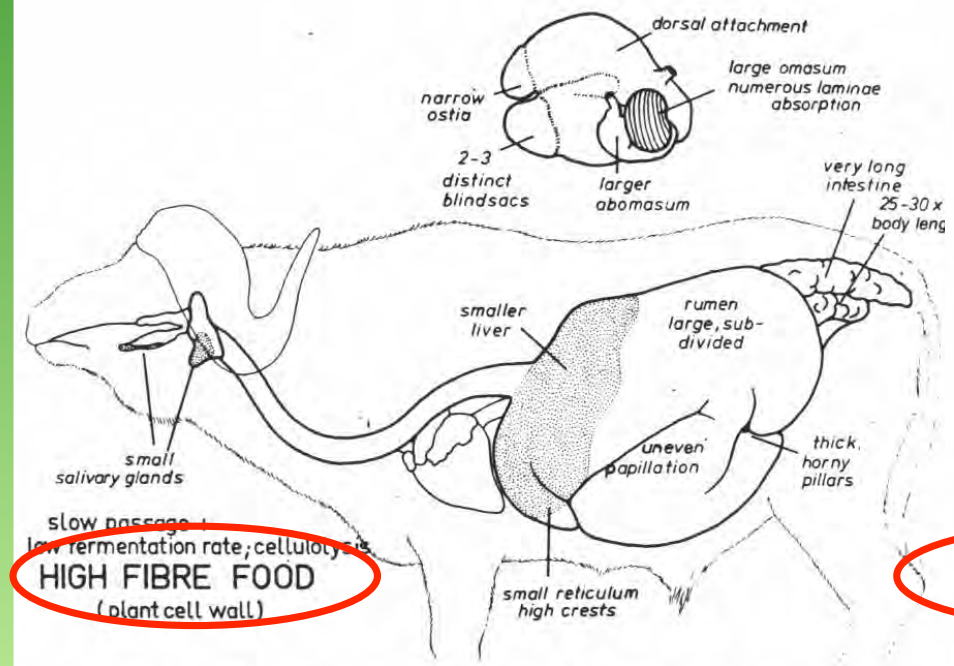

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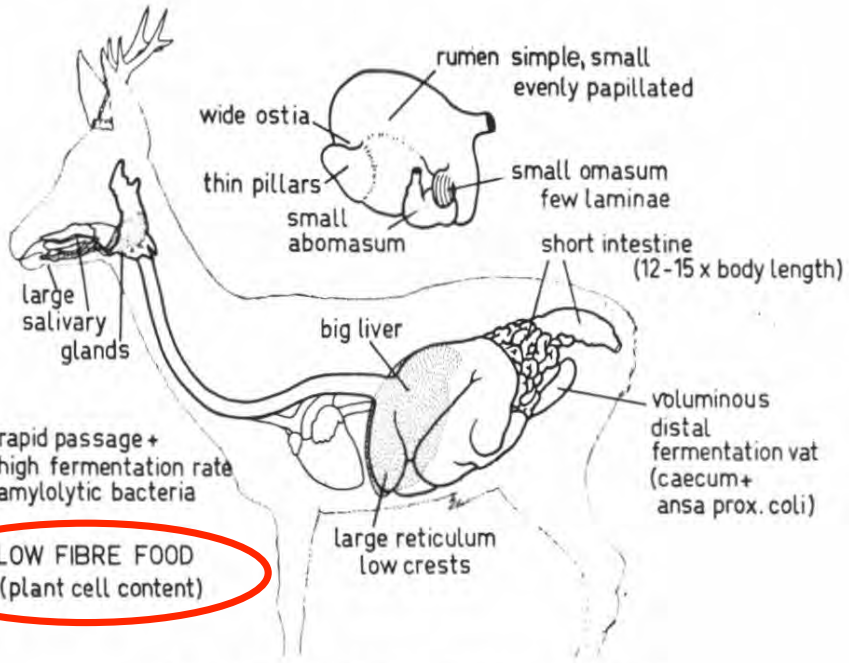

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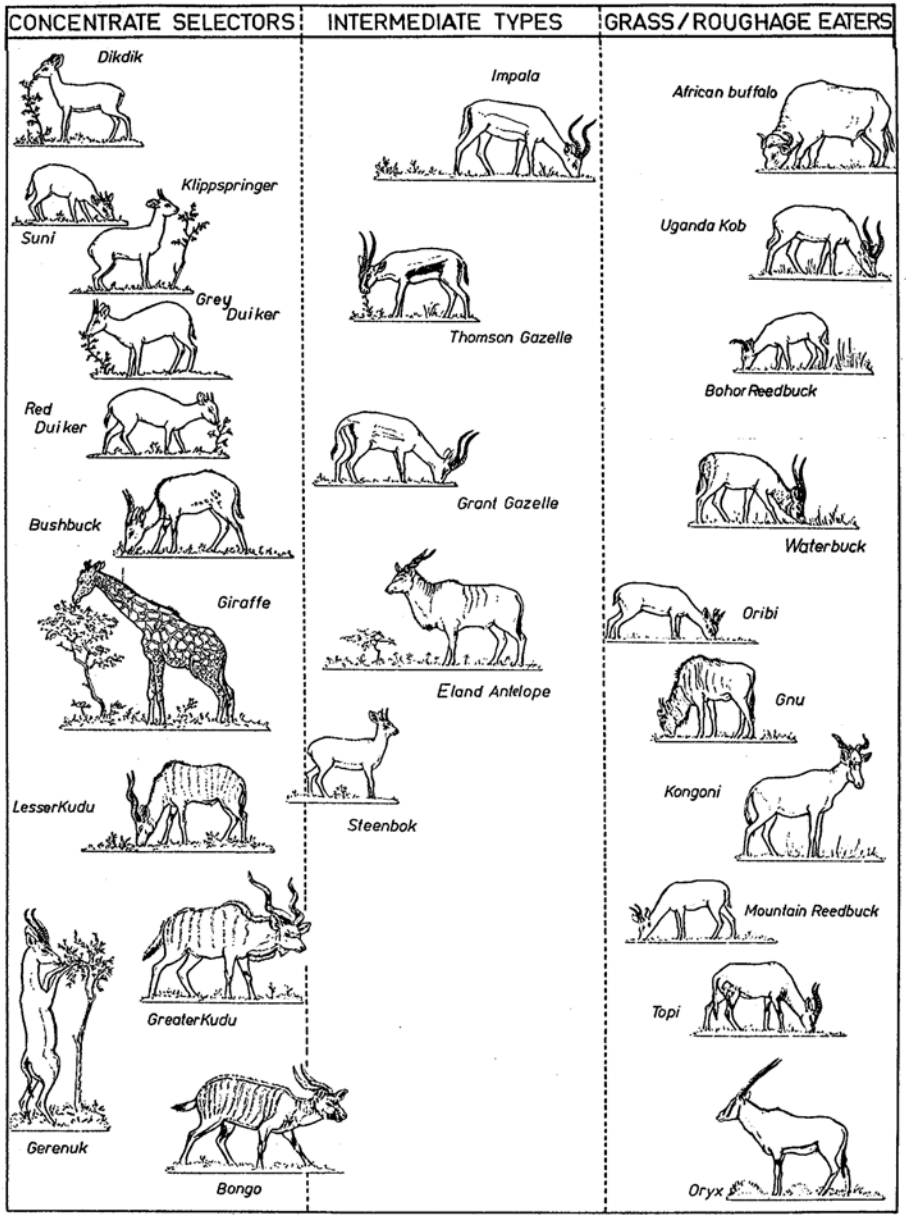
Do diets of grazers and browsers really differ?

Crude fibre in rumen contents (%DM)



from Hofmann (1989) and Woodall (1992)

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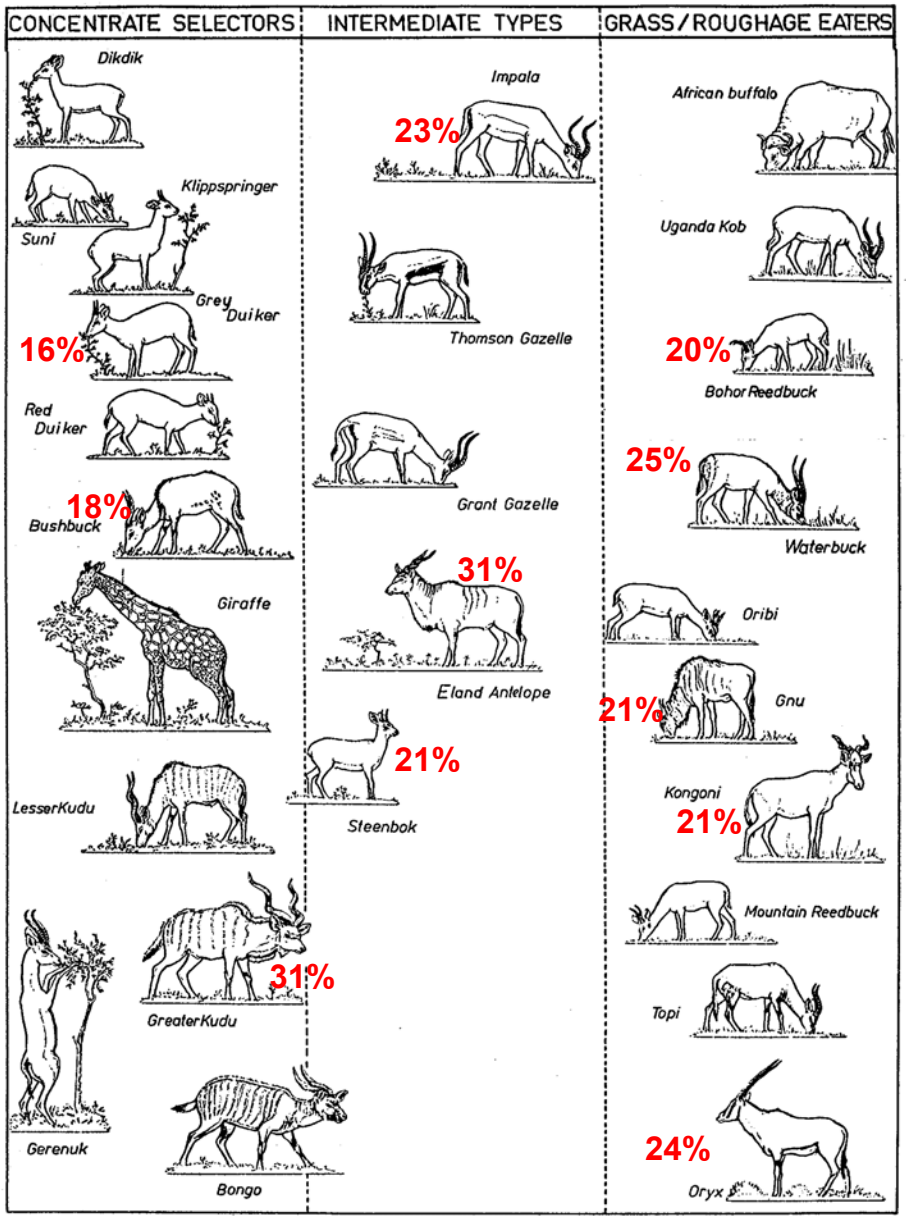

from Hofmann (1989) and Woodall (1992)

Sequence of hypotheses

Soft tissue variation and forestomach physiology is linked to

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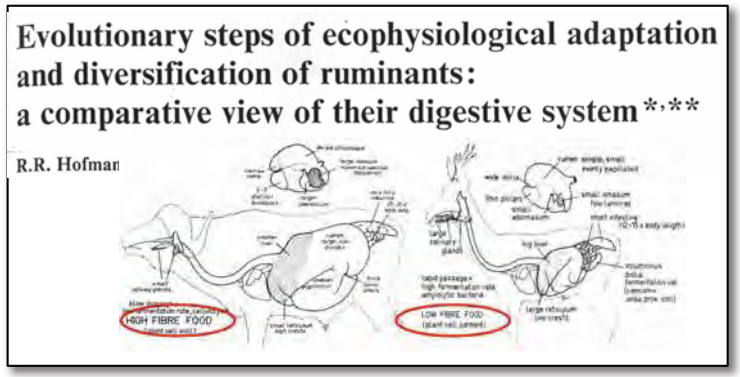

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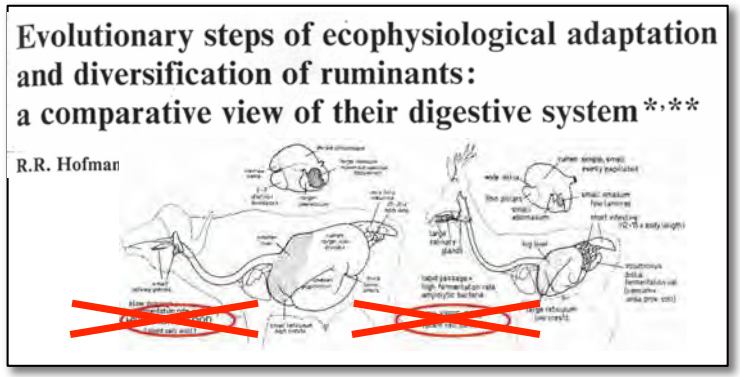
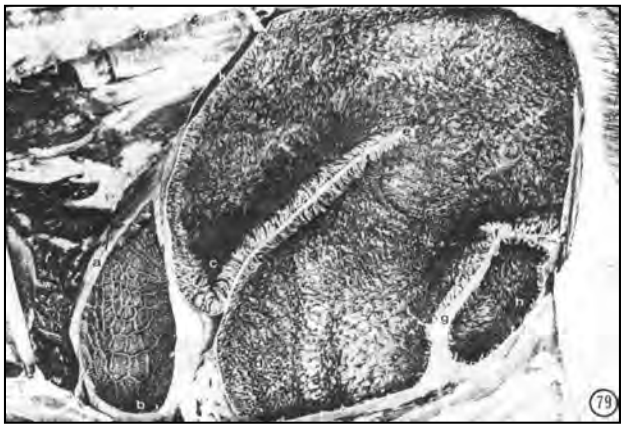
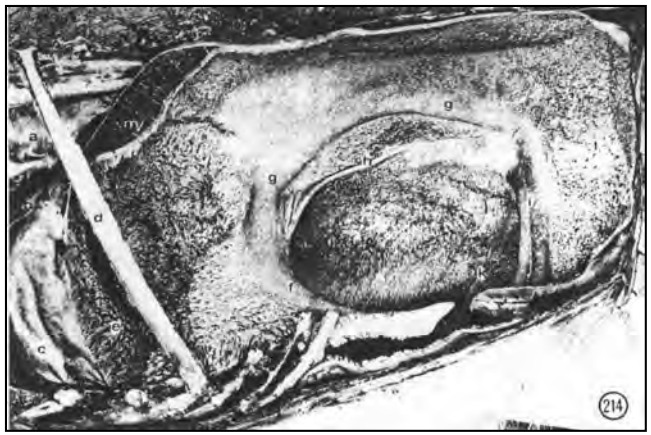
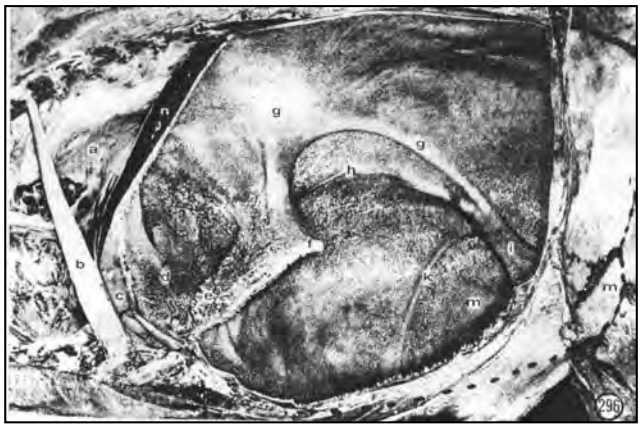


BROWSER



GRAZER



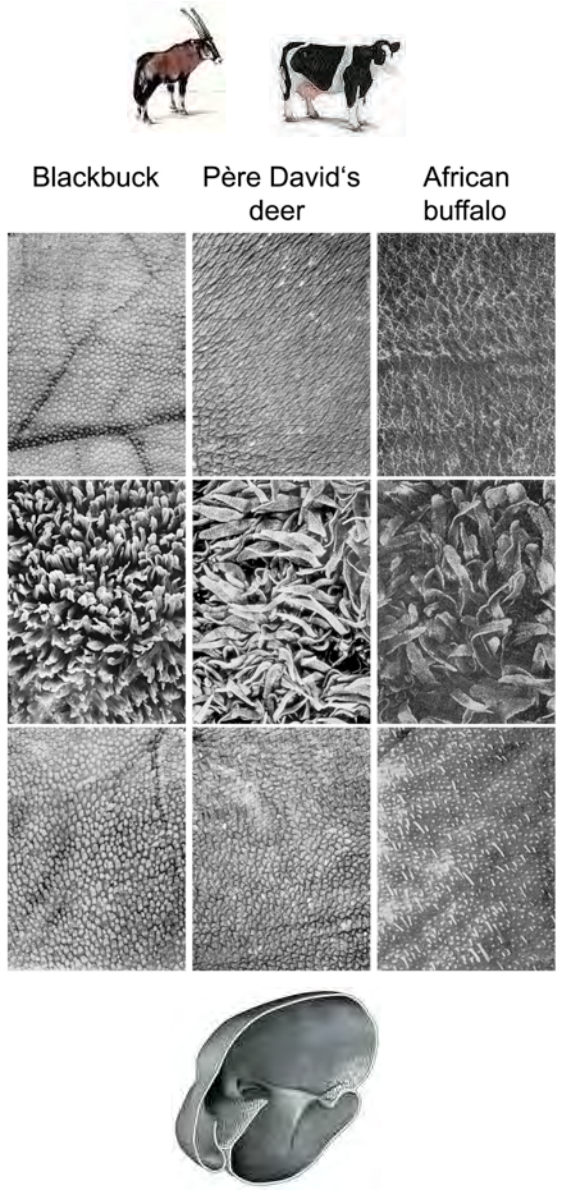


from Hofmann (1973)

No stratification - even rumen papillation

from Clauss, Hofmann et al. (2009)

Stratification and rumen papillation



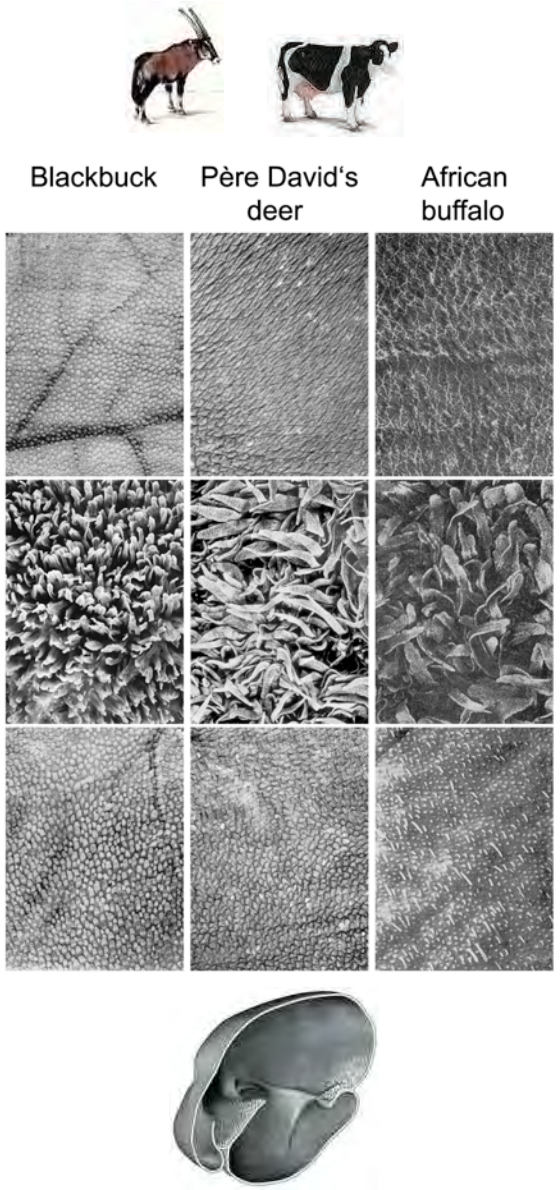
from Clauss, Hofmann et al. (2009)

Stratification and rumen papillation

dorsal

Atrium

ventral



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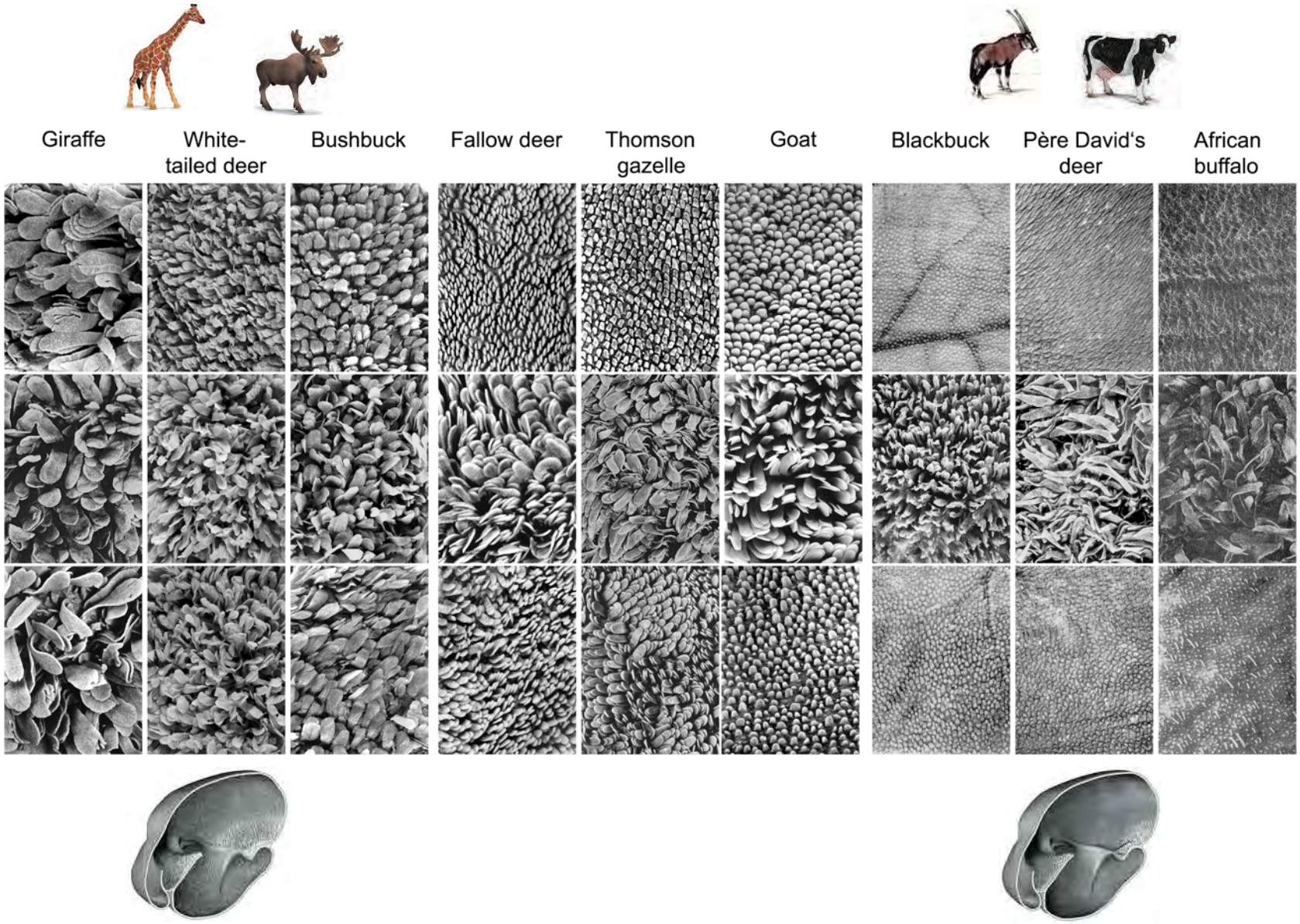
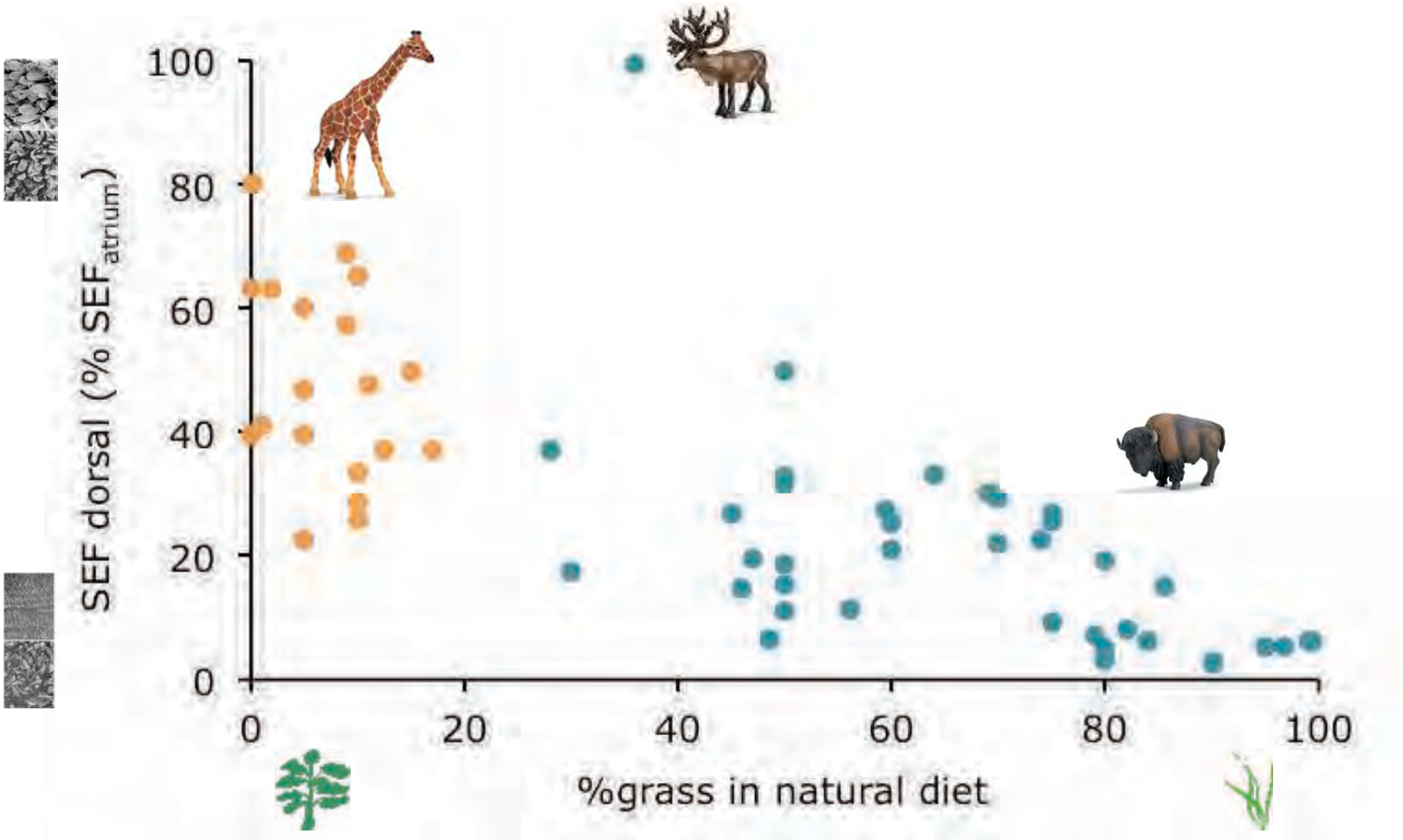


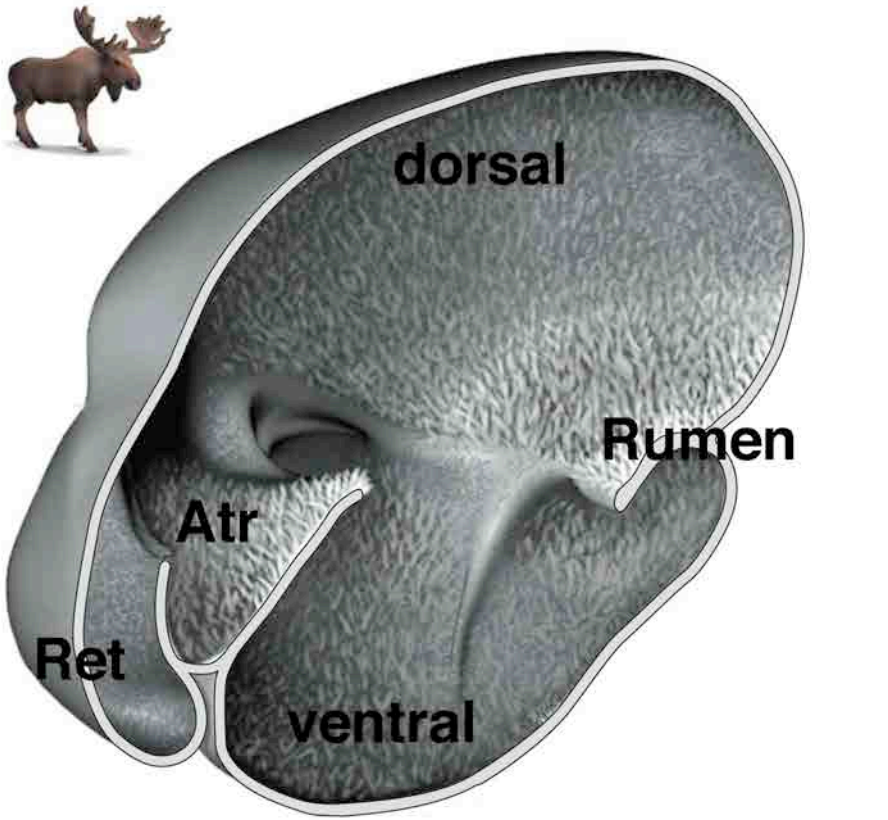
from Clauss, Hofmann et al. (2009)

A measure of ‘stratification’



from Clauss et al. (2009)

No stratification of rumen contents: ‘moose-type’



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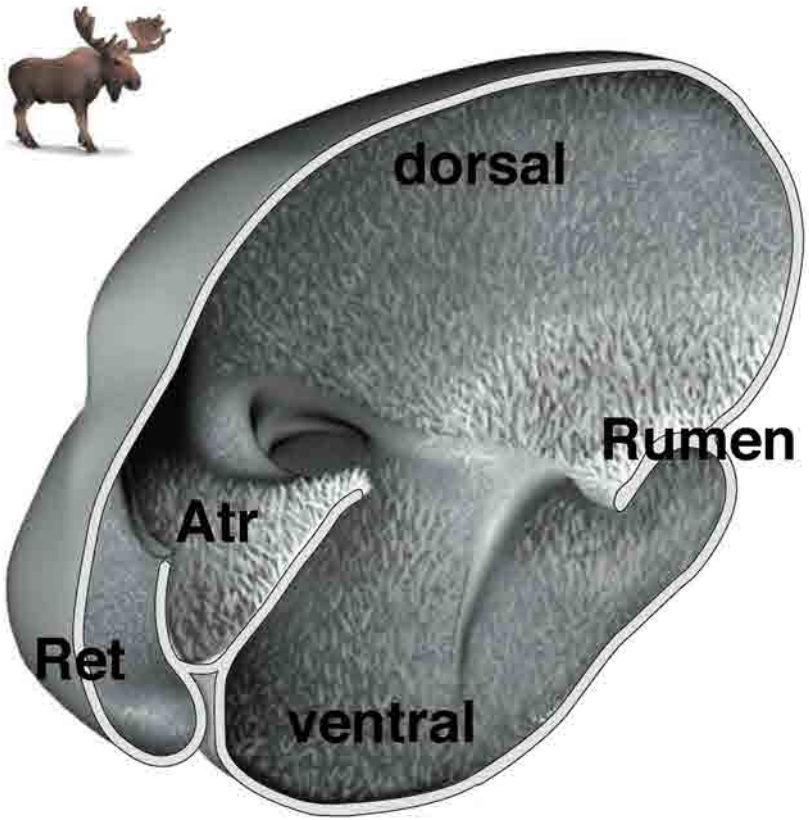

