Foregut and hindgut fermenters: How ruminants chew their way out of the foregut fermentation trap

Marcus Clauss

Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Switzerland

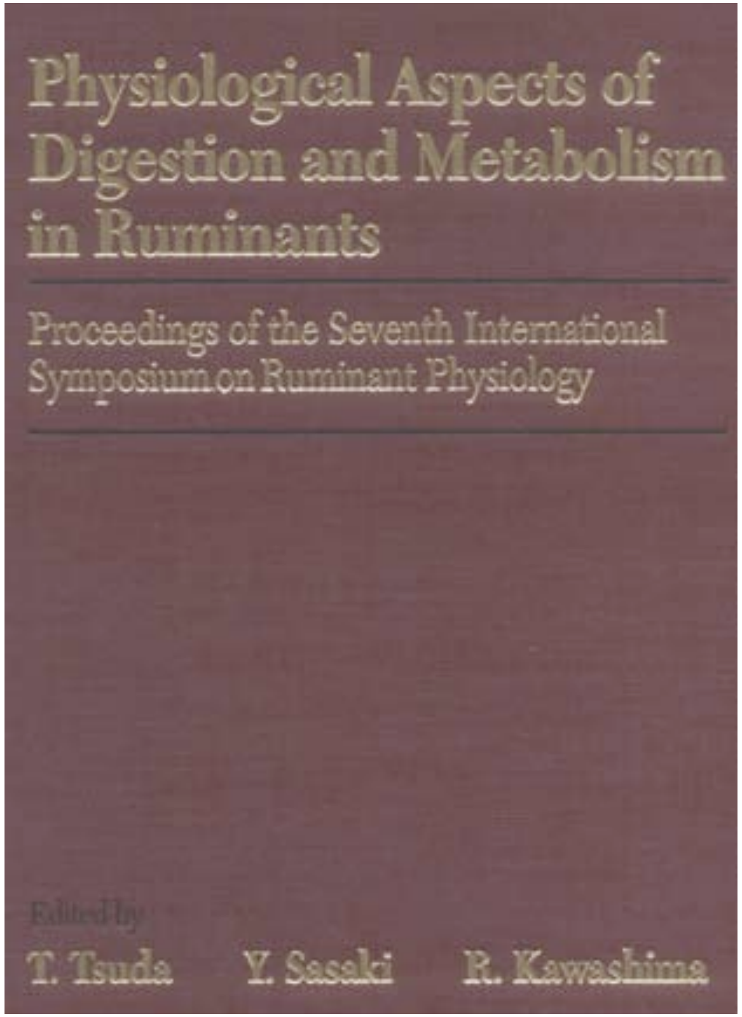
Wildlife Digestive Physiology Course Vienna 2013

University of Zurich
Vetsuisse Faculty

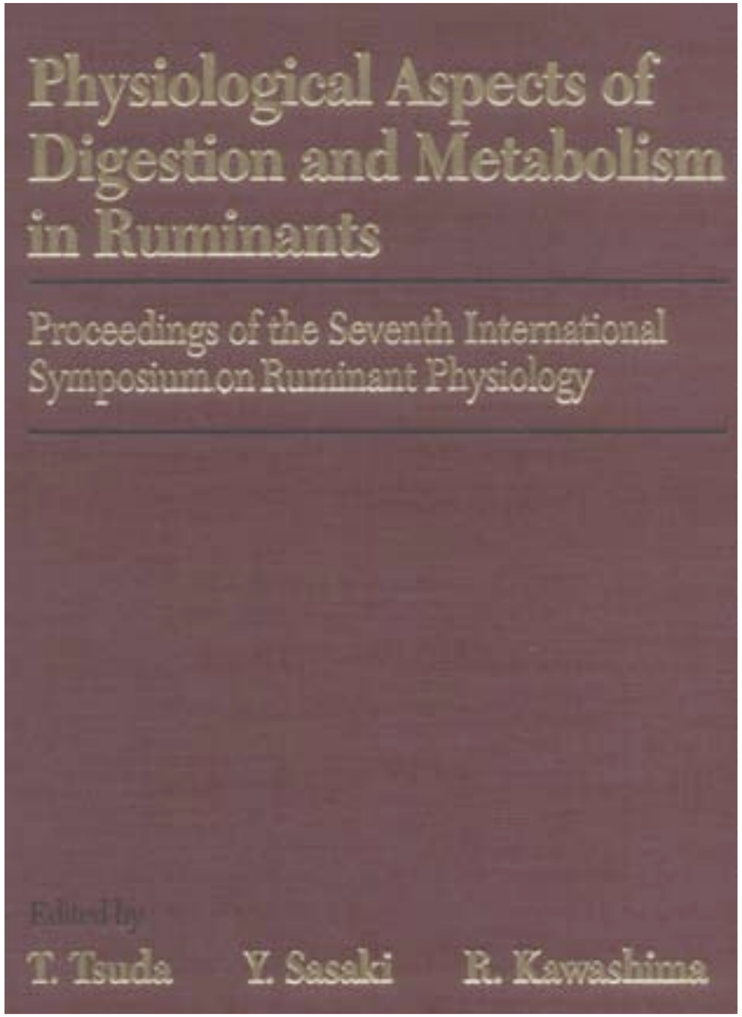
Clinic
of Zoo Animals, Exotic Pets and Wildlife

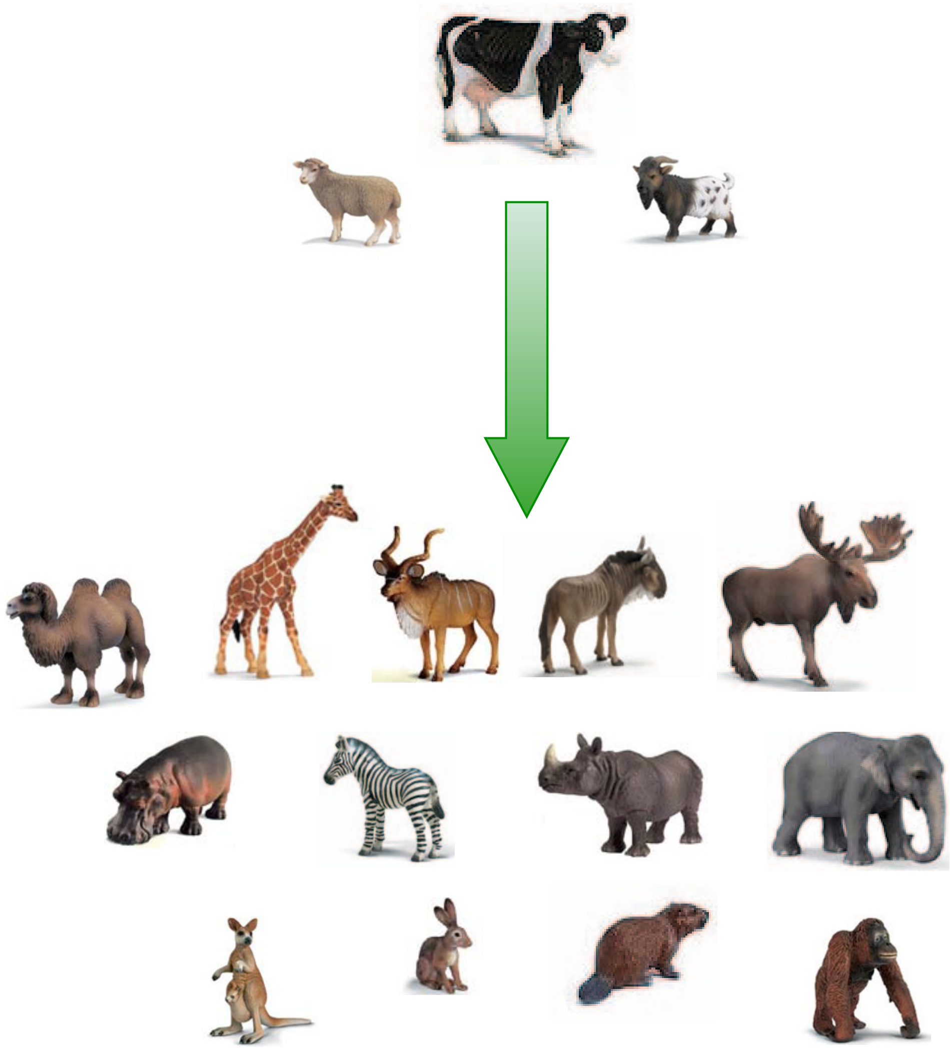
based on a true story

Digestive adaptations



Digestive adaptations





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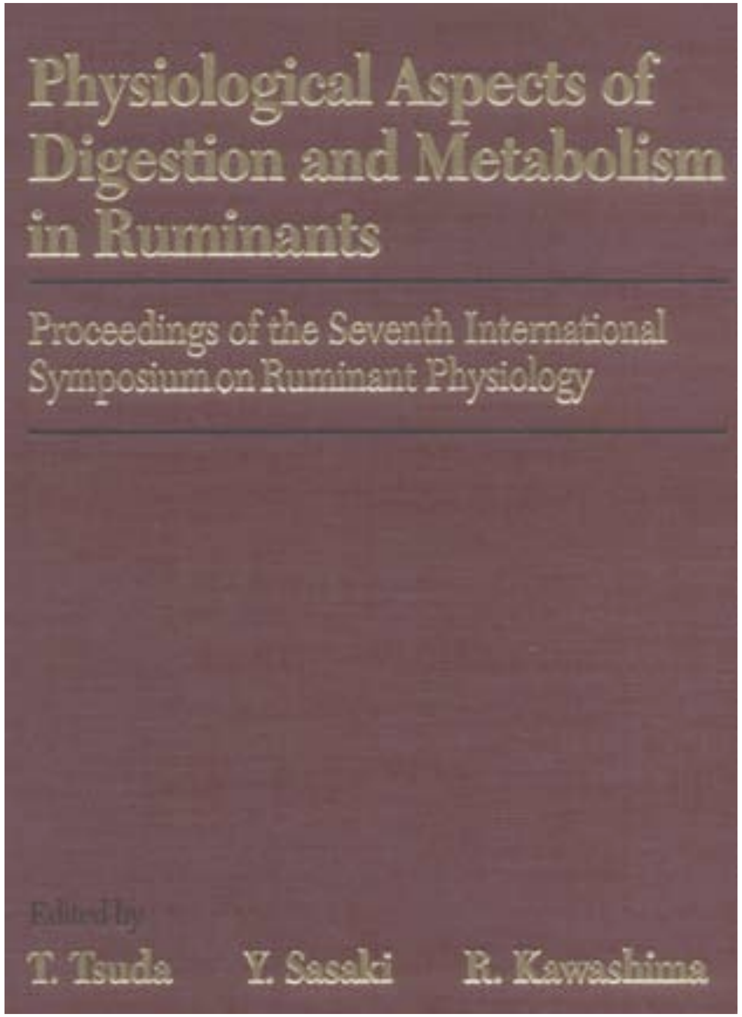

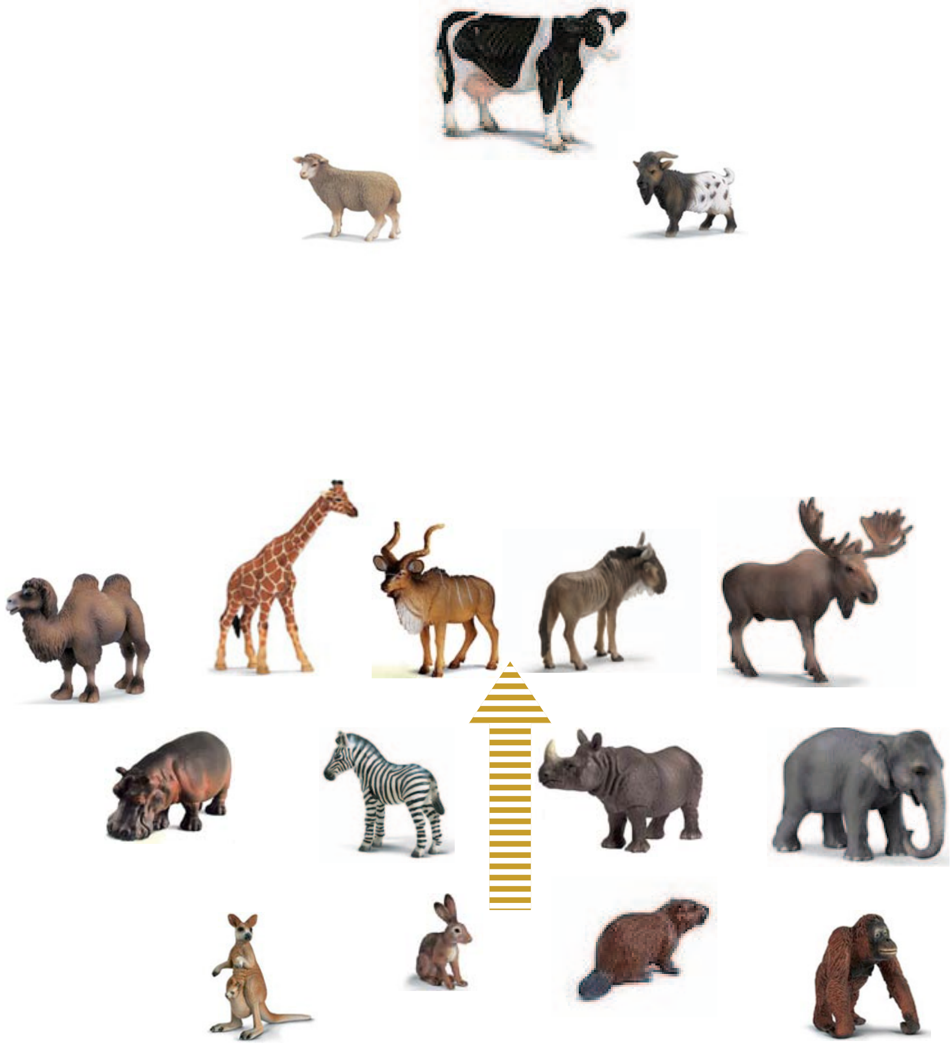

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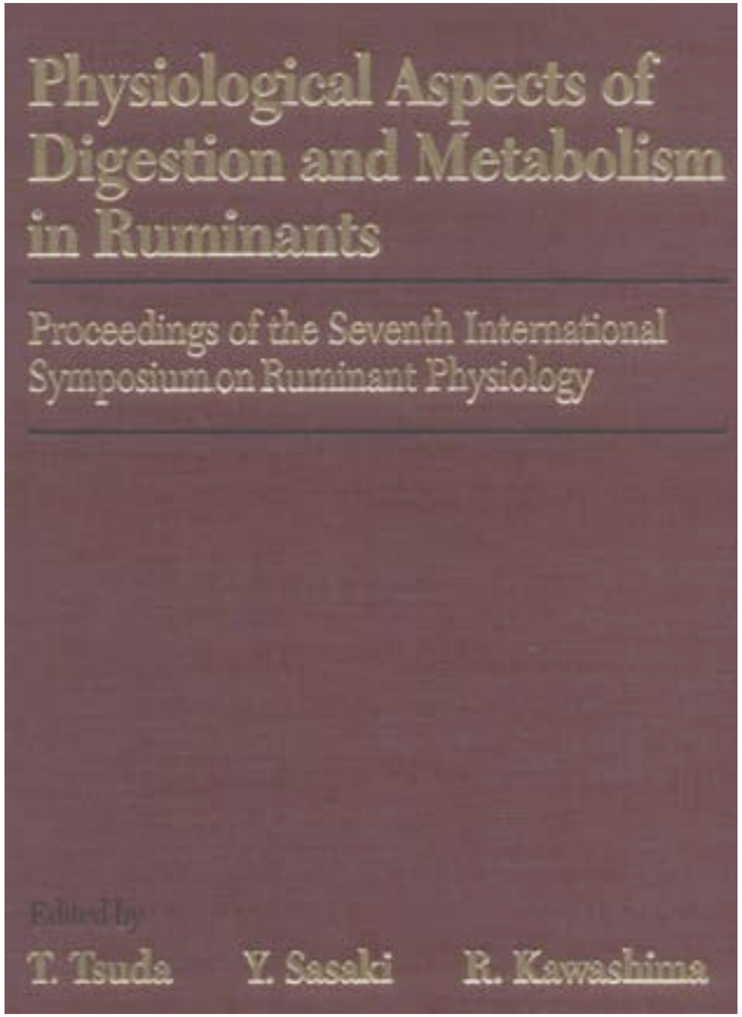
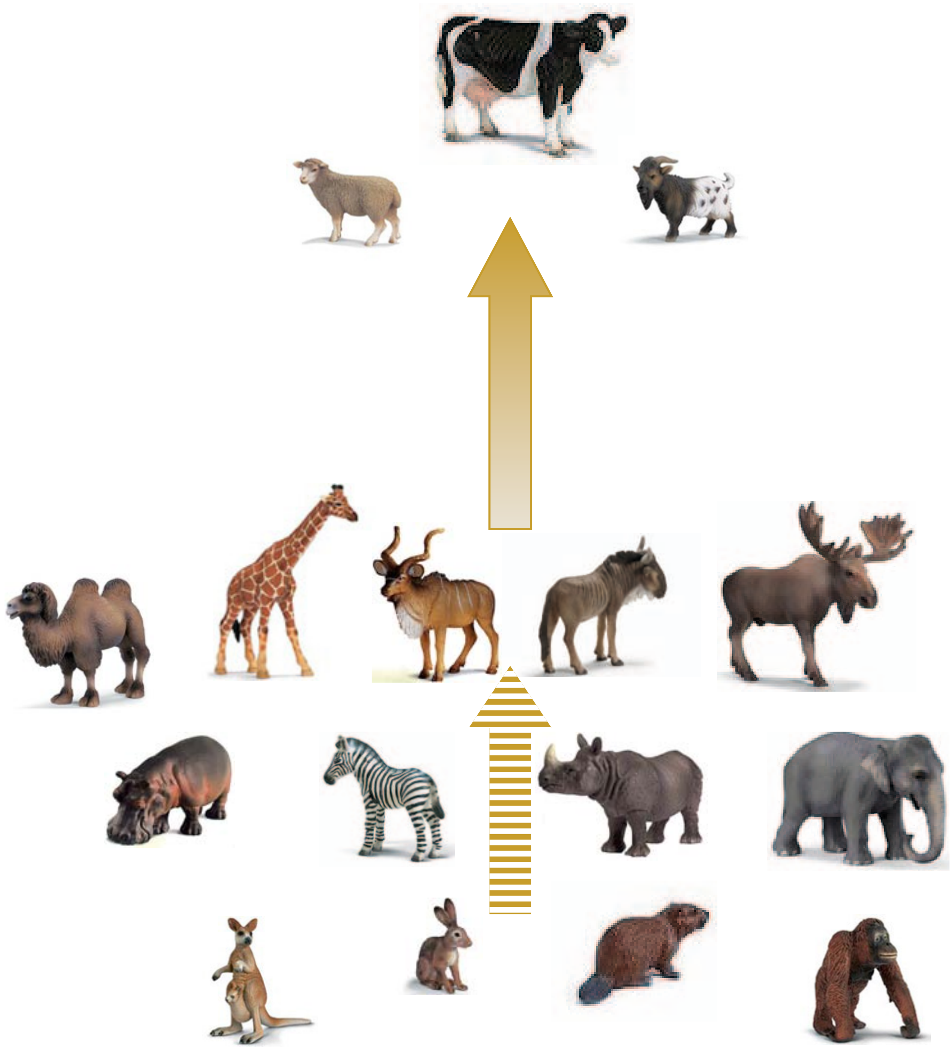
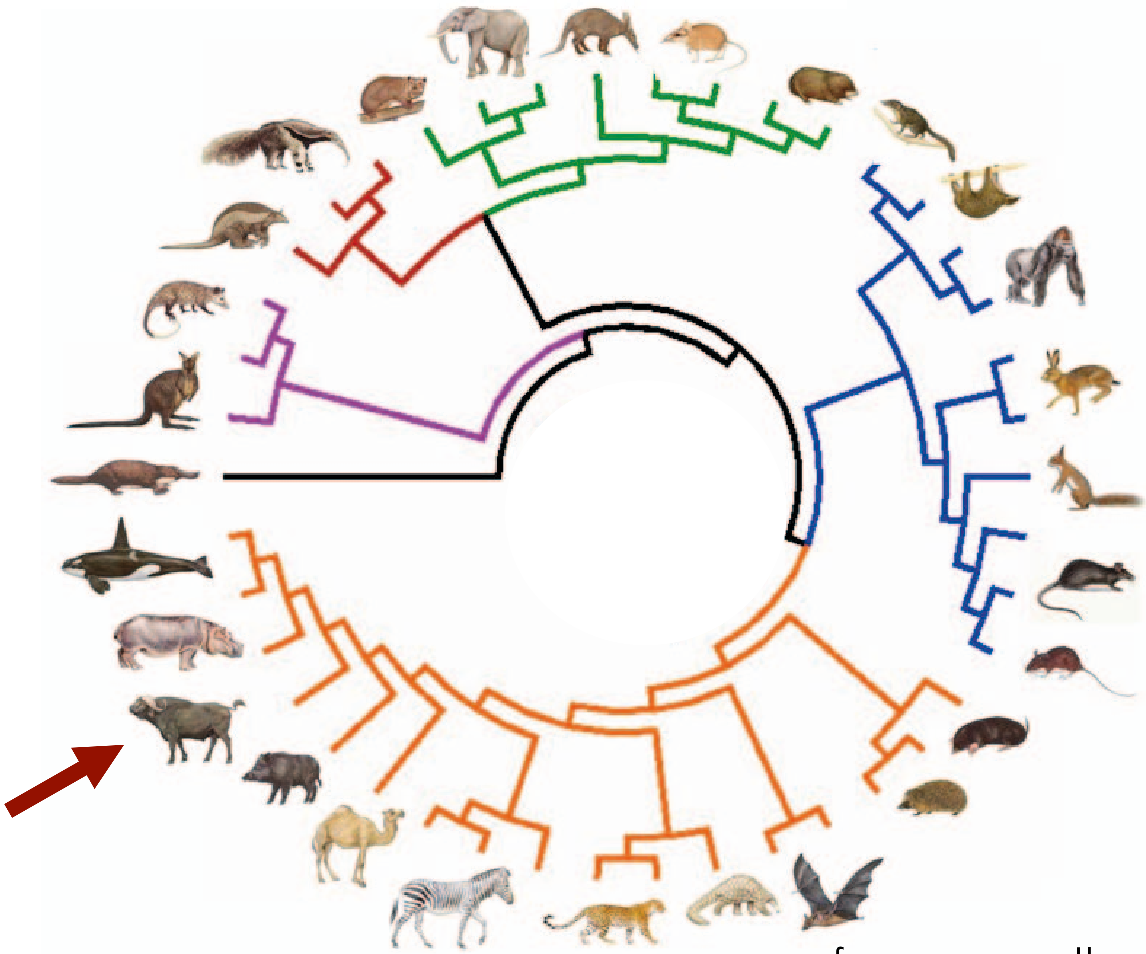




What comparative digestive physiology can offer to domestic ruminant research

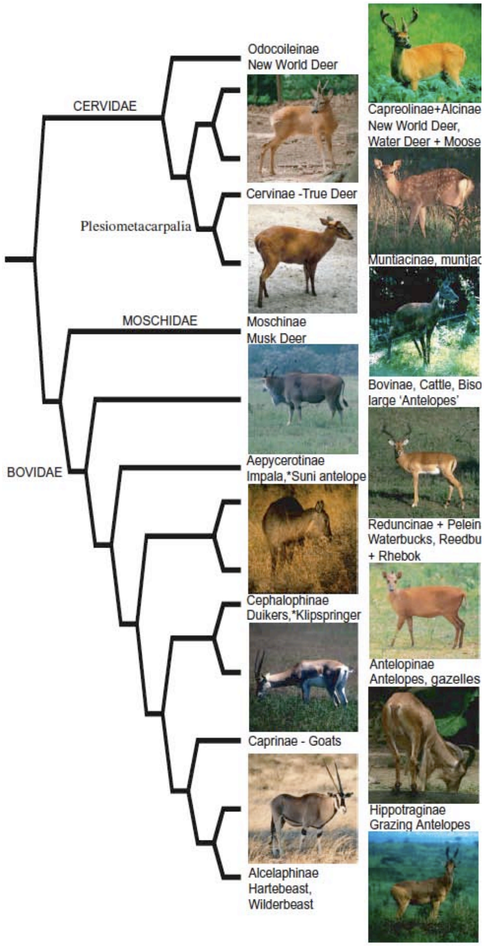
- Understanding where ruminants 'came from' in evolutionary terms



from www.orthomam.univ-montp2.fr

What comparative digestive physiology can offer to domestic ruminant research

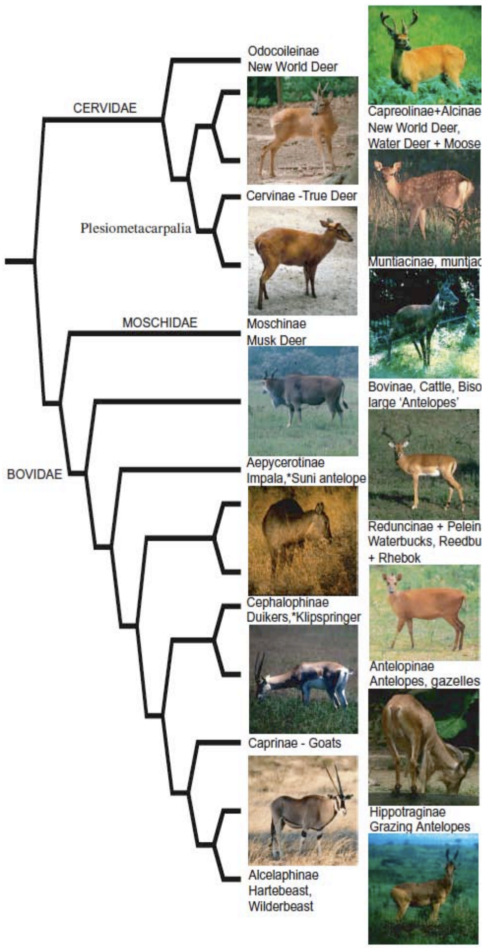
- Understanding where domestic ruminants 'came from' among the ruminants



from Agnarsson et al. (2008)

What comparative digestive physiology can offer to domestic ruminant research

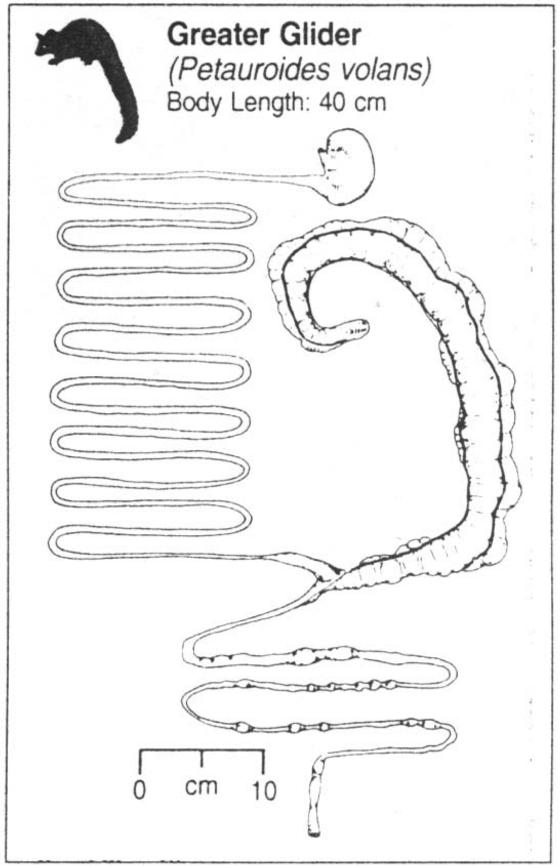
- Understanding where domestic ruminants 'came from' among the ruminants ...

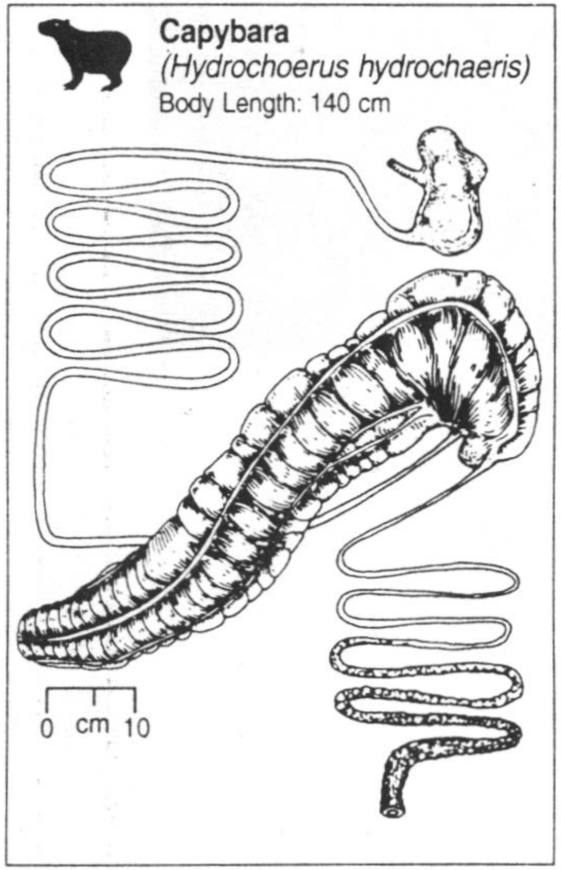


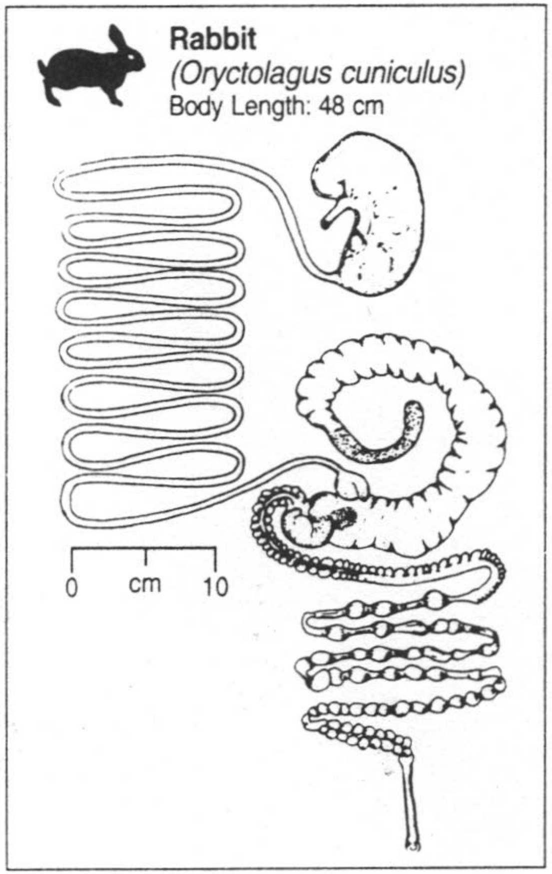
from Agnarsson et al. (2008)

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

Hindgut Fermentation - Caecum

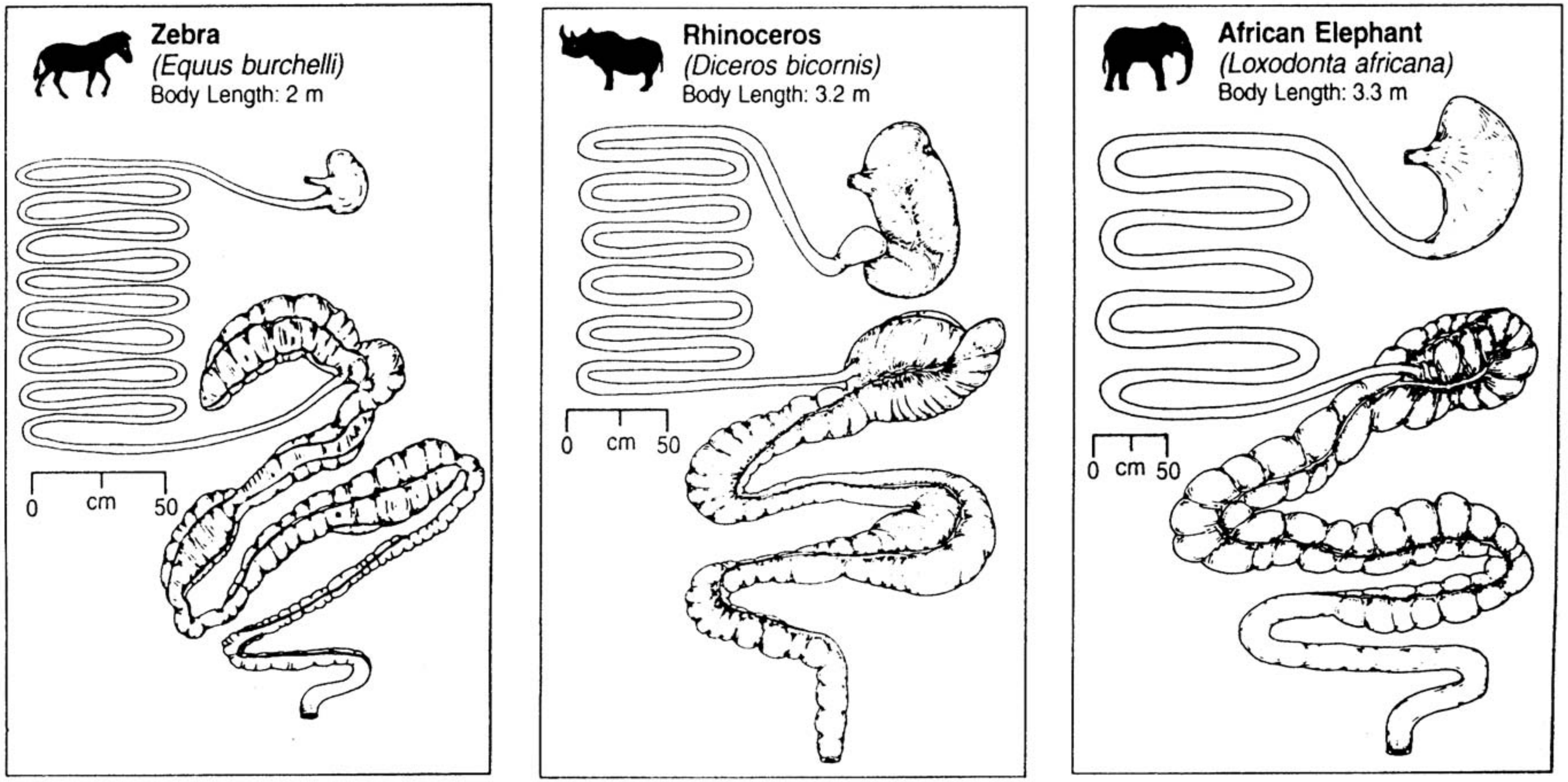






from Stevens & Hume (1995)

Hindgut Fermentation - Colon



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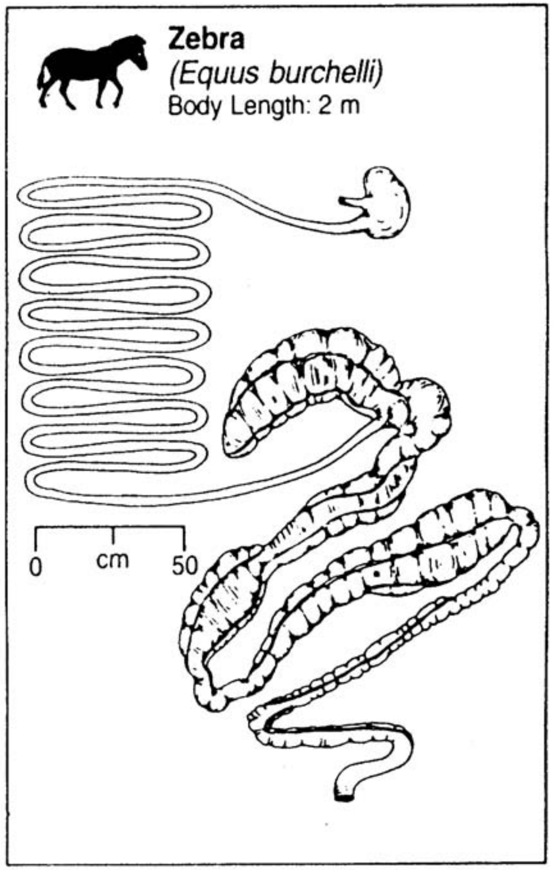
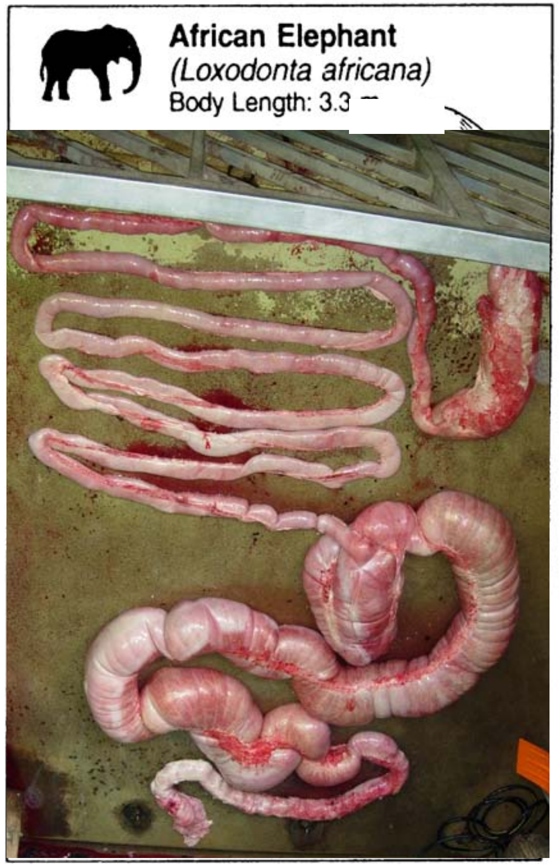
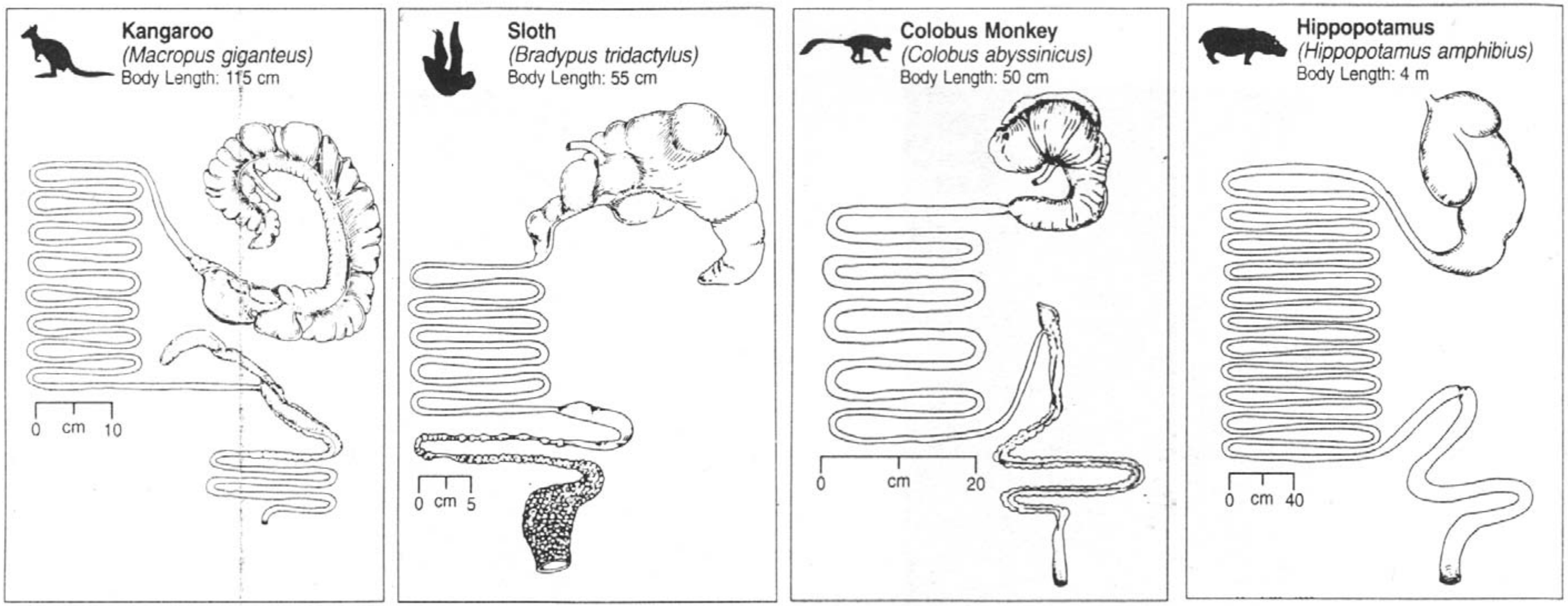




from Stevens & Hume (1995)

Foregut Fermentation

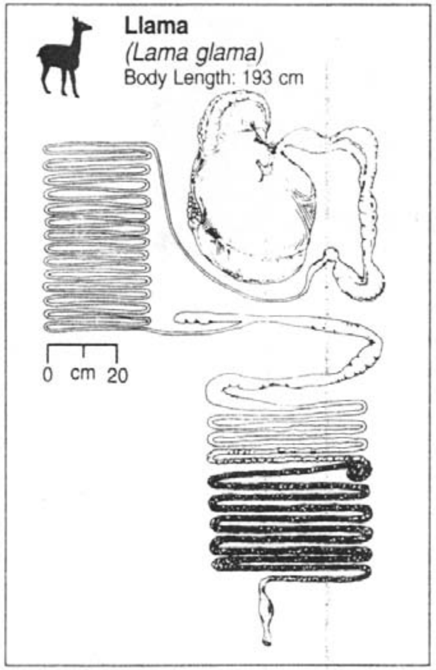


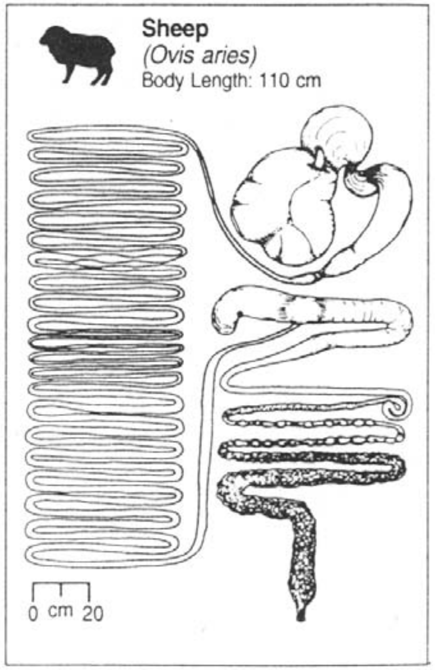
from Stevens & Hume (1995)

Foregut Fermentation

Photos A. Schwarm/
M. Clauss

Foregut Fermentation - Ruminant





aus Stevens & Hume (1995)
Photo Llama: A. Riek

Foregut fermentation = Ruminant digestion?

Ruminant-like Digestion in a Marsupial

R. J. Moir G. Sharman
M. Somers H. Waring
Institute of Agriculture, Zoology Department,
University of Western Australia,
Nedlands, Western Australia.
Sept. 24.

No. 4397 February 6, 1954 NATURE 269

Foregut fermentation = Ruminant digestion?

Ruminant-Like Digestion of the Langur Monkey

T. BAUCHOP
R. W. MARTUCCI

16 AUGUST 1968 SCIENCE, VOL. 161

Foregut fermentation = Ruminant digestion?