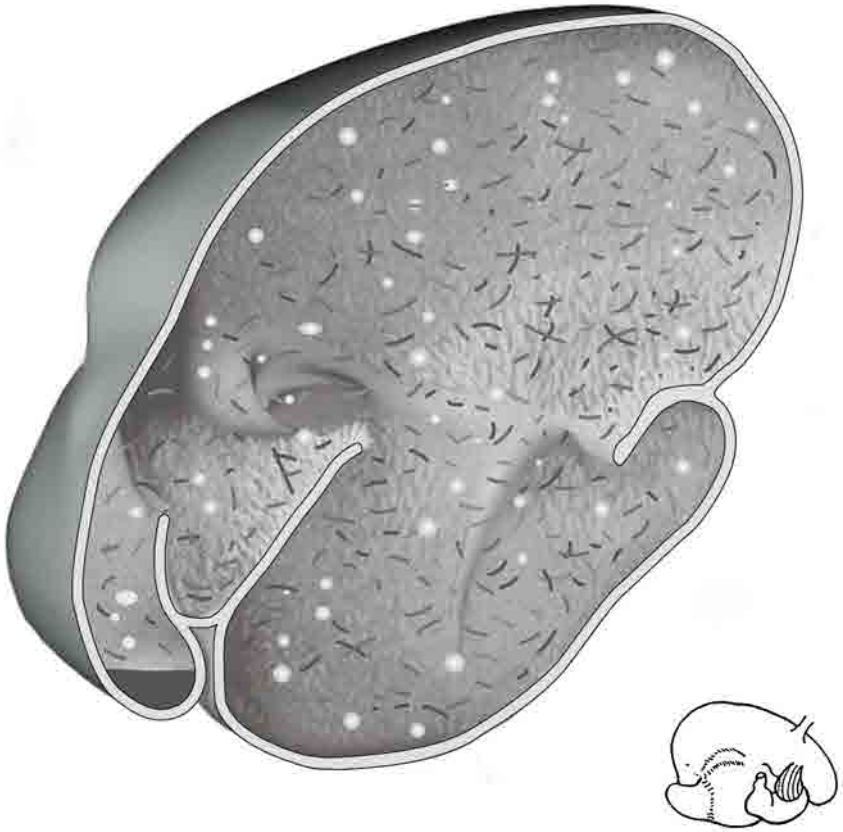

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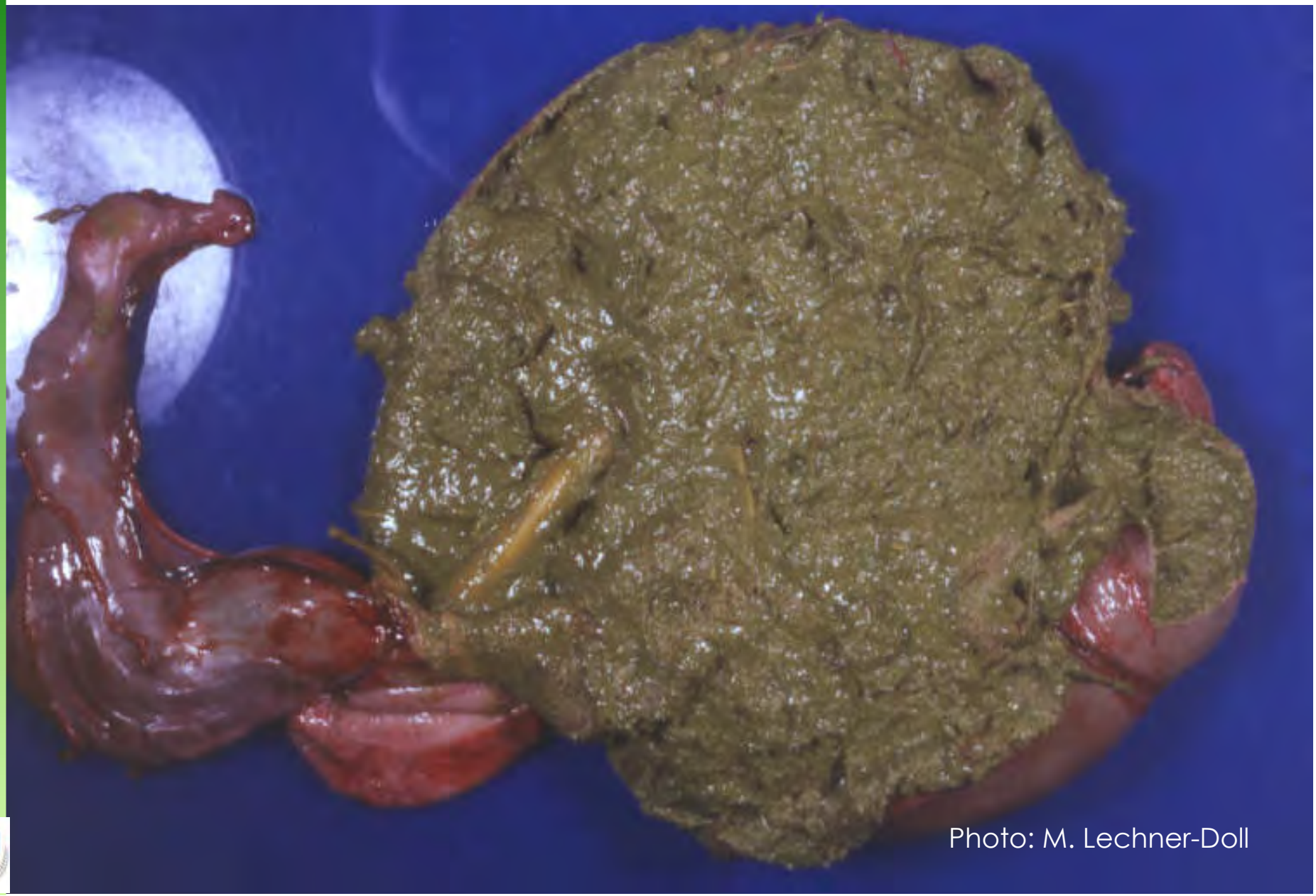

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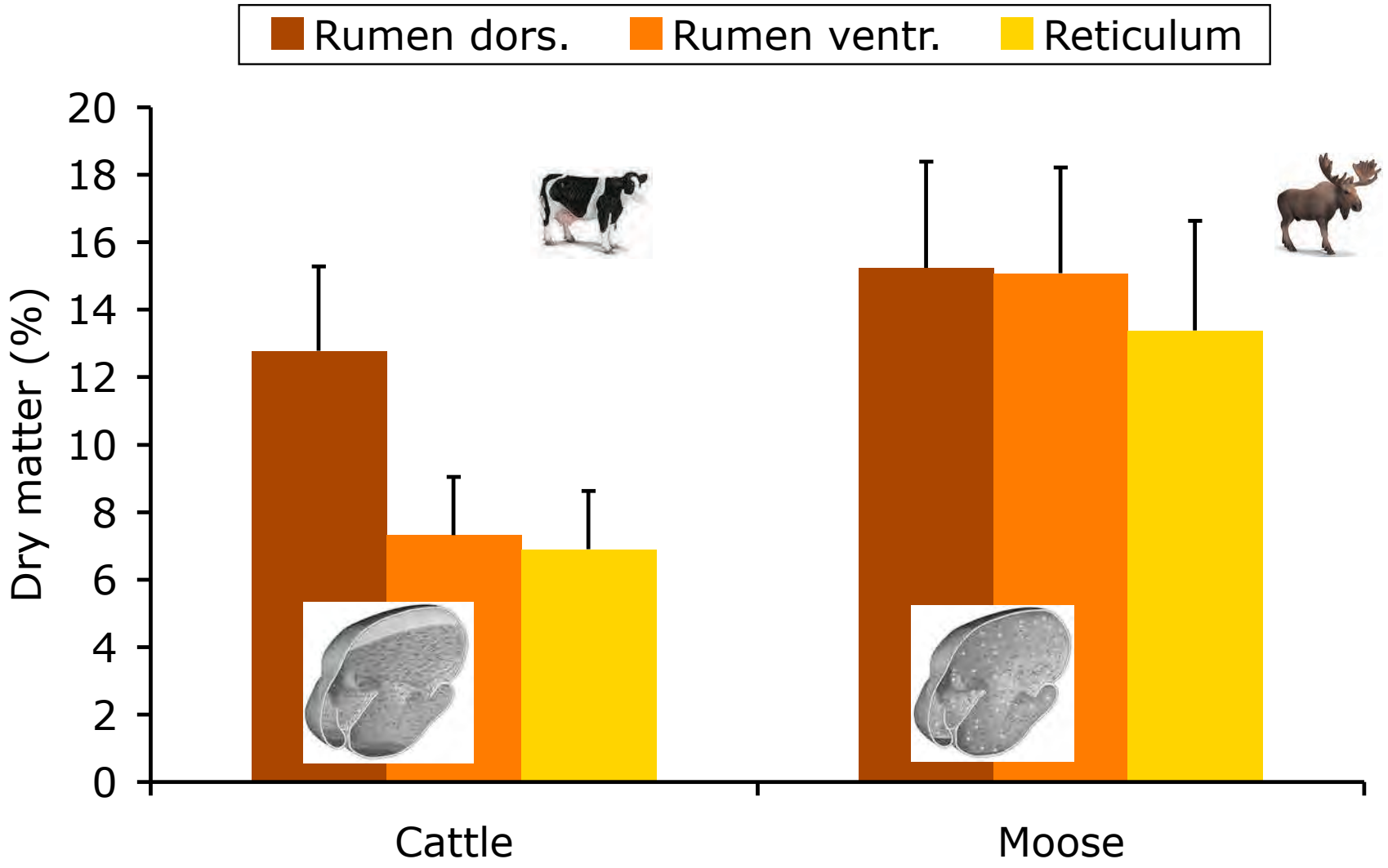

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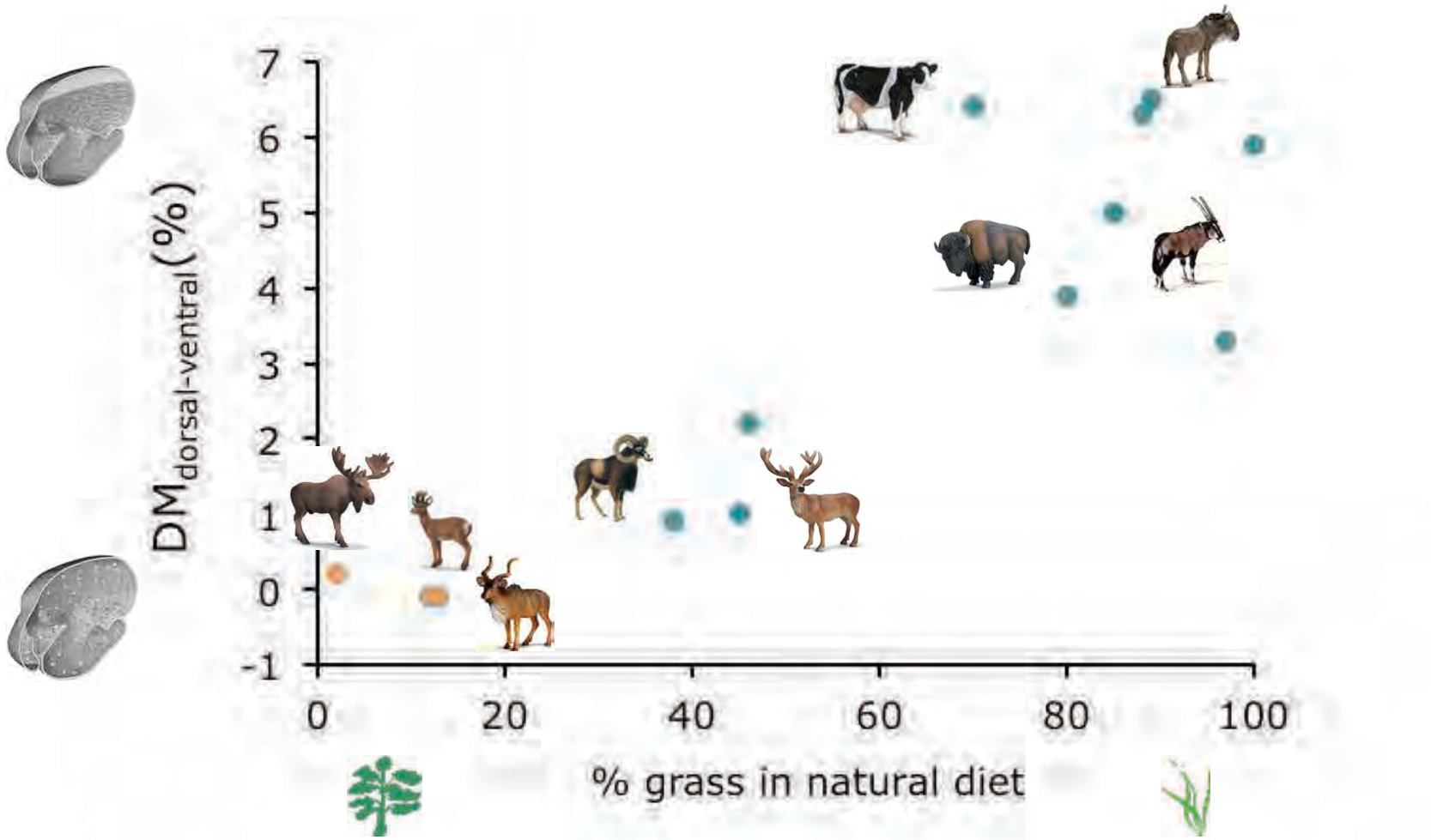
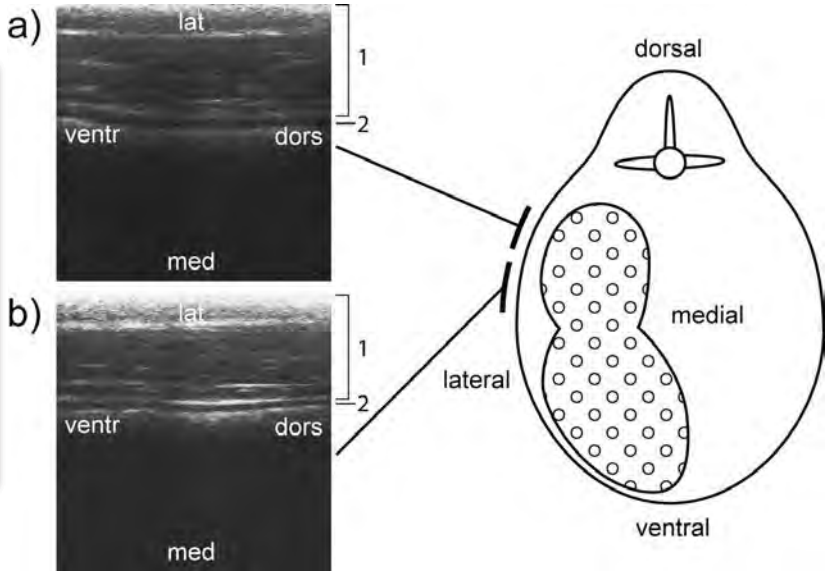
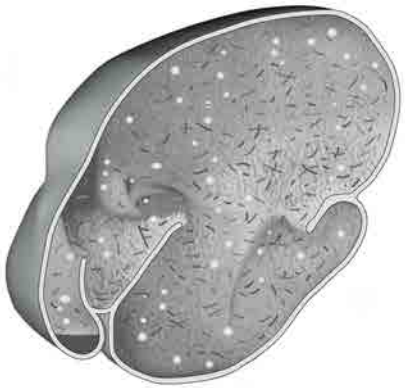
Another measure of ‘stratification’



from Clauss et al. (2009)

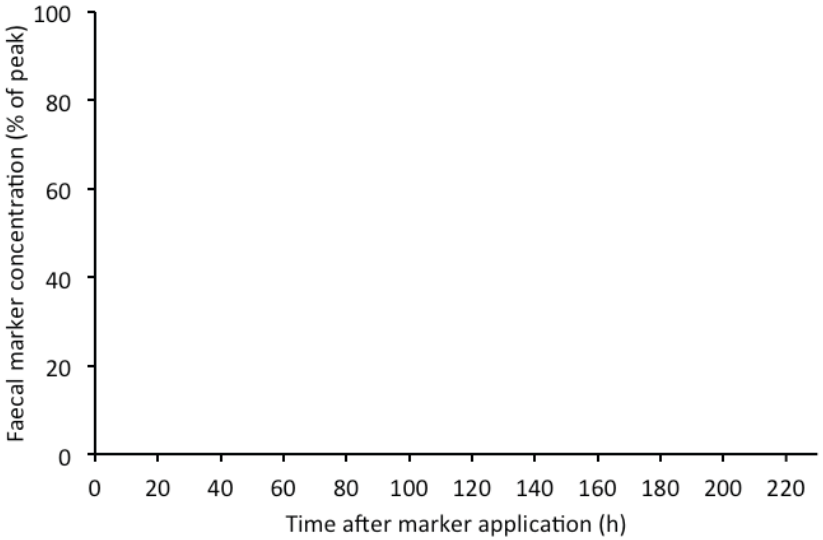
Testing stratification by ultrasound - moose

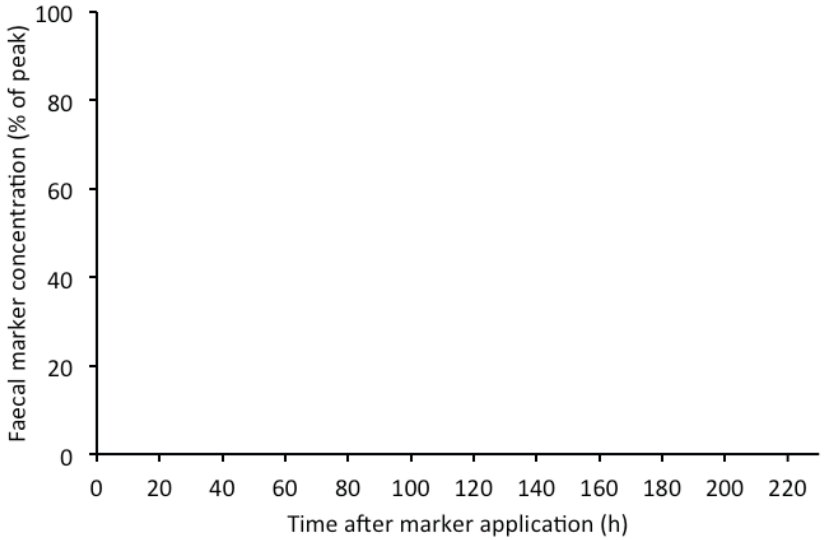




from Tschuor & Clauss (2008)

Passage kinetics of markers: ‘moose-type’





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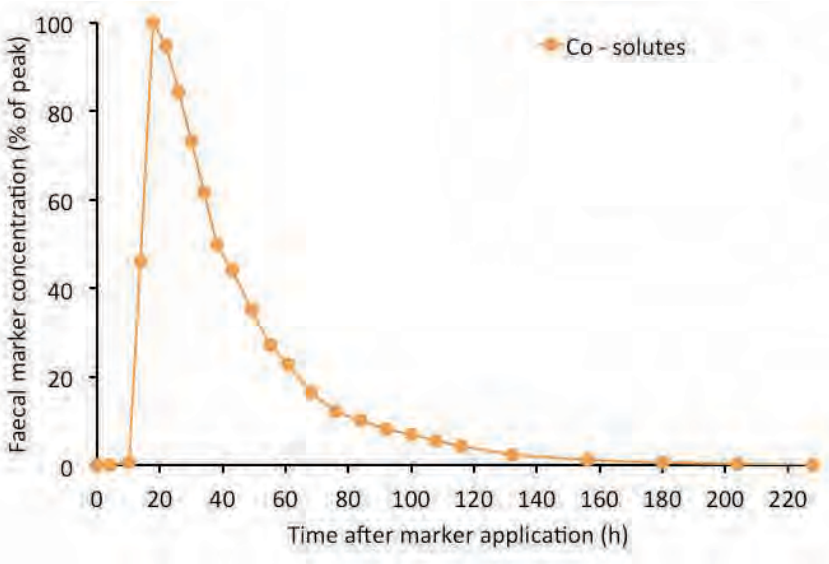

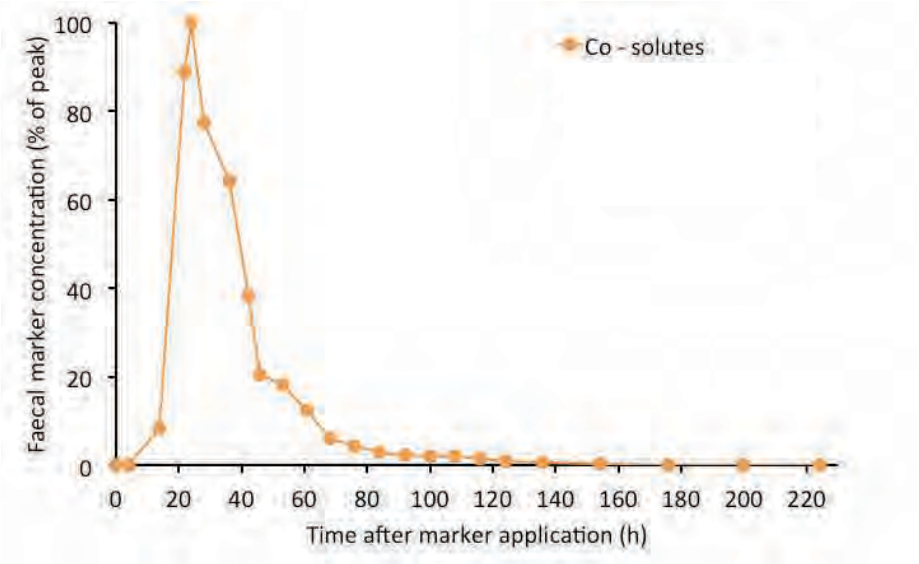

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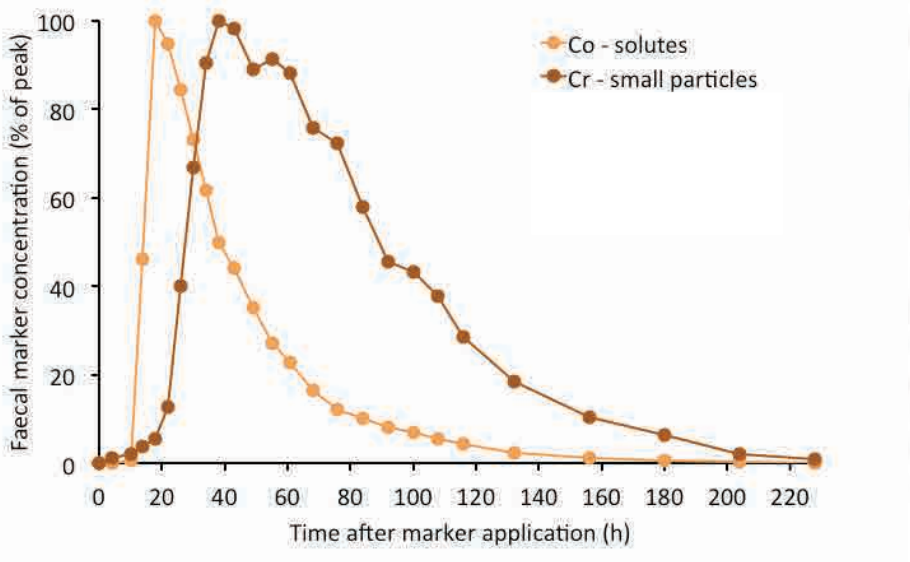

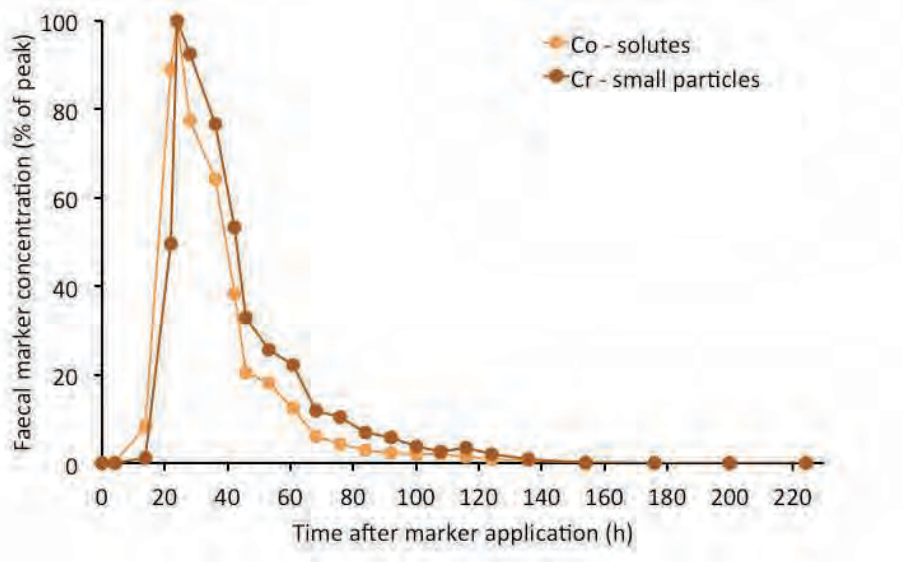

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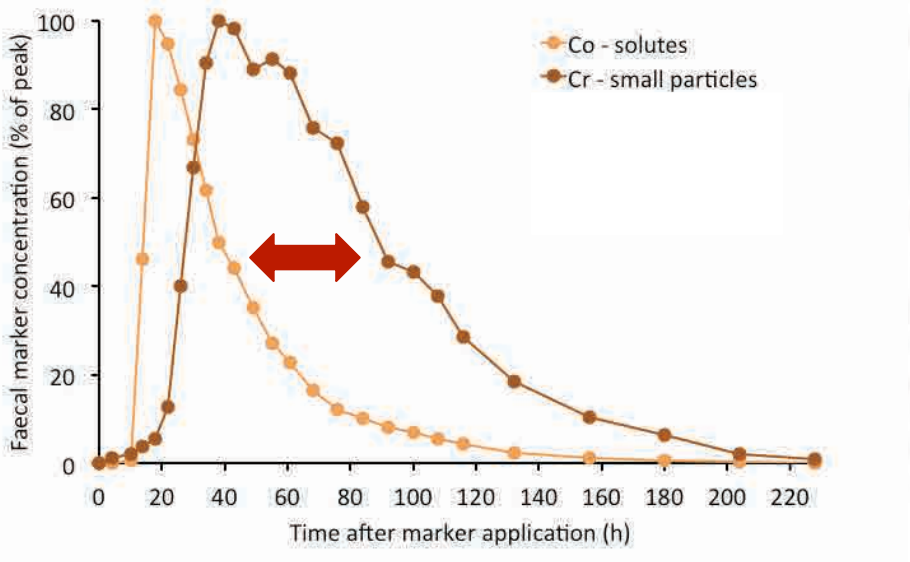

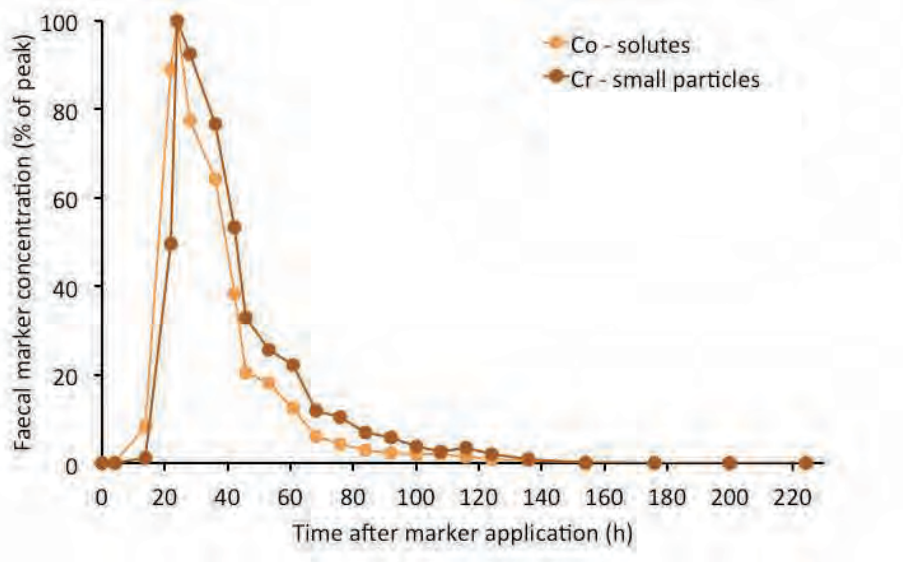

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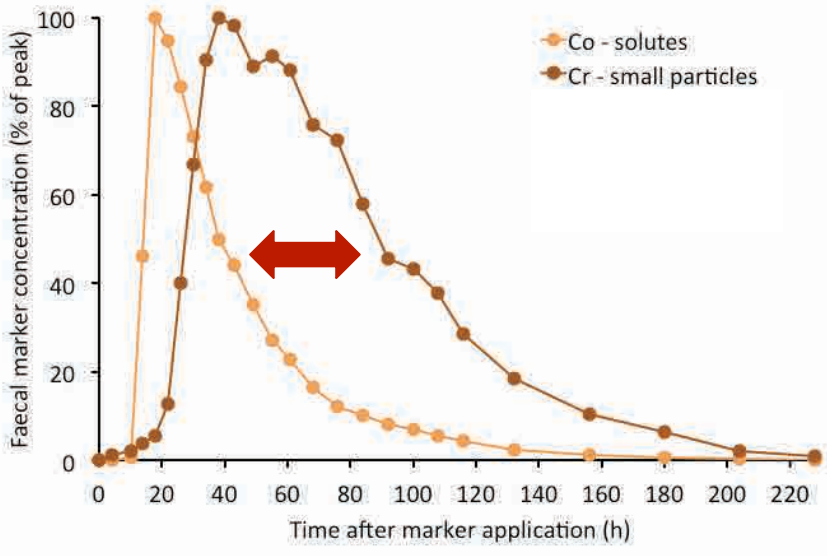