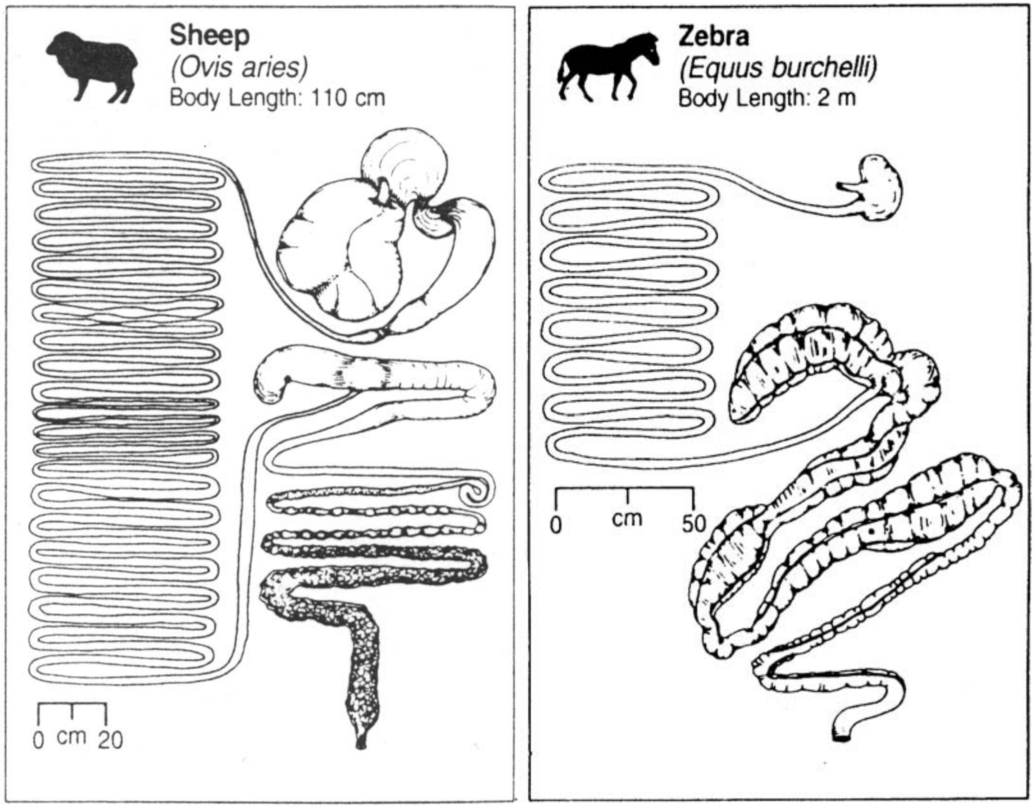
THE EVOLUTIONARY STRATEGY OF THE EQUIDAE AND THE ORIGINS OF RUMEN AND CECAL DIGESTION

CHRISTINE JANIS

EVOLUTION 30:757–774. December 1976

I will use "ruminant" to designate any animal that ferments cellulose in its forestomach.

Foregut vs. Hindgut Fermentation



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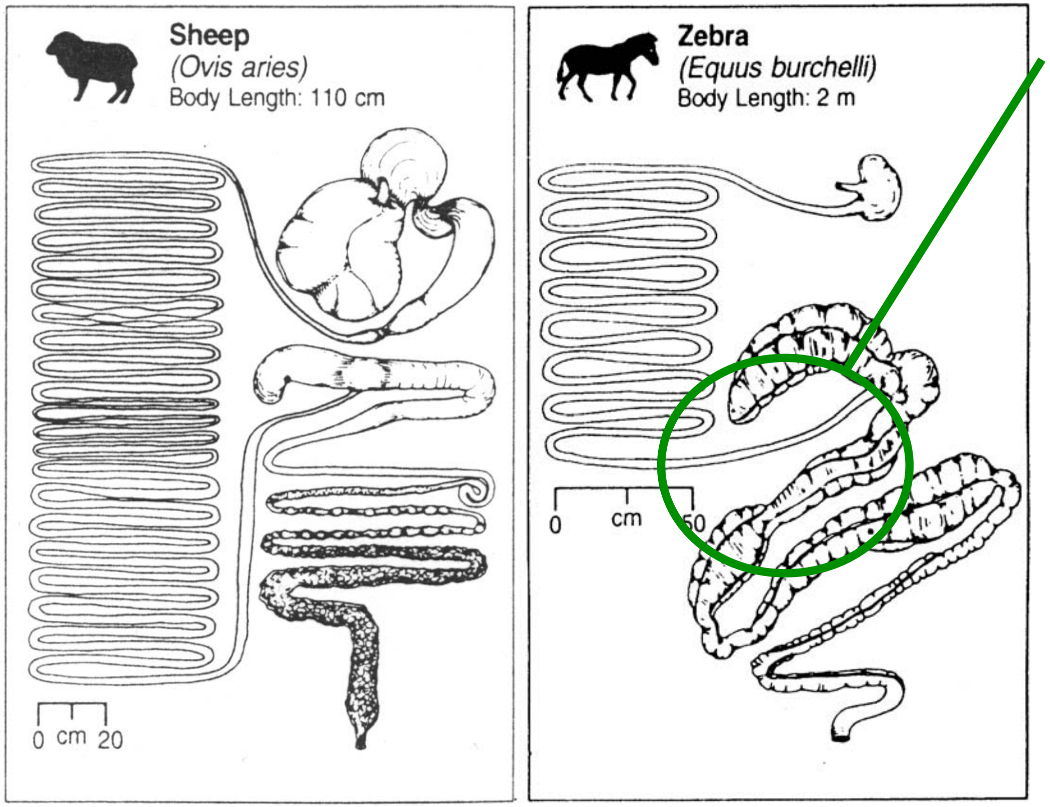
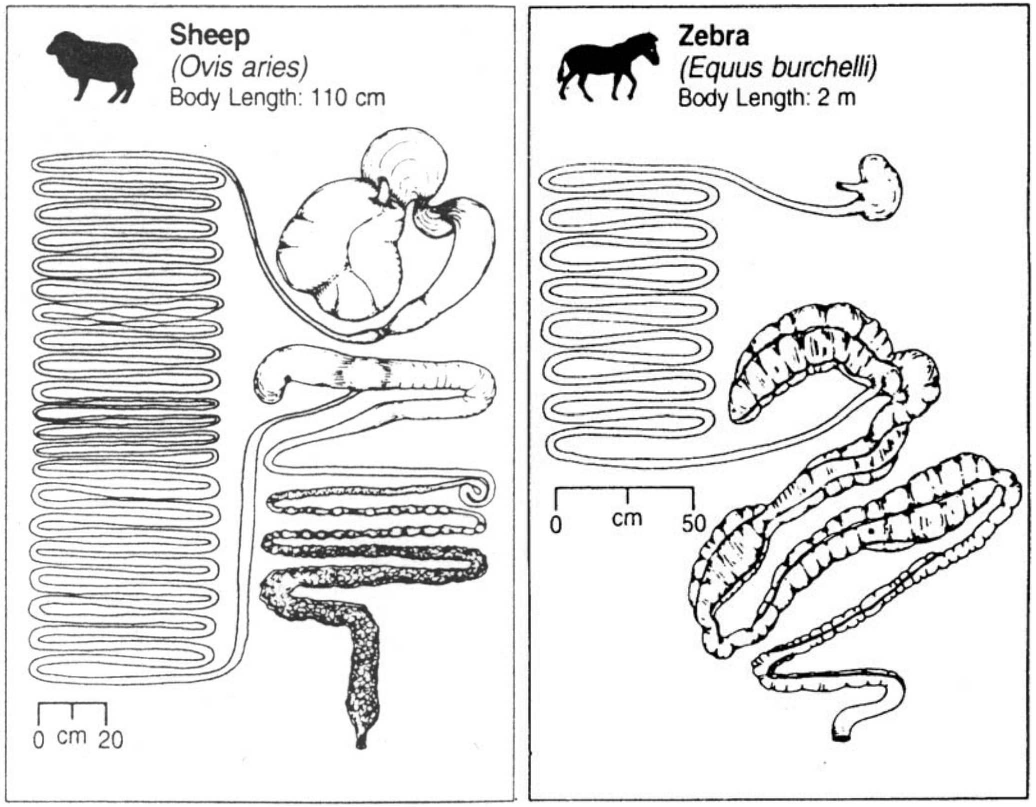


Fermentation <u>after</u> enzymatic digestion and absorption:

from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation



Fermentation <u>after</u> enzymatic digestion and absorption:

<u>'Loss'</u> of bacterial protein, bacterial products (B-Vitamins?)

from Stevens & Hume (1995)

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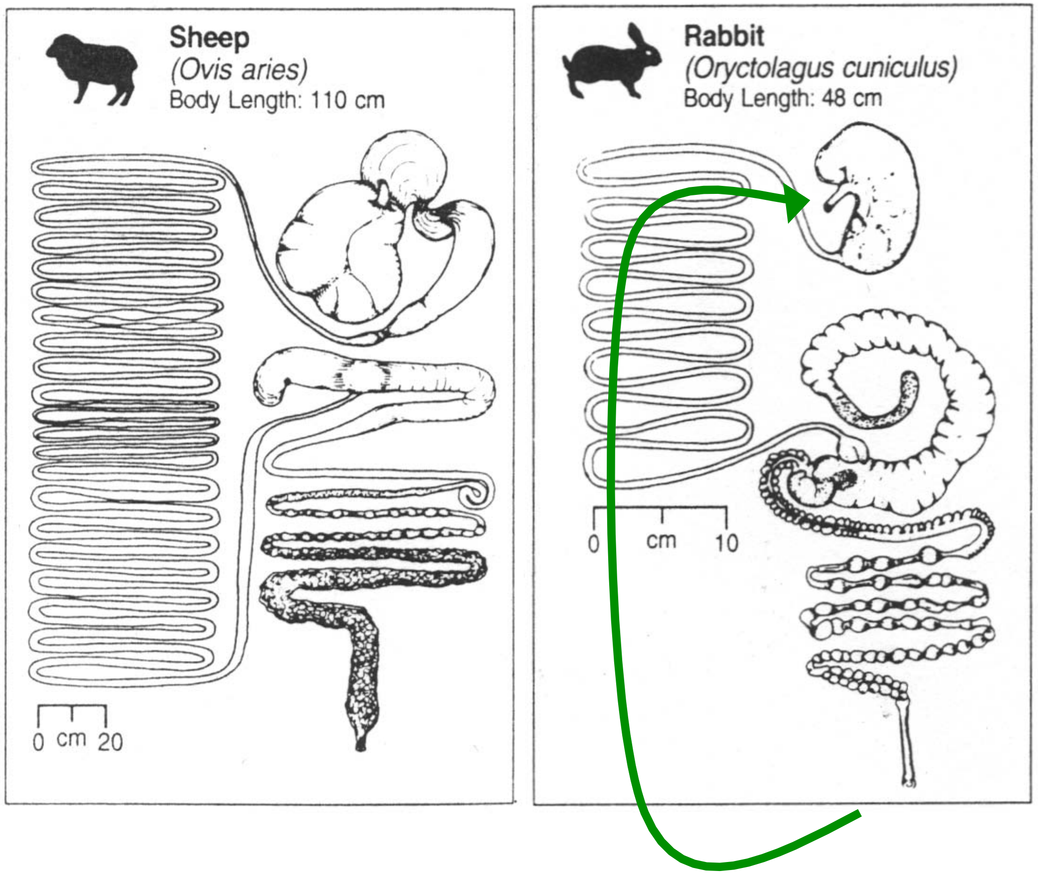

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(coprophagy)

from Stevens & Hume (1995)

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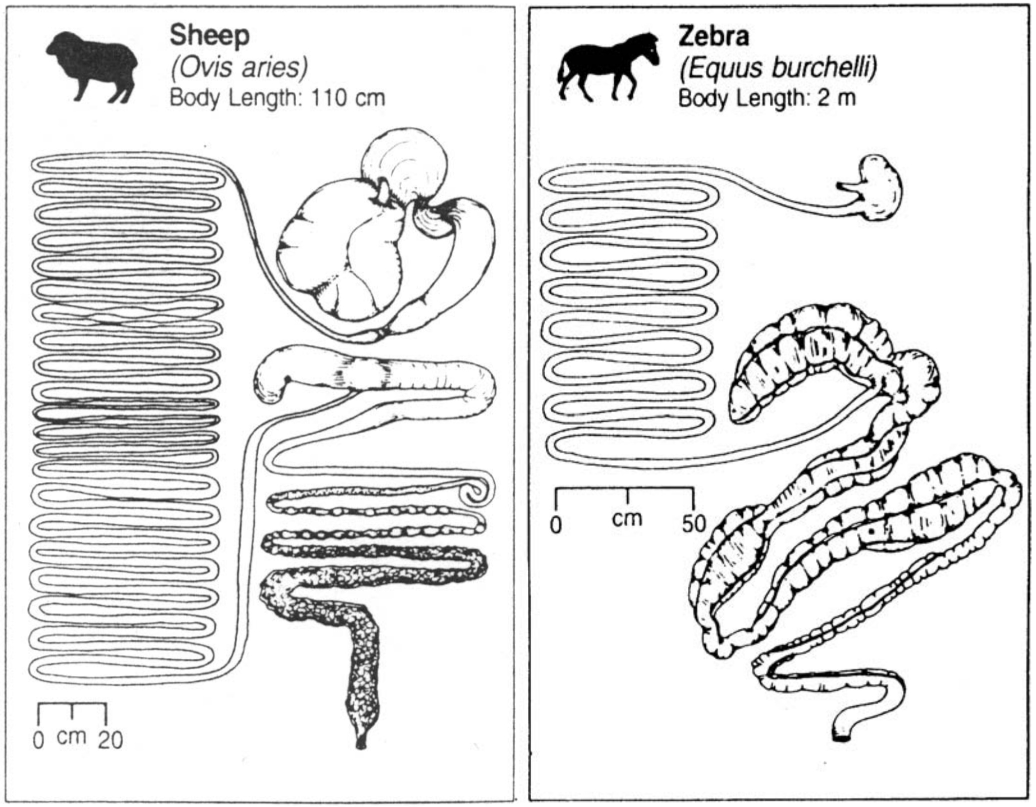

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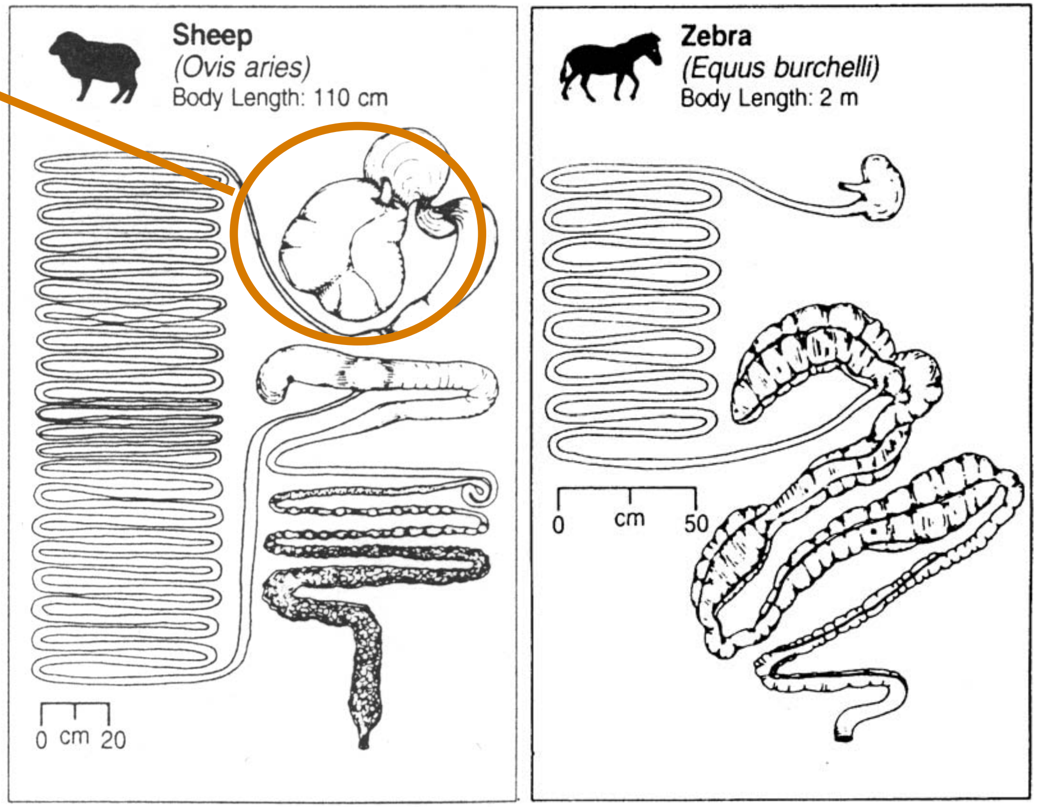
Use of easily digestible substrates

from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation

Fermentation prior to enzymatic digestion and absorption:



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Foregut vs. Hindgut Fermentation

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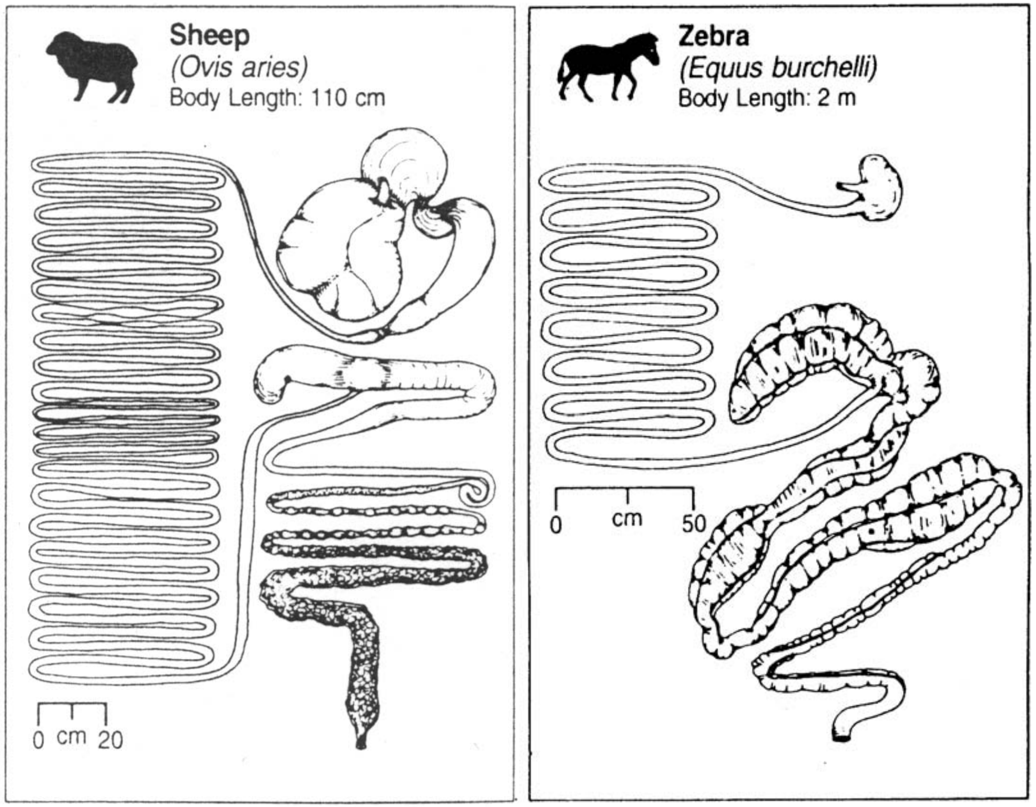

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Foregut vs. Hindgut Fermentation

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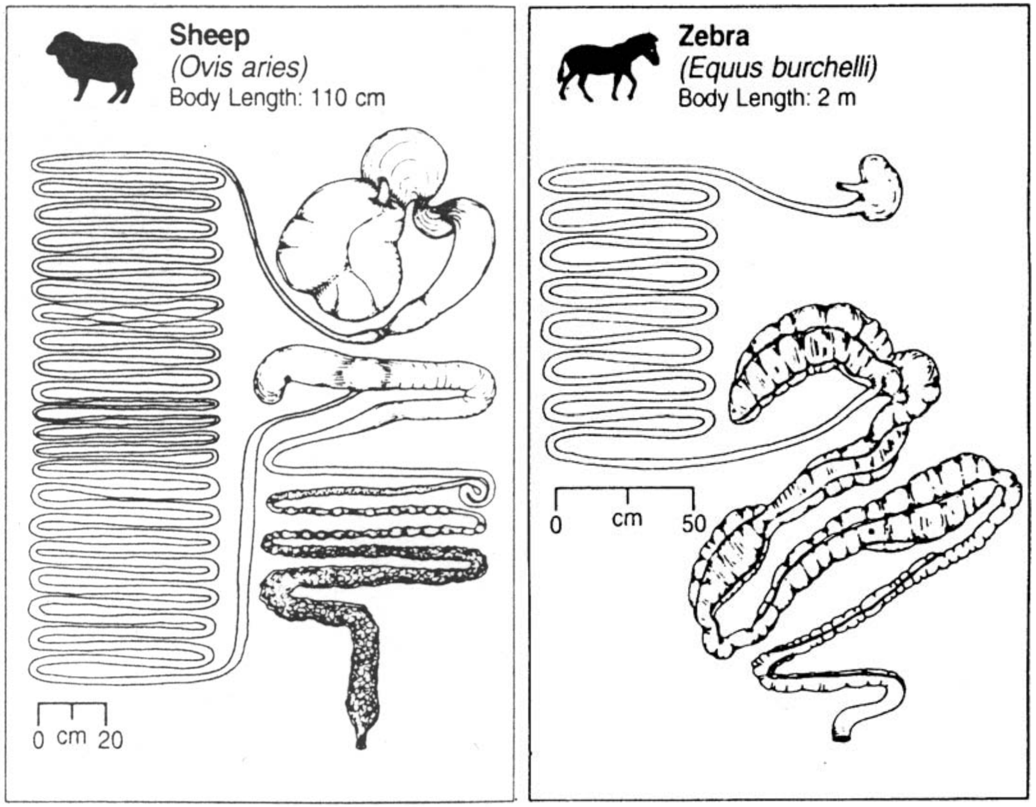
Bacterial detoxification?



Fermentation after enzymatic digestion and absorption:

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from Stevens & Hume (1995)

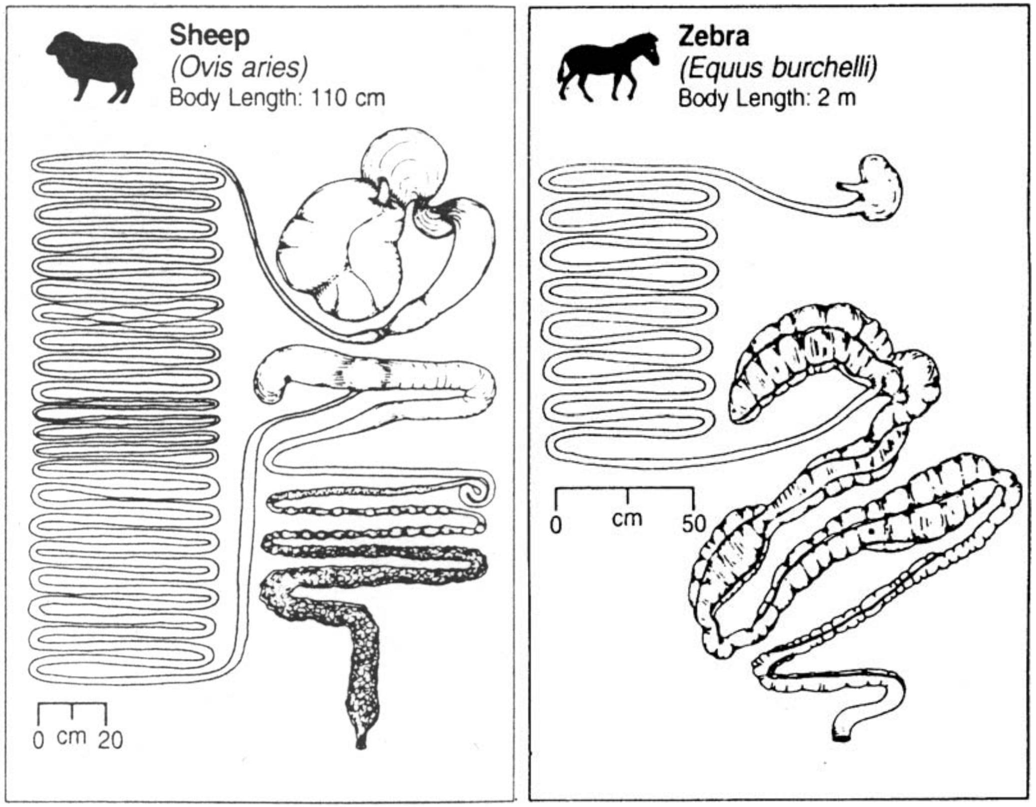
Foregut vs. Hindgut Fermentation

Fermentation prior to enzymatic digestion and absorption:

Use of bacterial protein, bacterial products (B-Vitamins)

Bacterial detoxification?

'Loss' of easily digestible substrates and bacterial modification



Fermentation after enzymatic digestion and absorption:

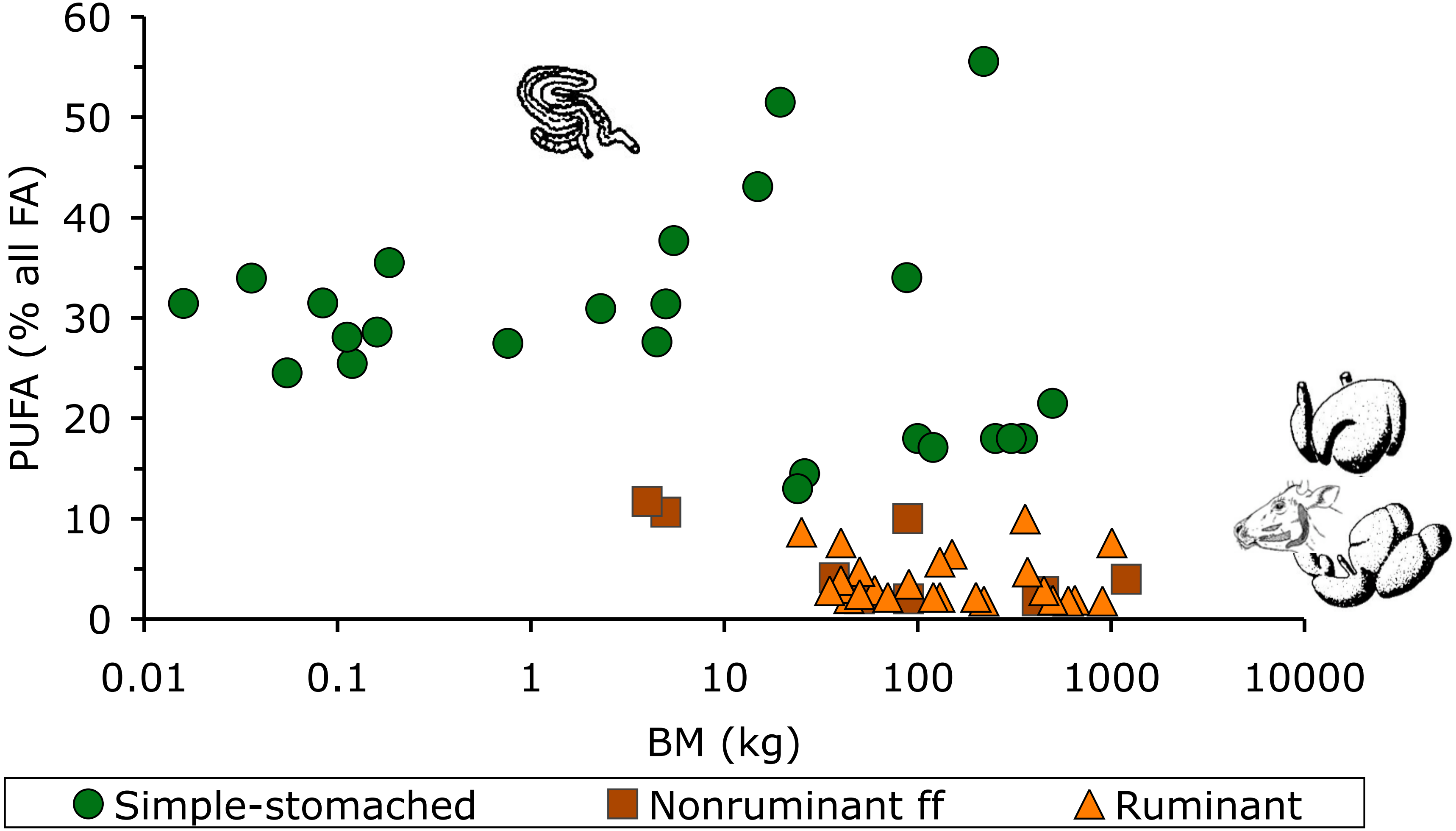
'Loss' of bacterial protein, bacterial products (B-Vitamins?)

(coprophagy)

Use of easily digestible substrates

from Stevens & Hume (1995)

Saturation of body fat

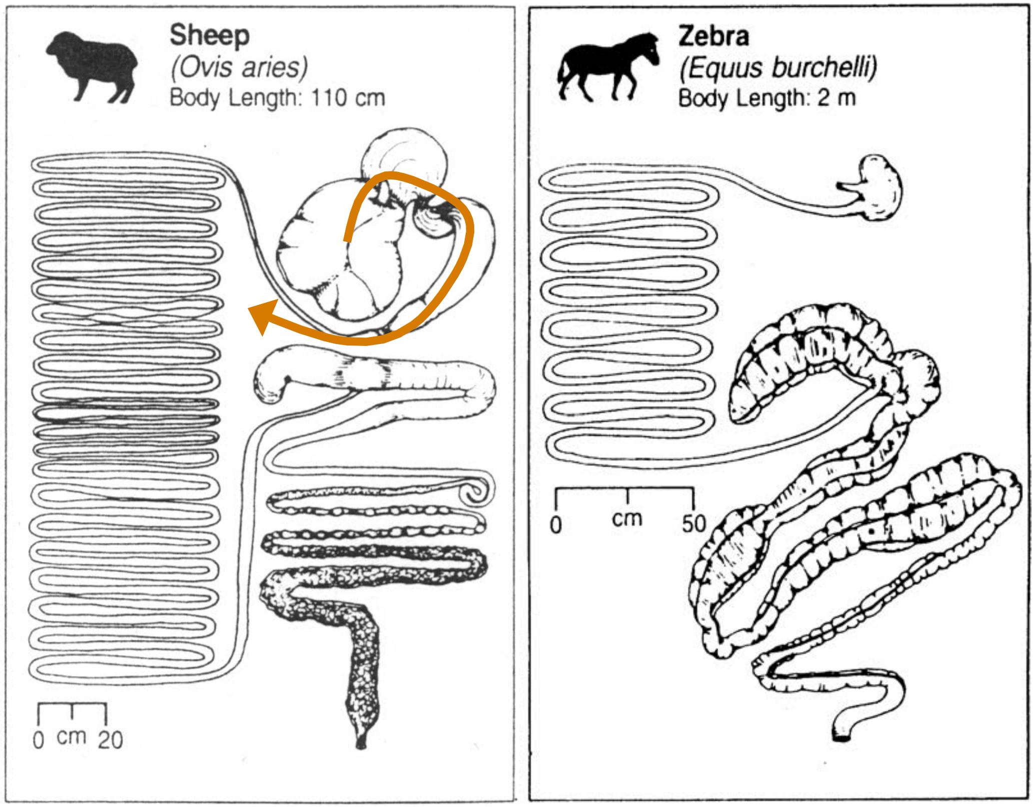


from Clauss et al. (2008)

Foregut vs. Hindgut Fermentation

Bacterially modified fatty acids

(e.g. CLA)



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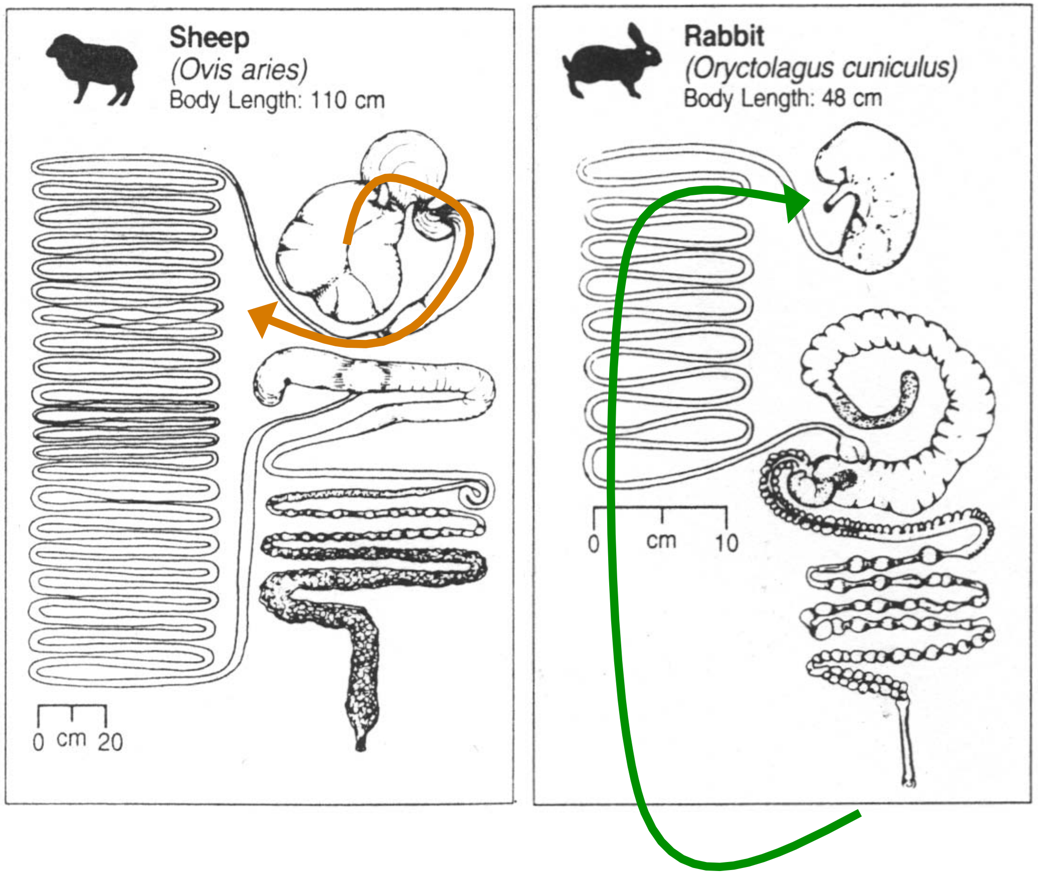
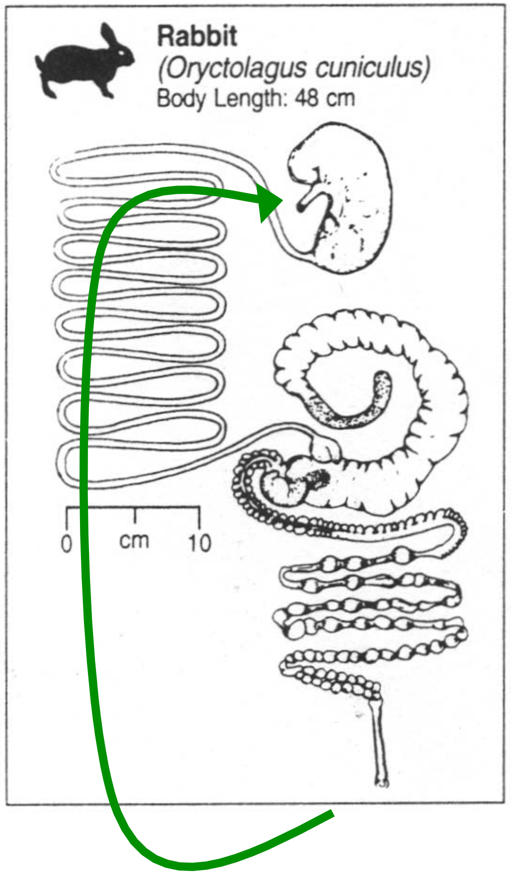


What about coprophagic small hindgut fermenters?

from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation

The FA profiles of caecotroph lipids of rabbits showed typical properties of an anaerobic microbial lipid metabolism comparable to that occurring during ruminal digestion.
Small amounts of BFA and *trans*-FA from caecotrophs are obviously ingested and metabolised. This could have significance for the evaluation of FA digestion and metabolism with small herbivore animal models. It seems possible to develop markers for the occurrence of significant levels of coprophagy in non-ruminant herbivores particularly on the basis of BFA and *trans*18:1 FA.



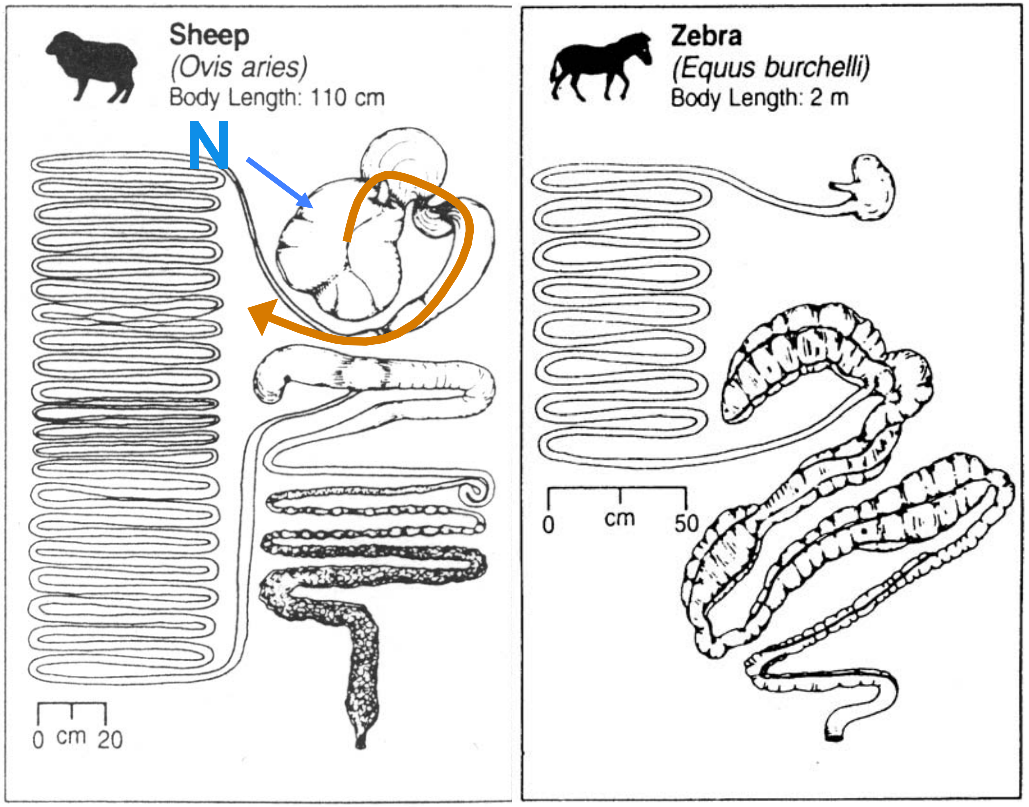
What about coprophagic small hindgut fermenters?

Leiber et al. (2008)

from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation

Endogenous nitrogen products (urea) can be recycled by introducing them into the fermentation chamber - use by microbes - re-digestion of N as bacterial amino acids



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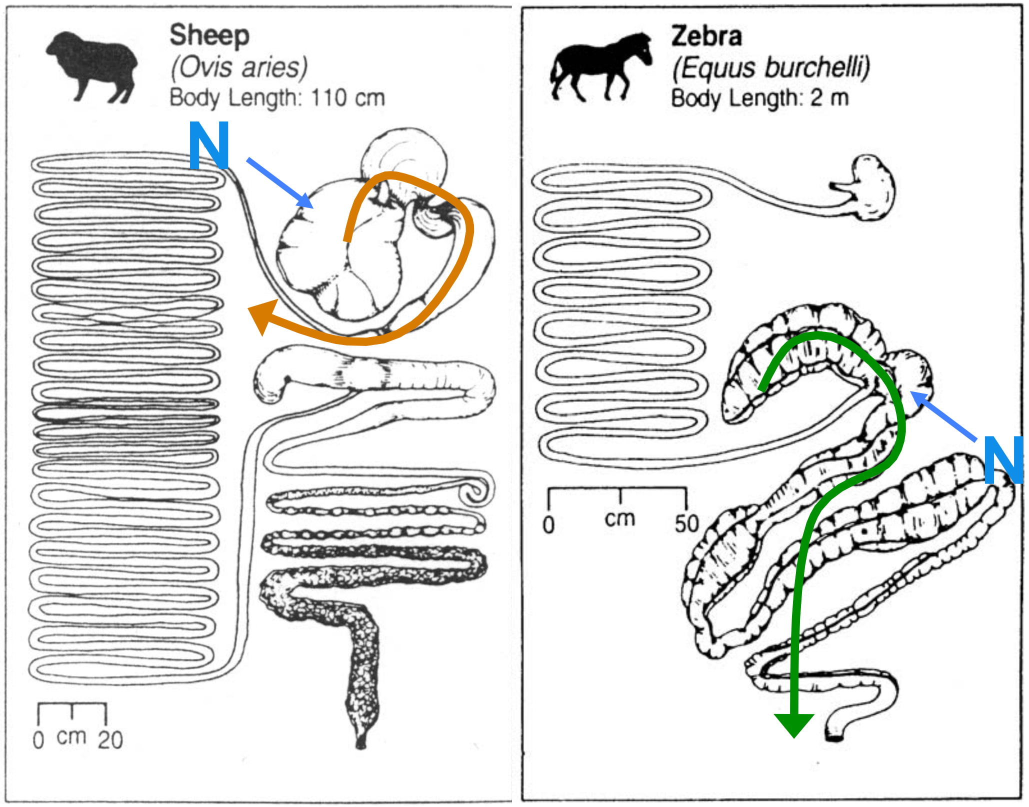