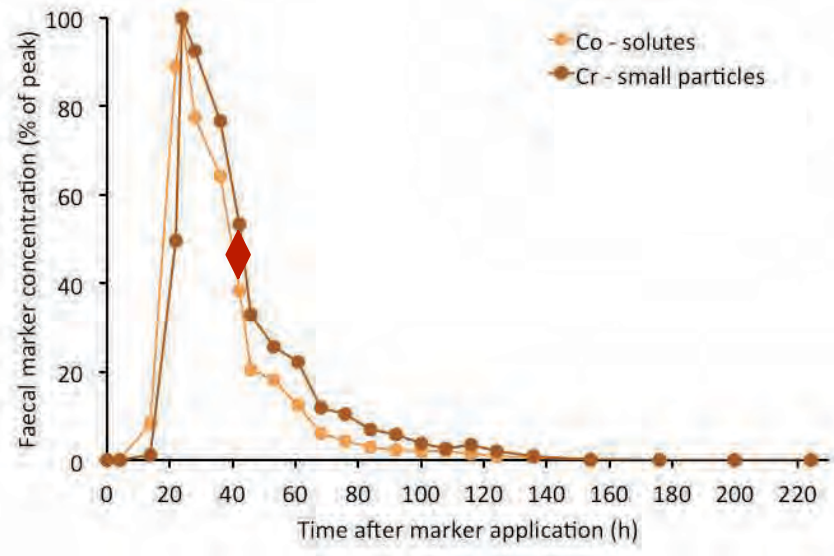

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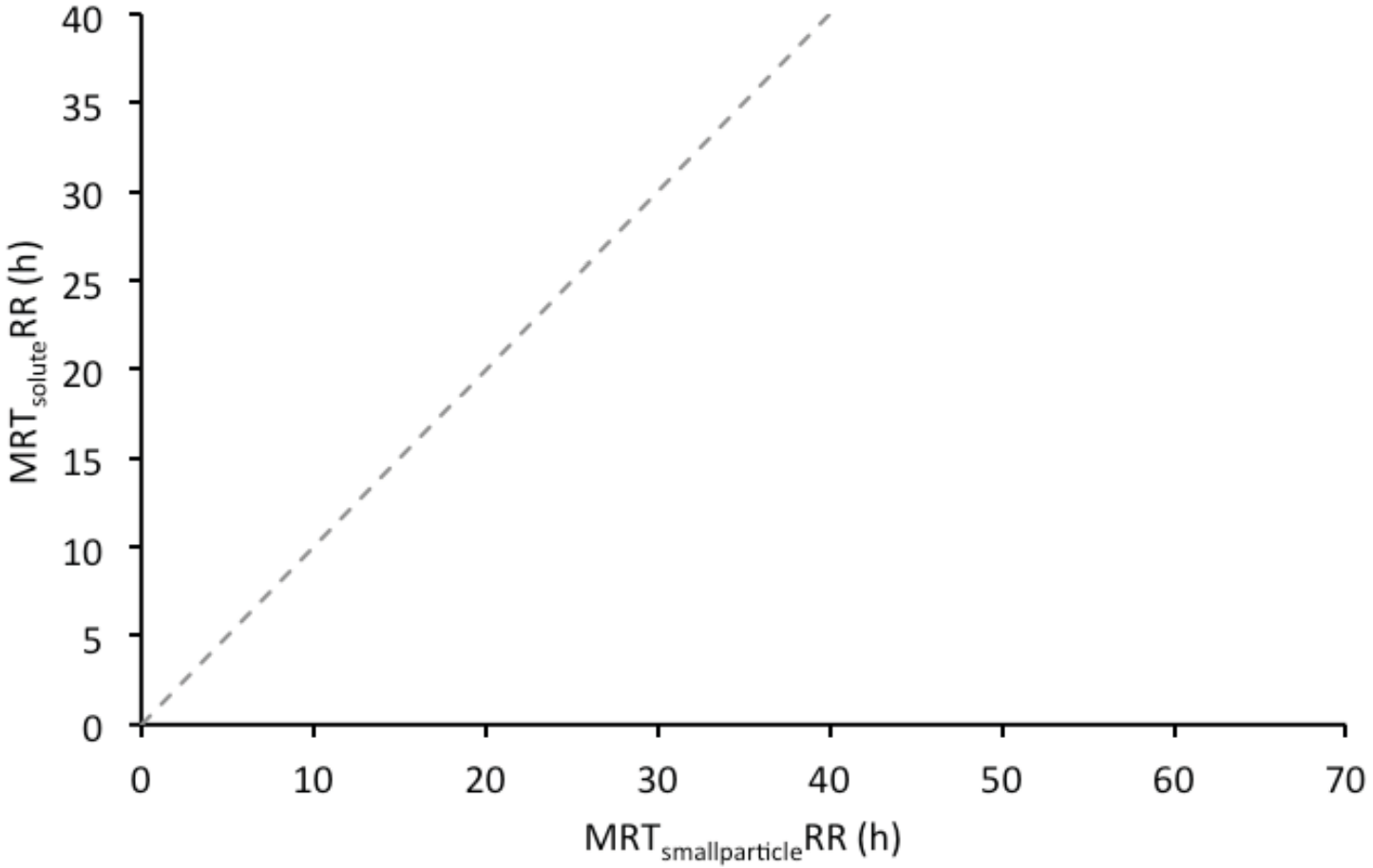
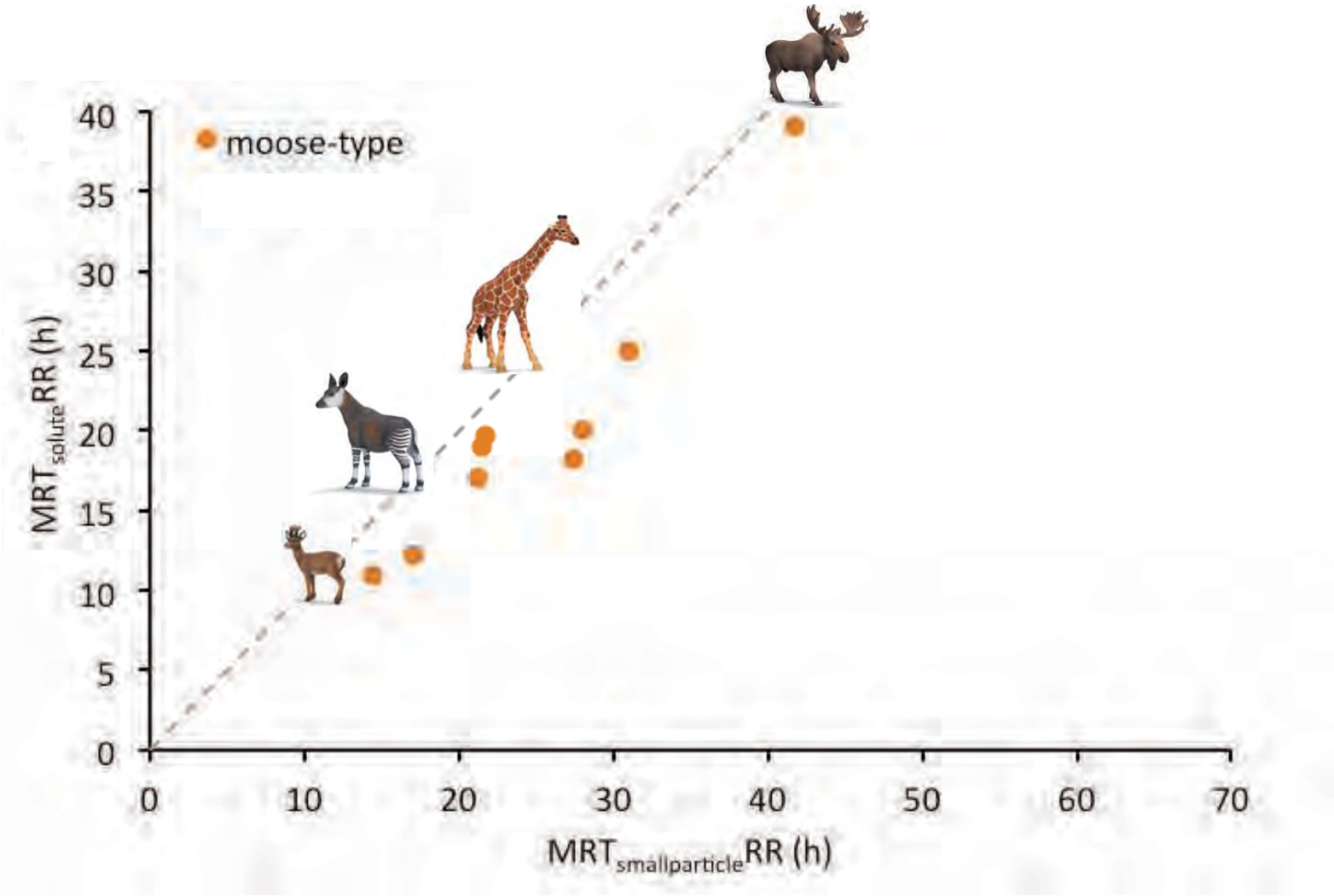
Passage kinetics of markers:



from Dittmann et al. (2015)

Passage kinetics of markers: ‘moose-type’



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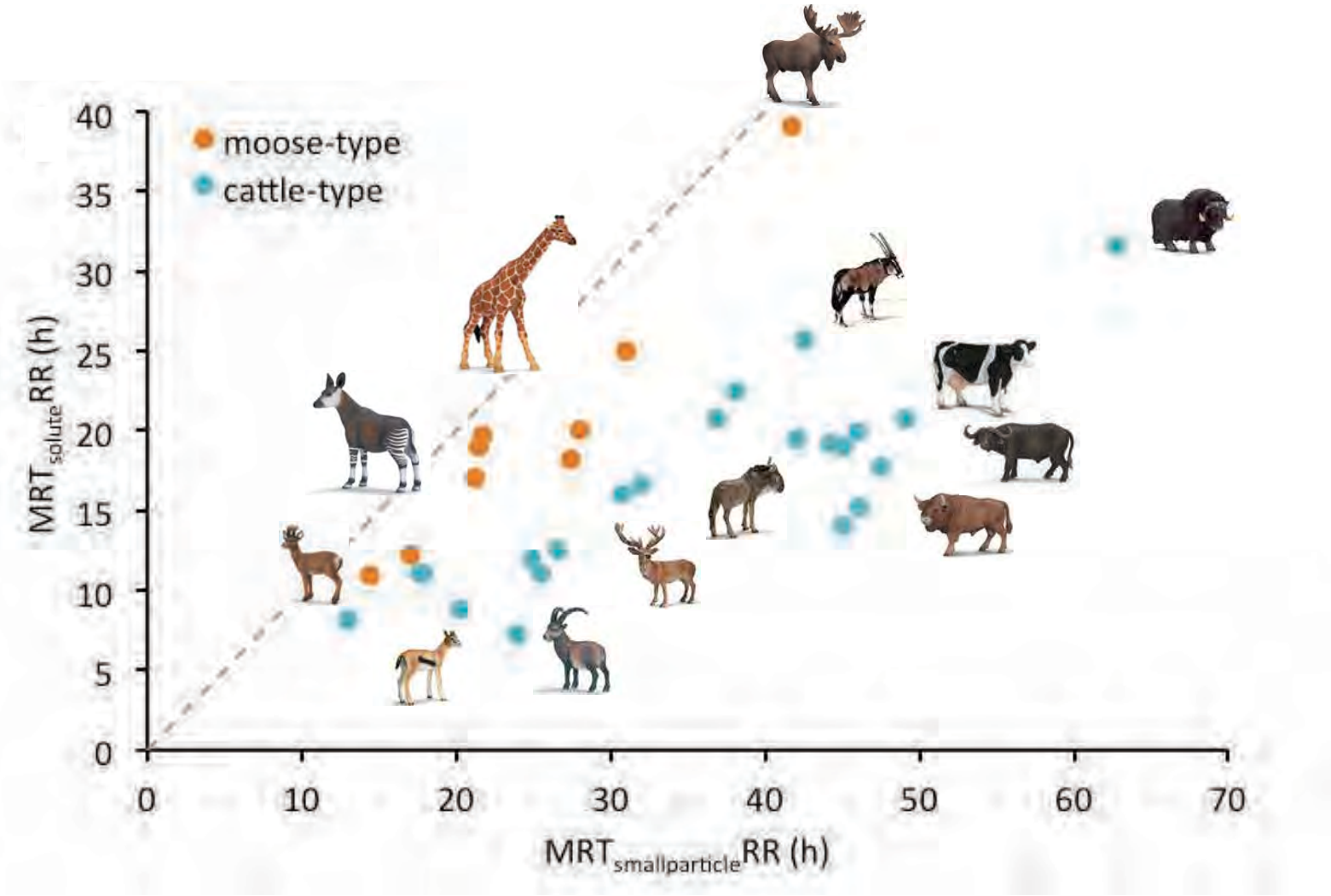
Passage kinetics of markers: ‘cattle-type’



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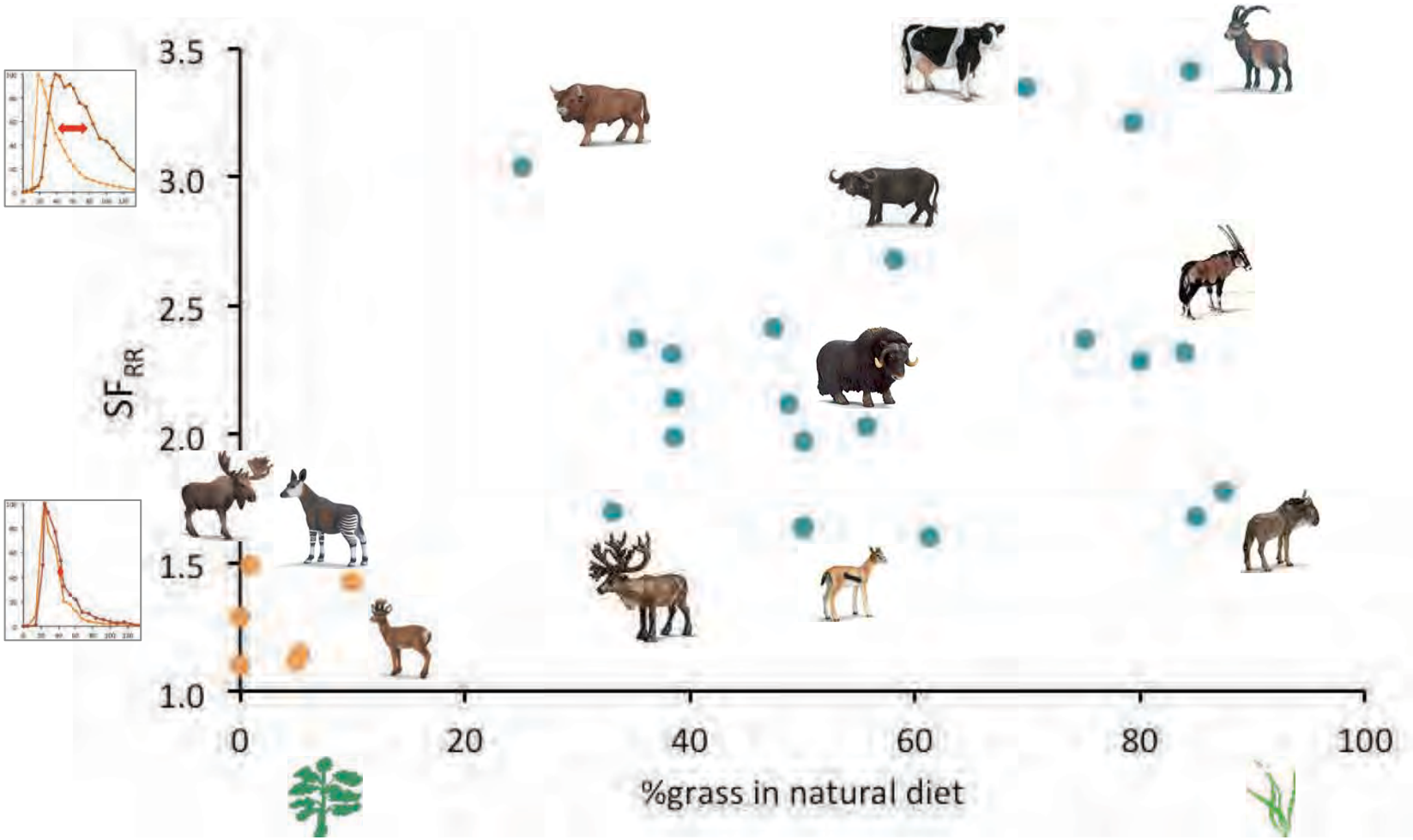
Another measure of ‘stratification’



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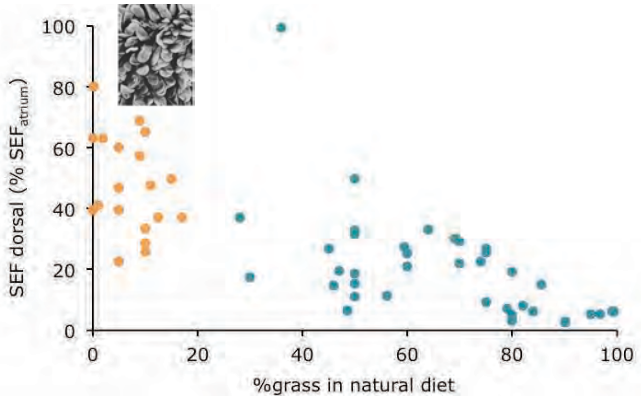
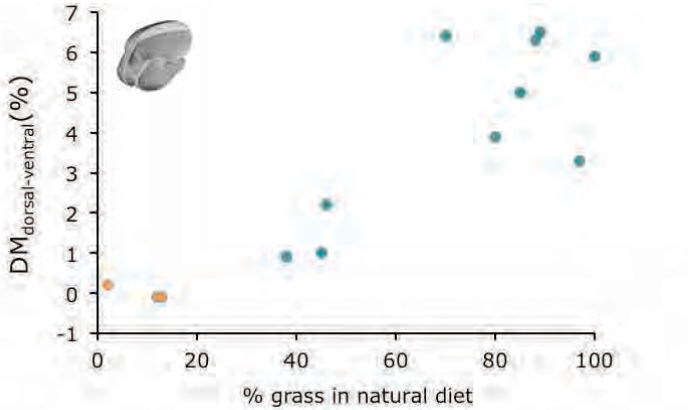
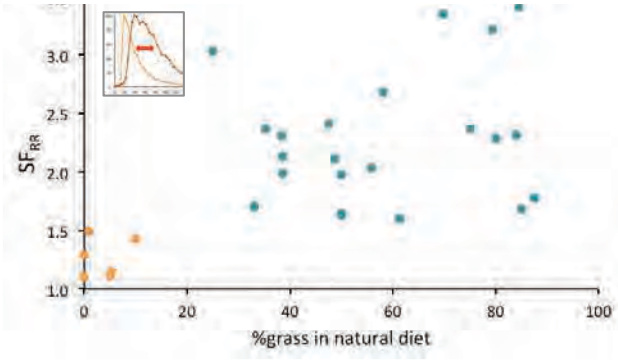
Three measures of ‘stratification’

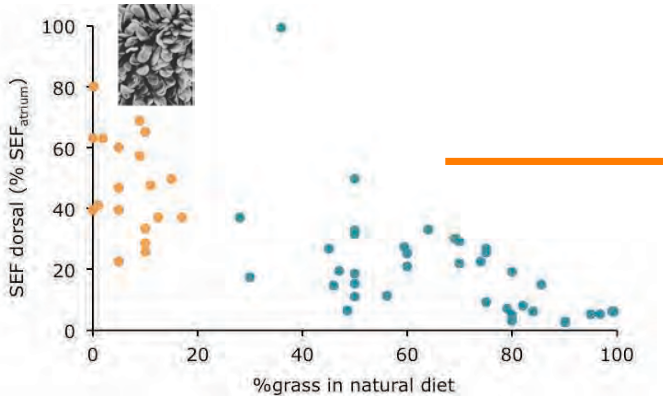


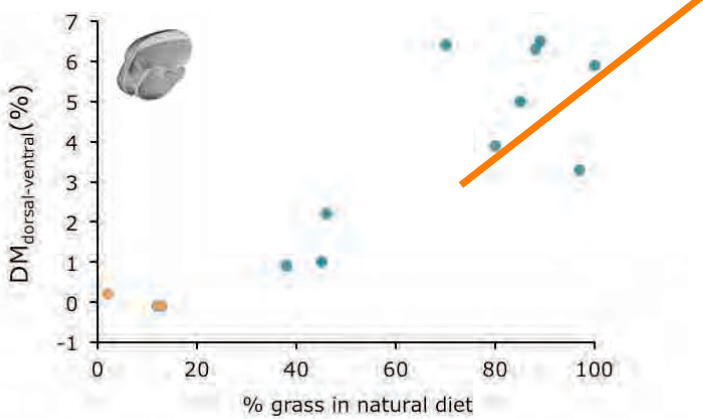


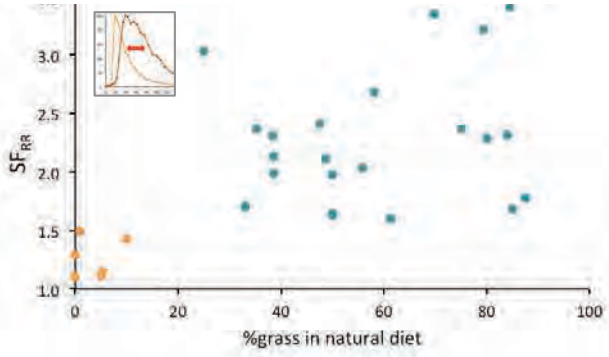


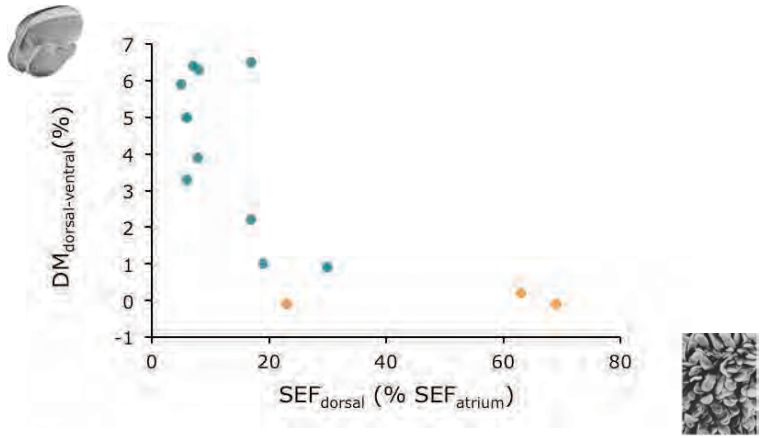
from Clauss et al. (2009), Codron & Clauss (2010), Dittmann et al. (2015), Tahas et al. (subm.)

Three measures of ‘stratification’









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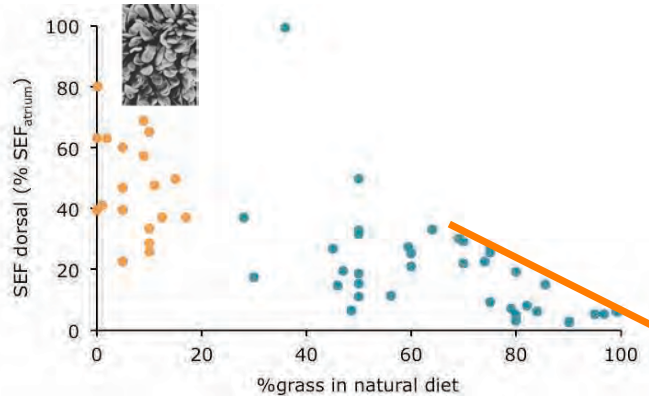

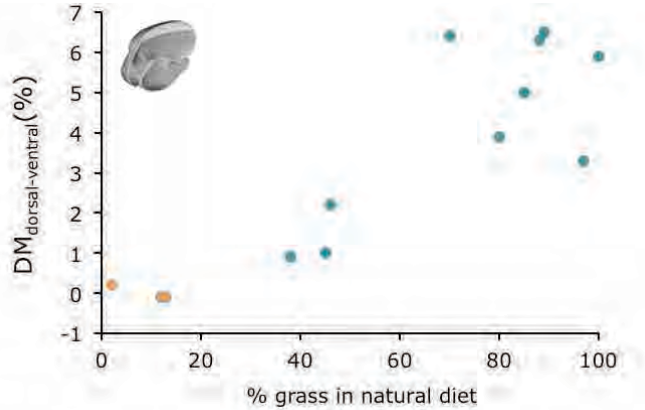

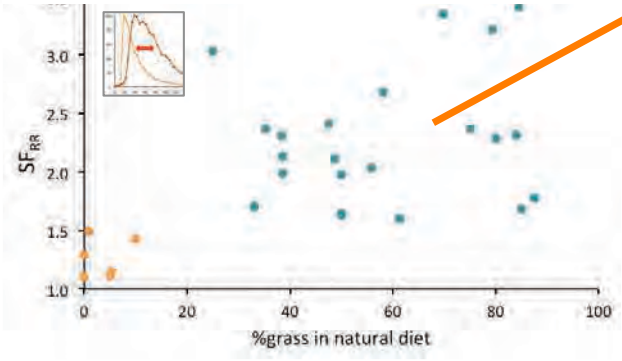

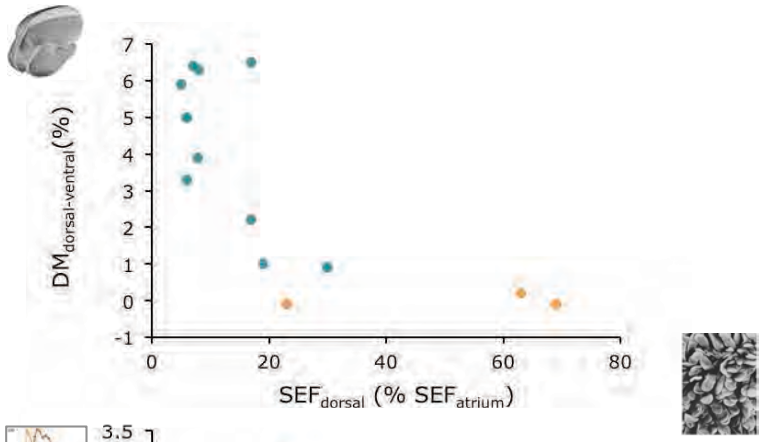

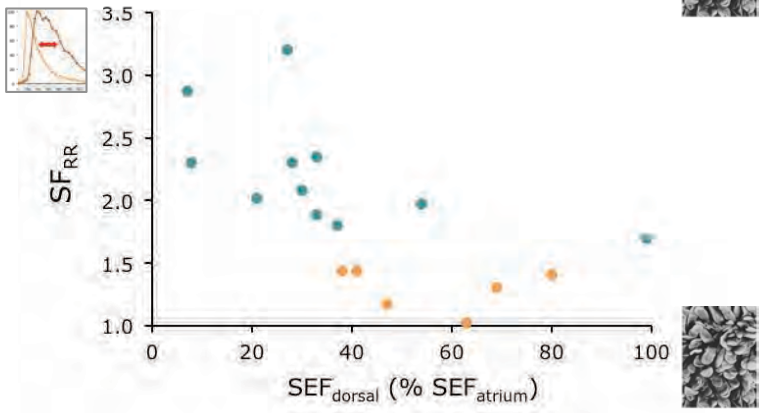

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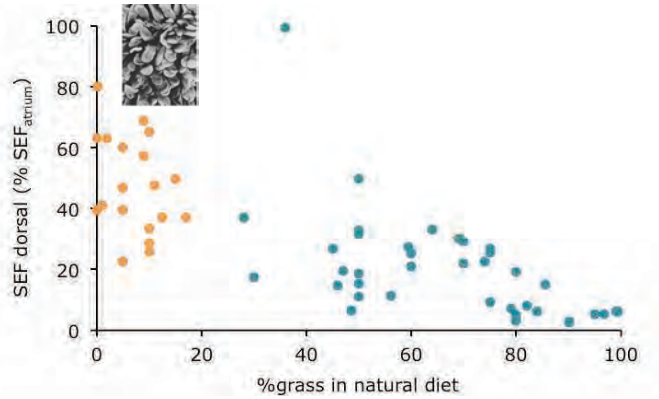

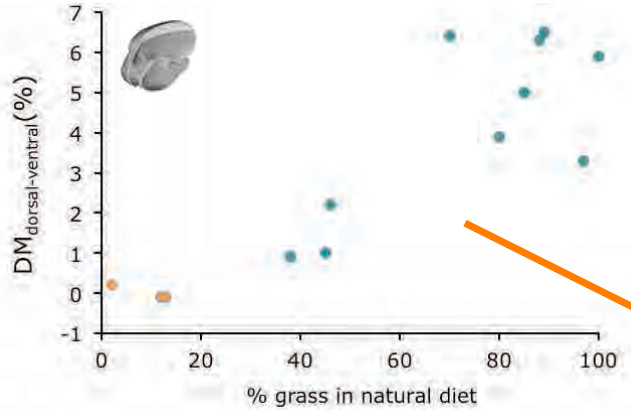

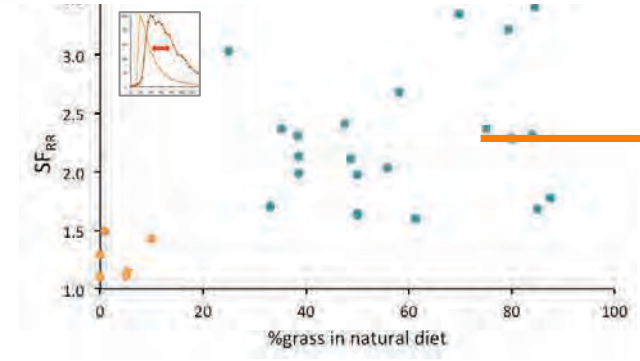

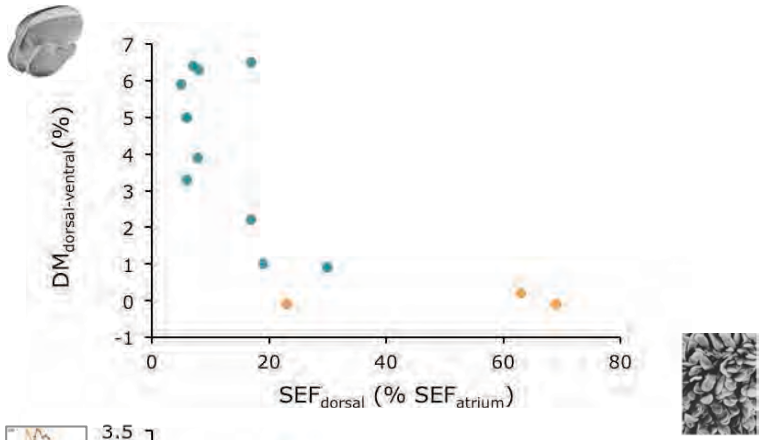

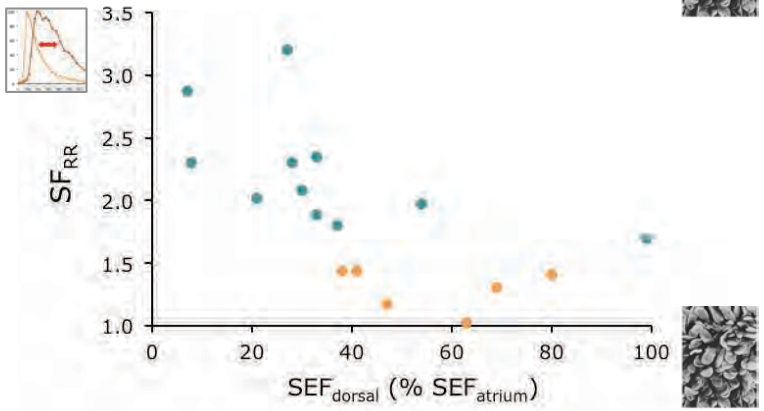

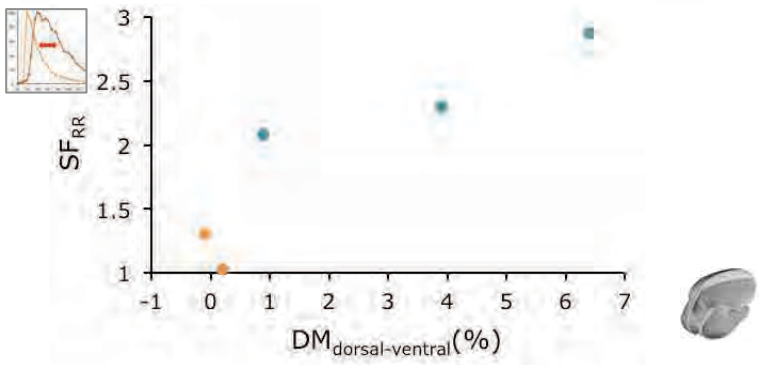

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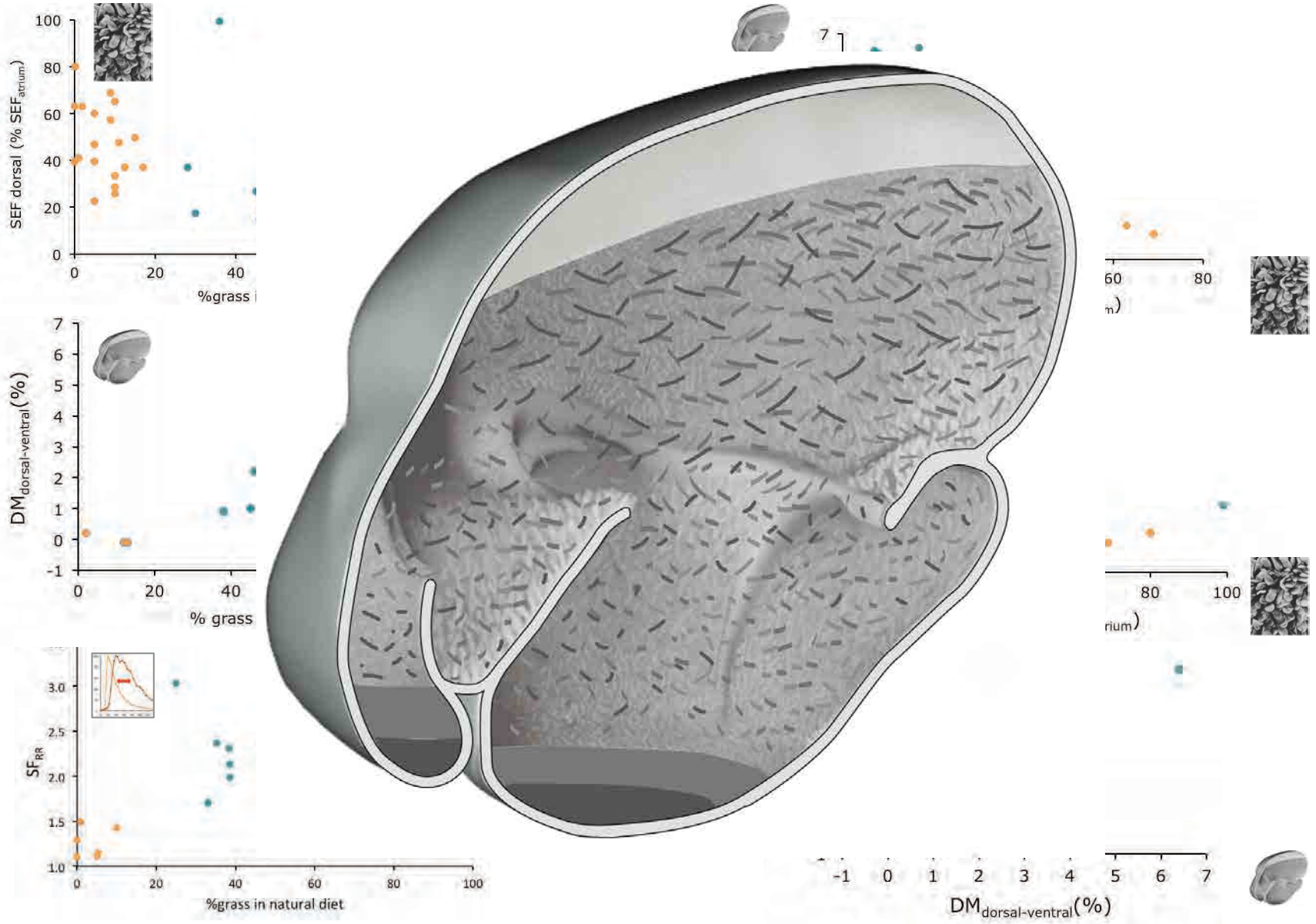