Urea could be available for bacteria in hindgut fermenters, but it would not be recycled

from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation

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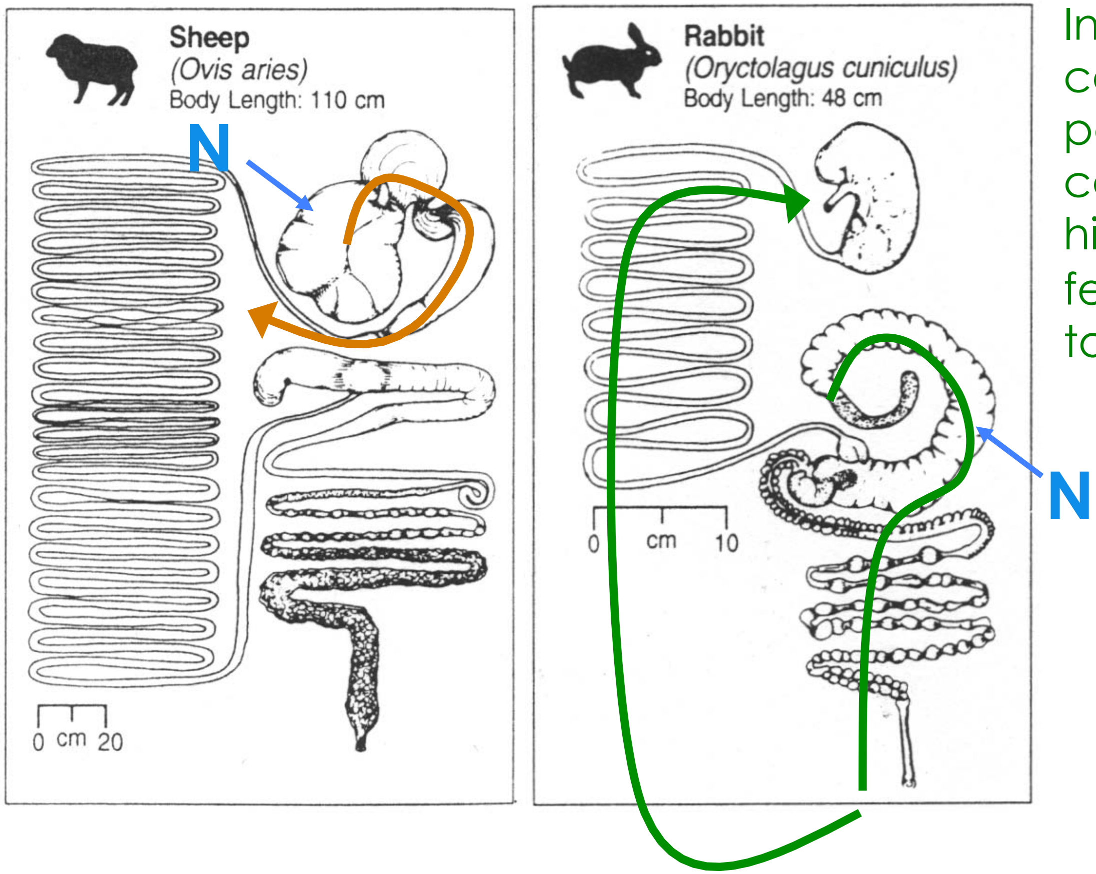
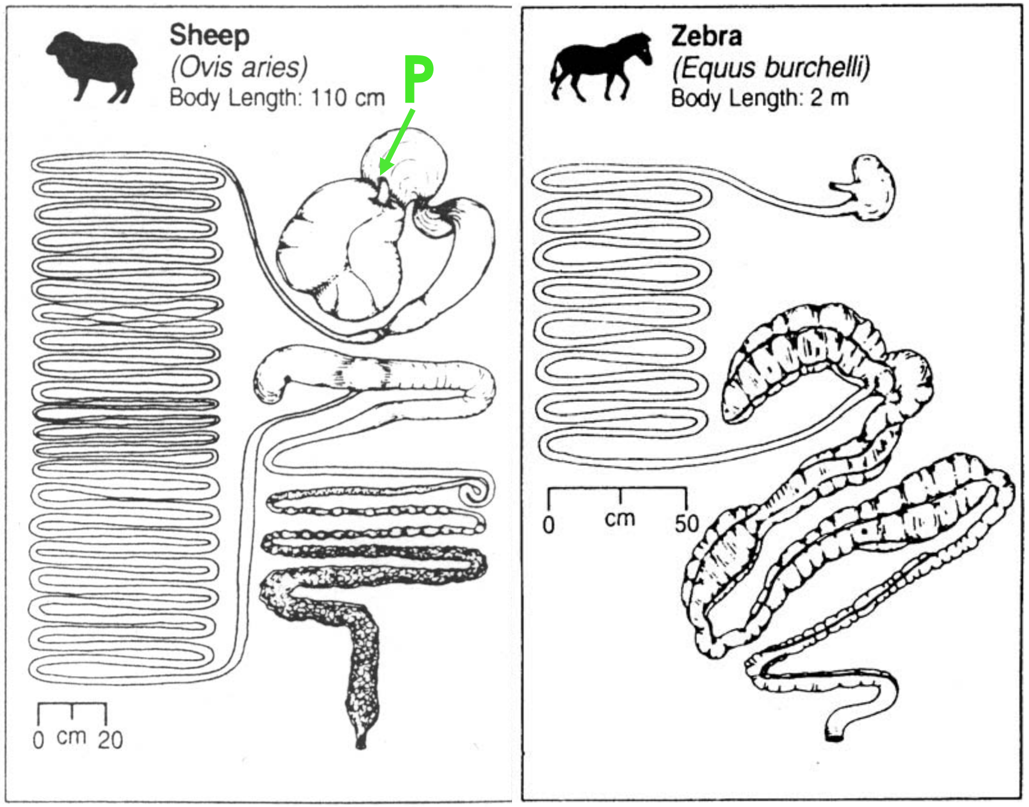


In theory, this could be possible in coprophagic hindgut fermenters, too

from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation

Phosphorus is supplied directly to microbes via saliva



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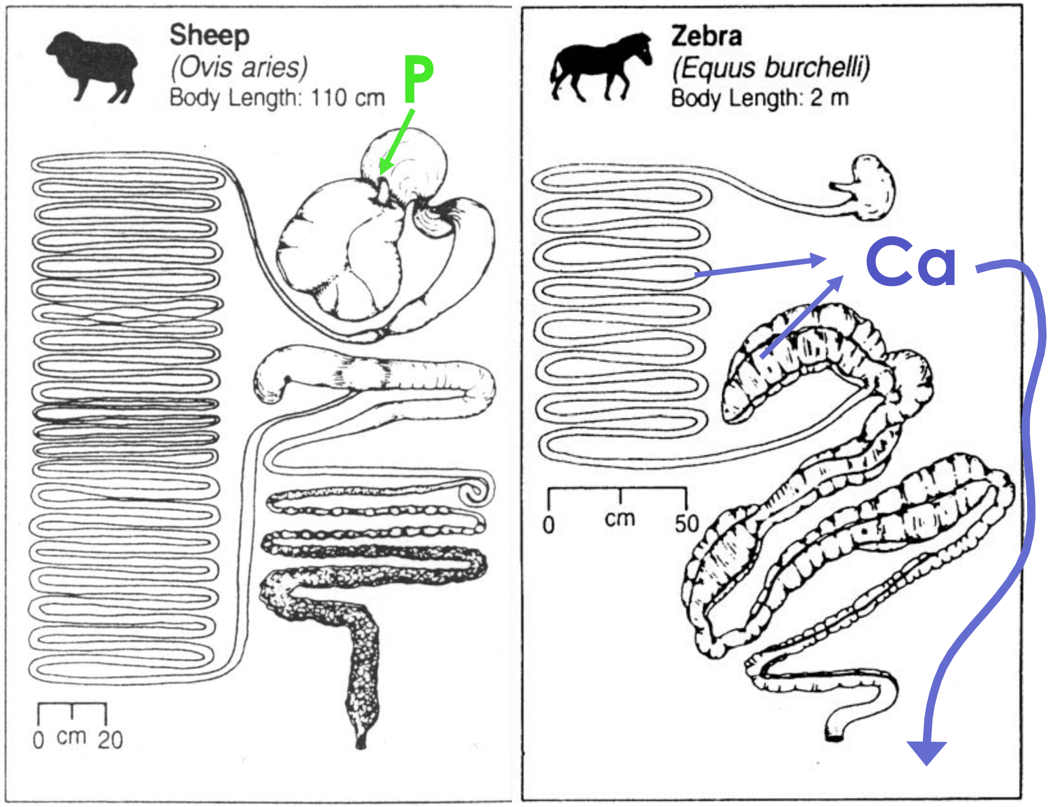


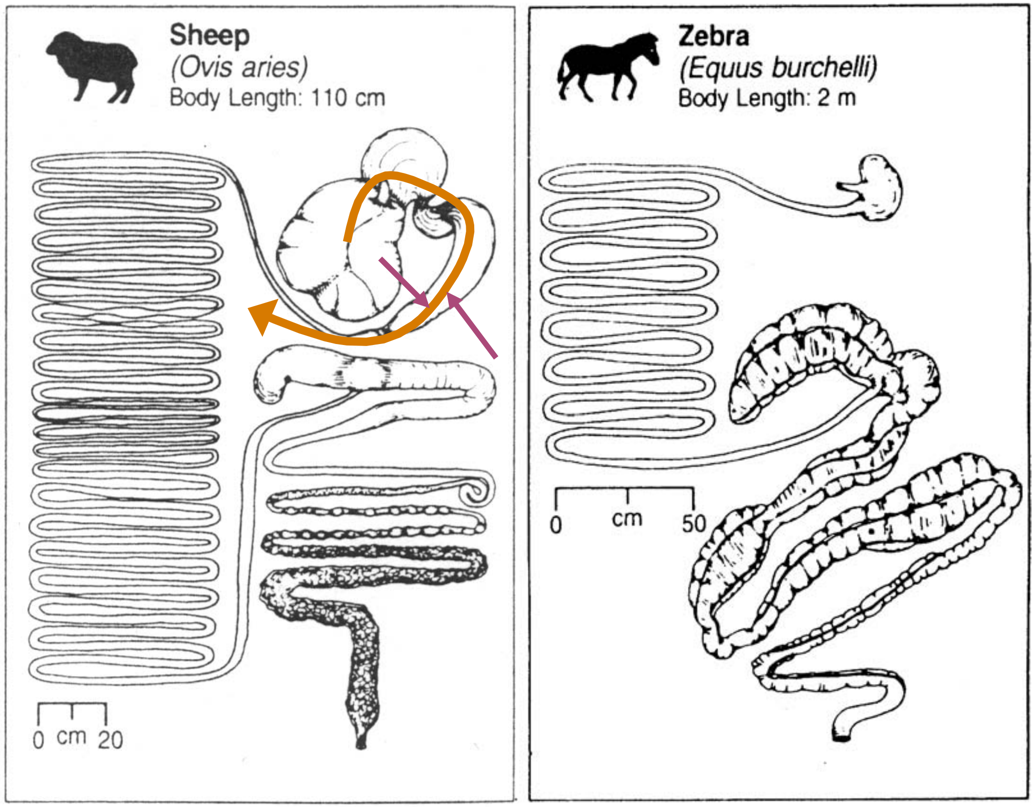
In order to guarantee **phosphorus** availability in the hindgut, **calcium** is actively absorbed from ingesta and excreted via urine

from Stevens & Hume (1995)
hypothesis by Clauss & Hummel (2008)

Foregut vs. Hindgut Fermentation

Lysozyme secretion in the glandular stomach (and ribonuclease in the duodenum) as an example of convergent evolution of enzymes

(for the digestion of bacteria)



from Stevens & Hume (1995), Karasov & Martinez del Rio (2007)

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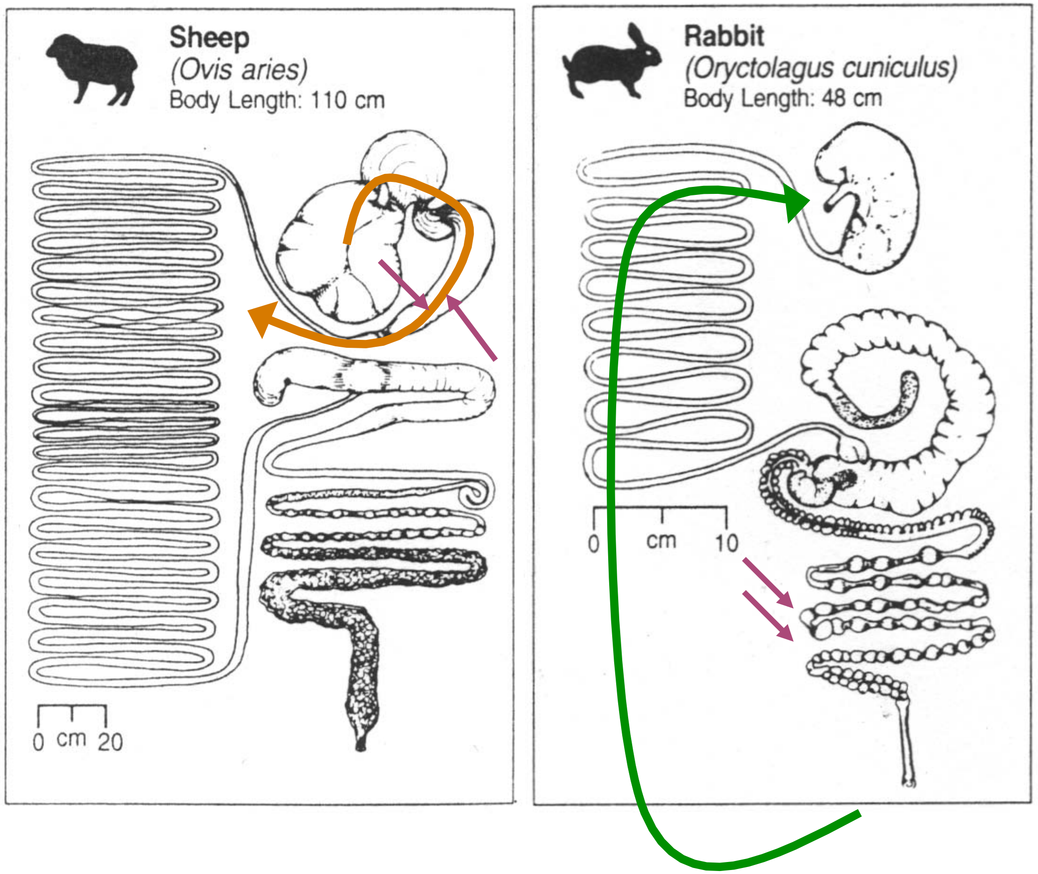
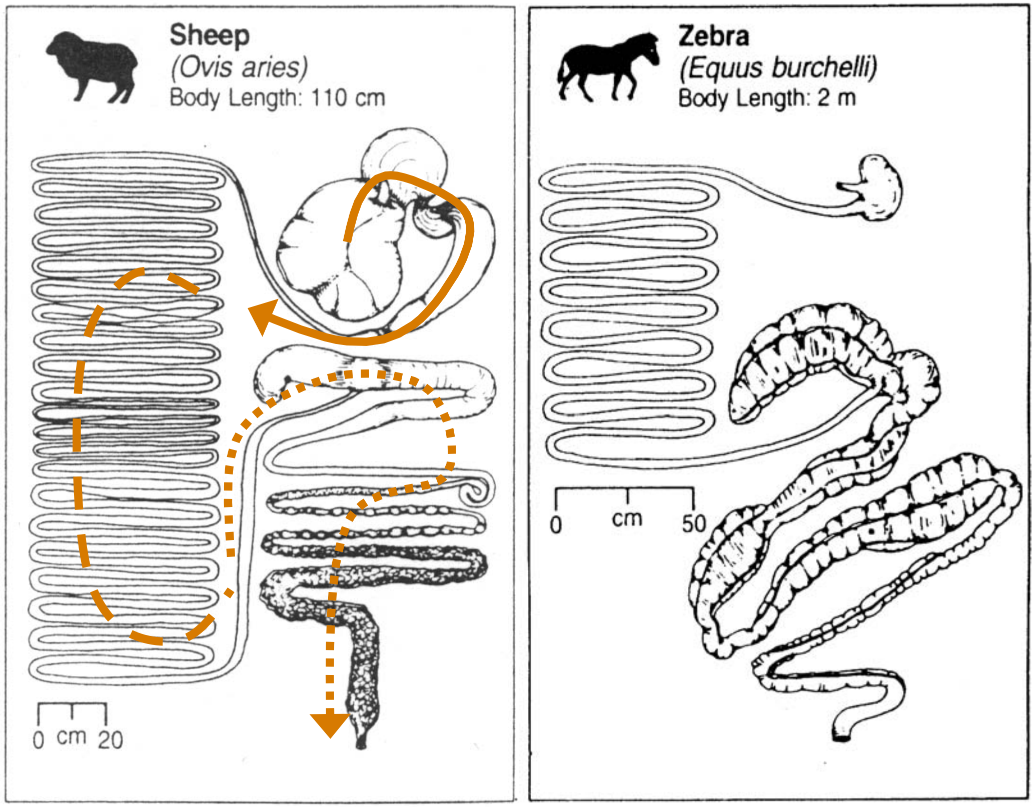


Intermittent colonic **lysozyme** secretion in synchrony with caecotroph formation

from Stevens & Hume (1995), Karasov & Martinez del Rio (2007), Camara & Prieur (1984)

Foregut vs. Hindgut Fermentation

Lower bacterial nitrogen losses in the faeces?



from Stevens & Hume (1995)

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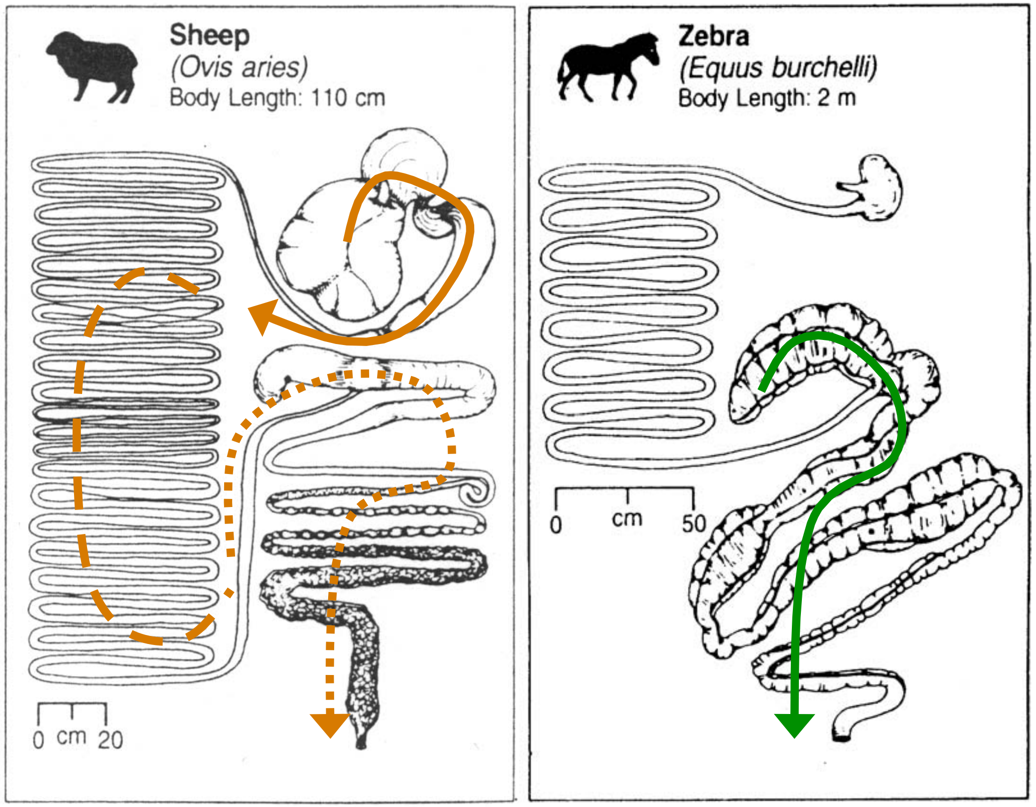
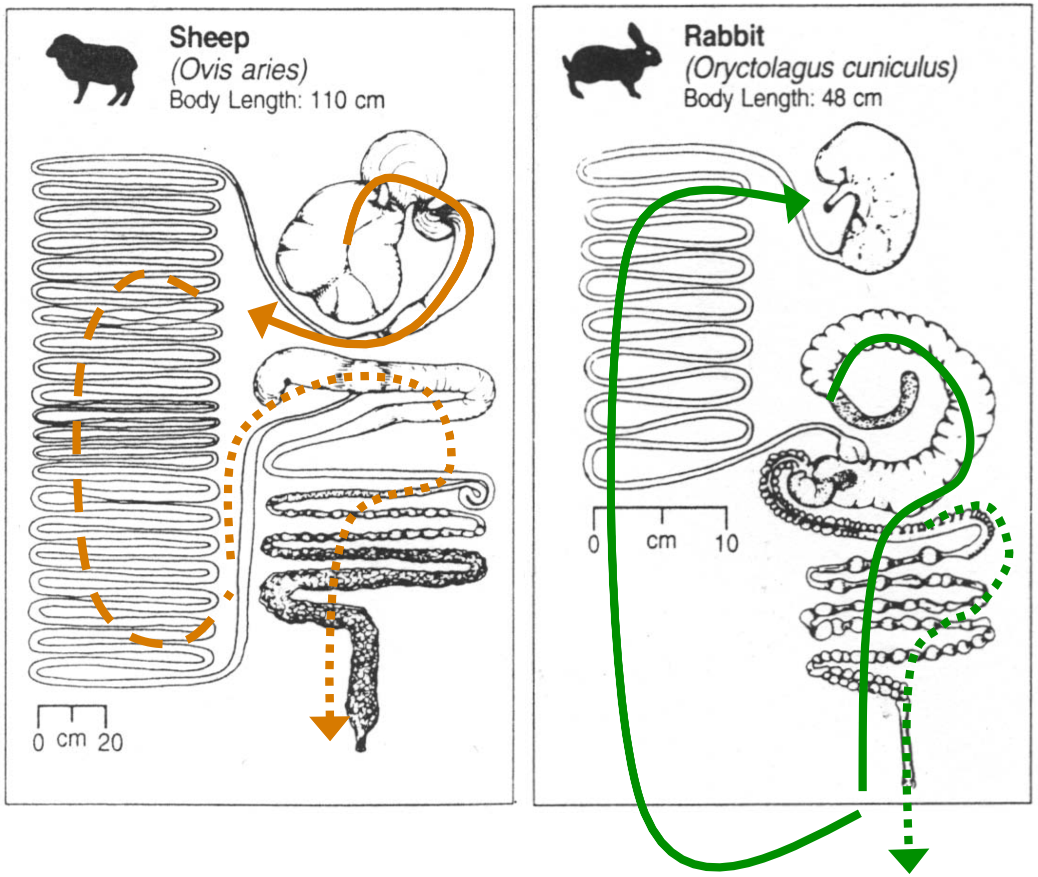


Higher bacterial nitrogen losses in the faeces?

from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation

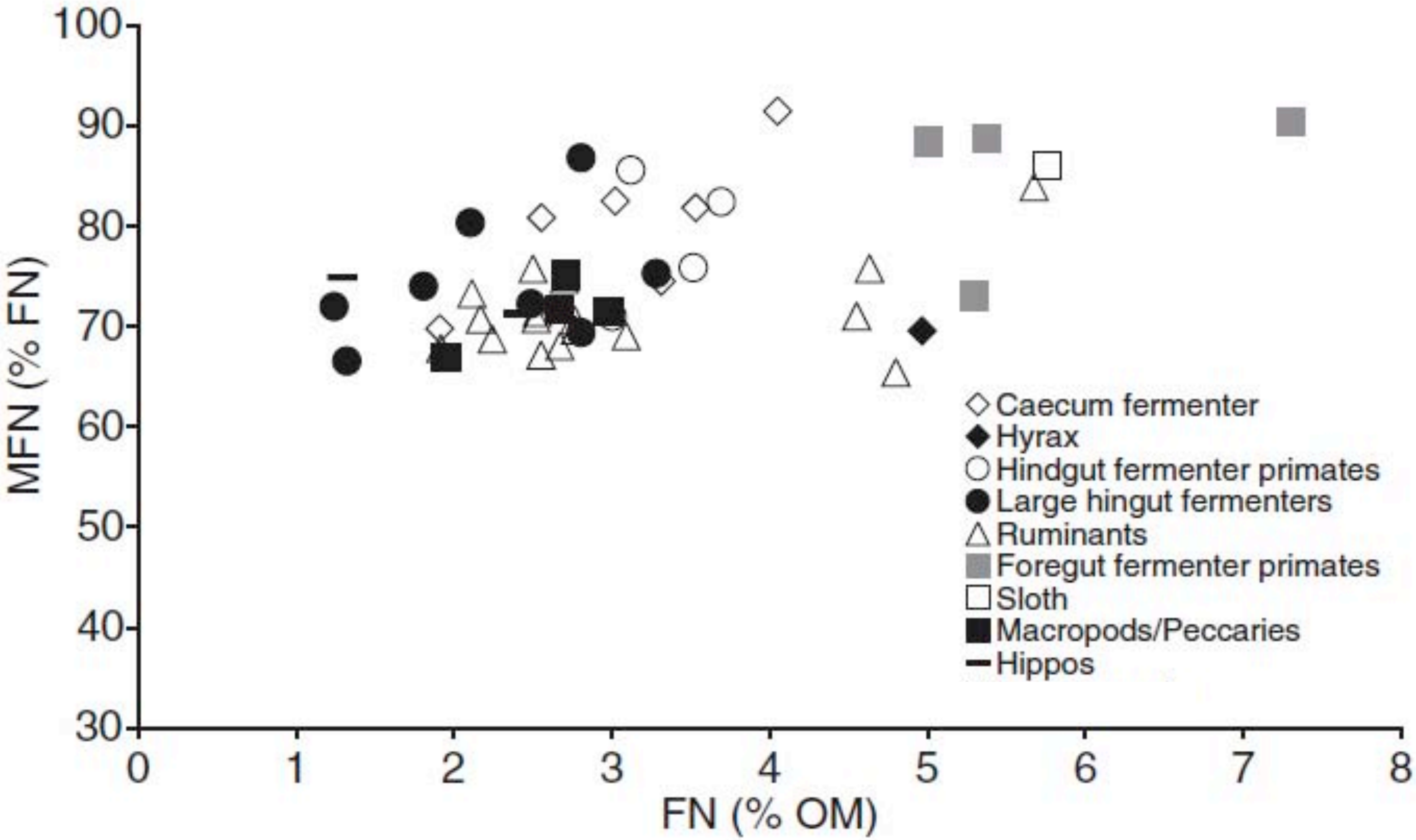
Lower bacterial nitrogen losses in the faeces?