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Sequence of hypotheses

Soft tissue variation and forestomach physiology is linked to

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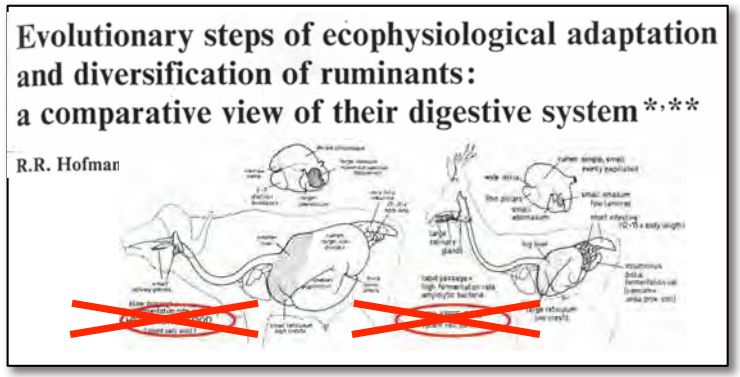

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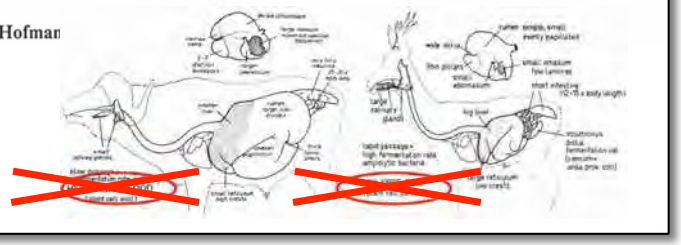

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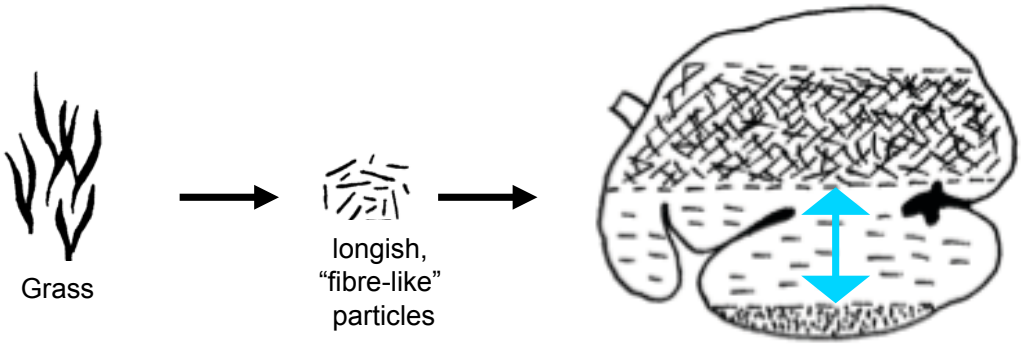
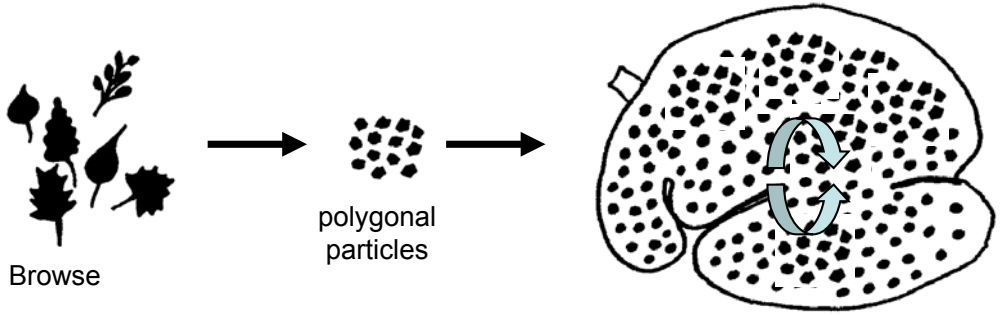
OIKOS 102: 253–262, 2003

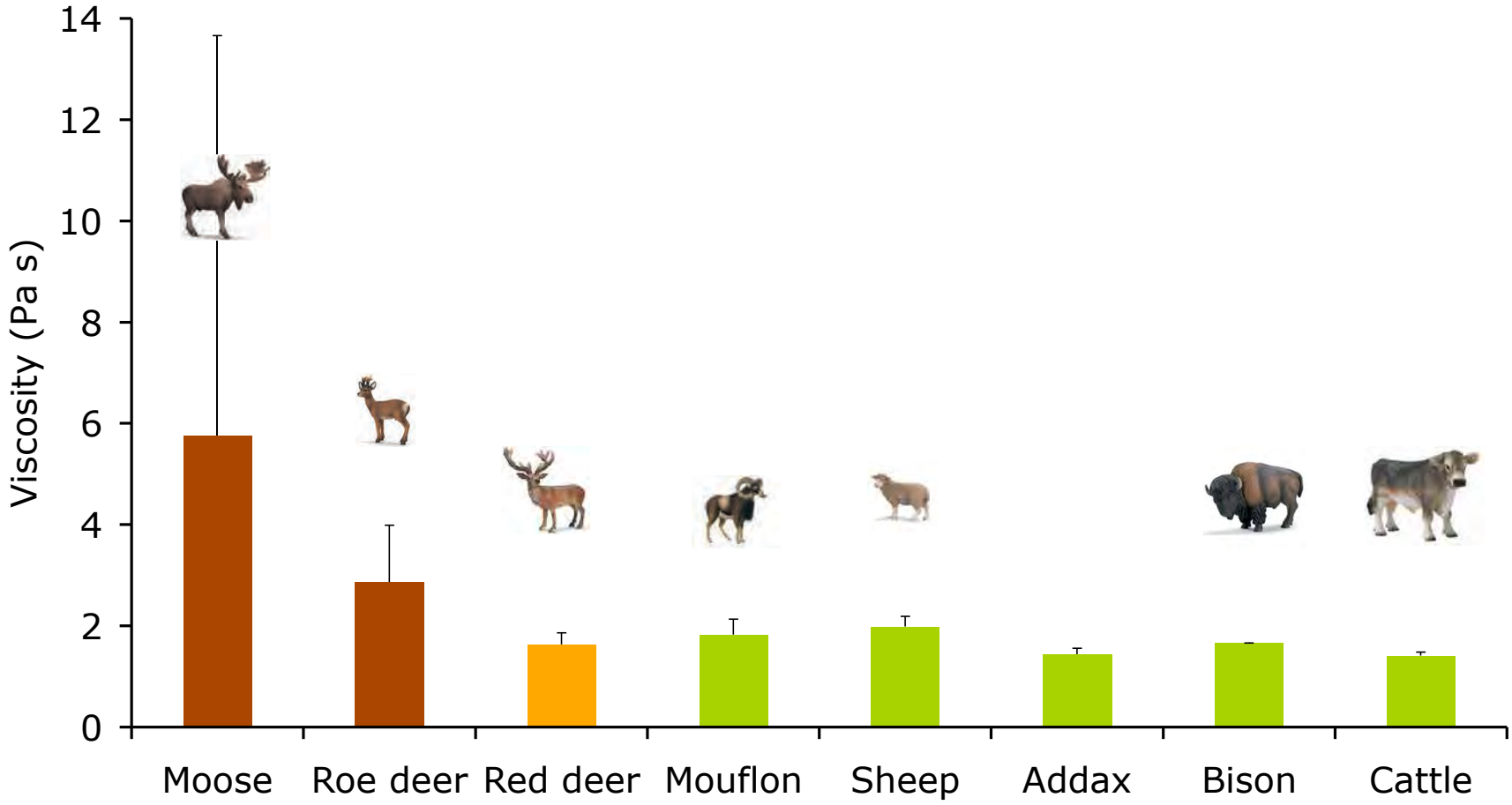


Low viscosity fluid: Separation due to flotations/sedimentation; clear separation of gas dome



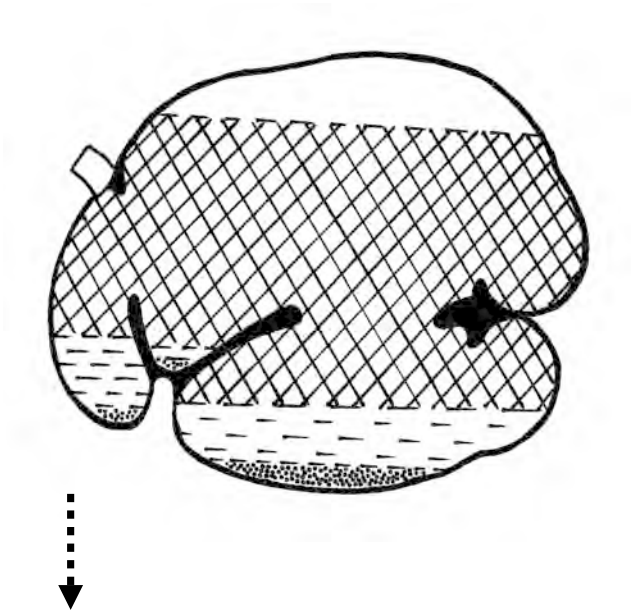
High viscosity fluid: Separation due to flotation/sedimentation less possible; gas bubbles distributed evenly in the contents

Rumen fluid viscosity

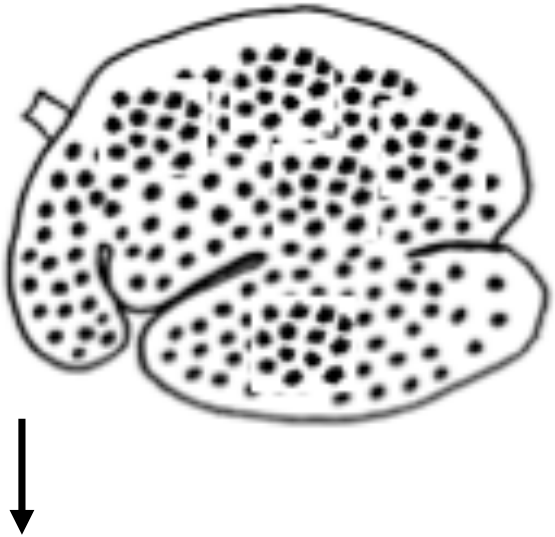


from Hummel et al. (2009) and Clauss et al. (2009ab)

Differences in RR contents stratification could mean ...



only small particles escape the rumen



escape of larger particles possible

Marcus Clauss · Matthias Lechner-Doll
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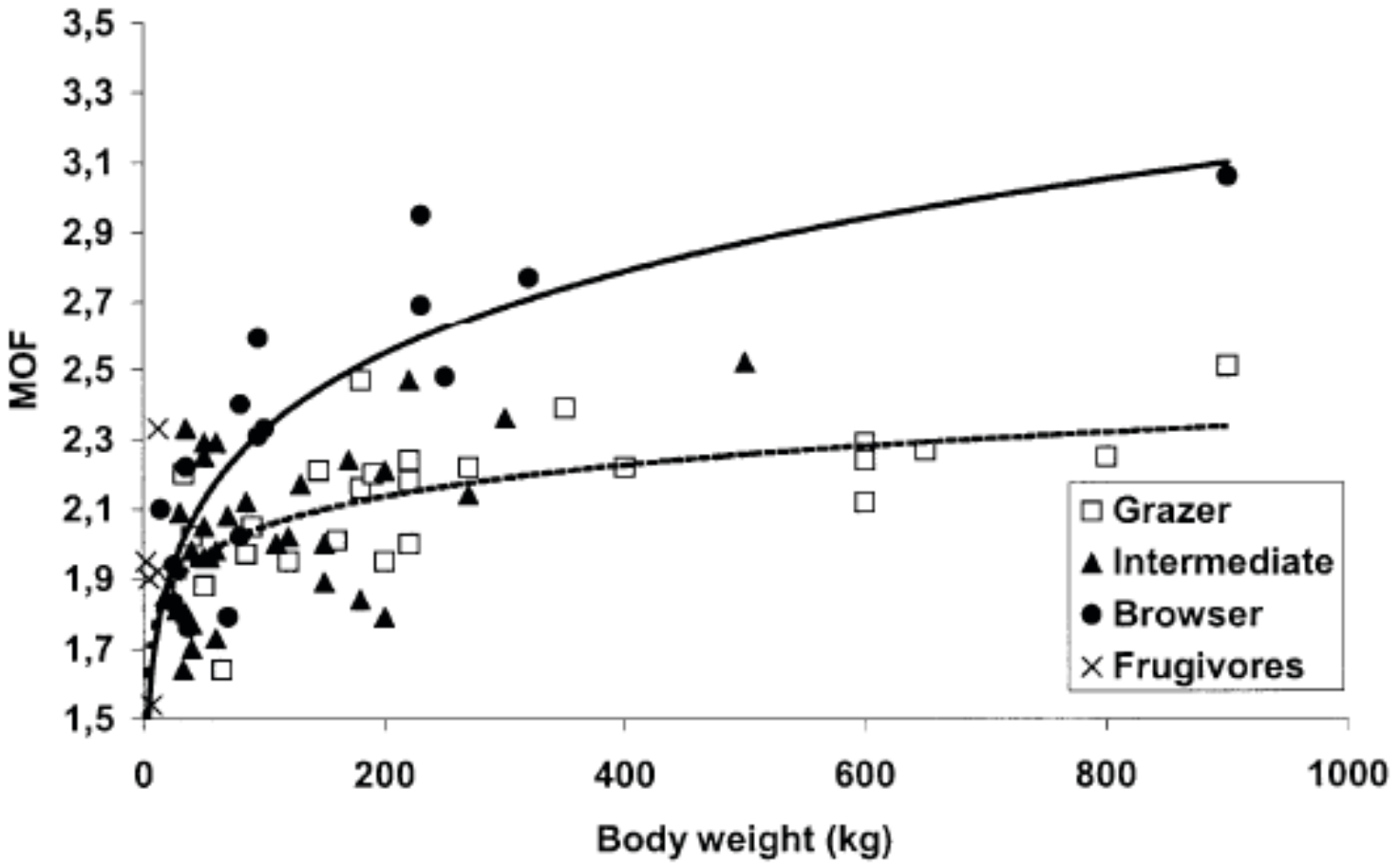
Oecologia (2002) 131:343–349

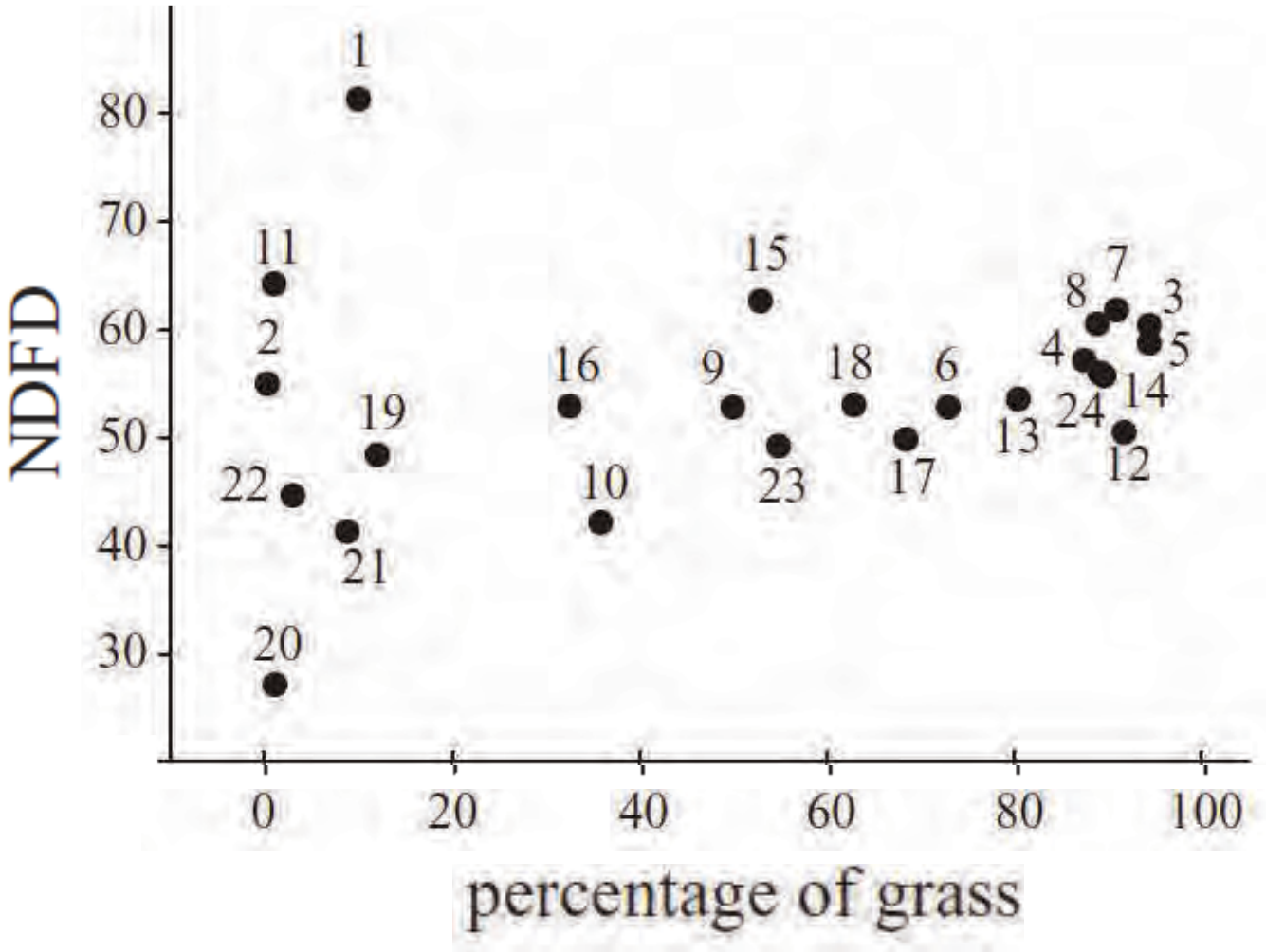
Faecal particle size distribution in captive wild ruminants: an approach to the browser/grazer dichotomy from the other end



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

F. J. Pérez-Barbería[1*], D. A. Elston[2], I. J. Gordon[1†] and A. W. Illius[3]

Proc. R. Soc. Lond. B (2004) 271, 1081–1090



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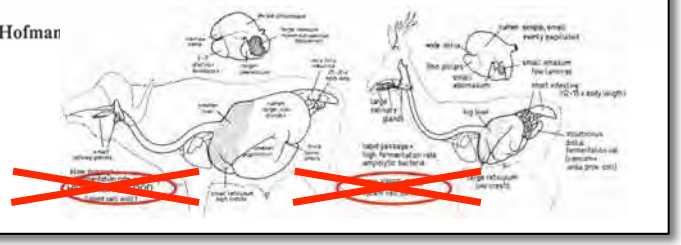

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from Lechner et al. (2010)

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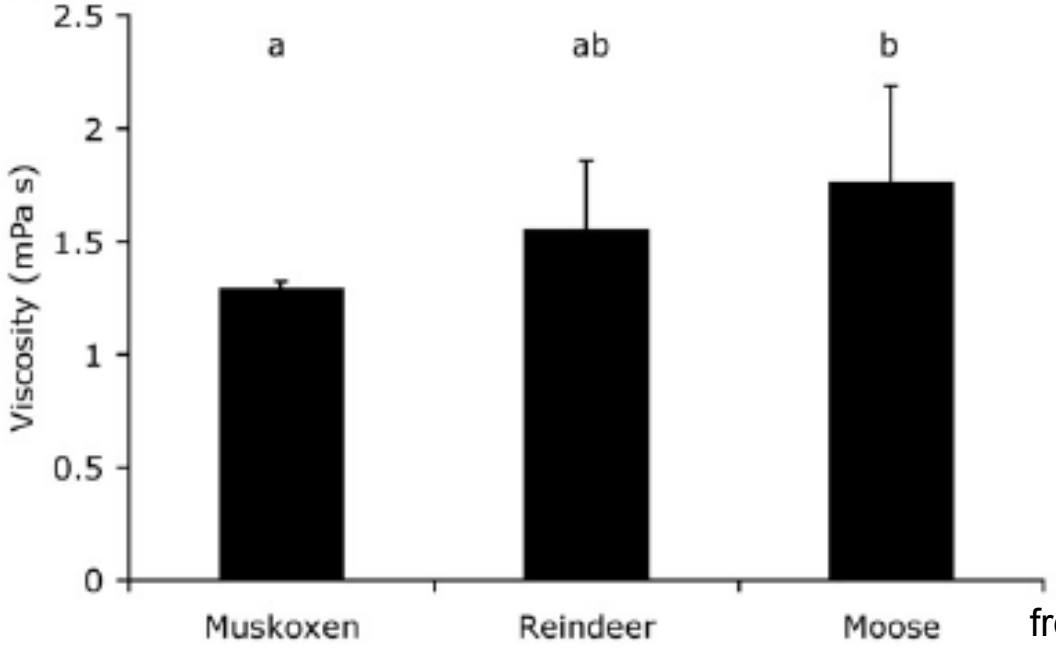

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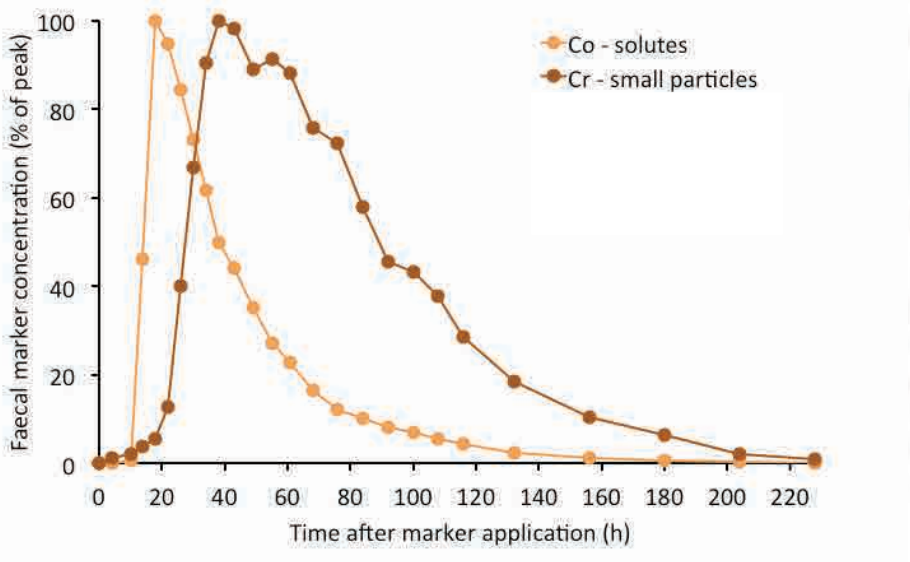
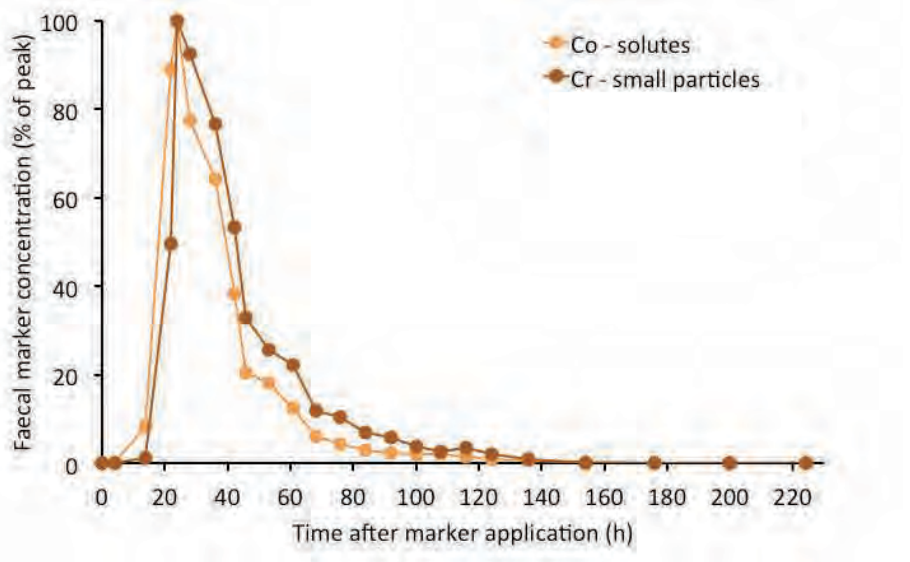
Passage kinetics of markers: ‘moose-type’





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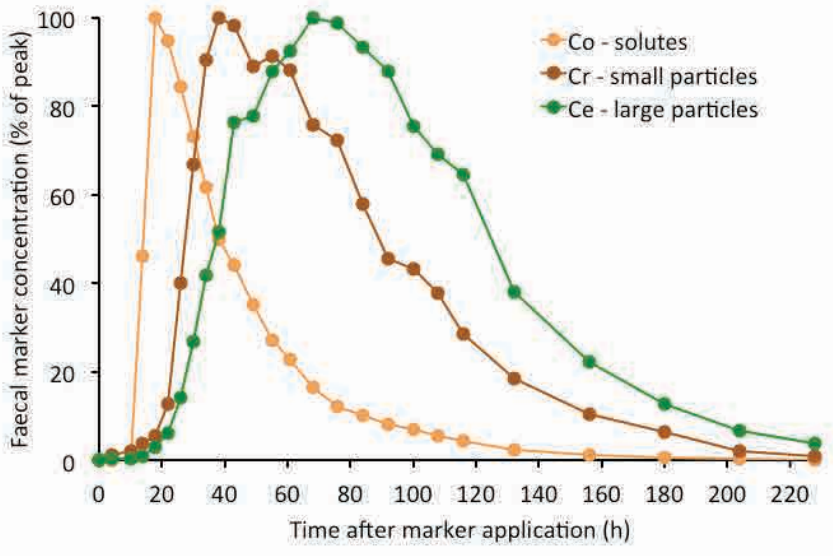

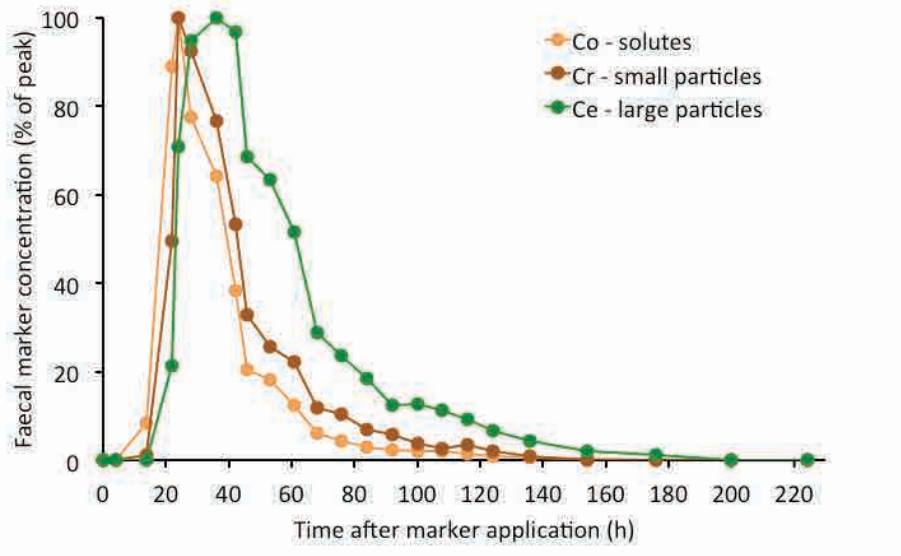

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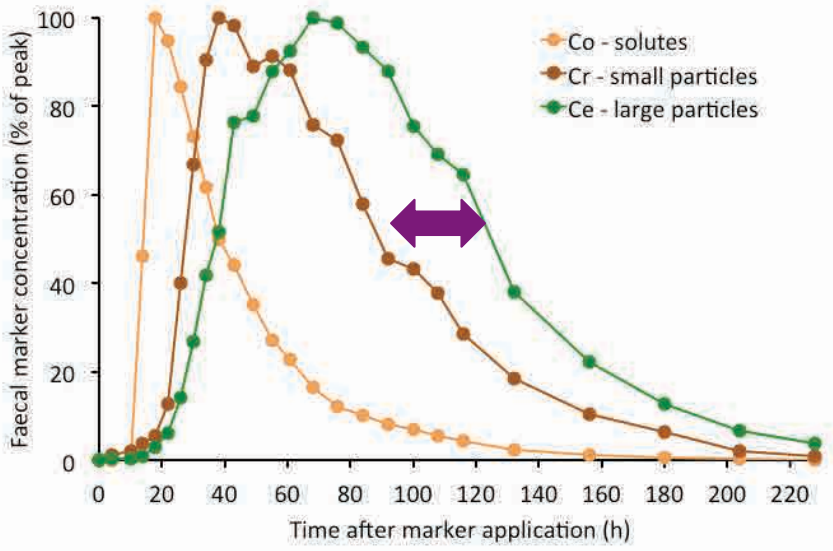

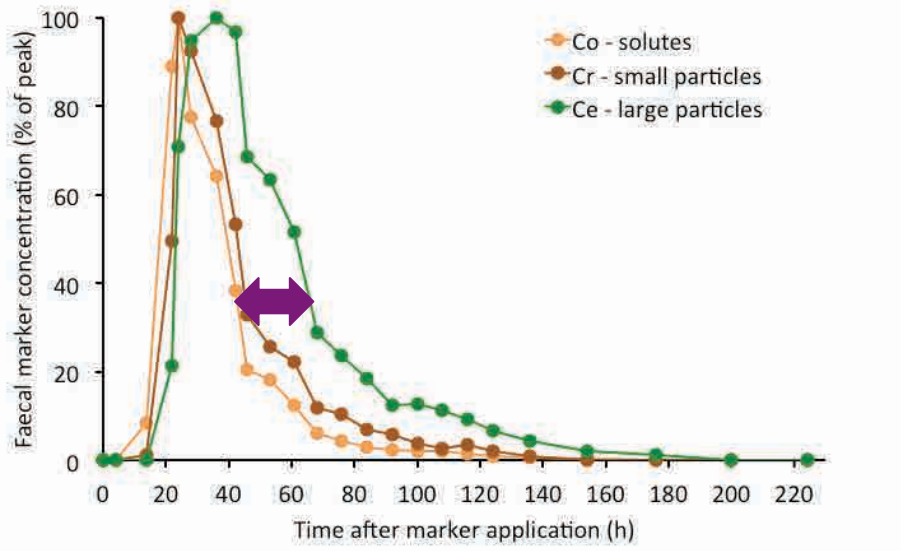

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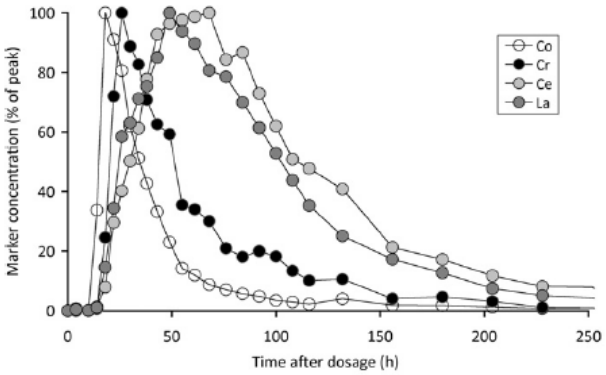
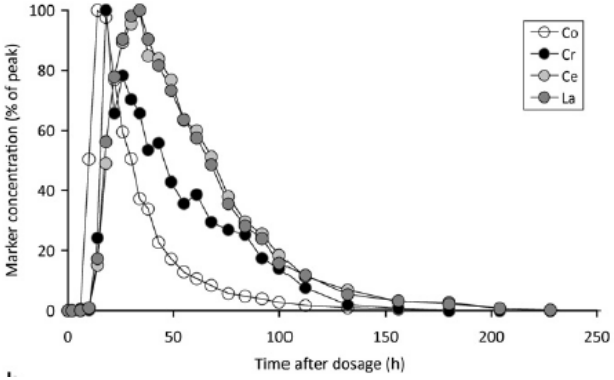
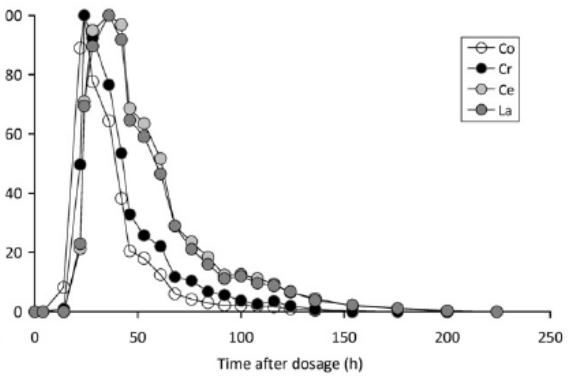
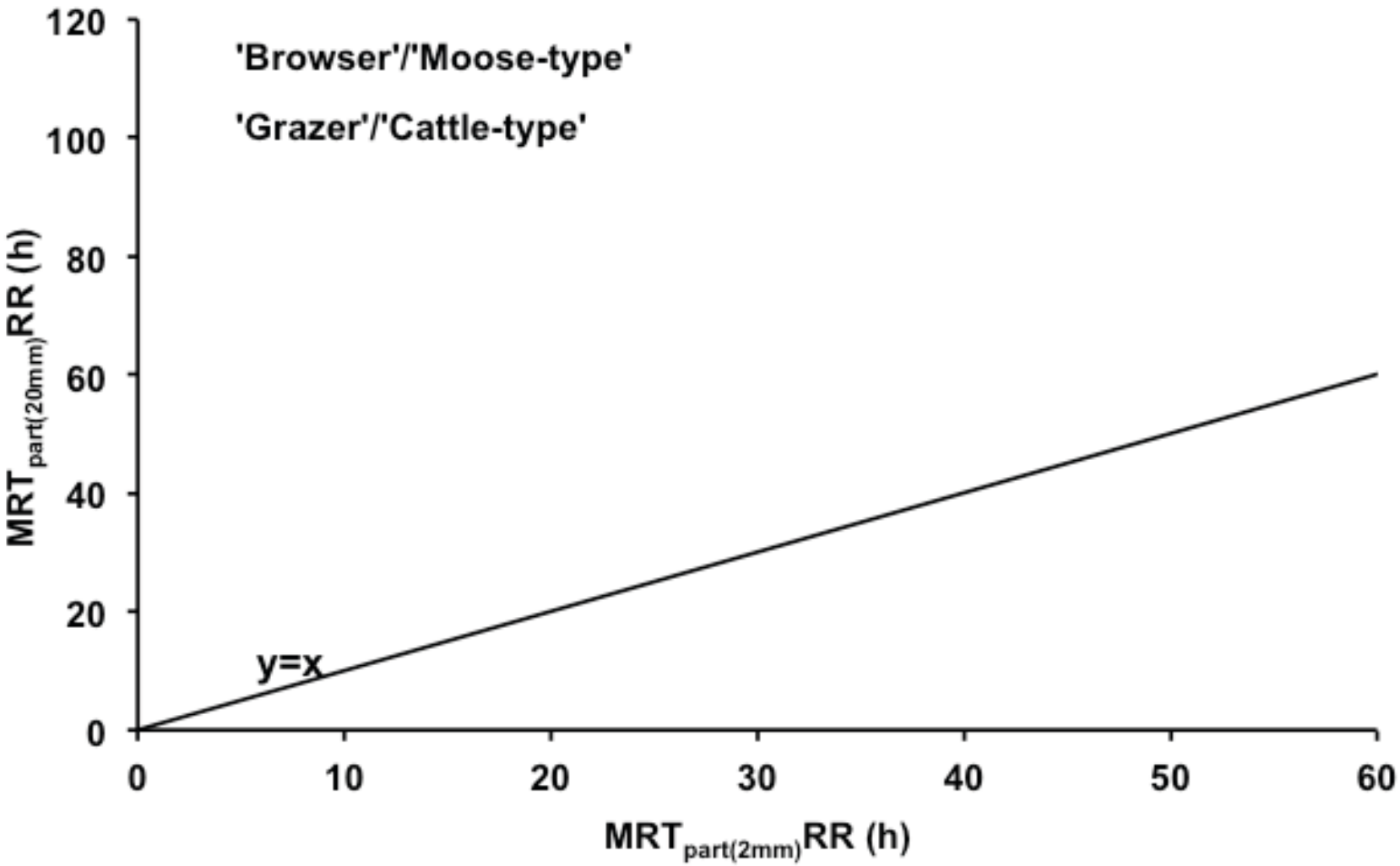






from Lechner et al. (2010)

No difference in sorting mechanism



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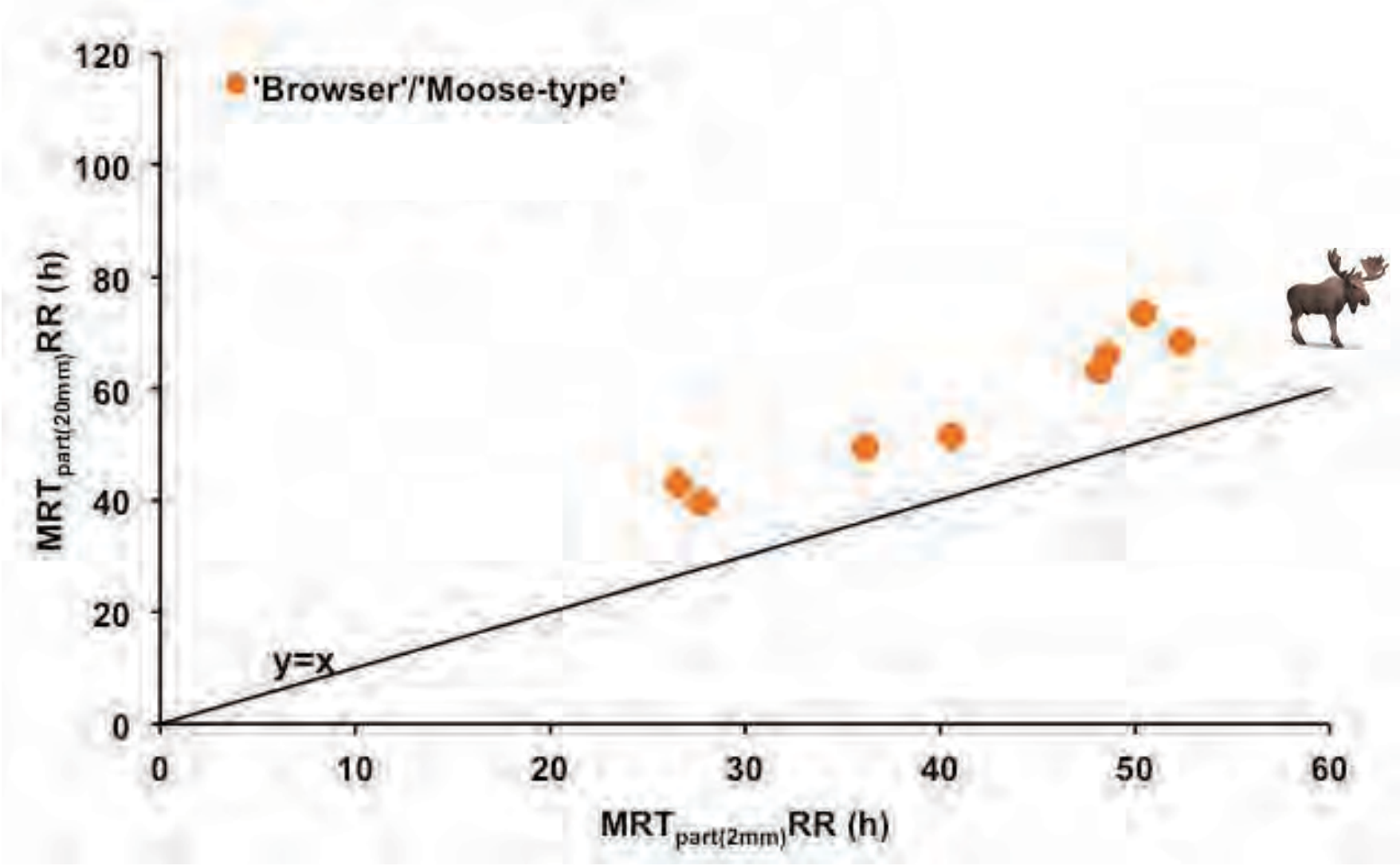

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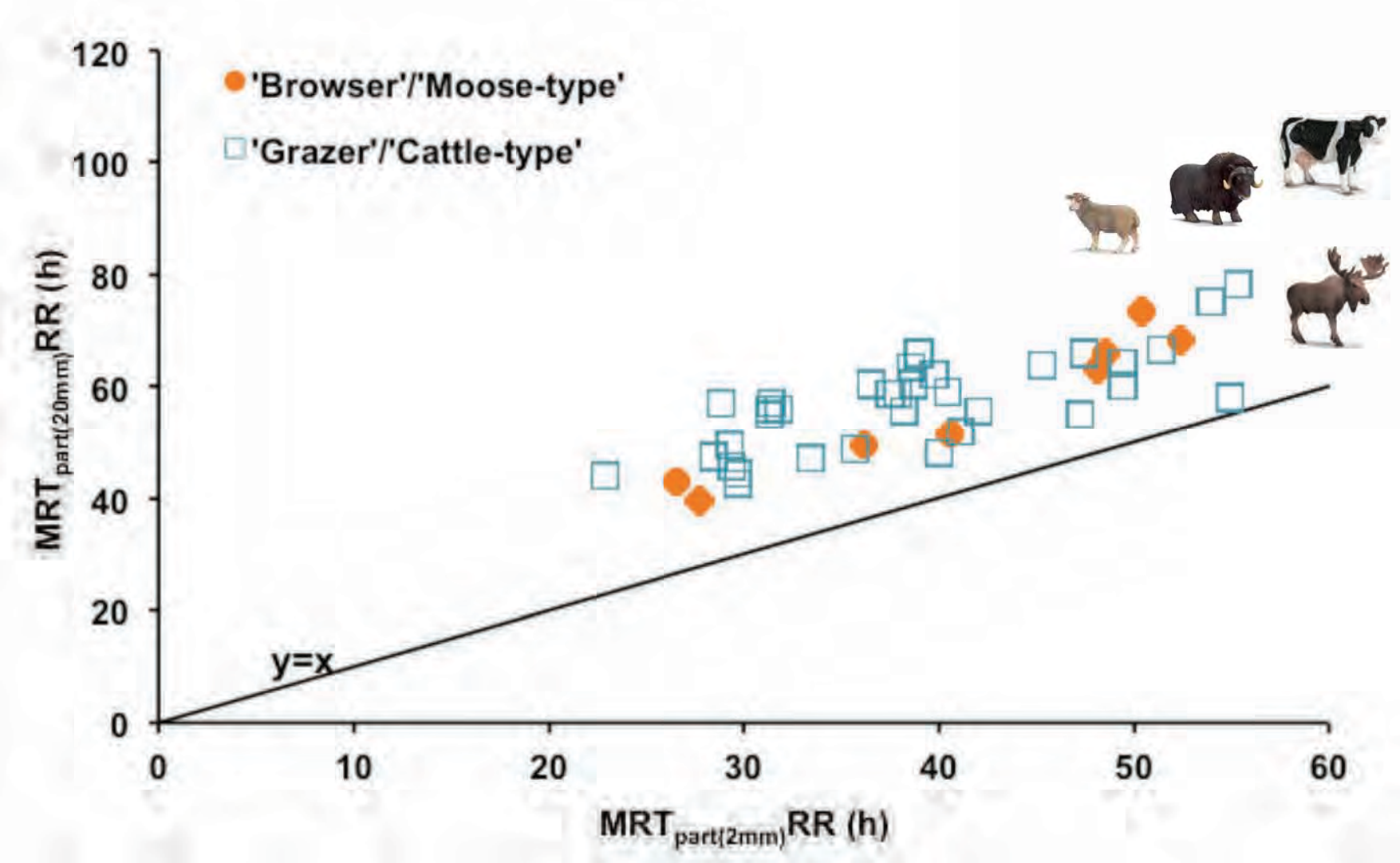

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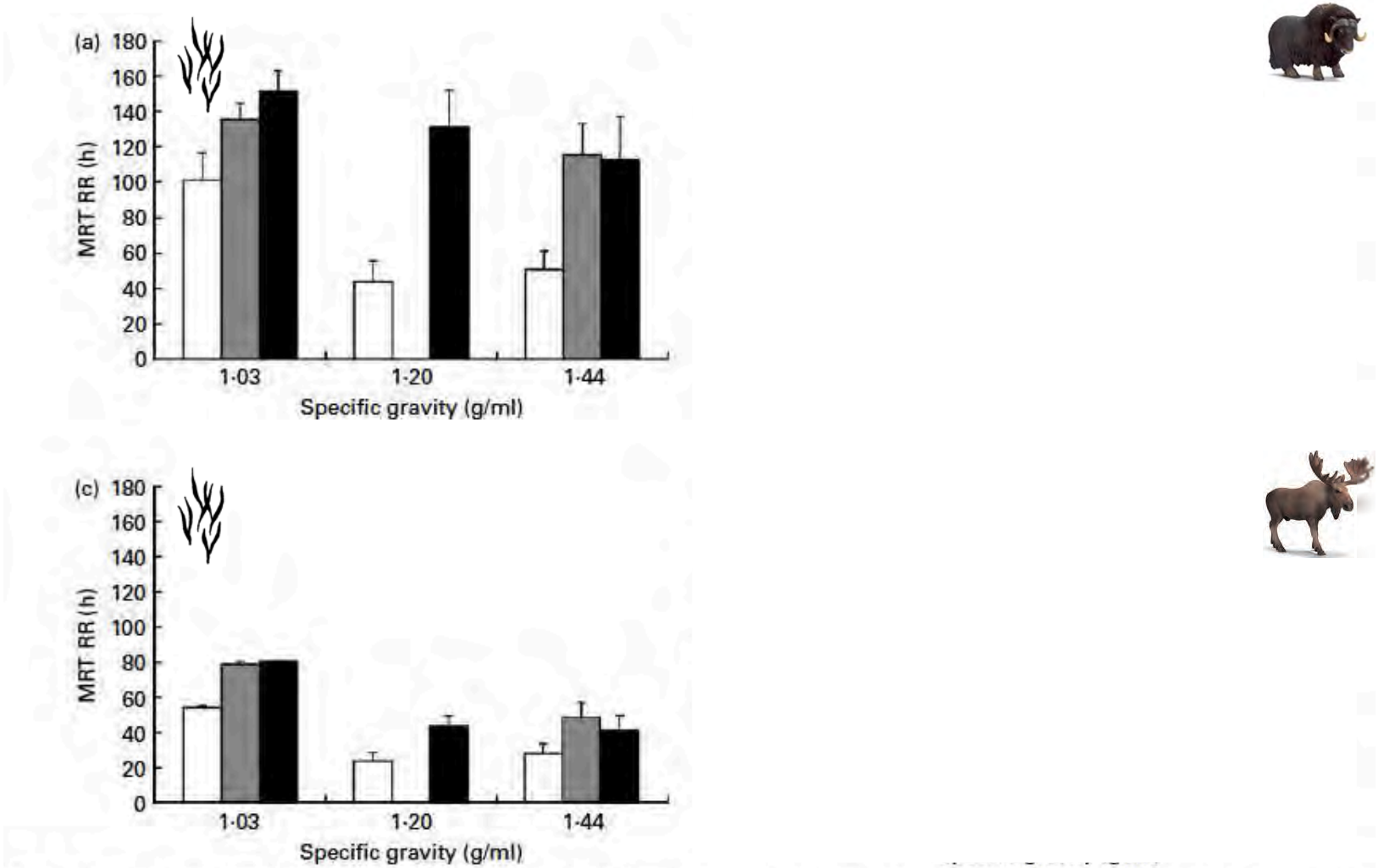

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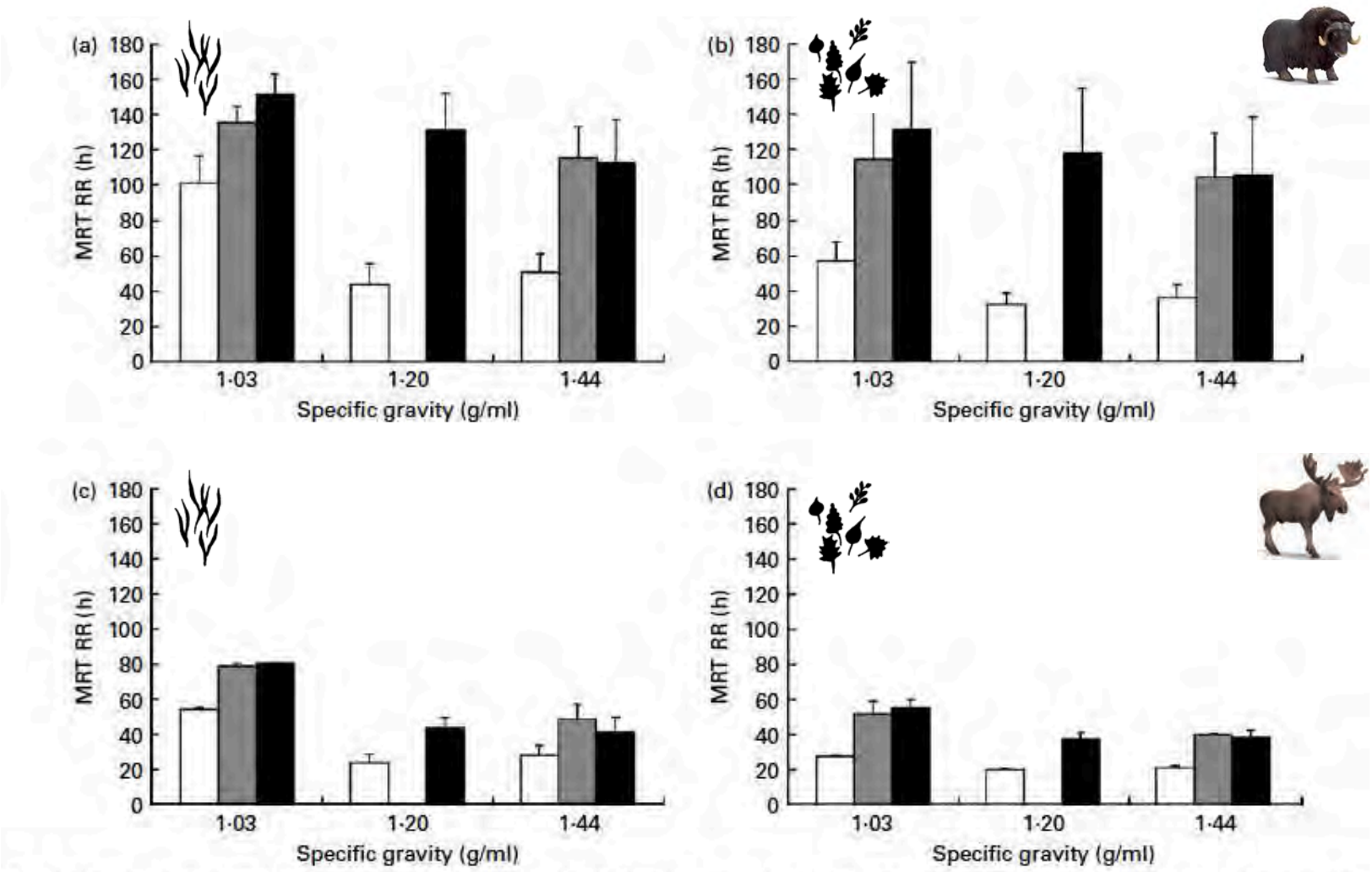

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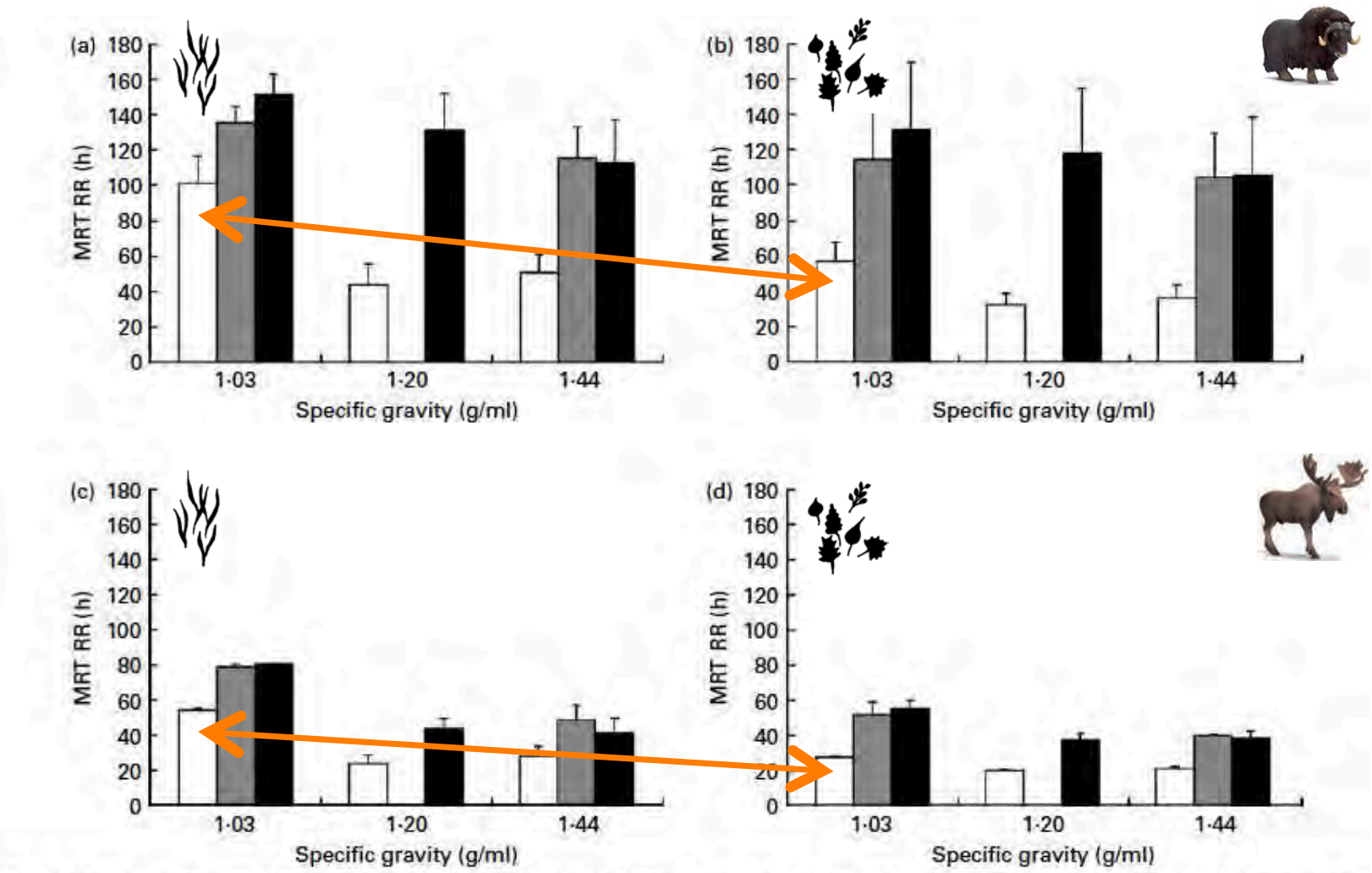

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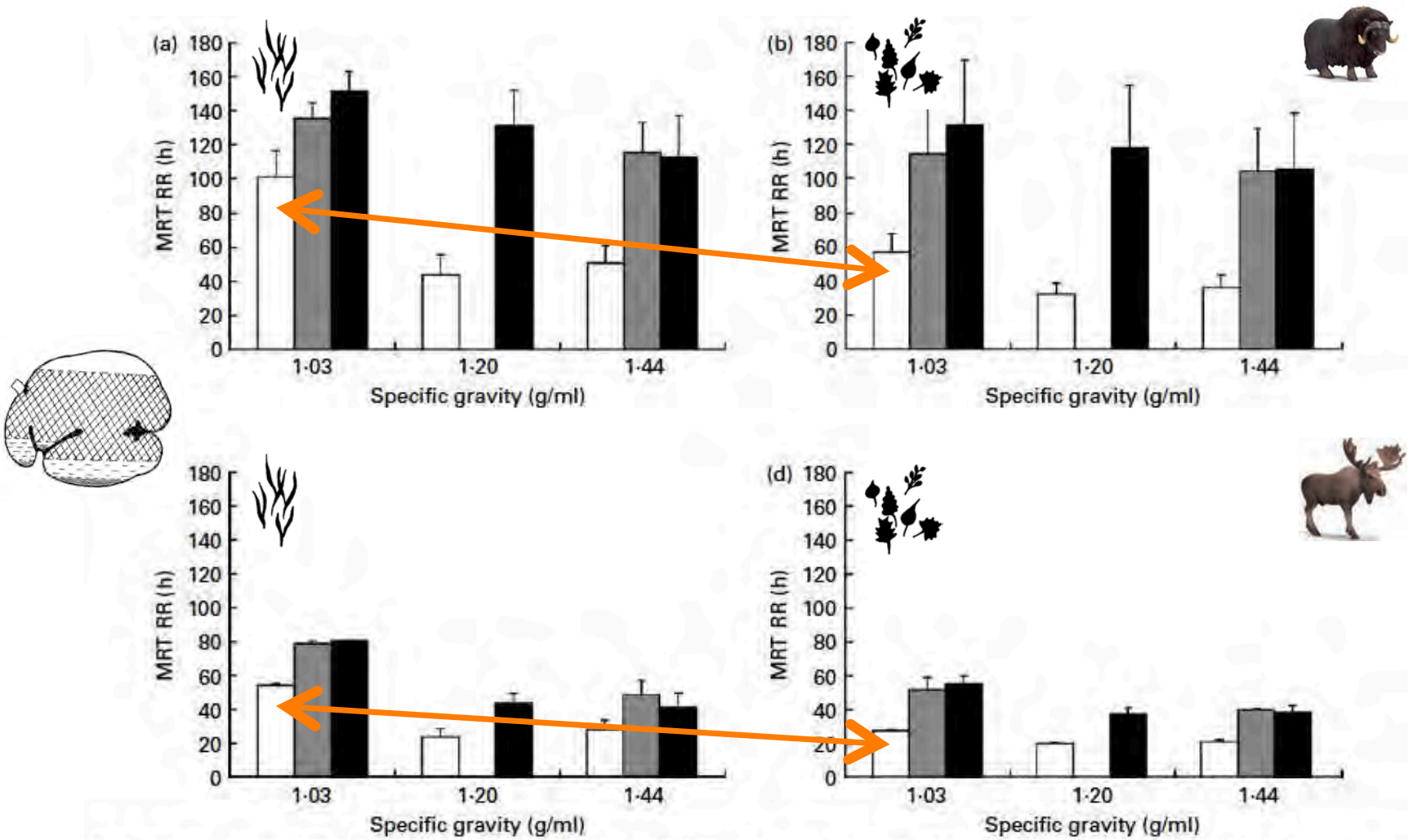