Lower bacterial nitrogen losses in hard faeces in coprophagic hindgut fermenters due to bacterial accumulation in caecotrophs?

from Stevens & Hume (1995)

Metabolic faecal nitrogen in zoo herbivores



from Schwarm et al. (2009)

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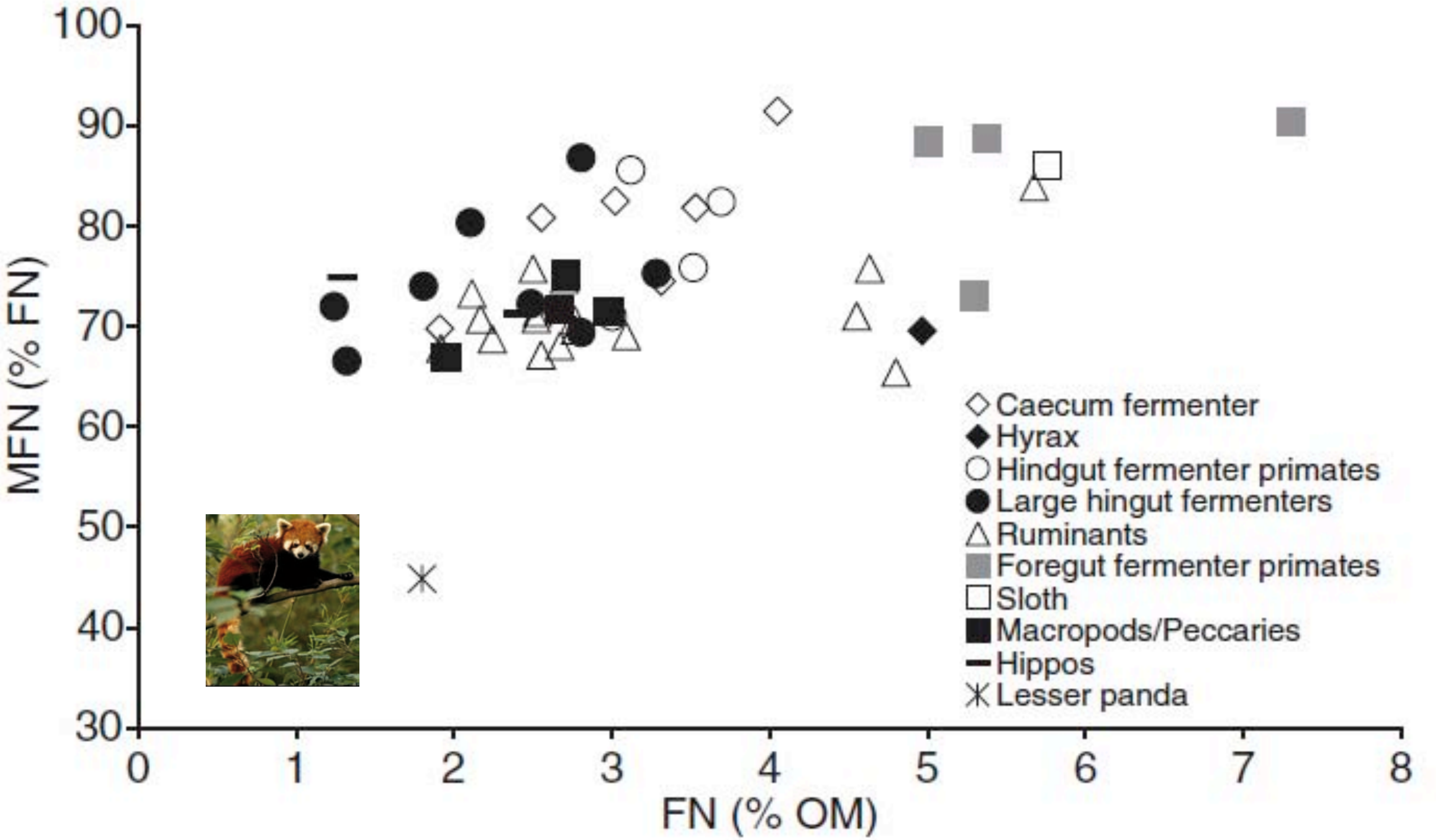

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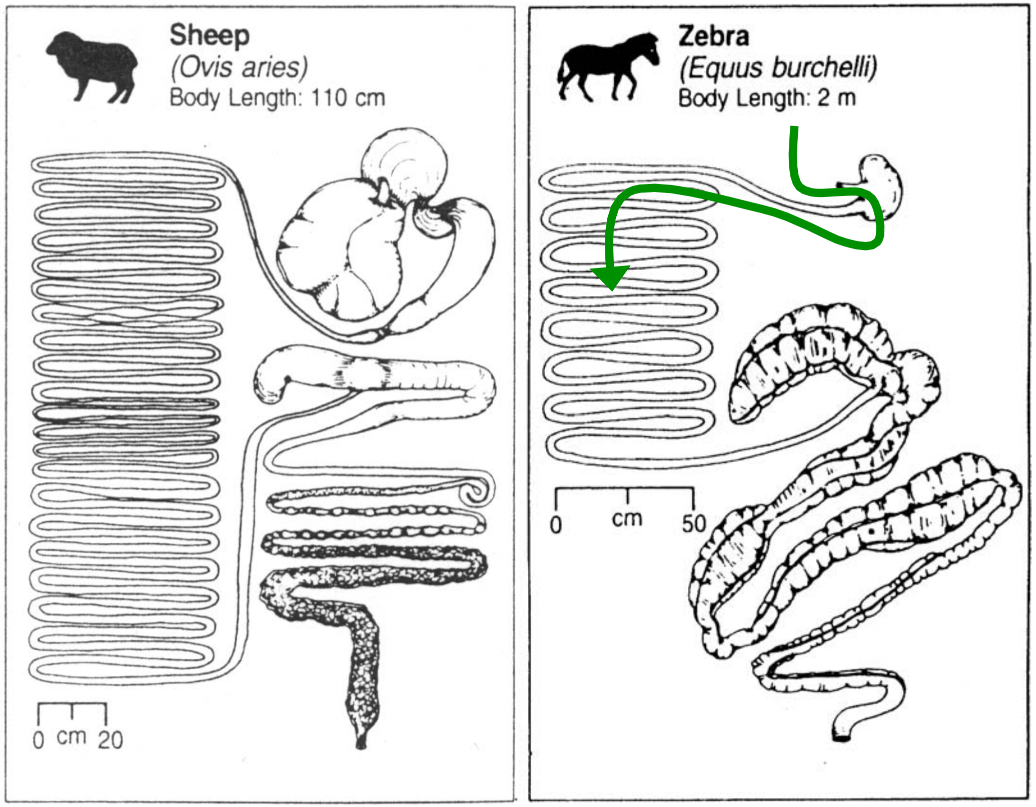
Foregut vs. Hindgut Fermentation

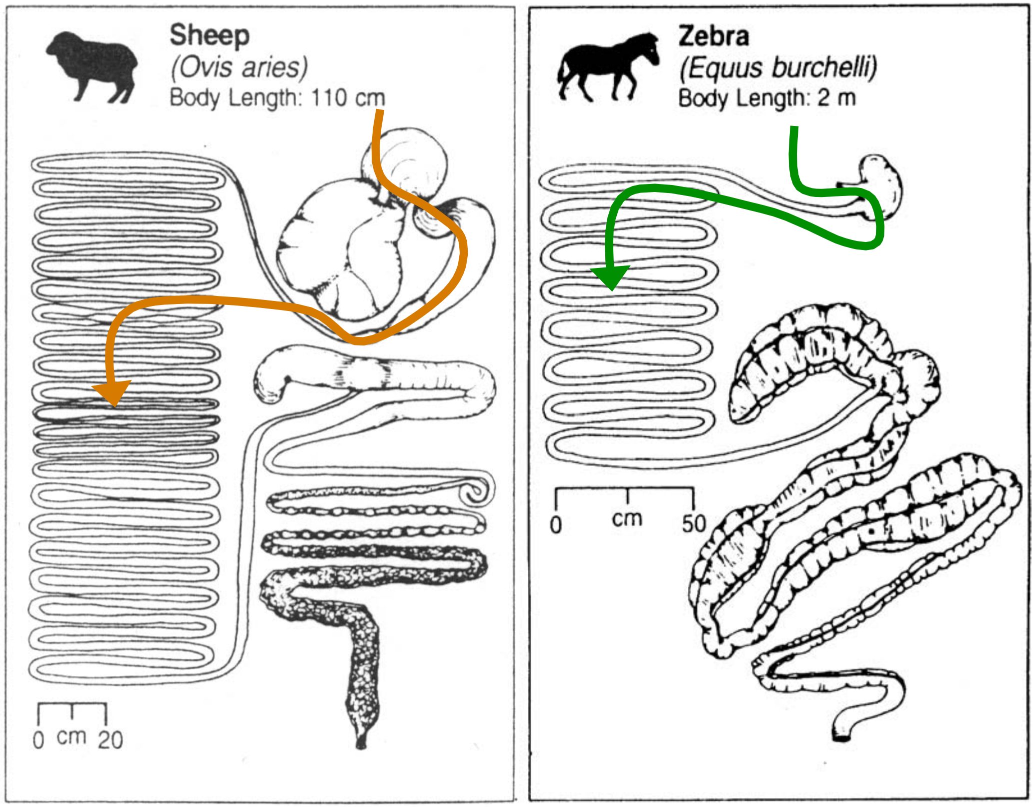


Ontogenetic diet shifts are no problem because all ingested material is always digested enzymatically first

from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation

Ontogenetic diet shifting: animal food must be directed past the foregut to prevent mal-fermentation!



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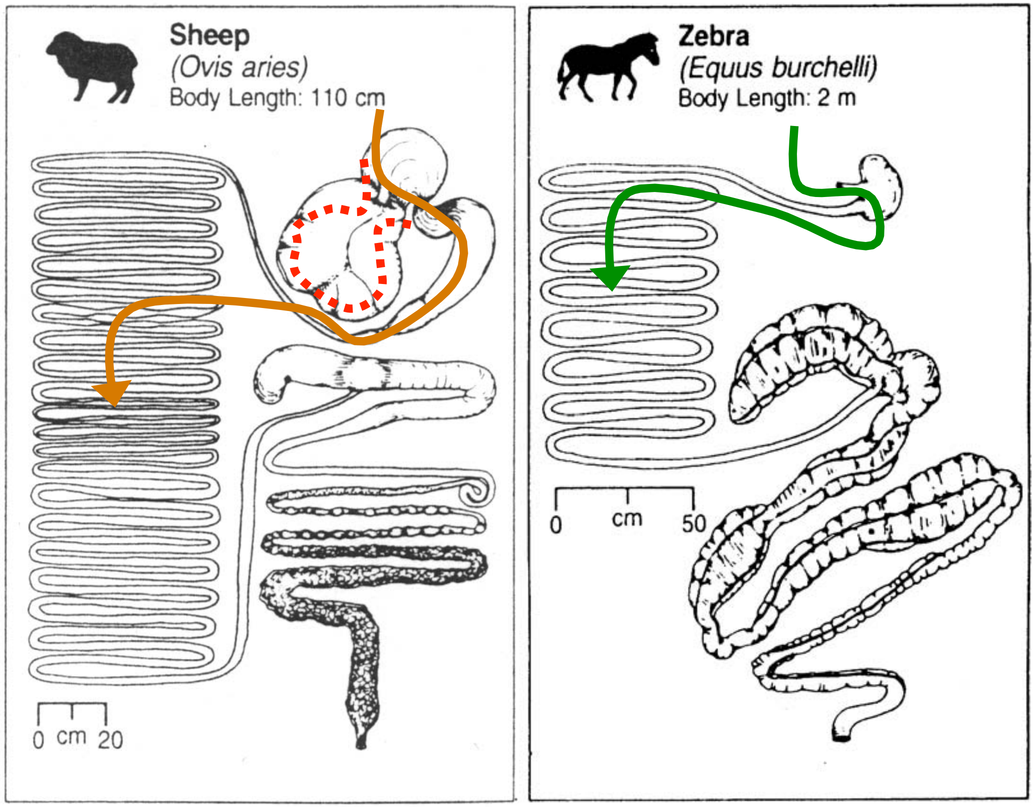

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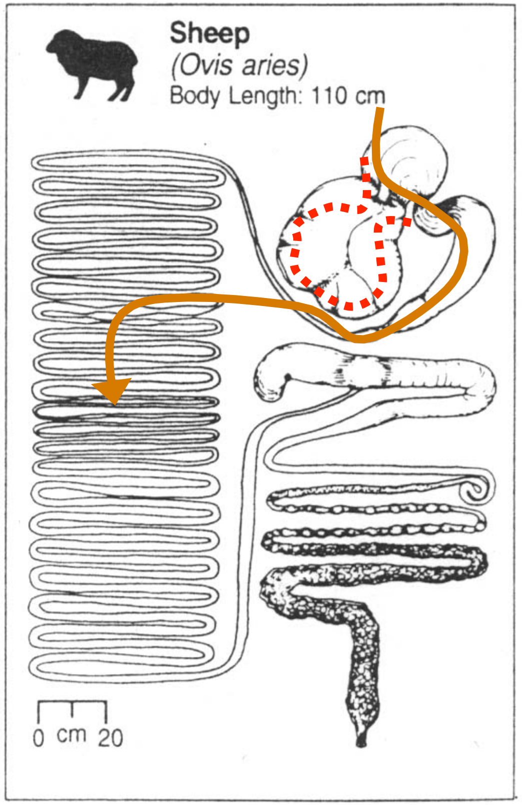
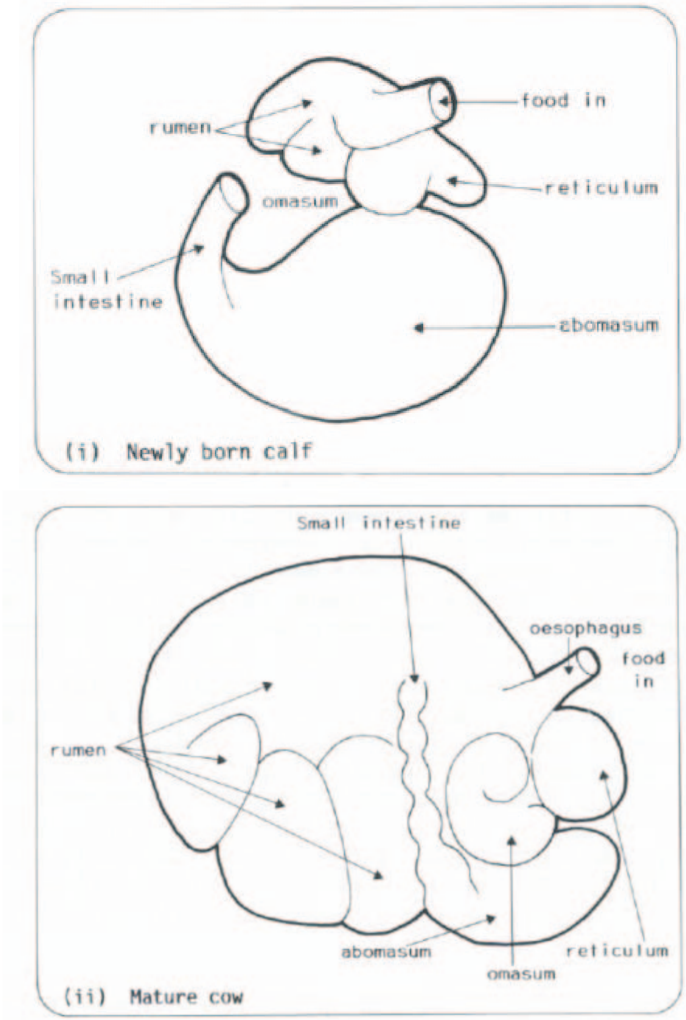
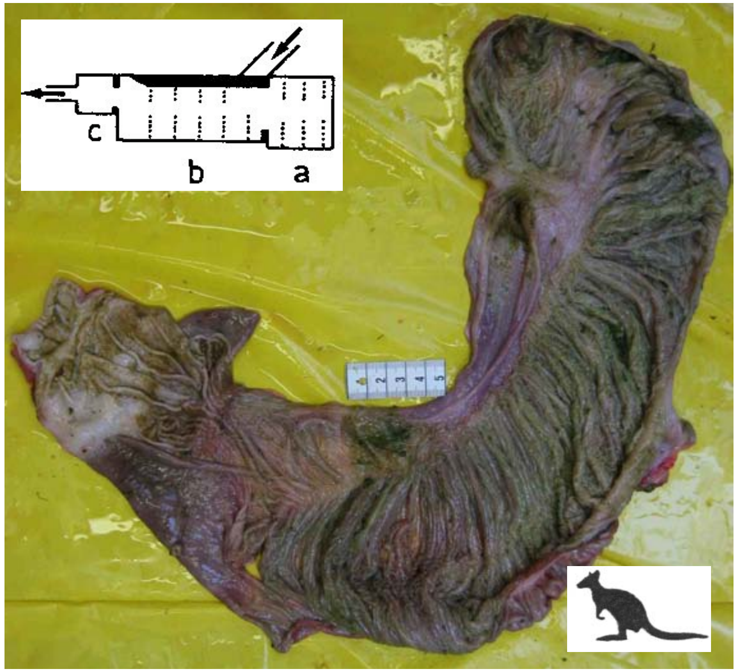
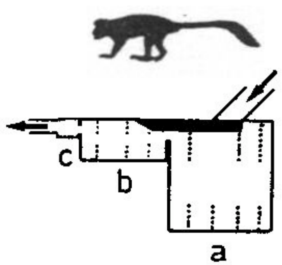


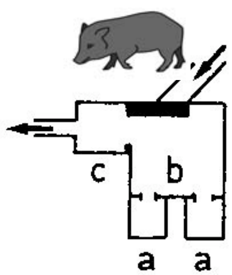


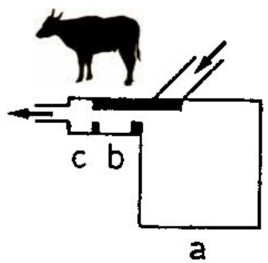
from Stevens & Hume (1995), Moss et al. (2003)

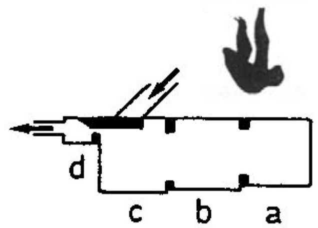
Bypass structures in foregut fermenters





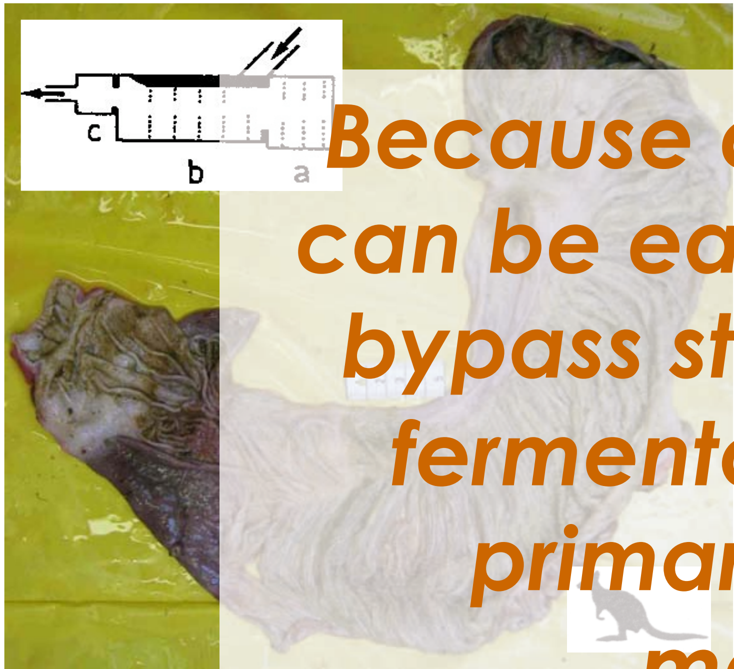




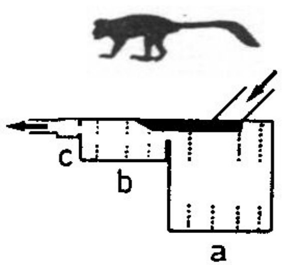


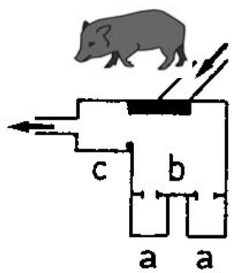
from Langer (1988)
Photos A. Schwarm

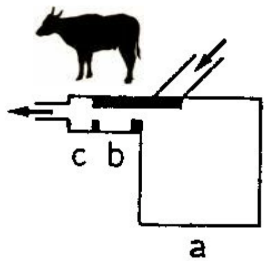
Bypass structures in foregut fermenters

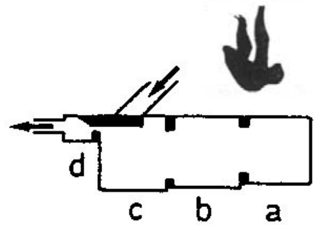


Because only a fluid food can be easily diverted in a bypass structure, foregut fermentation might be primarily limited to mammals.