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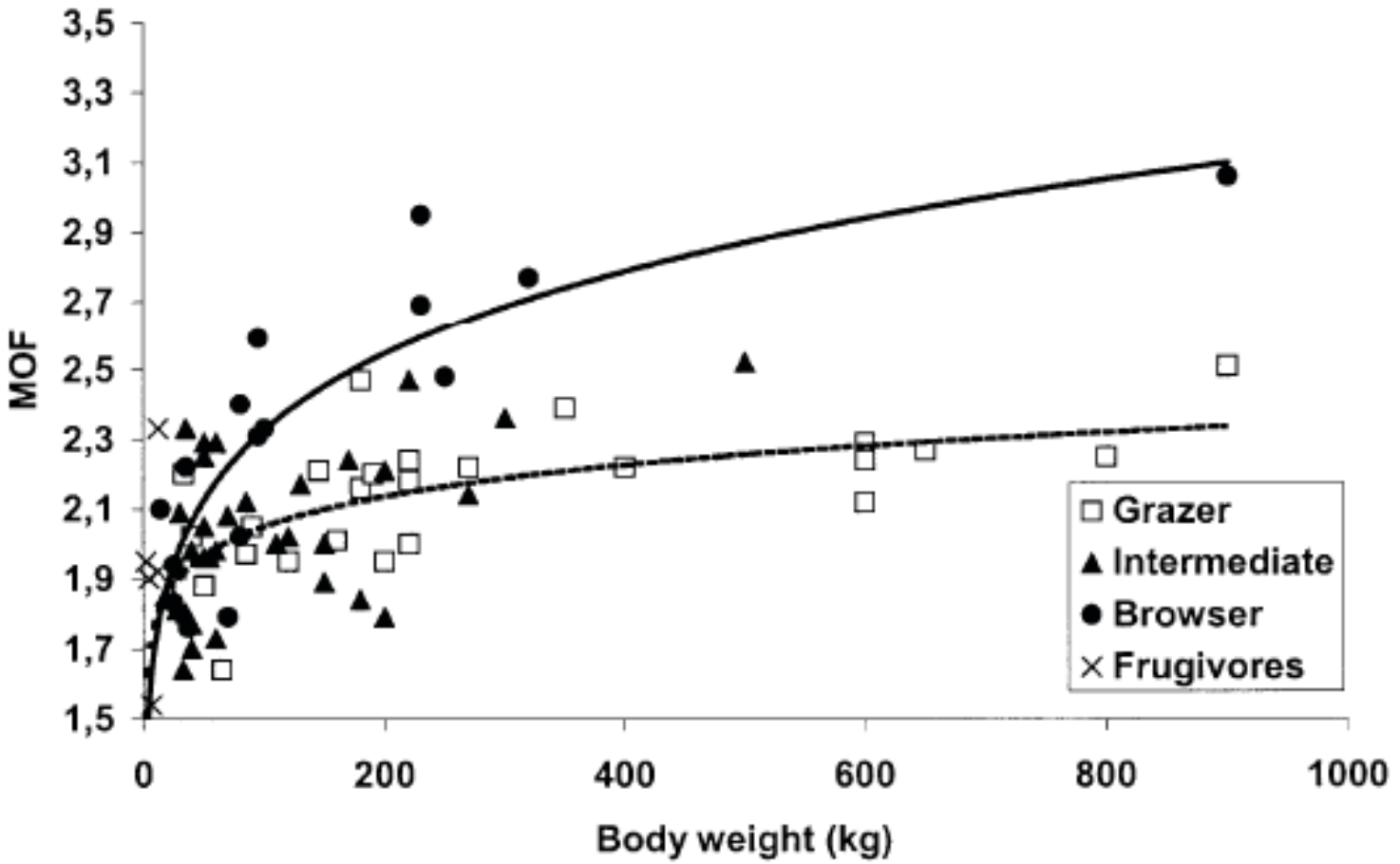
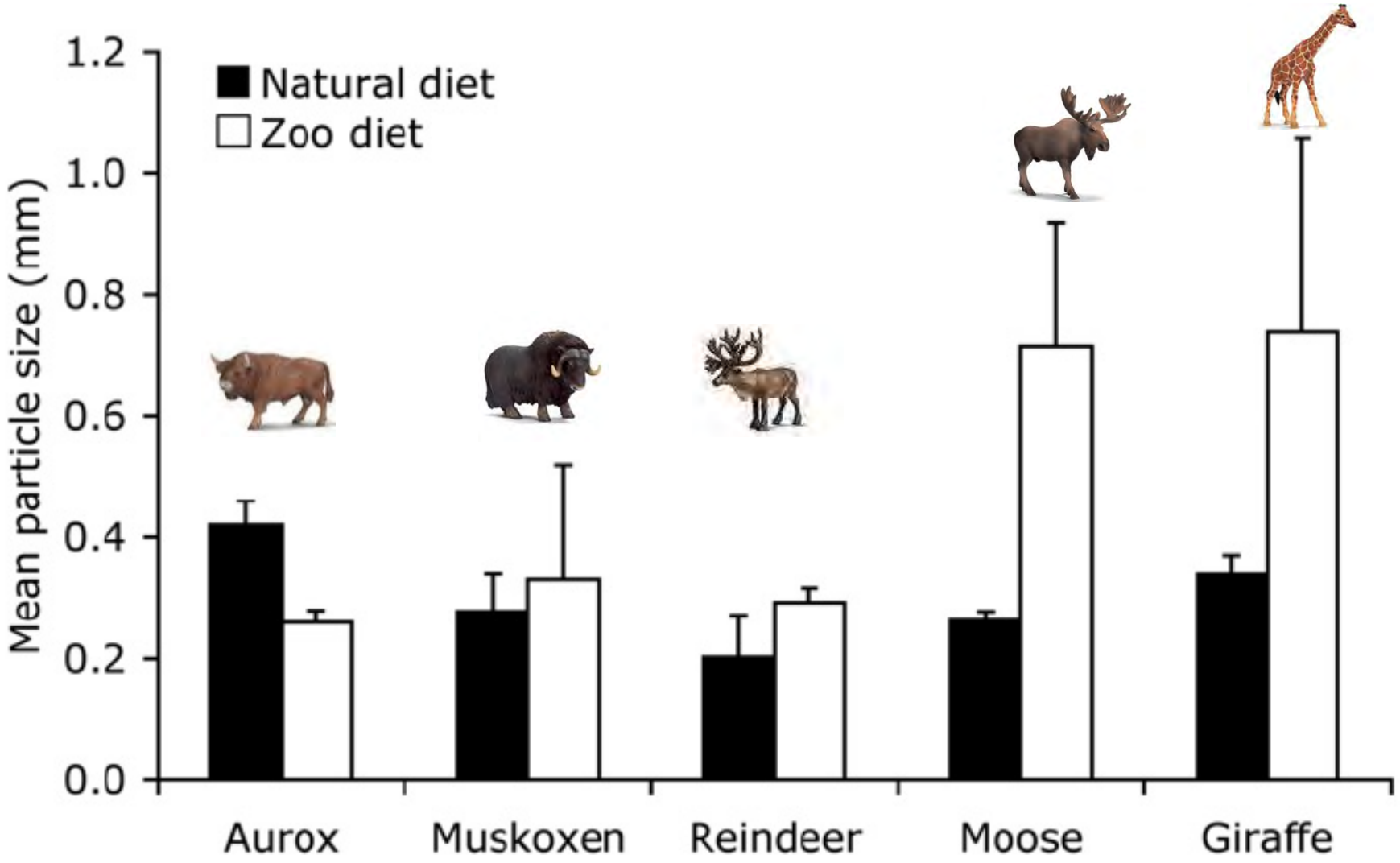


Faecal particle size in ruminants



from Lechner et al. (2010)

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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,*]

Comparative Biochemistry and Physiology, Part A 155 (2010) 211–222

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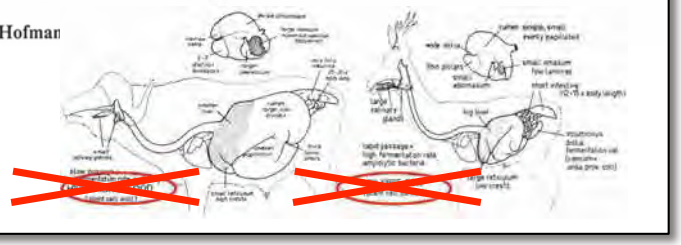

RR stratification enhancement for better fibre use – fibre mat – 'filter bed-effect'

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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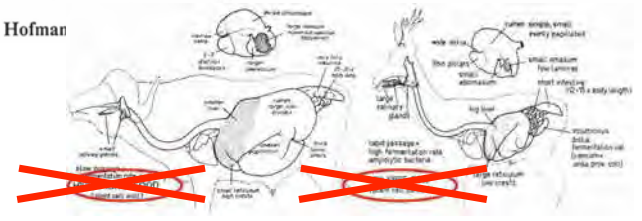

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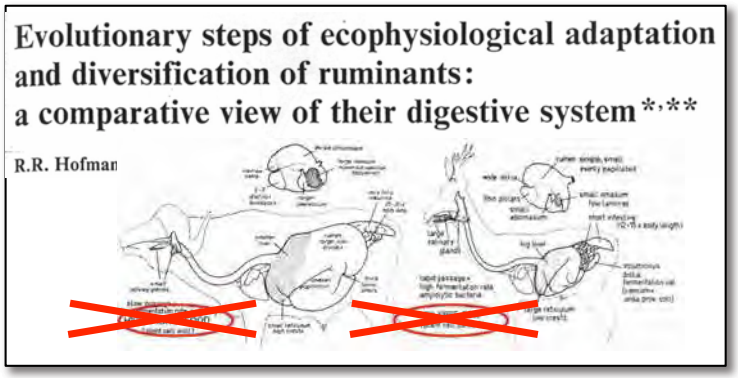
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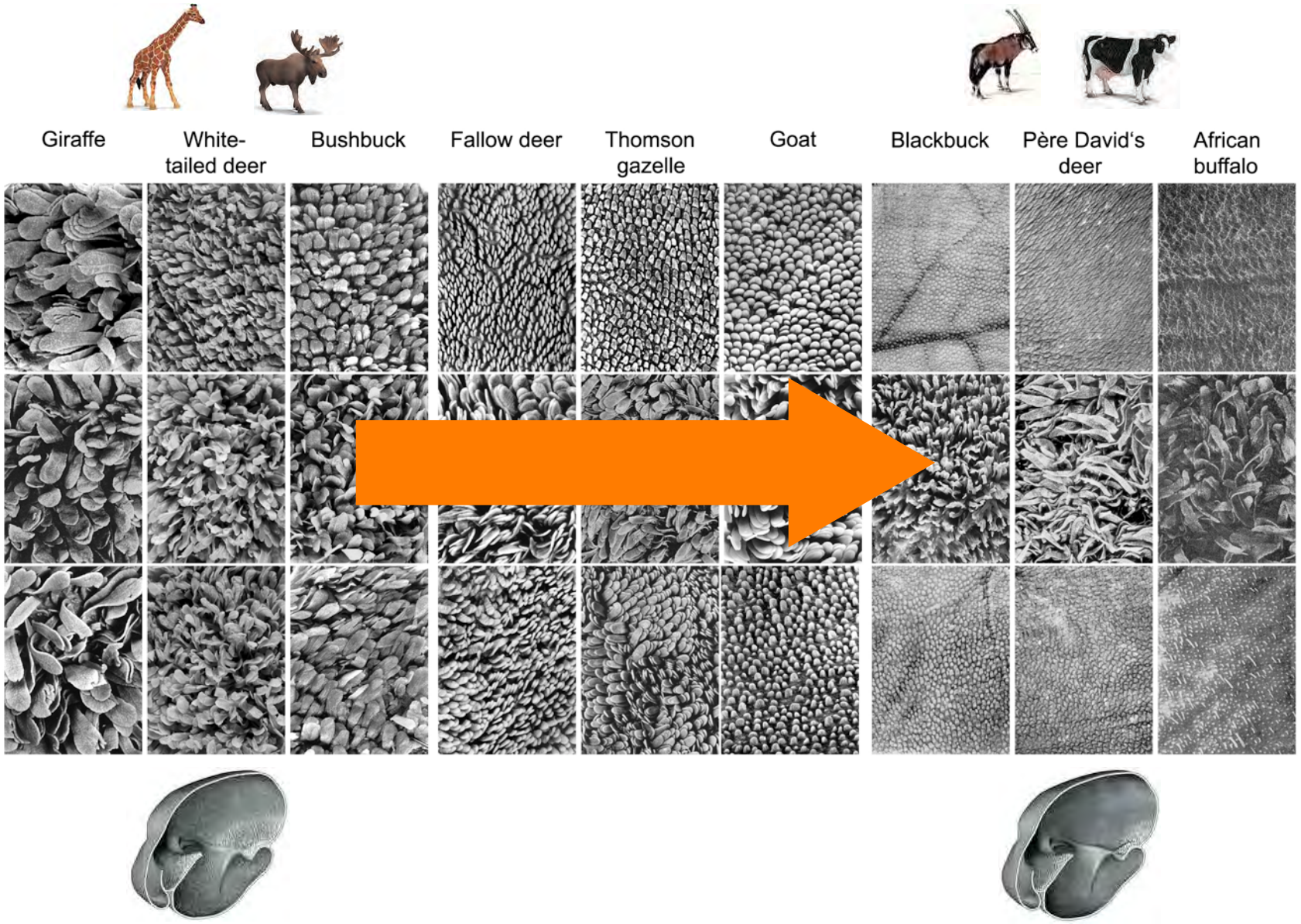
difference in salivary defence and potential for RR microbial harvest

Stratification and rumen papillation



from Clauss, Hofmann et al. (2009)

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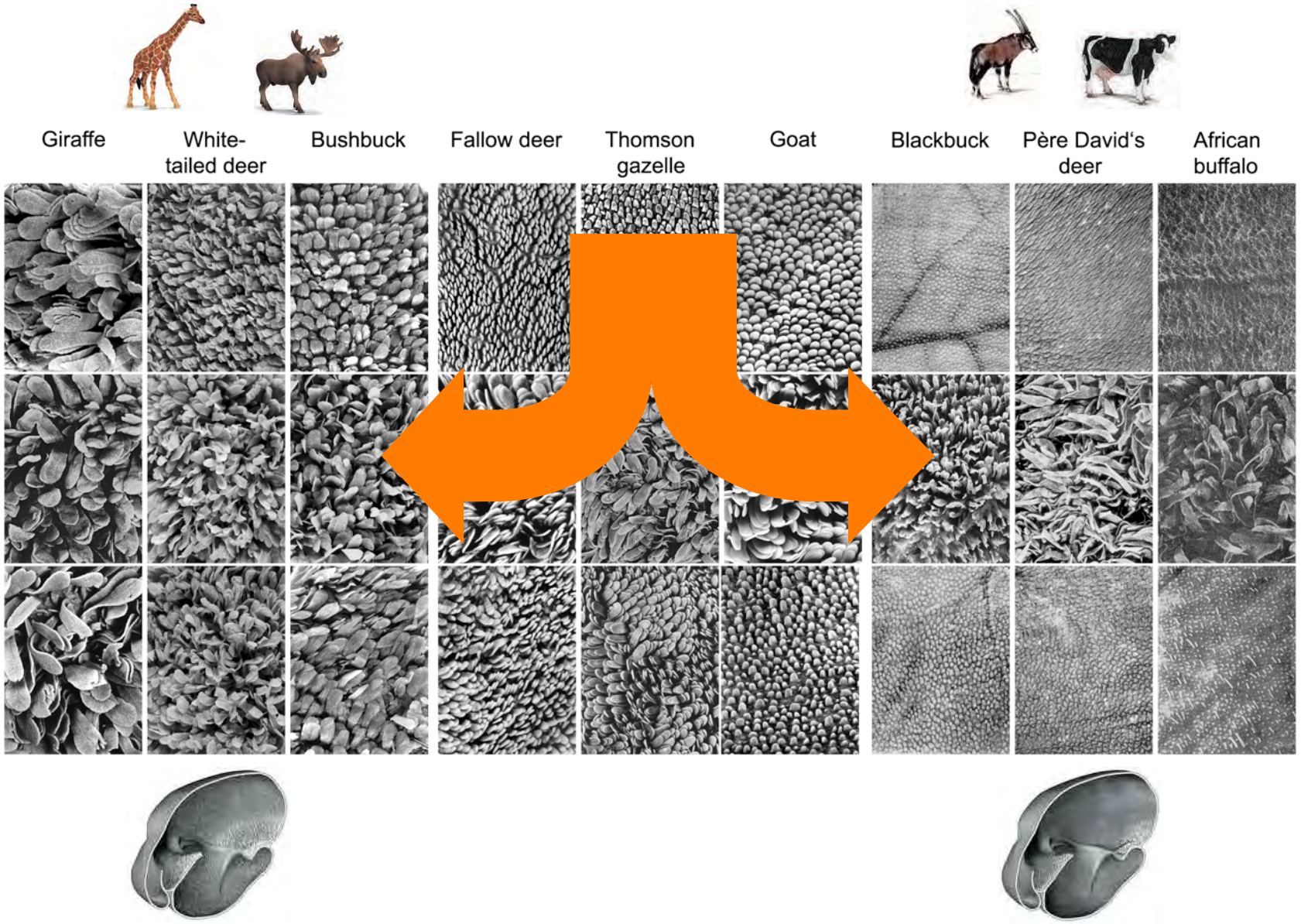

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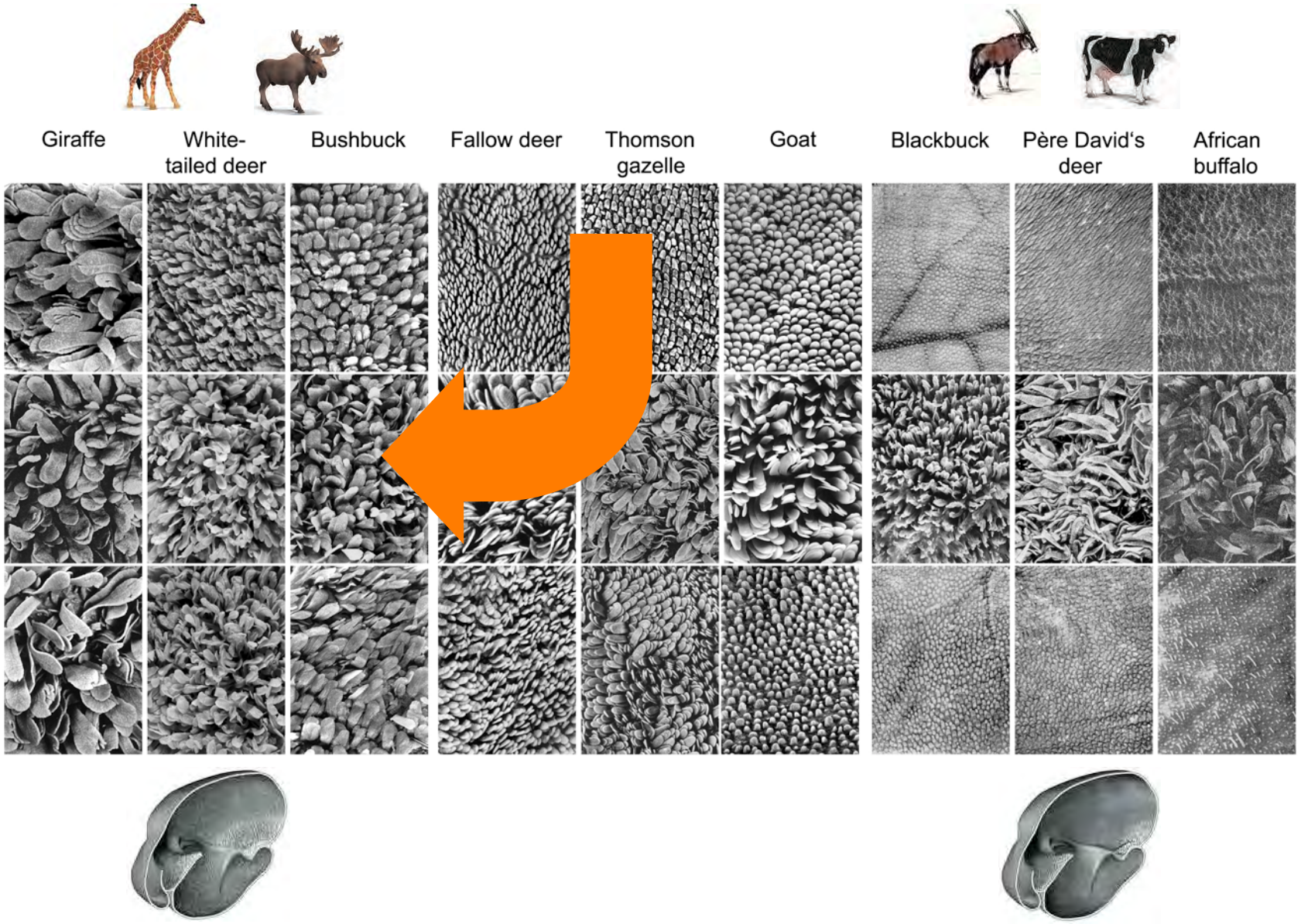


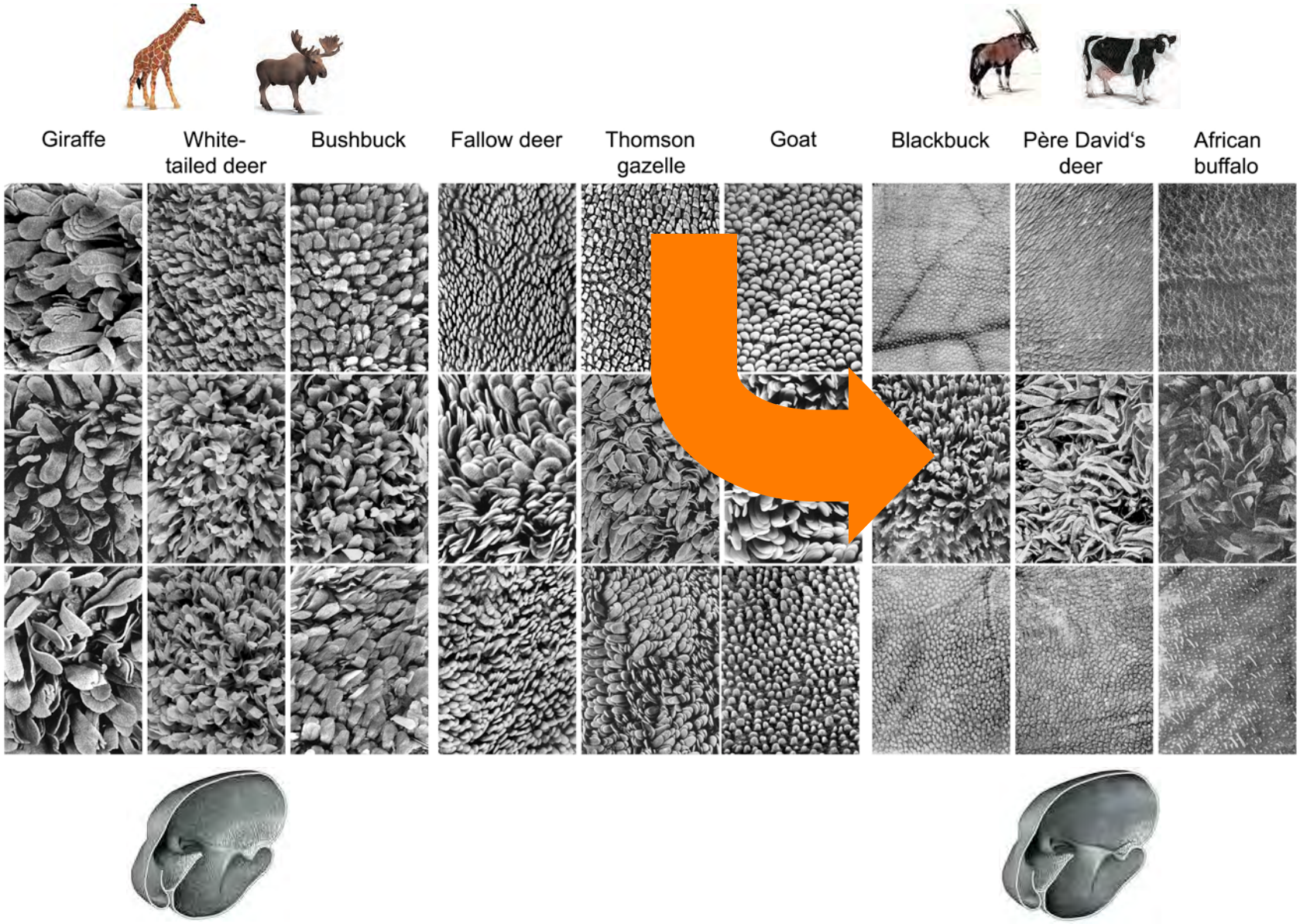
from Clauss, Hofmann et al. (2009)

Stratification and rumen papillation

- Large salivary glands
- Protein-rich (=viscous) saliva contains tannin-binding proteins as a defence against tannins
- High fluid throughput not possible

from Clauss, Hofmann et al. (2009)

Stratification and rumen papillation



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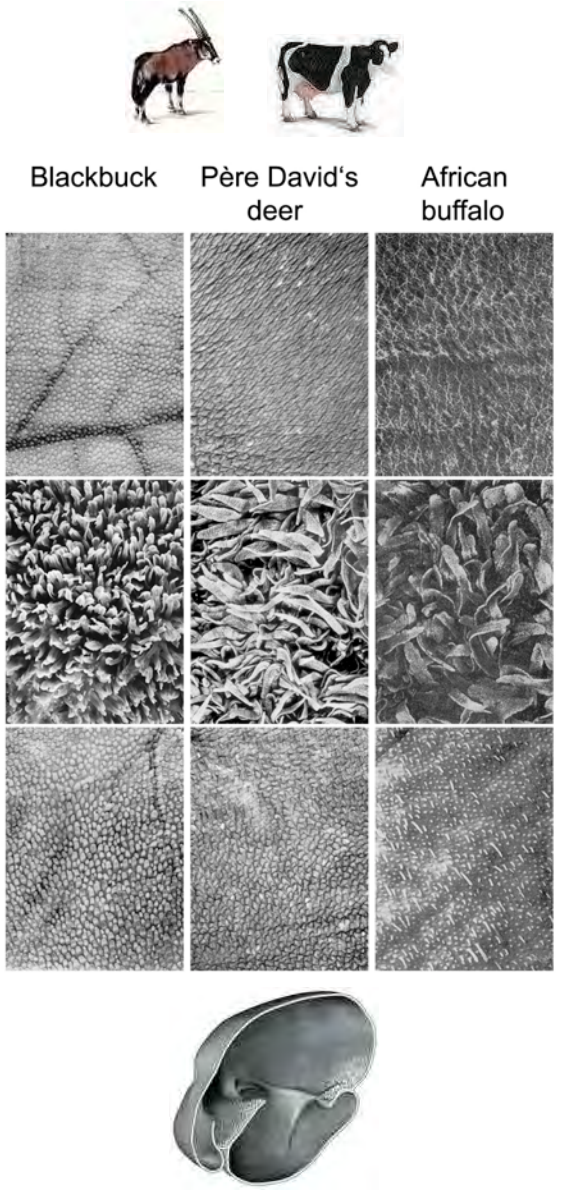

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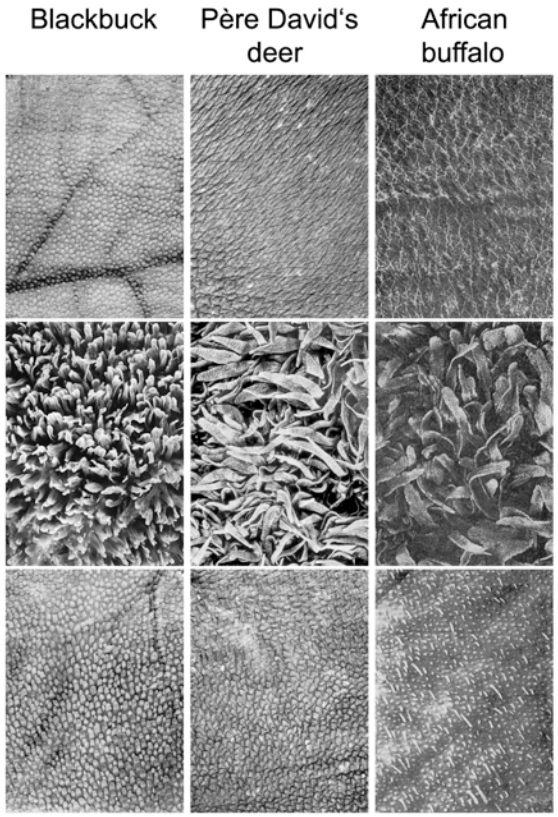

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Why a higher fluid throughput?