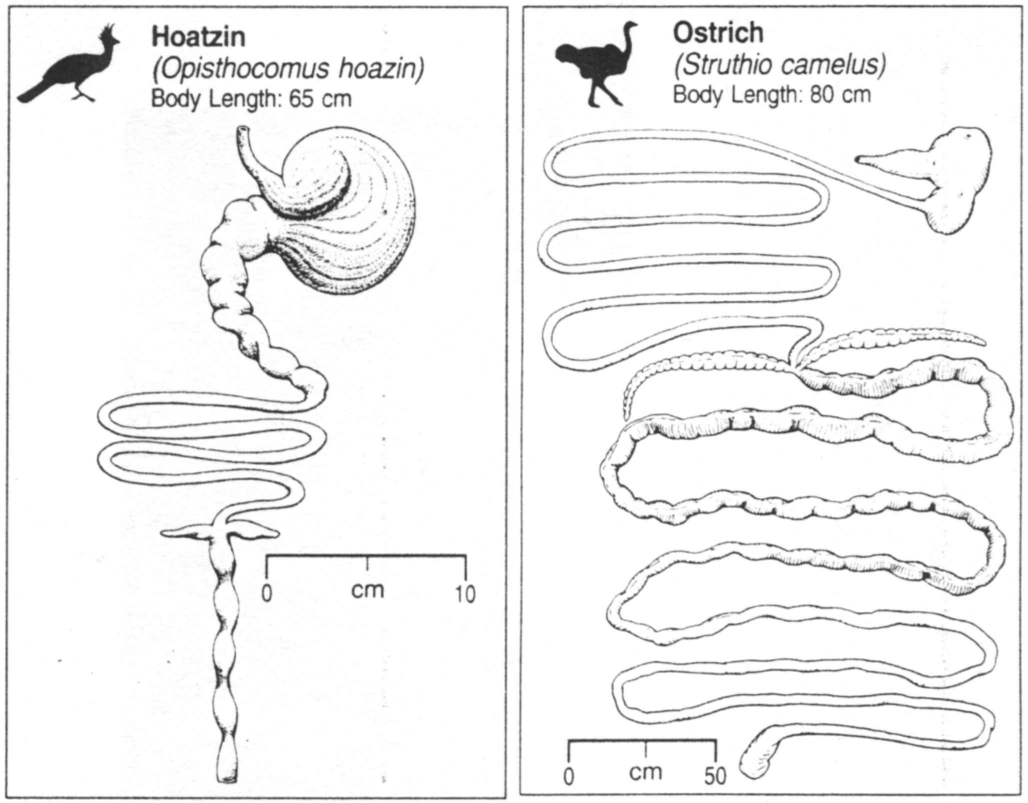






from Langer (1988)
Photos A. Schwarm

Foregut vs. Hindgut Fermentation



Foregut fermentation occurs in just one avian and no reptilian species.

from Stevens & Hume (1995)

Foregut fermentation = Ruminant digestion?

THE EVOLUTIONARY STRATEGY OF THE EQUIDAE AND THE ORIGINS OF RUMEN AND CECAL DIGESTION

CHRISTINE JANIS

EVOLUTION 30:757–774. December 1976

I will use "ruminant" to designate any animal that ferments cellulose in its forestomach.

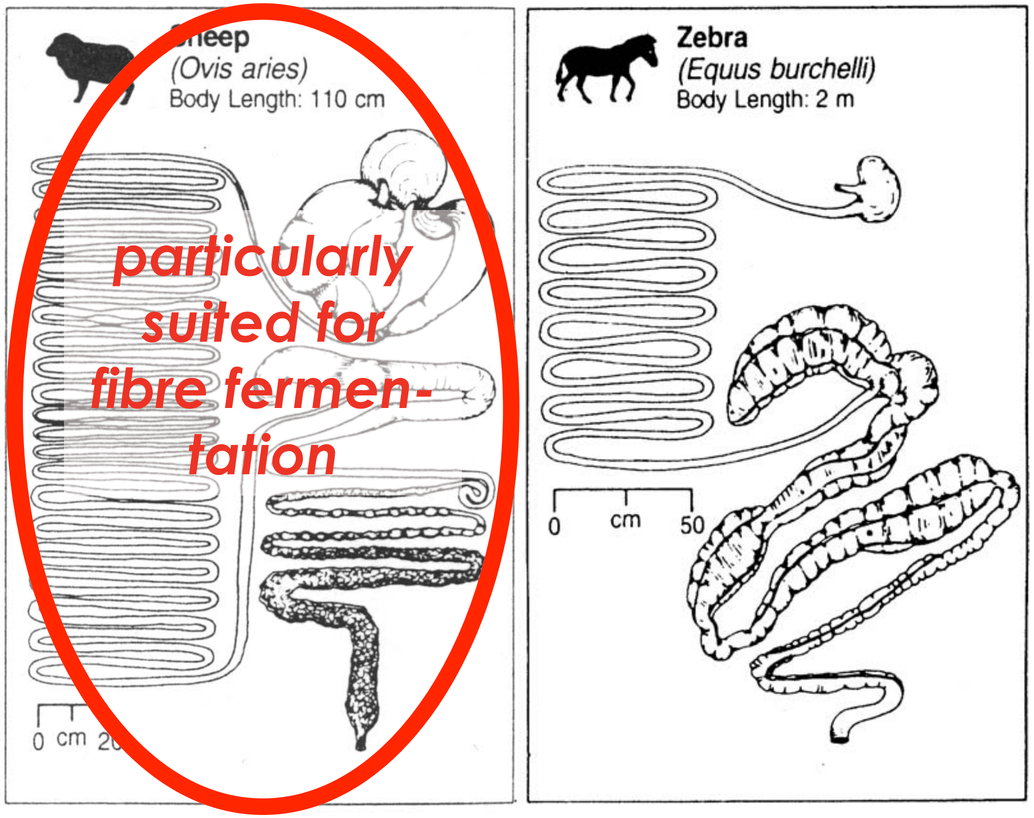
Foregut vs. Hindgut Fermentation

Fermentation prior to enzymatic digestion and absorption:

Use of bacterial protein, bacterial products (B-Vitamins)

Bacterial detoxification?

'Loss' of easily digestible substrates



Fermentation after enzymatic digestion and absorption:

'Loss' of bacterial protein, bacterial products (B-Vitamins?)

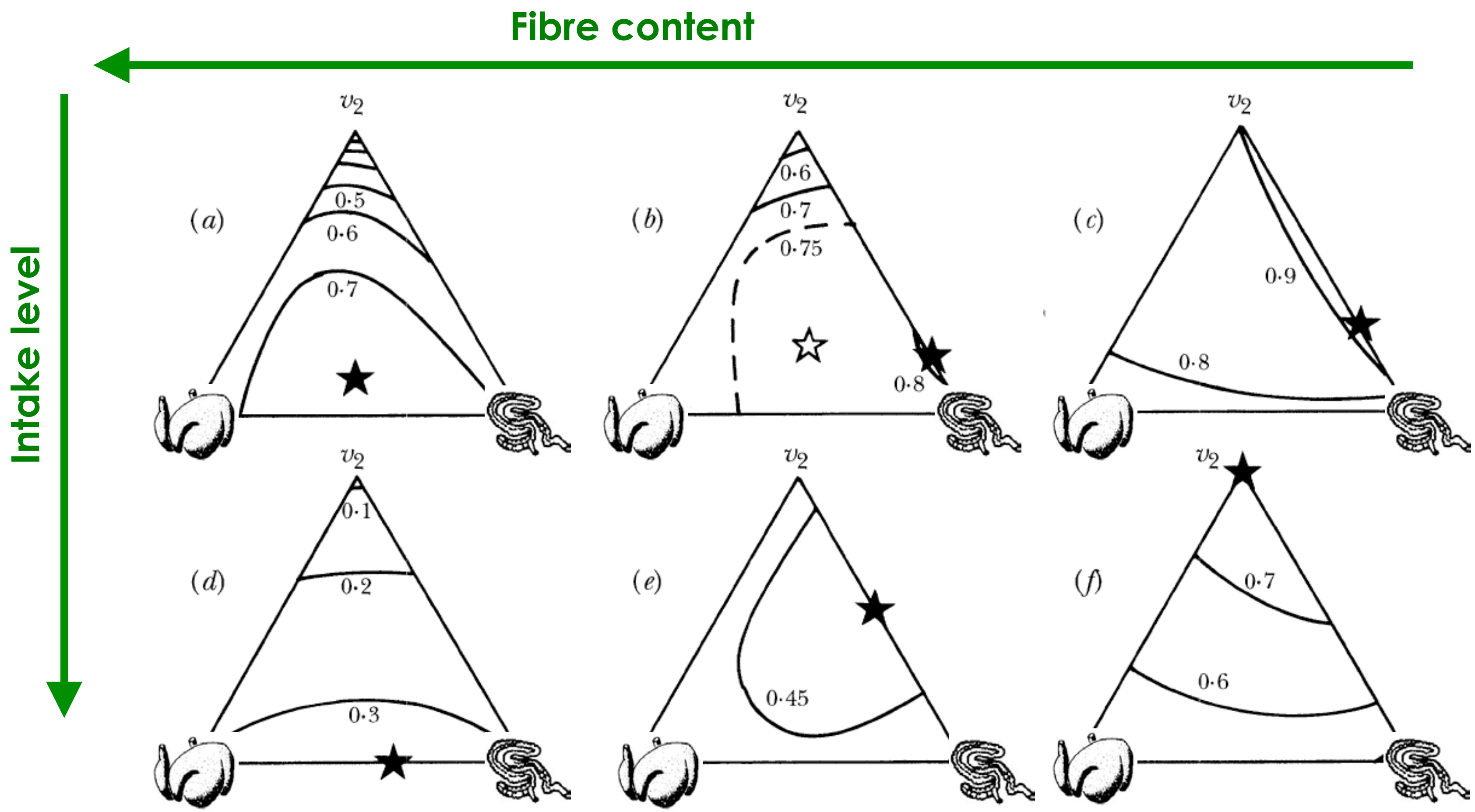
(coprophagy)

Use of easily digestible substrates

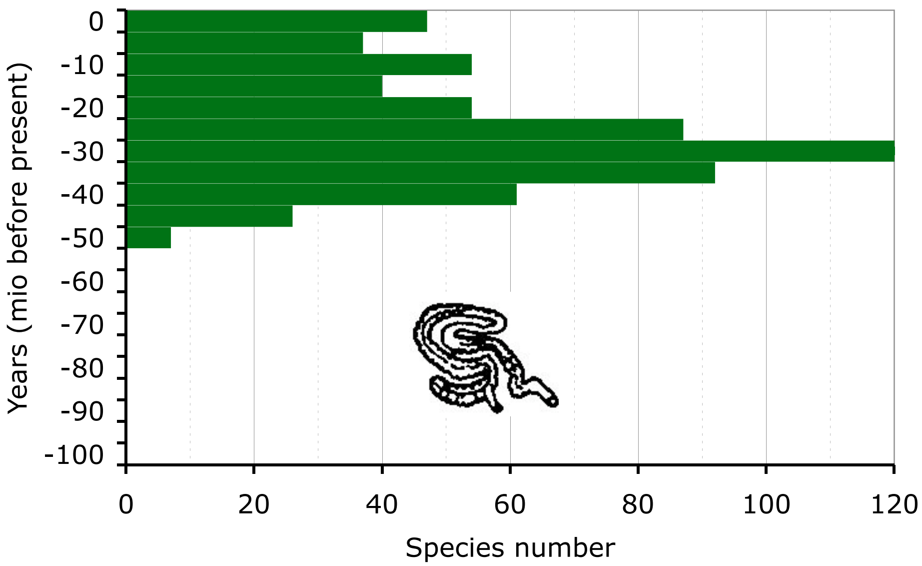
from Stevens und Hume (1995)

Optimization of gut structure and diet for higher vertebrate herbivores

R. McN. ALEXANDER
Phil. Trans. R. Soc. Lond. B (1991) **333**, 249–255

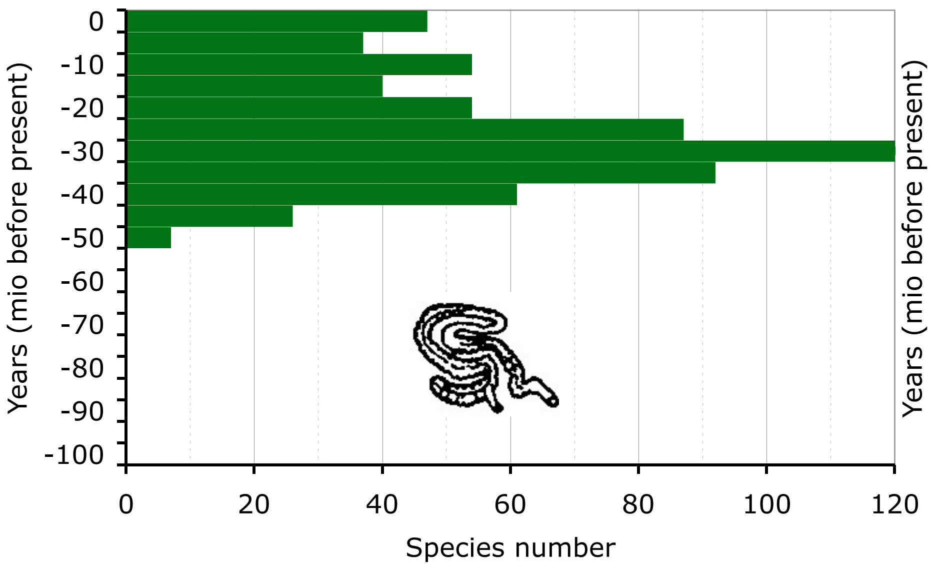


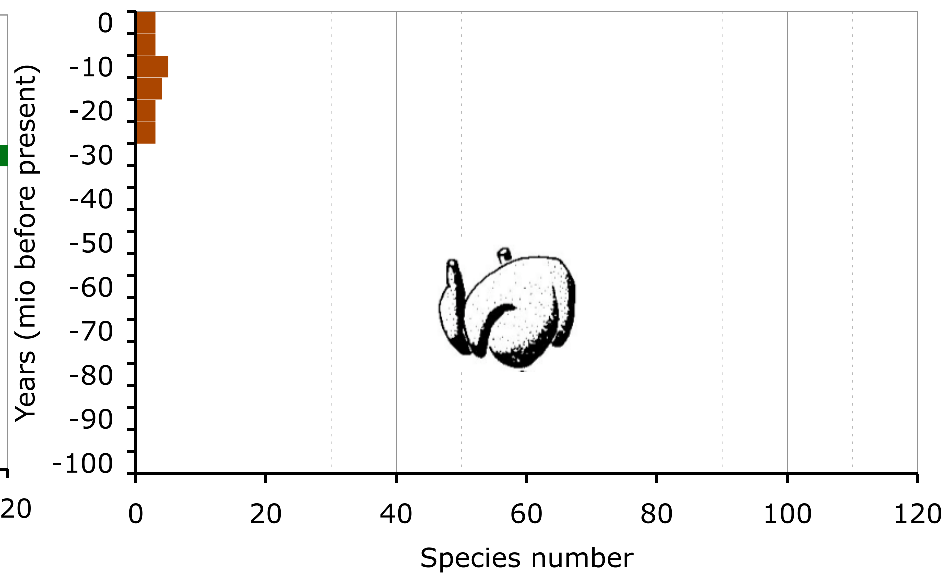
European Mammal Herbivores in Deep Time



from Langer (1991)

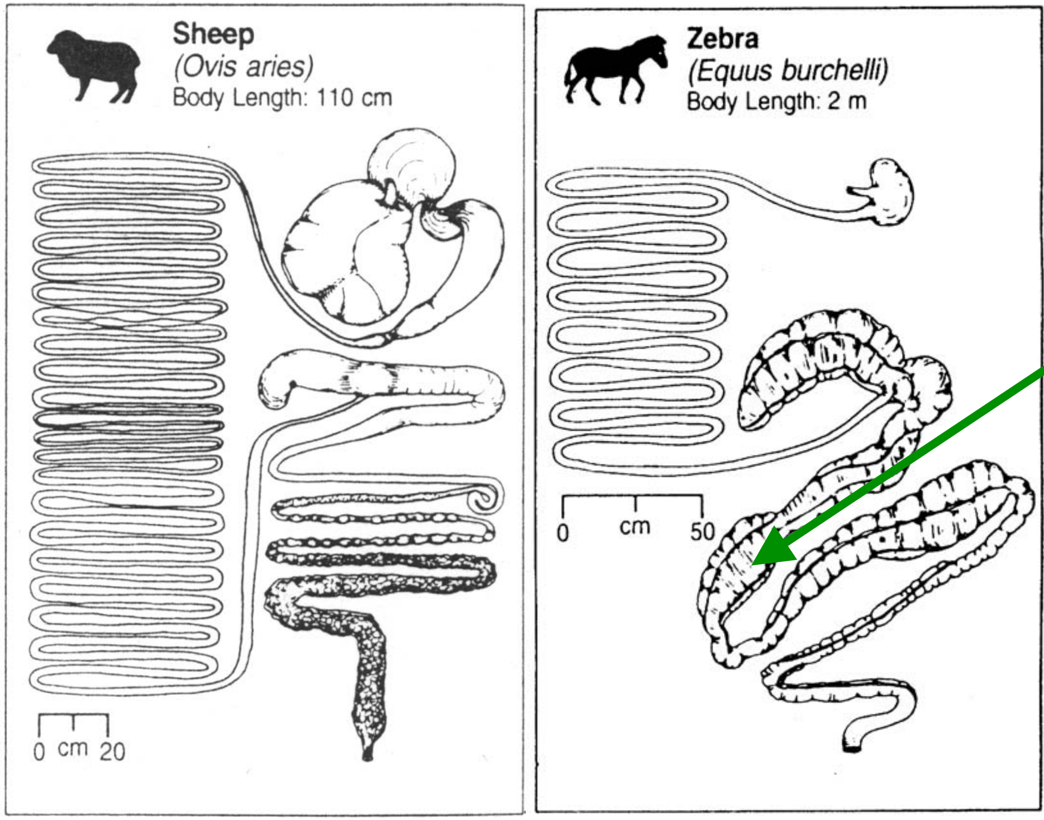
European Mammal Herbivores in Deep Time





from Langer (1991)

Foregut vs. Hindgut Fermentation



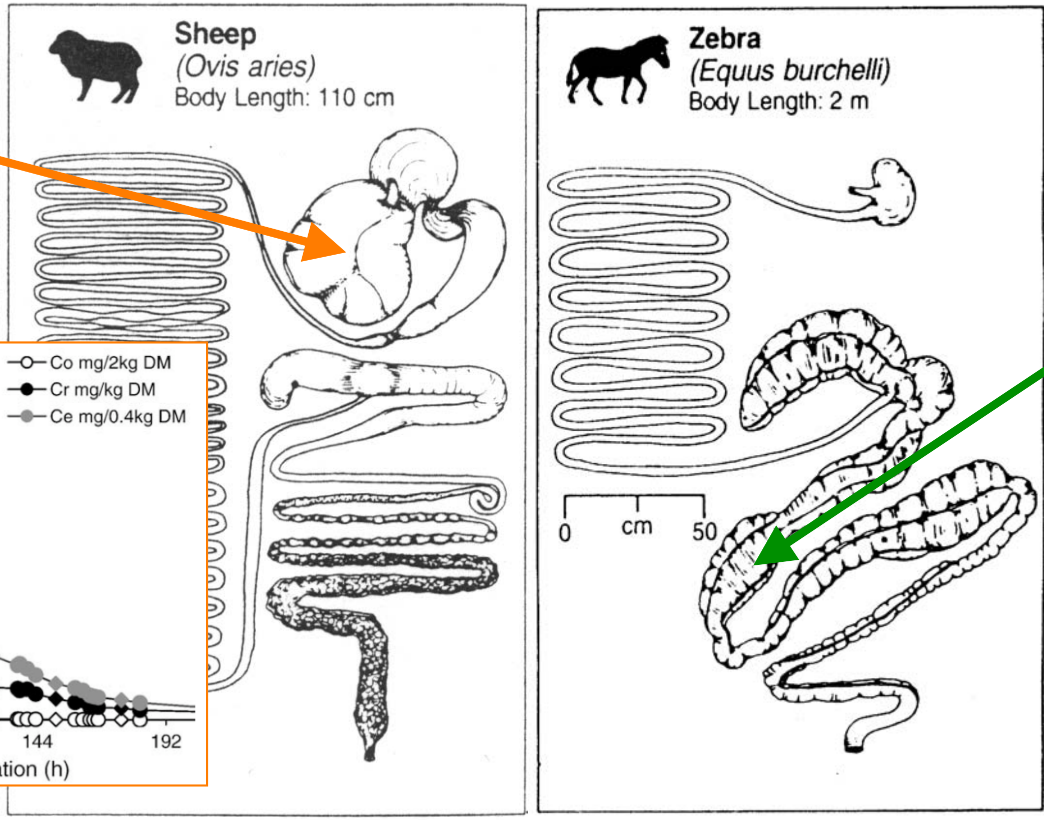
No selective particle retention!