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The Continuous Culture of Bacteria; a Theoretical and Experimental Study

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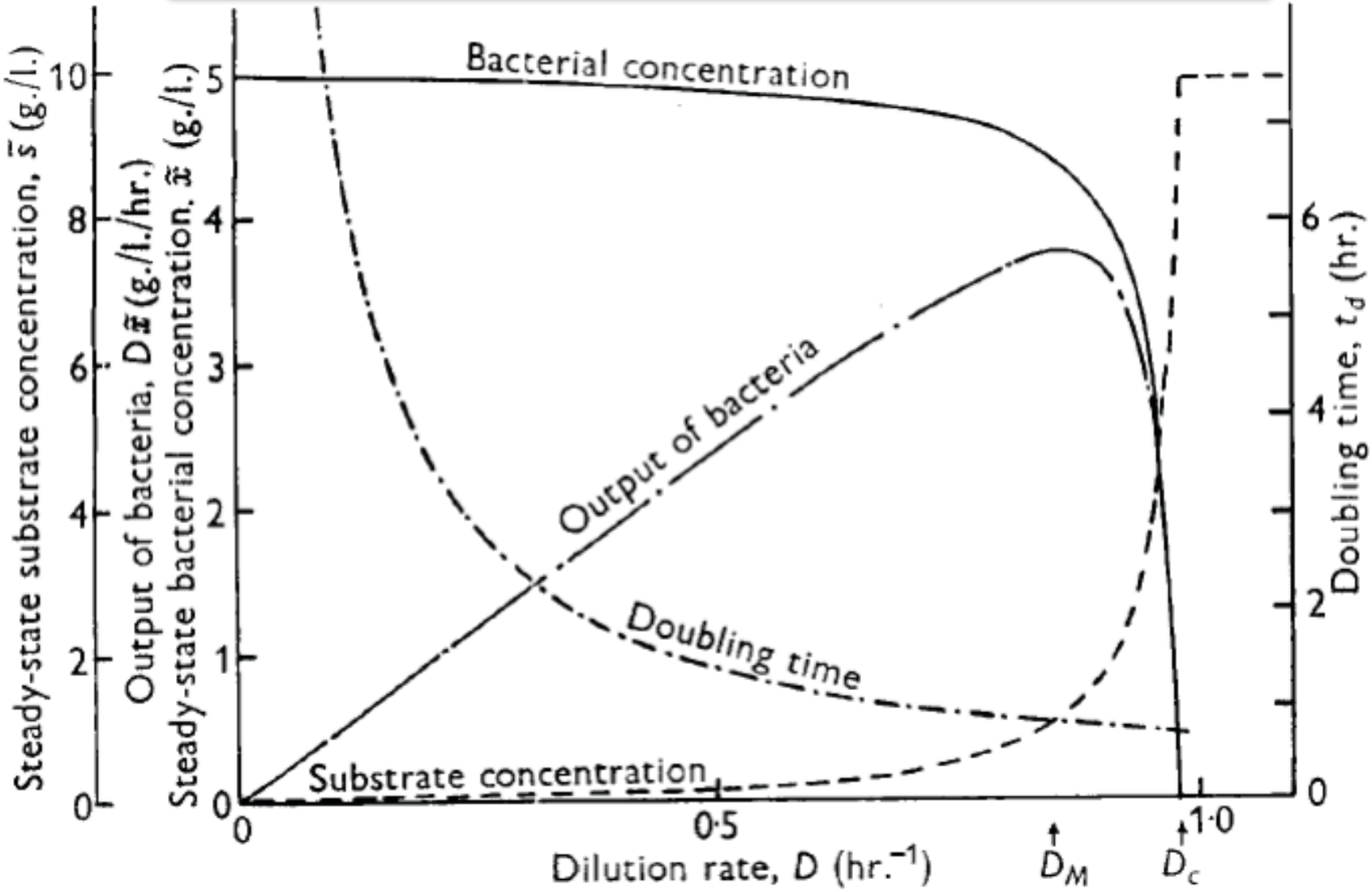

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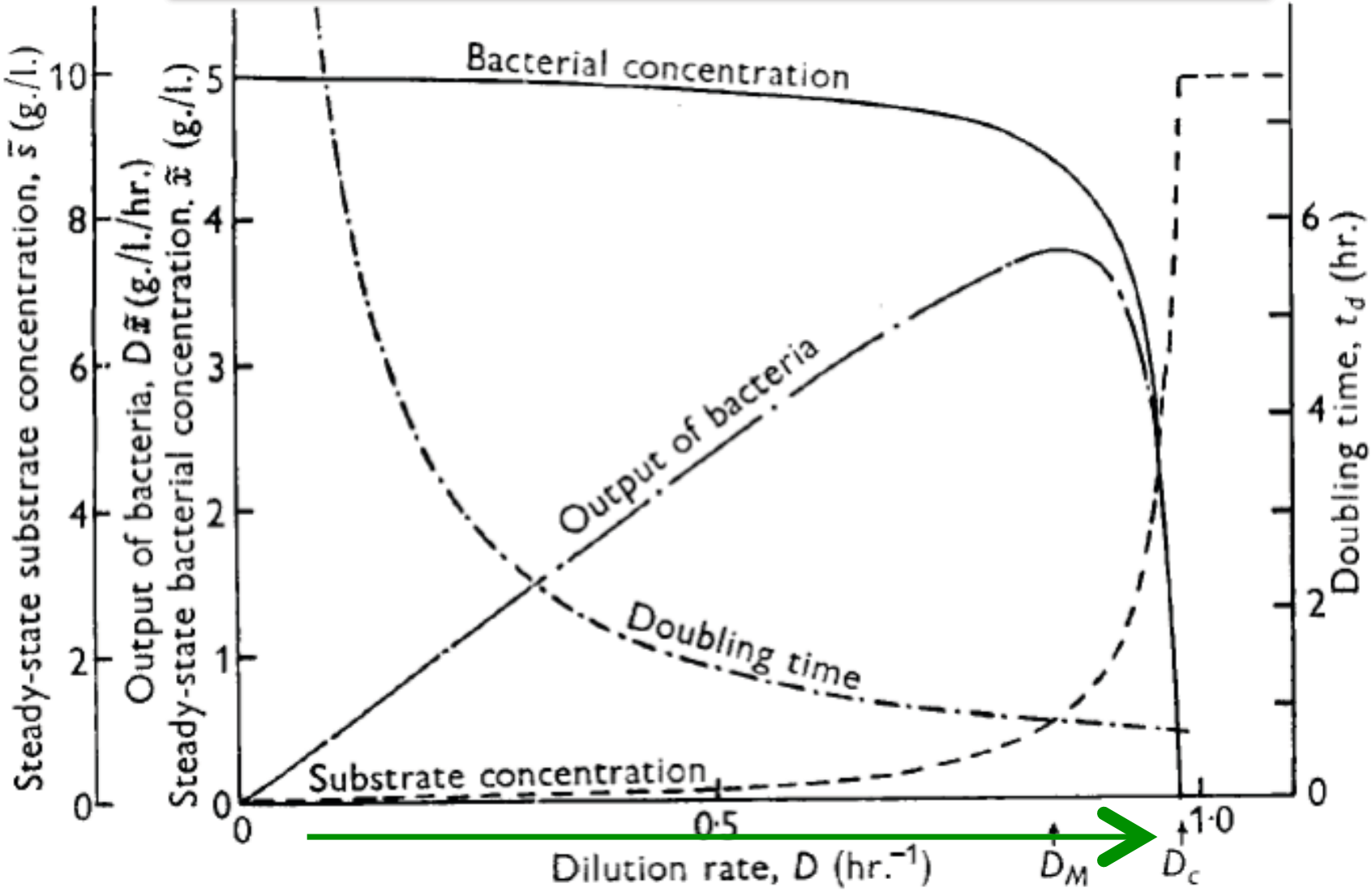

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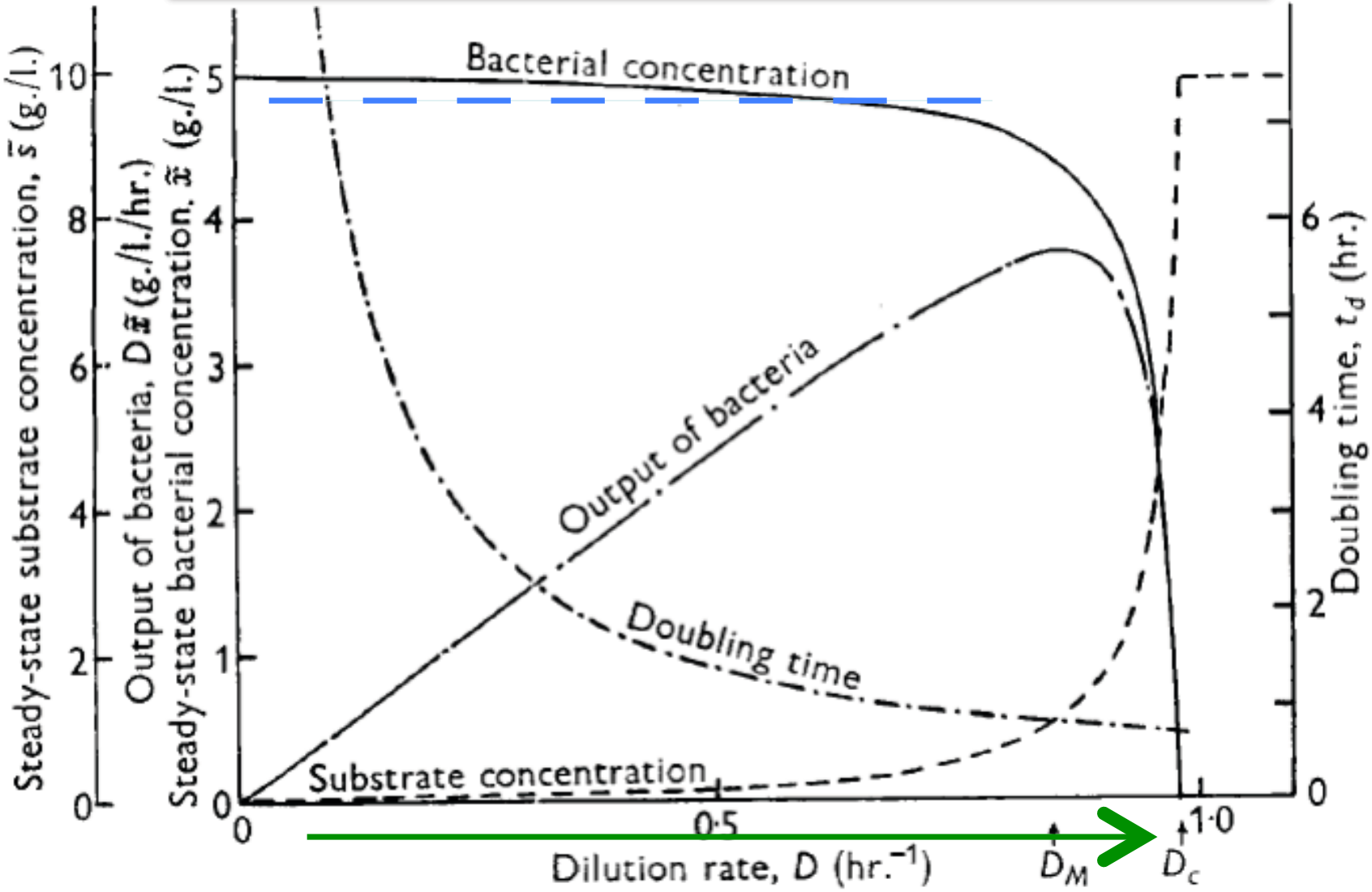

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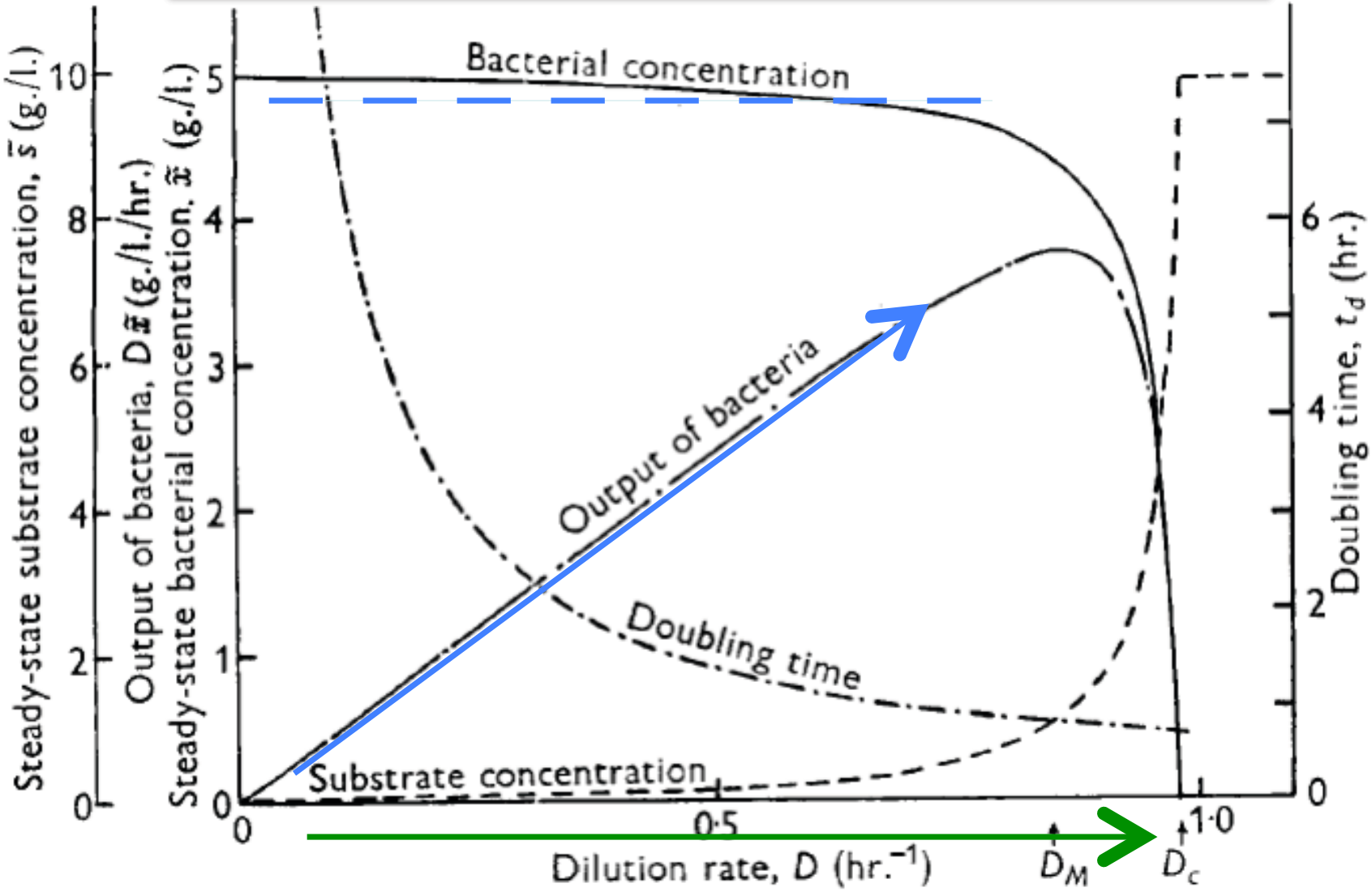

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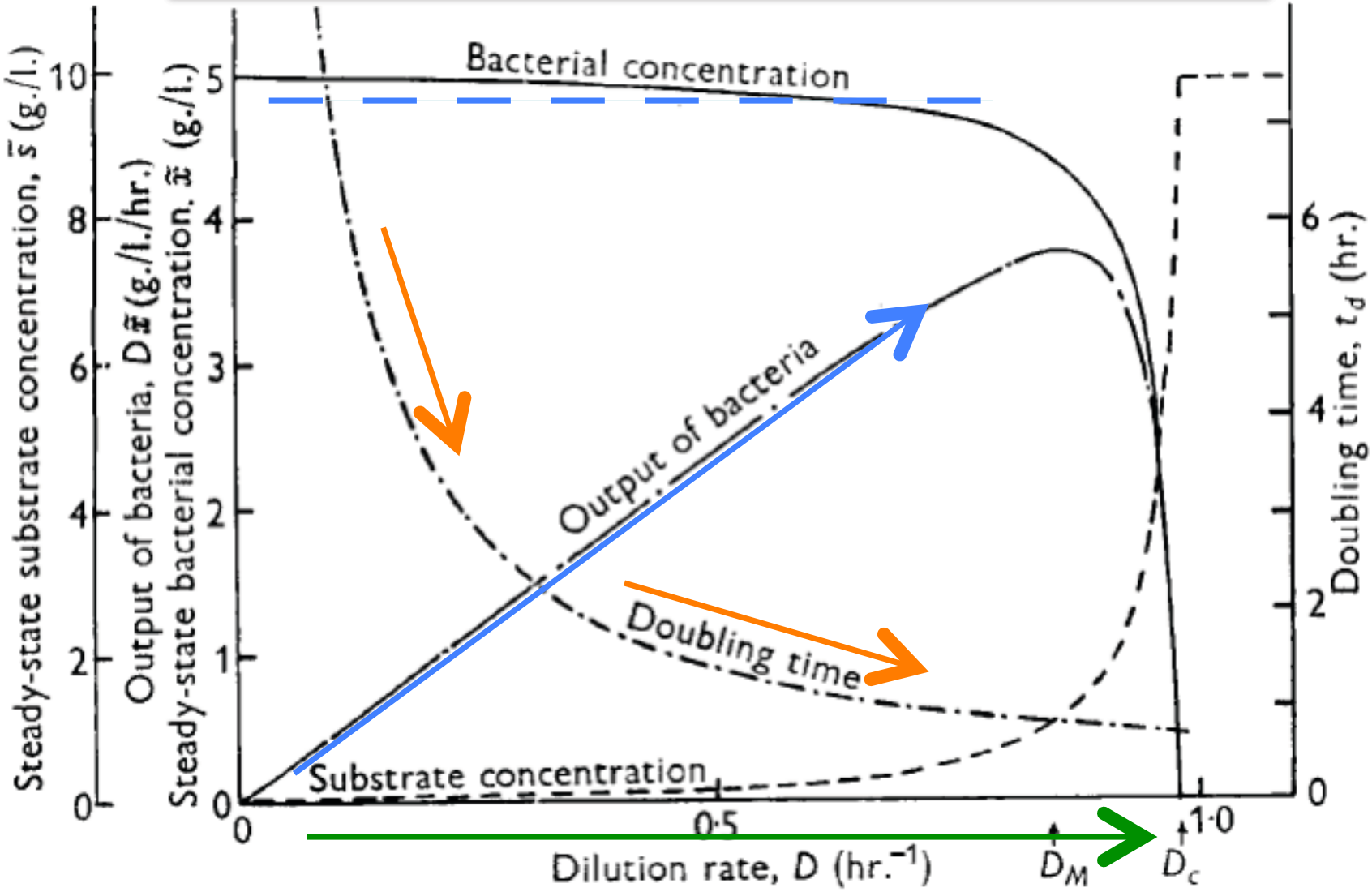

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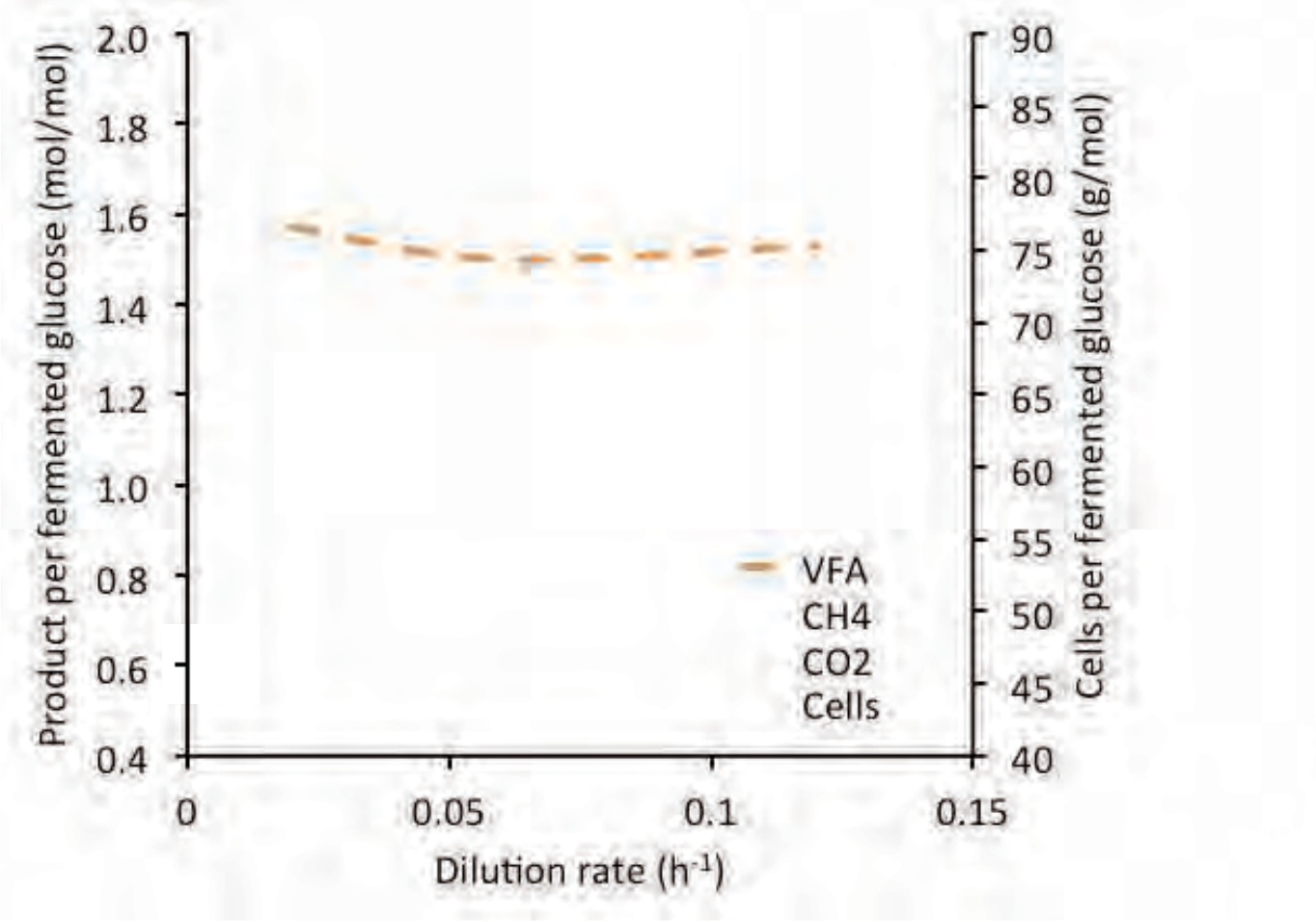

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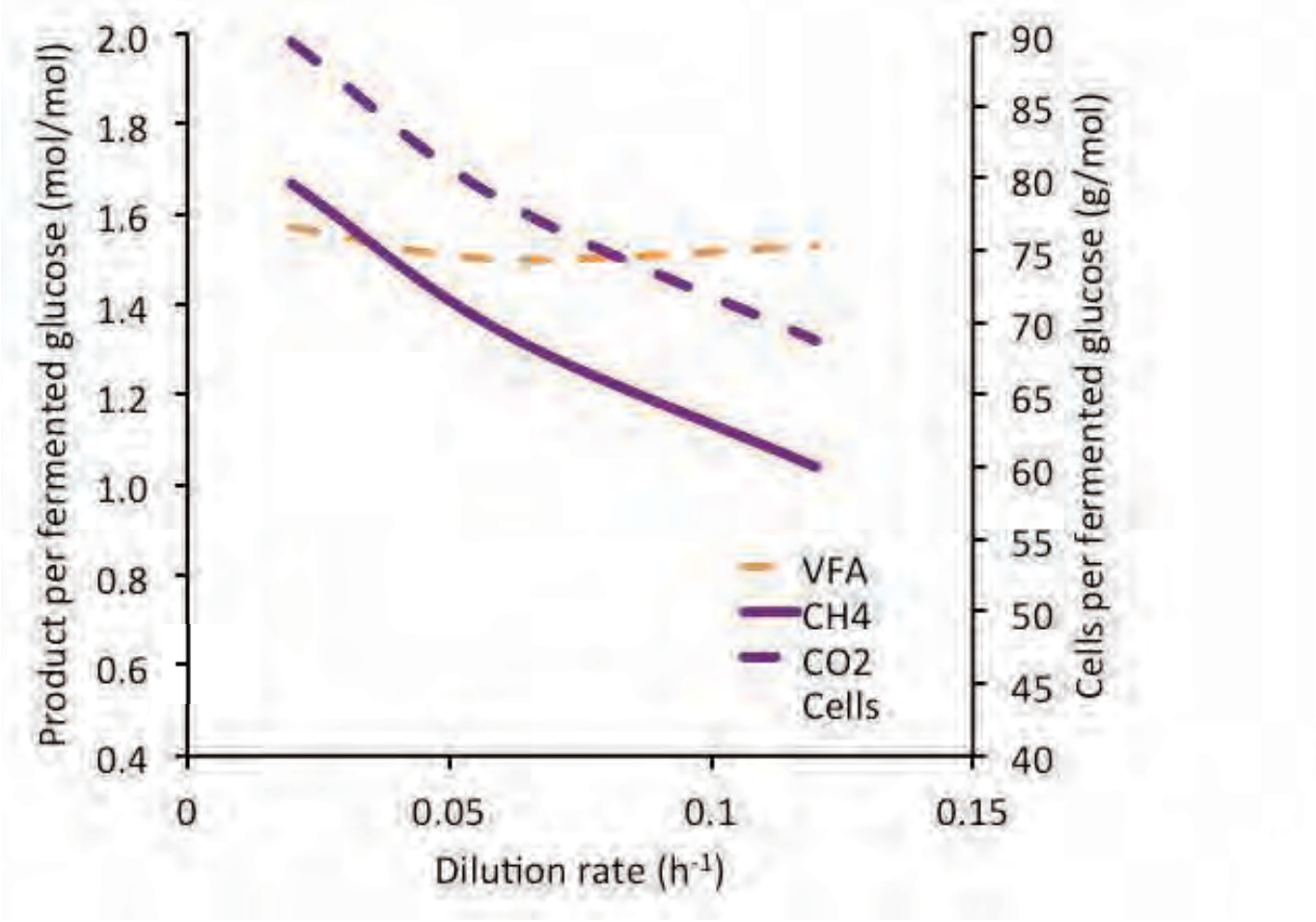

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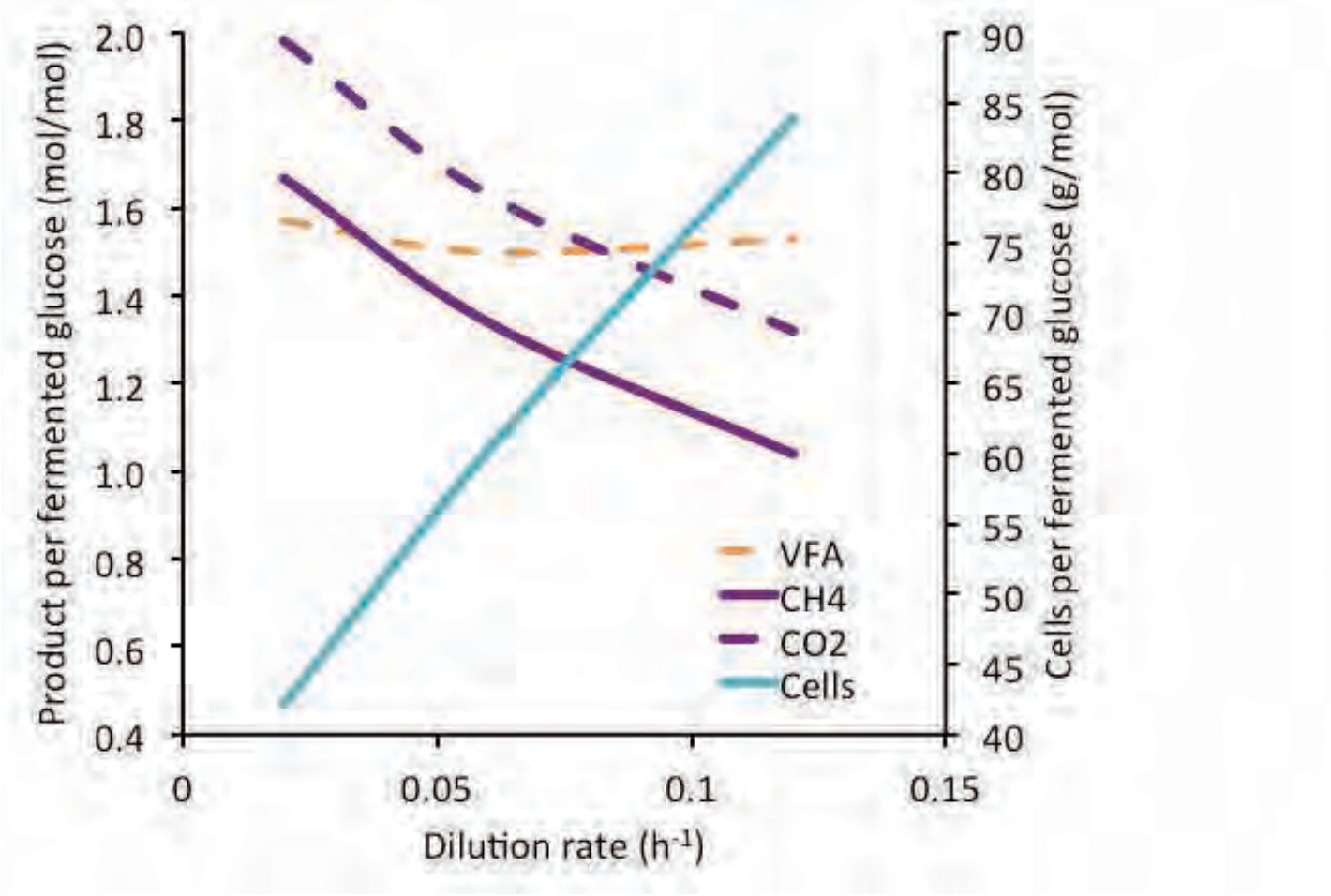

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Attempts to increase rumen fluid throughput

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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

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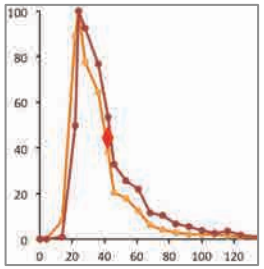

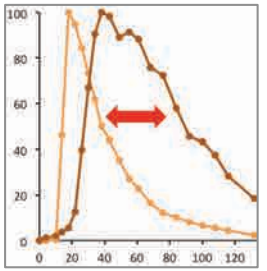

from Hummel et al. (2015)

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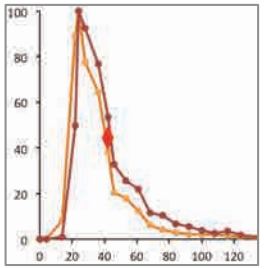
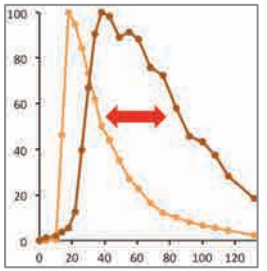


model calculation for a ration of
50:50 alfalfa hay:concentrates



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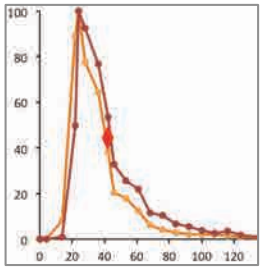

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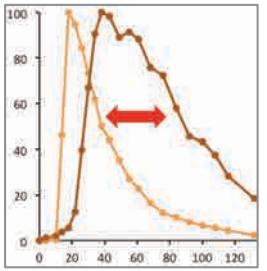
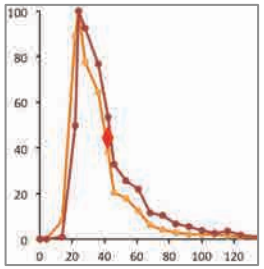
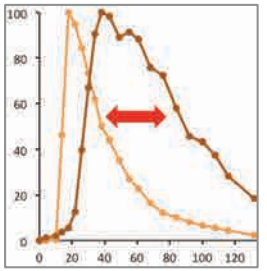


microbial efficiency
(microbial N g / kg fermented organic matter)

from Hummel et al. (2015)

Ecological consequences





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microbial efficiency
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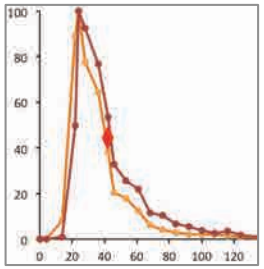
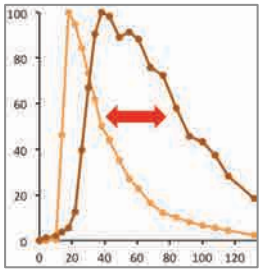
↓

34.7

from Hummel et al. (2015)

Ecological consequences





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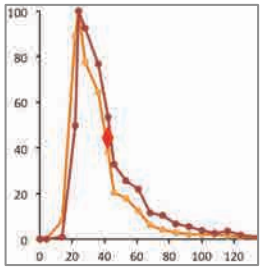
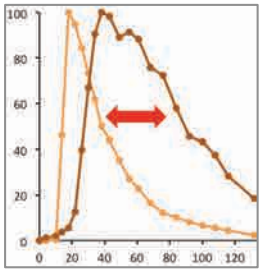
34.7

38.5

from Hummel et al. (2015)

Ecological consequences





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34.7

38.5

10 % higher

from Hummel et al. (2015)

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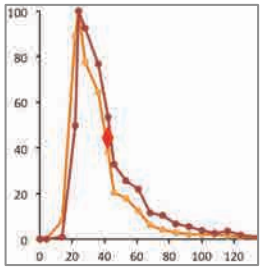
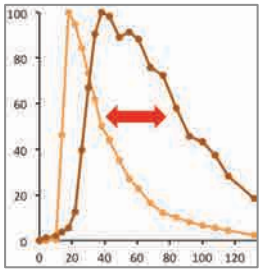


restricted to strict browse diets

('non-grazers')



broader diet spectrum

('mixed feeders/ grazers')

from Clauss et al. (2010)

Cattle question

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

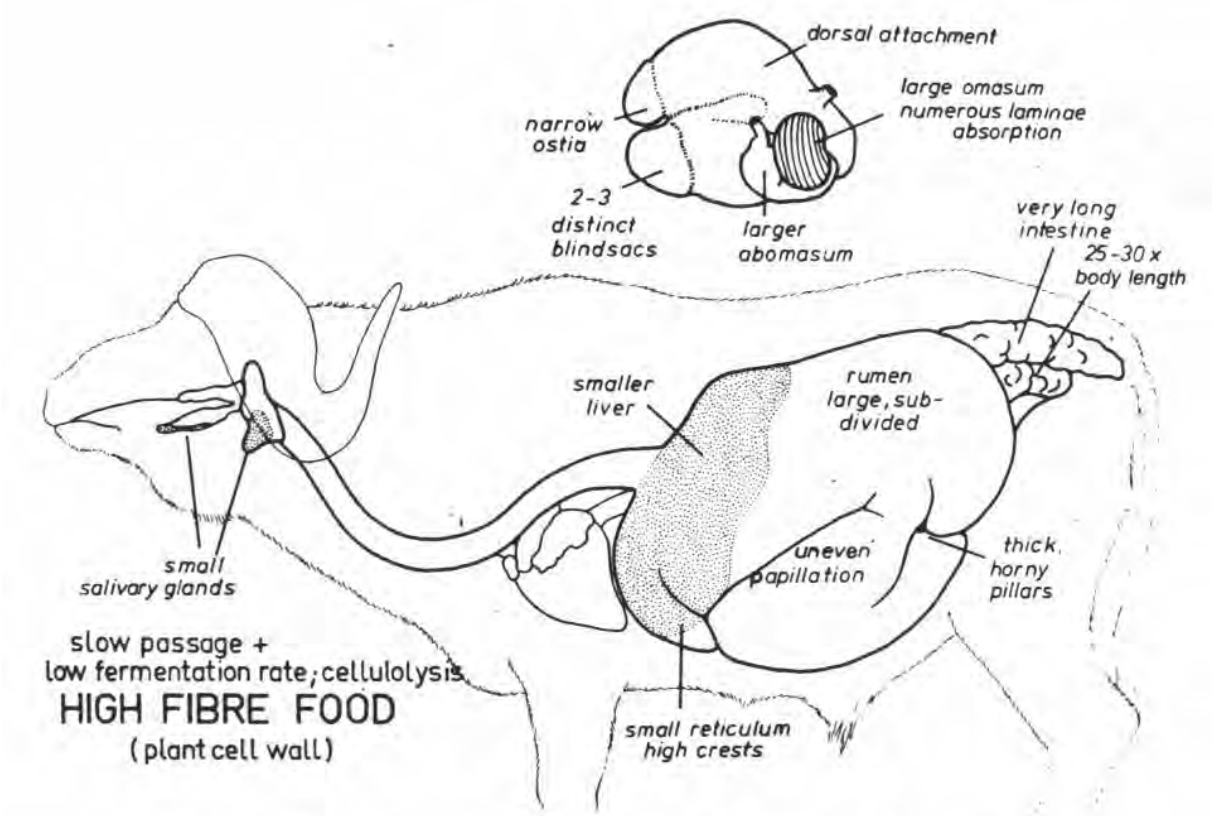
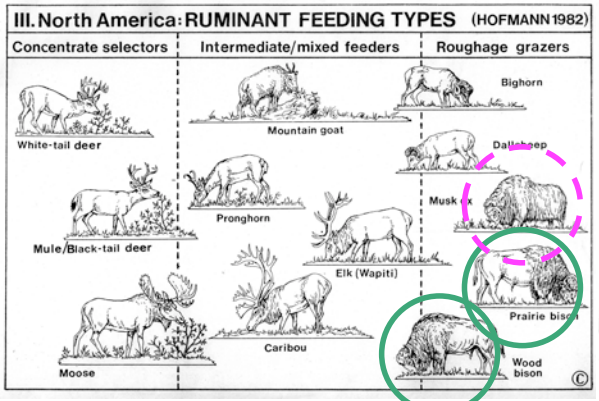


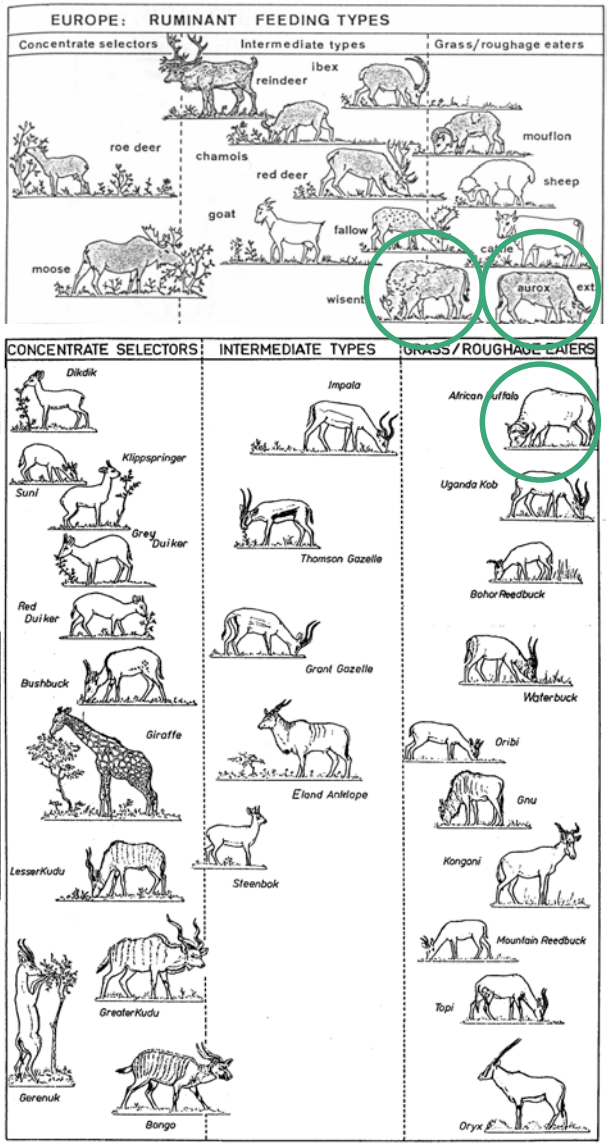
Fig. 1: The African buffalo, a non-selective roughage grazer.

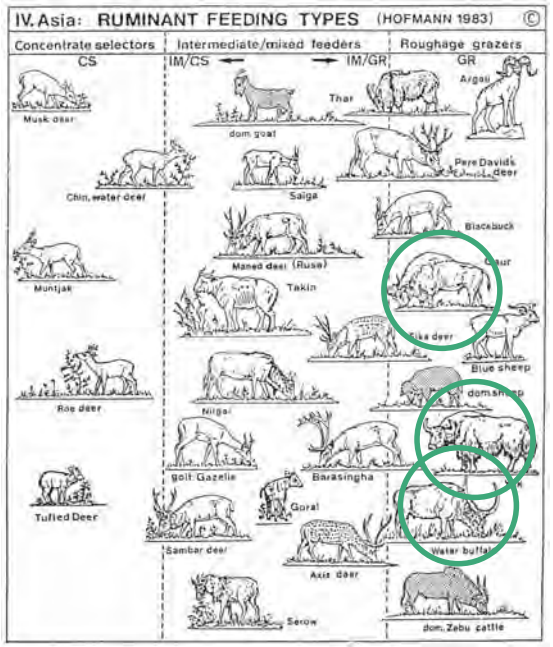
Is it really linked to a specific 'grazer' diet ?

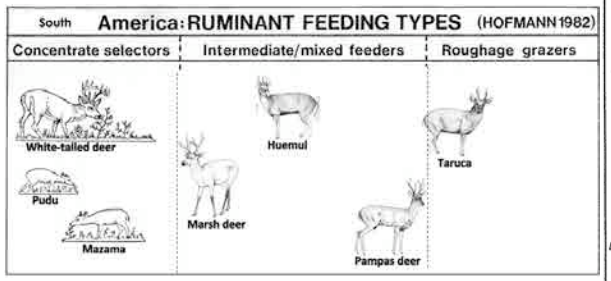
from Hofmann (1989)

Ruminant feeding types (Hofmann)









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

Ruminant questions

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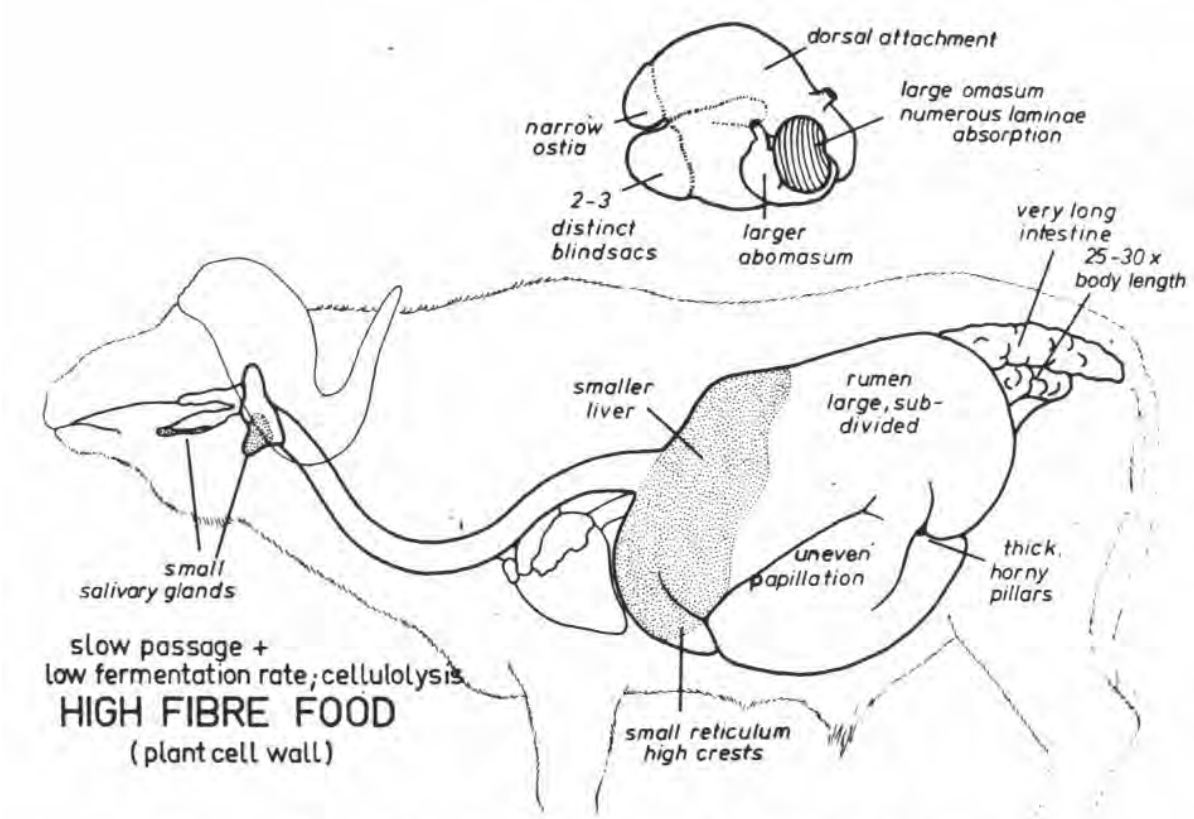

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  African buffalo - Red forest buffalo

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  Yak - Gaur - Banteng

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  Yak - Gaur - Banteng

  Muskoxen

  tradition of supplementing cattle with browse

Form & Function

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

... does not increase particle sorting efficiency

... but it might:

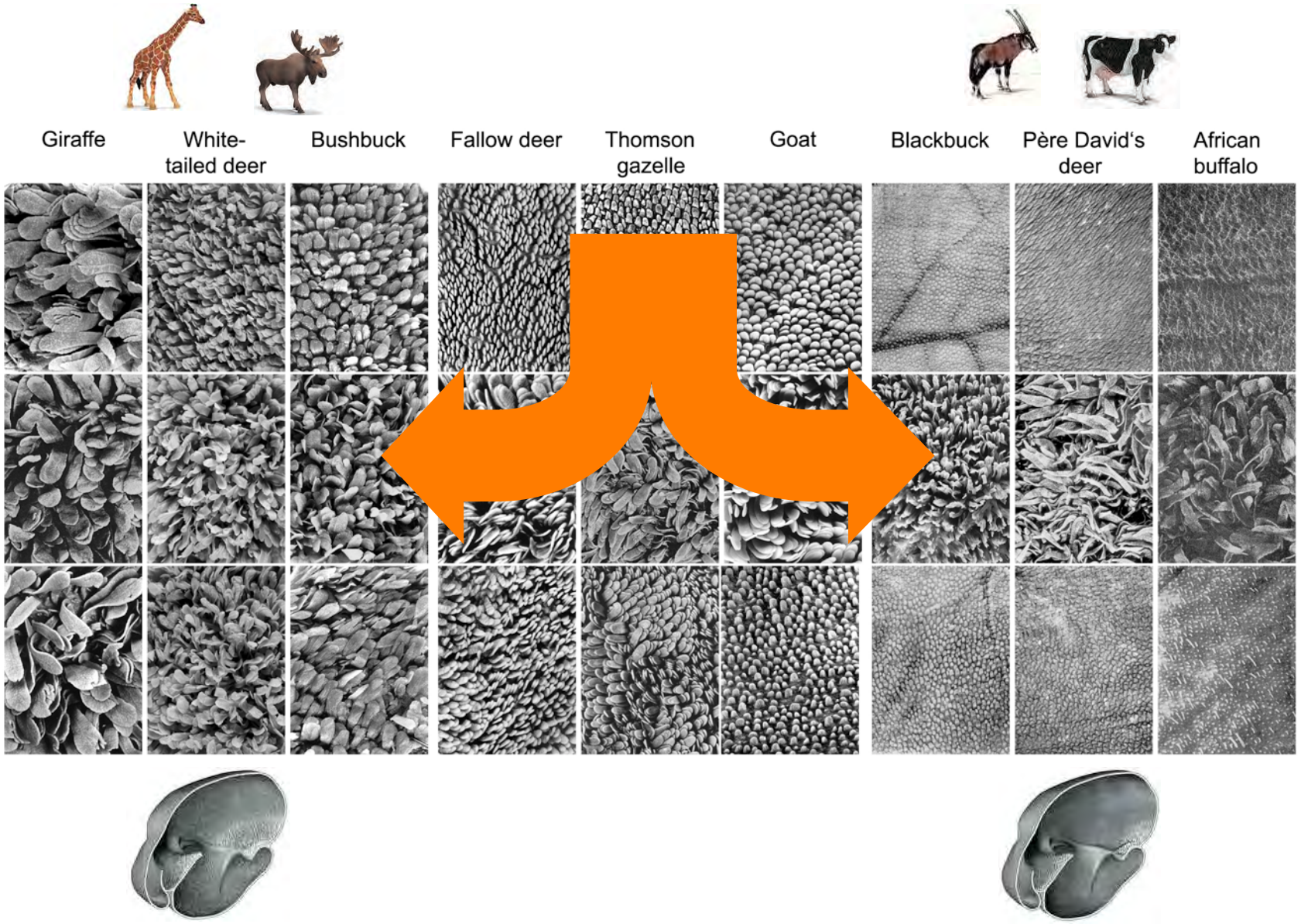
- Enhance harvesting of forestomach microbe populations and keeping methane losses at bay ?

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?

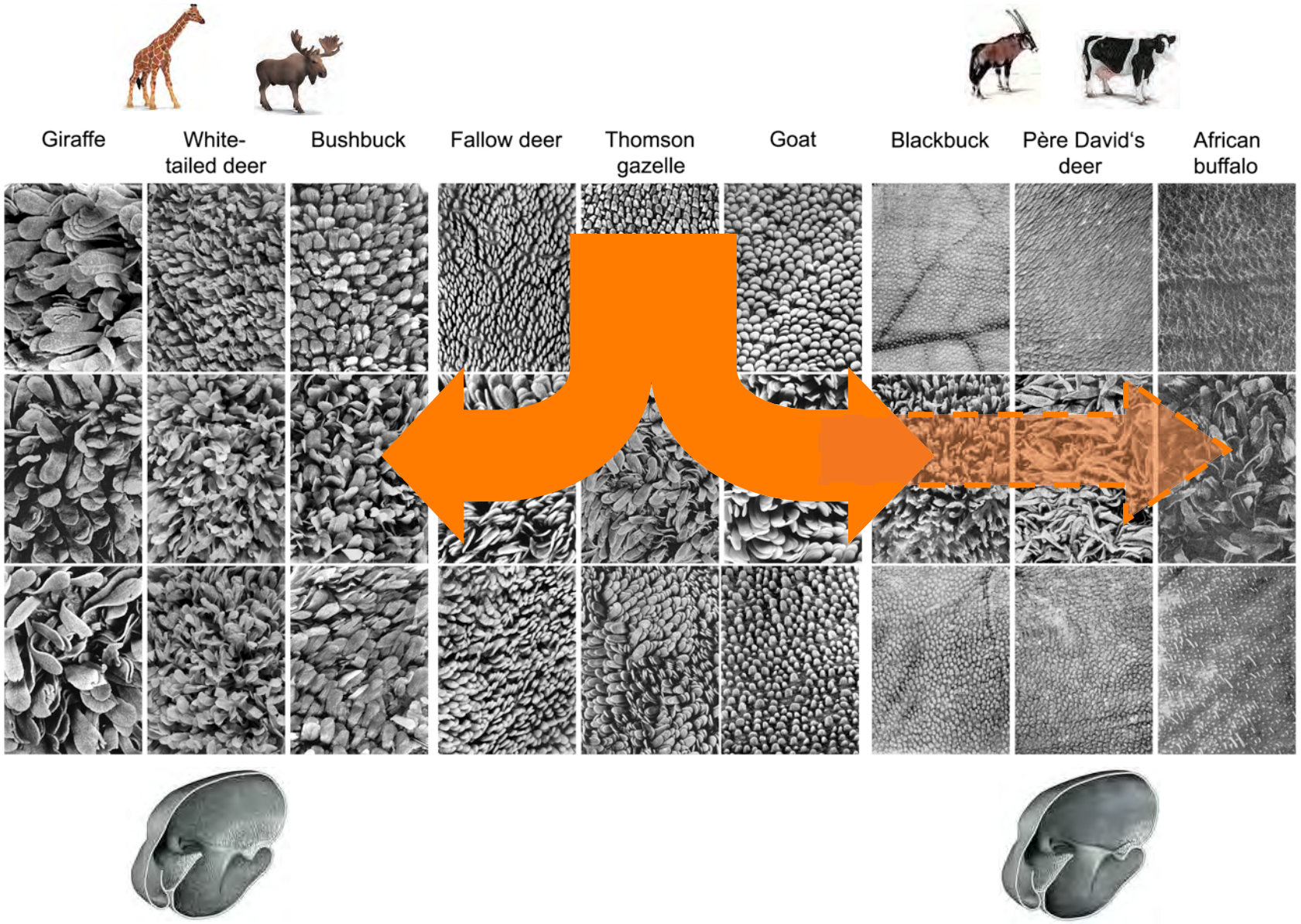
Chalupa (1977) Manipulating rumen fermentation. J Anim Sci 46, 585
Harrison & McAllan (1980) Factors affecting microbial growth yields in the reticulo-rumen. In Digestive physiology and metabolism in ruminants (eds. Ruckebush & Thivend), p 205, MTP Press, Lancaster
Croom et al. (1993) Manipulation of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

Stratification and rumen papillation



from Clauss, Hofmann et al. (2009)

Stratification and rumen papillation



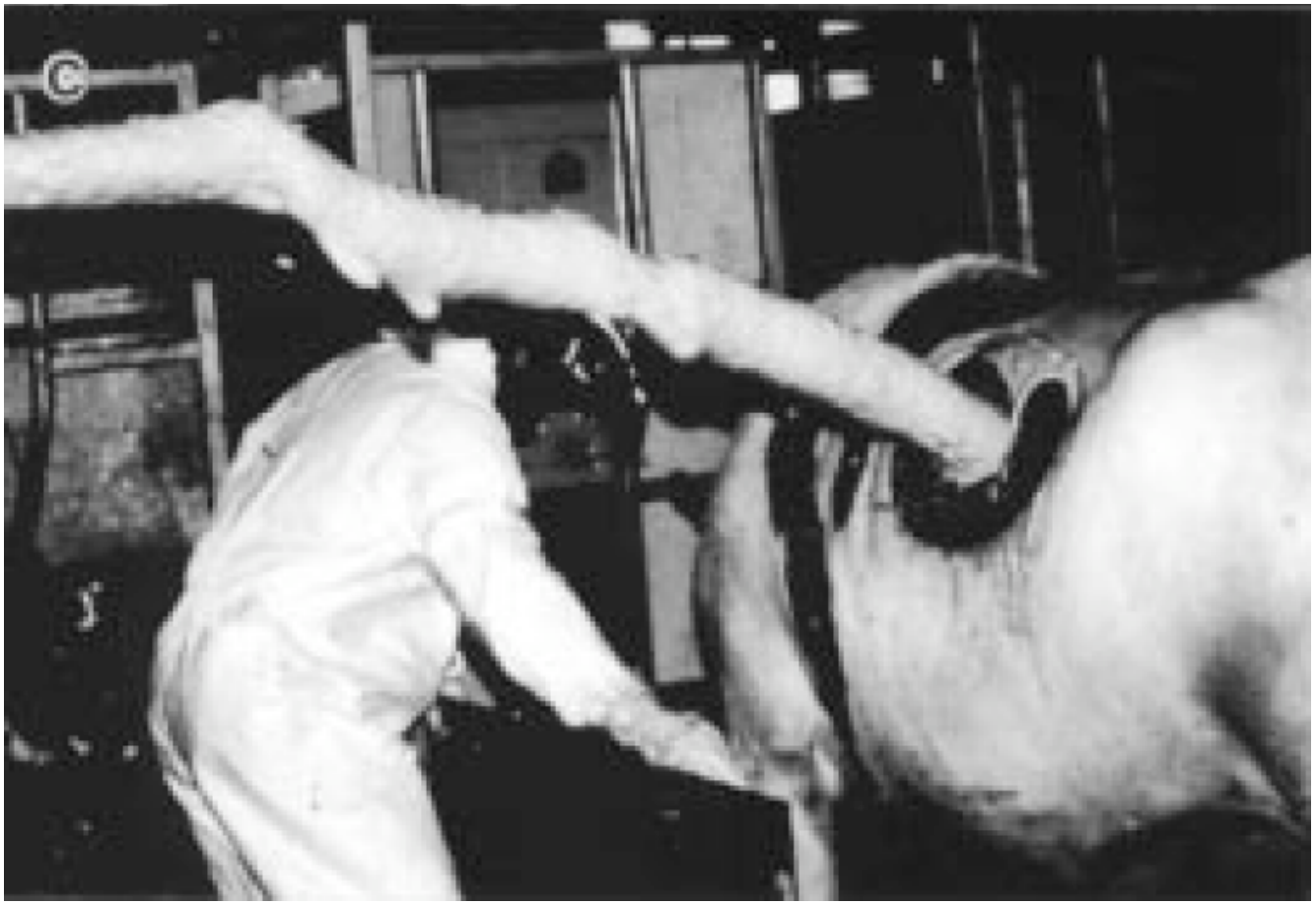
from Clauss, Hofmann et al. (2009)

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?

- *... selective breeding ?*

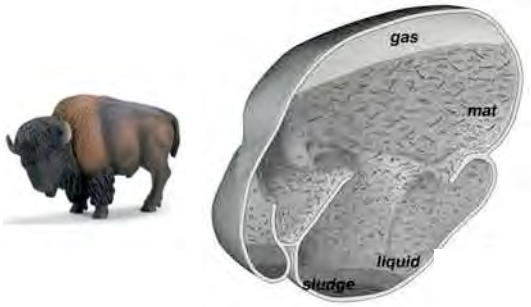
Frothy bloat



from Cheng et al. (1998)

Frothy bloat

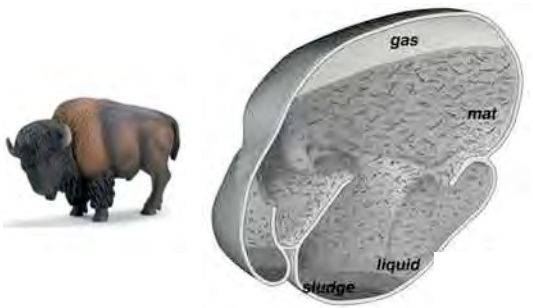
frothy rumen contents



'dry' rumen contents

from Cheng et al. (1998)

Frothy bloat



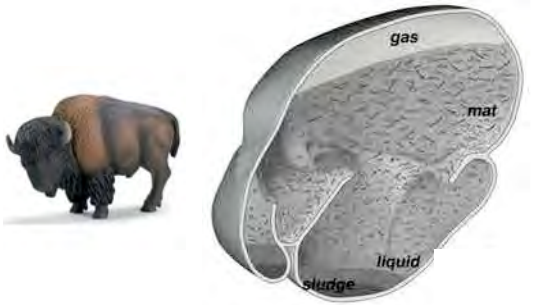
low saliva production
low RR fluid throughput

frothy rumen contents

'dry' rumen contents

from Cheng et al. (1998), Morris et al. (1997)

Frothy bloat



frothy rumen contents

low saliva production
low RR fluid throughput

selective breeding against bloat susceptibility possible

'dry' rumen contents

from Cheng et al. (1998), Morris et al. (1997)

Not only different species, but different phenotypes exist

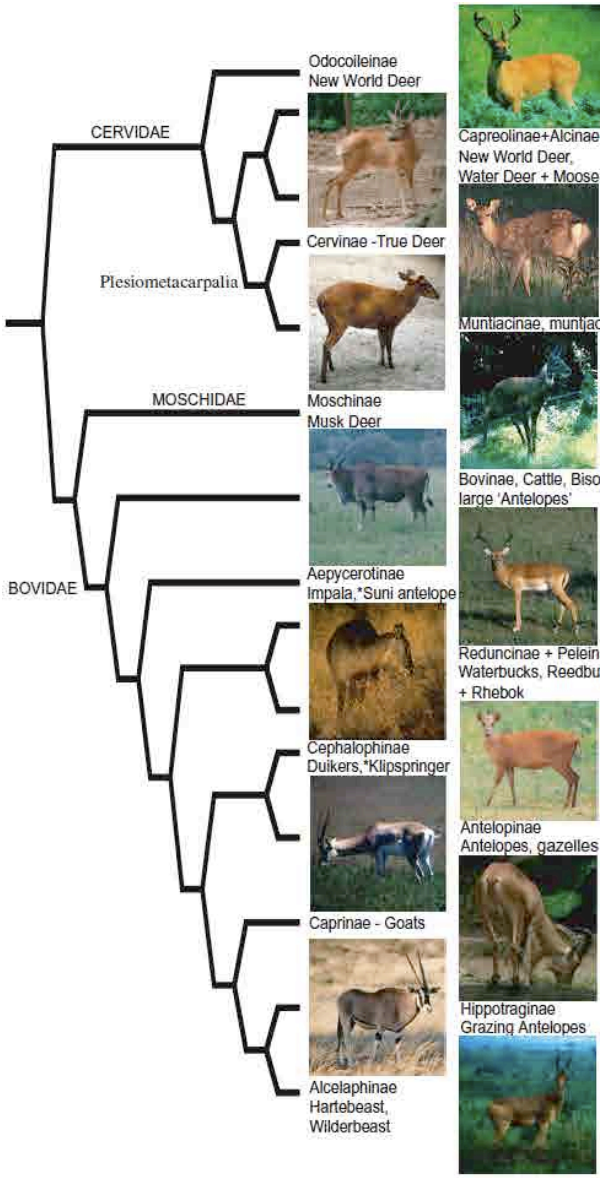
Not only different species, but different phenotypes exist

British Journal of Nutrition (2014), **111**, 578–585

Low-methane yield sheep have smaller rumens and shorter rumen retention time

John P. Goopy[1]*†, Alastair Donaldson[1], Roger Hegarty[2], Philip E. Vercoe[3,4], Fay Haynes[2], Mark Barnett[2] and V. Hutton Oddy[1]

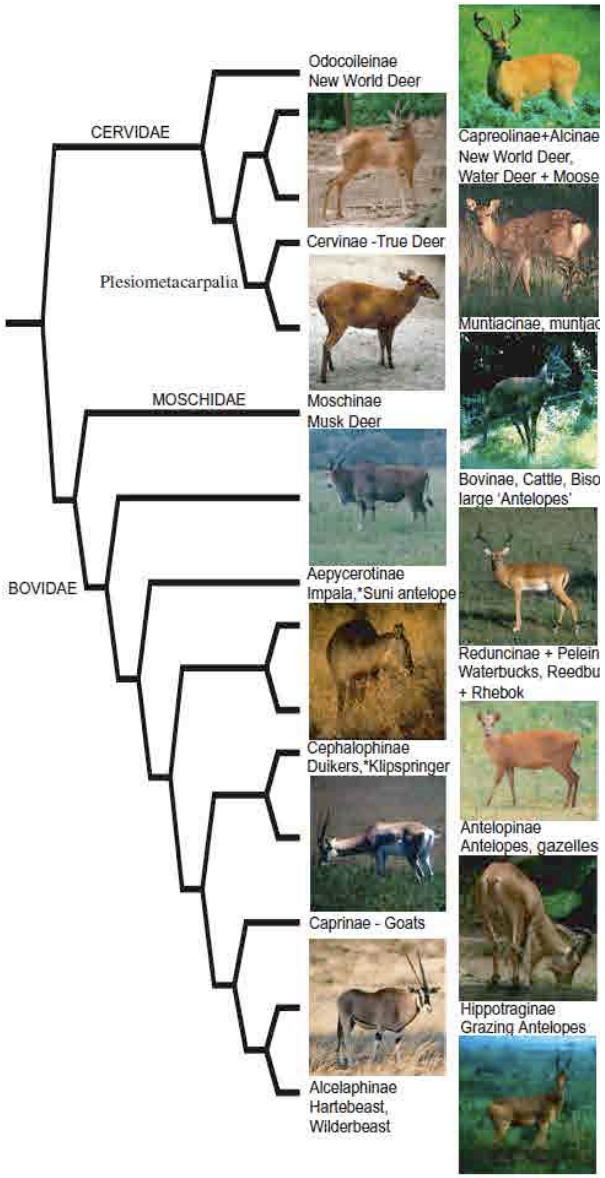
Conclusion: ruminants and fluids



from Agnarsson et al. (2008)

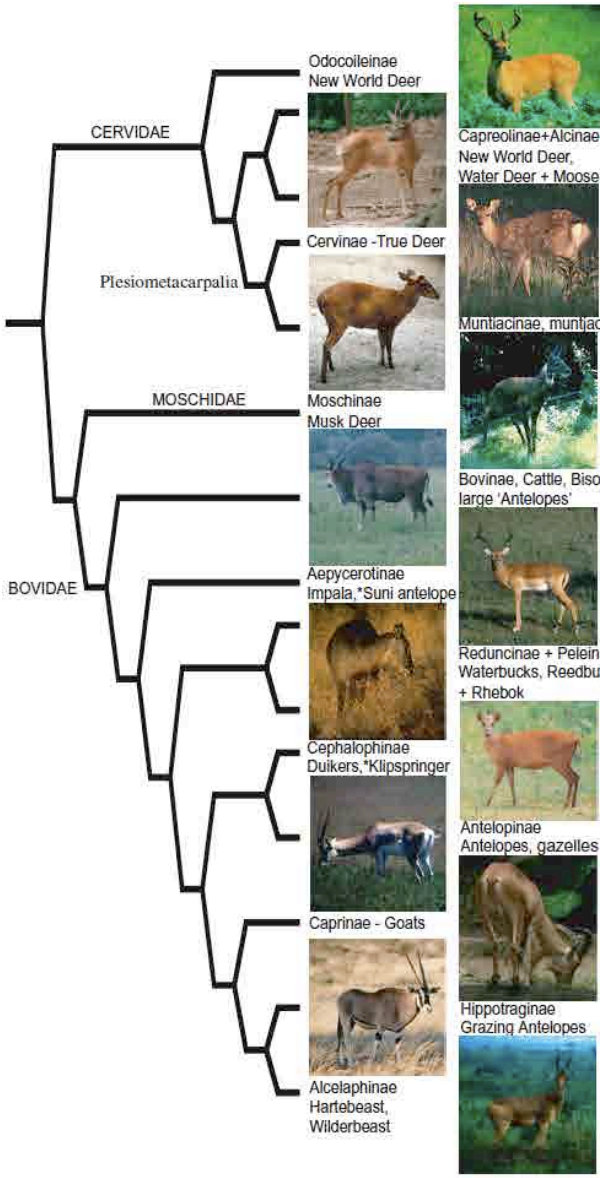
Evidence for convergent evolution of high fluid throughput in ruminant lineages suggests that benefits are substantial.

Conclusion: ruminants and fluids



from Agnarsson et al. (2008)

Conclusion: ruminants and fluids



from Agnarsson et al. (2008)

Further increase of RR fluid throughput by selective breeding could

- increase microbial yield from RR
- increase buffering capacity (capacity to deal with concentrate diets)
- reduce methane emissions

Work to be done

- Proof of concept (experiments with fistulated animals/fluid infusions & salivary stimulation) in which not only microbial N yield but also CH_4 and complete energy budgets are measured

- Develop a proxy to identify high-fluid-throughput phenotypes that is easier to measure than ‘mean retention times’