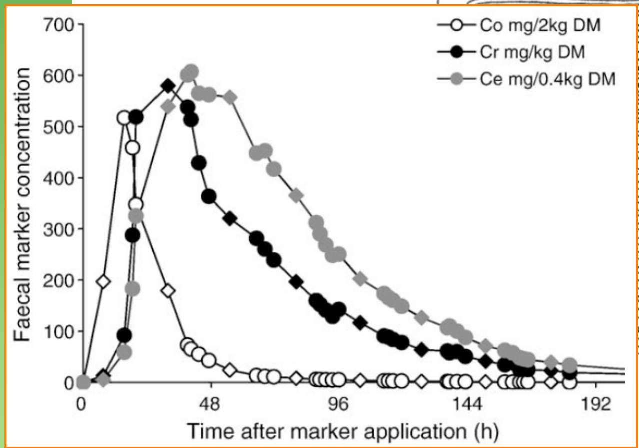
"no intake limitation"

from Stevens und Hume (1995)

Foregut vs. Hindgut Fermentation

Selective retention of large particles!



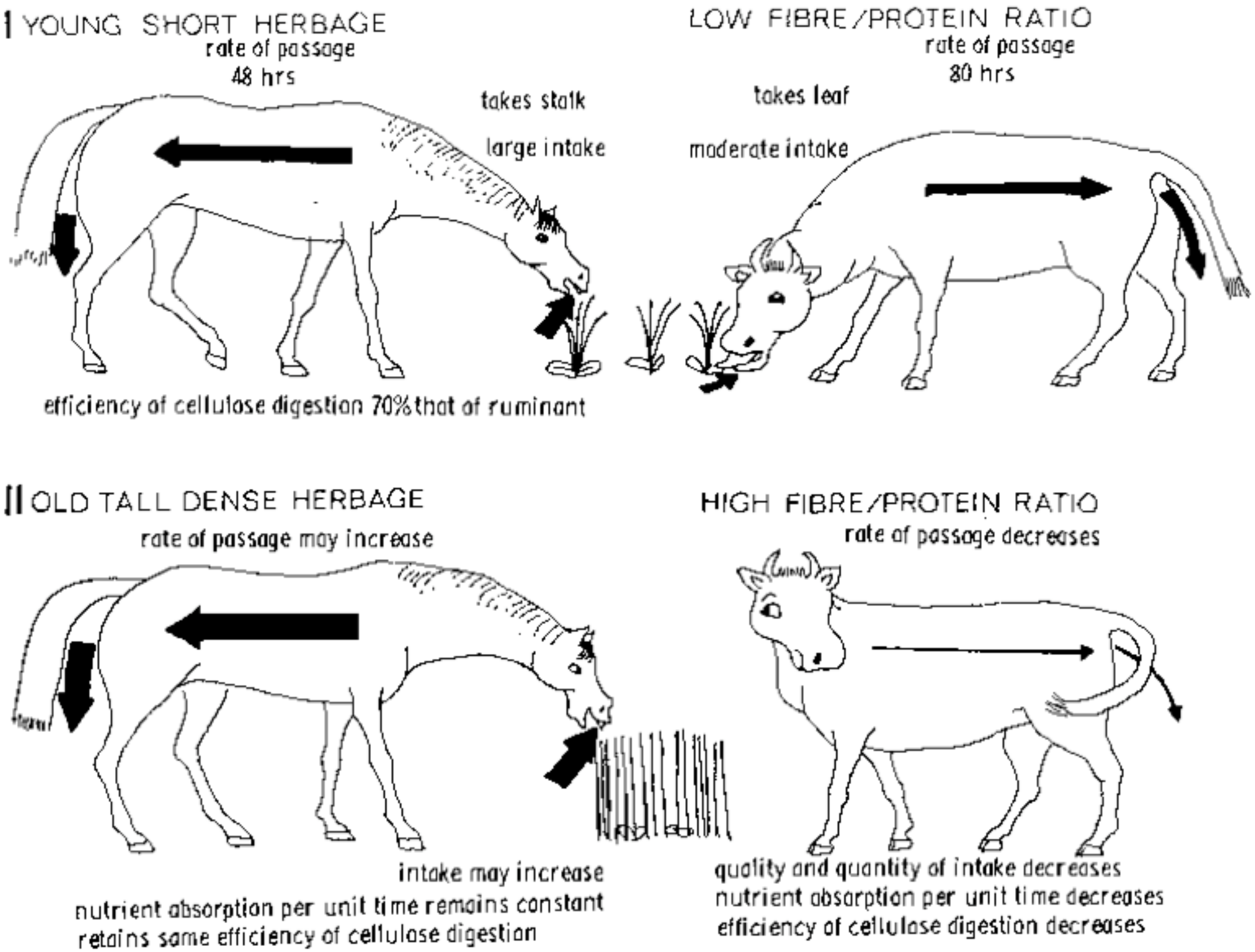


No selective particle retention!

"distinct intake limitation" ***"no intake limitation"***

from Stevens und Hume (1995); Schwarm et al. (2008)

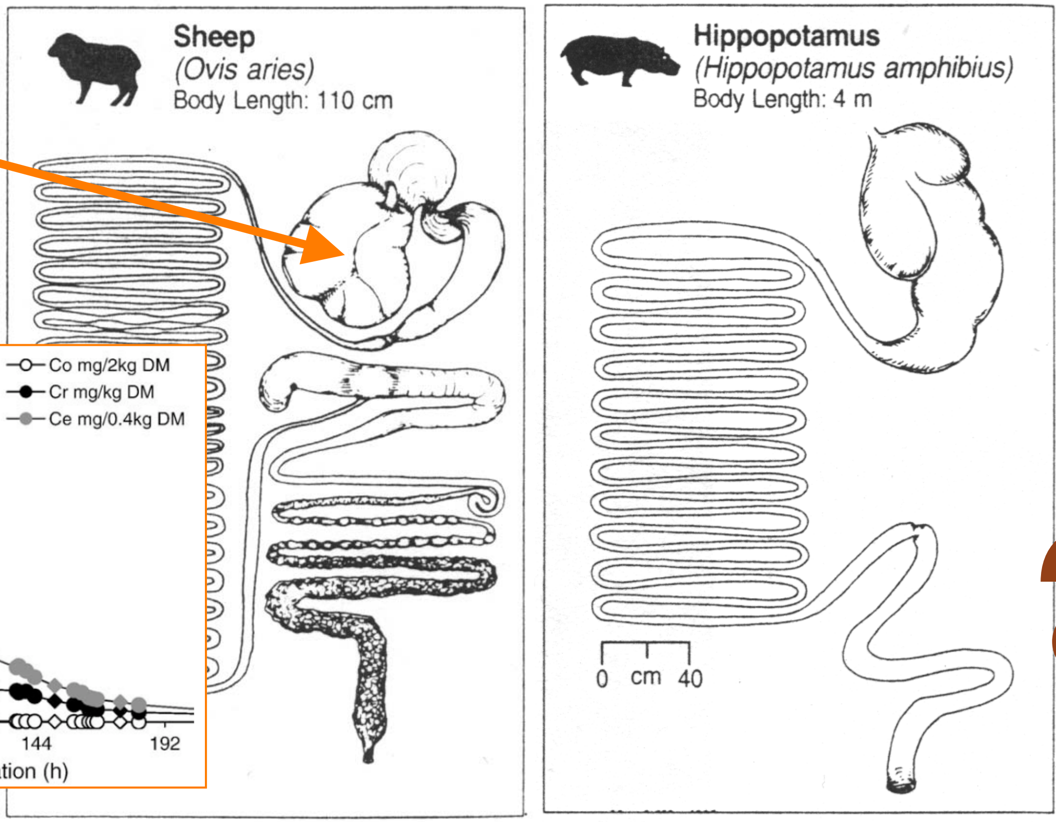
Foregut vs. Hindgut Fermentation



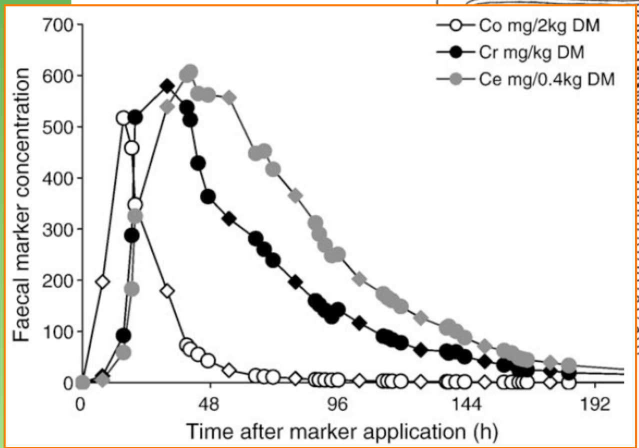
from Janis (1976)

Ruminant vs. Nonruminant Foregut Fermentation

Selective retention of large particles!



?



"distinct intake limitation"

from Stevens und Hume (1995); Schwarm et al. (2008)

Ruminant vs. Nonruminant Foregut Fermentation

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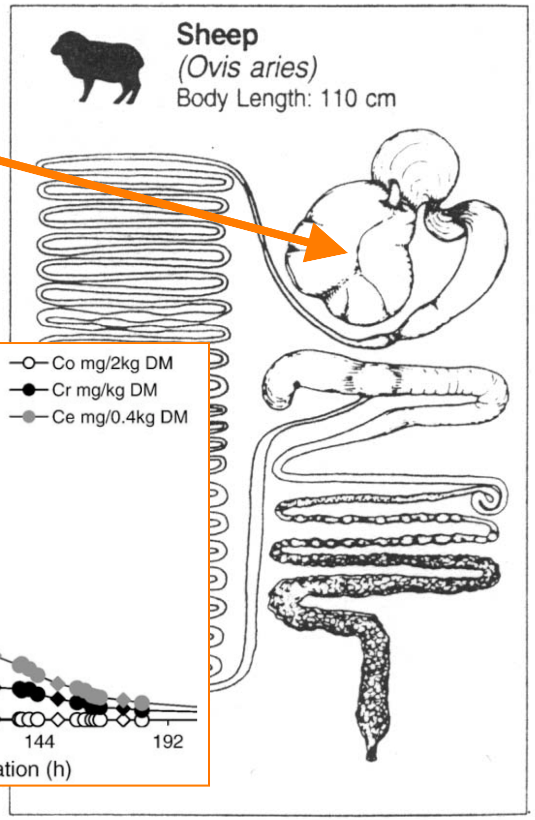
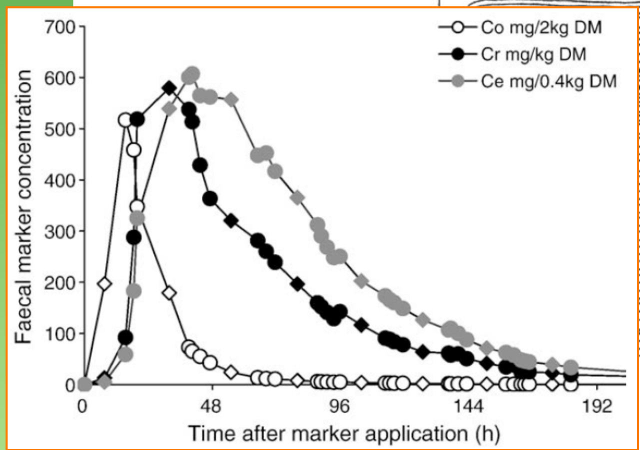
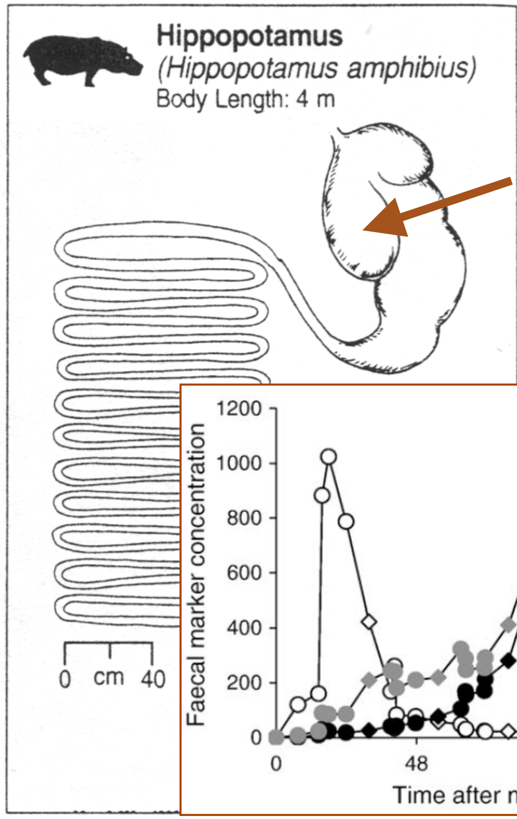
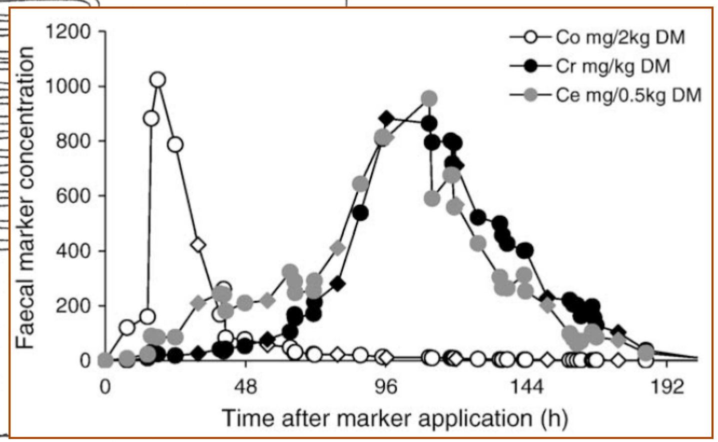






No selective retention of large particles!



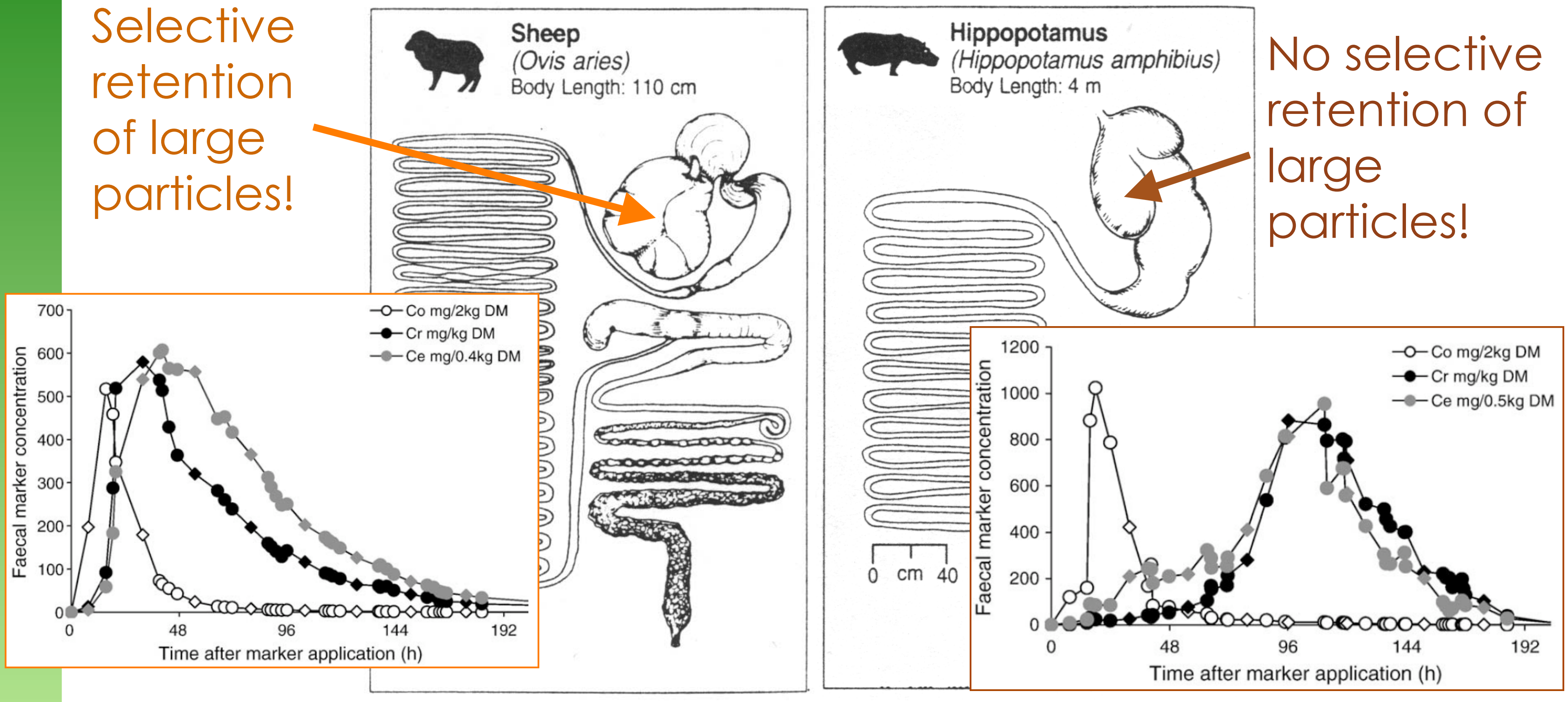
"distinct intake limitation"

from Stevens und Hume (1995);
Schwarm et al. (2008)

Ruminant vs. Nonruminant Foregut Fermentation

Selective retention of large particles!

No selective retention of large particles!



"distinct intake limitation"

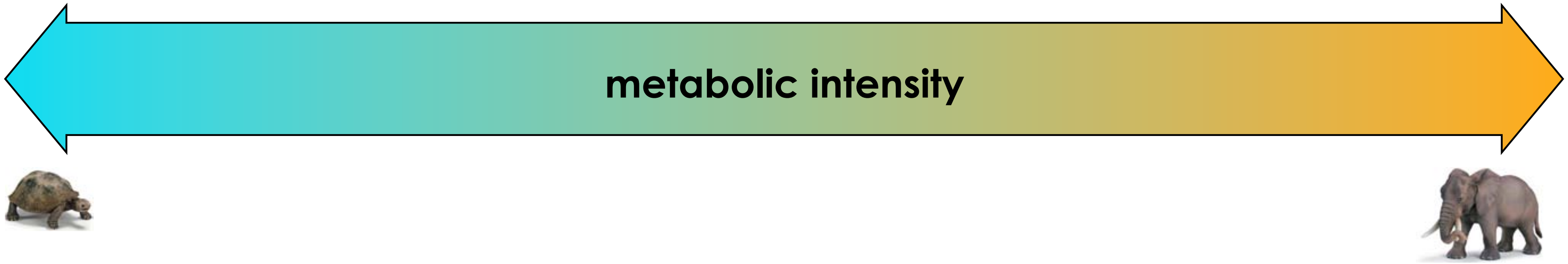
"no intake limitation"

... but ...

from Stevens und Hume (1995);
Schwarm et al. (2008)

Conceptualizing herbivore diversity

Conceptualizing herbivore diversity



Conceptualizing herbivore diversity

metabolic intensity

To achieve a high metabolic intensity, you need

Conceptualizing herbivore diversity

To achieve a high metabolic intensity, you need

- *a high food intake*

Conceptualizing herbivore diversity

To achieve a high metabolic intensity, you need

- ***a high food intake***

- ***a high digestive efficiency***

Conceptualizing herbivore diversity

metabolic intensity

To achieve a high metabolic intensity, you need

- ***a high food intake***

- ***a high digestive efficiency***
  - ***long retention times***
  - ***intensive particle size reduction***
  - ***(high feeding selectivity)***

Conceptualizing herbivore diversity

metabolic intensity

To achieve a high metabolic intensity, you need

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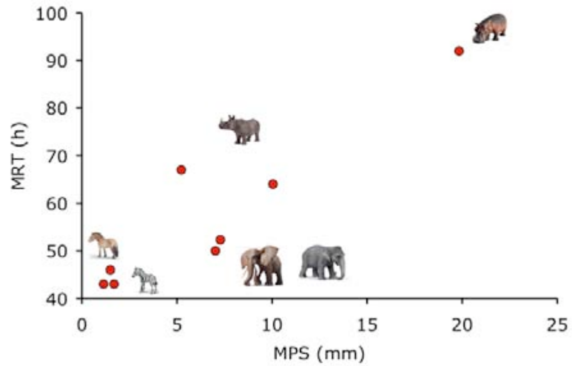
?

Conceptualizing herbivore diversity

metabolic intensity

To achieve a high metabolic intensity, you need



- ***a high food intake***

- ***a high digestive efficiency***
  - ***long retention times***
  - ***intensive particle size reduction***
  - ***(high feeding selectivity)***

from Clauss et al. (2009; data from Foose 1982)

Conceptualizing herbivore diversity

metabolic intensity

To achieve a high metabolic intensity, you need

- ***a high food intake***

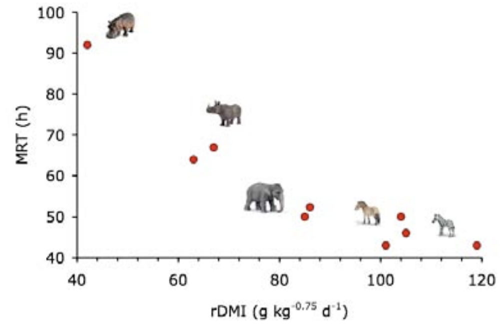
?

- ***a high digestive efficiency***
  - ***long retention times***
  - ***intensive particle size reduction***
  - ***(high feeding selectivity)***

Conceptualizing herbivore diversity

metabolic intensity

To achieve a high metabolic intensity, you need



- *a high food intake*

- *a high digestive efficiency*
  - *long retention times*
  - *intensive particle size reduction*
  - *(high feeding selectivity)*

Conceptualizing herbivore diversity

metabolic intensity

To achieve a high metabolic intensity, you need

- *a high food intake*

Compensation via gut capacity?

- *a high digestive efficiency*
  - *- long retention times*
  - *- intensive particle size reduction*
  - *- (high feeding selectivity)*

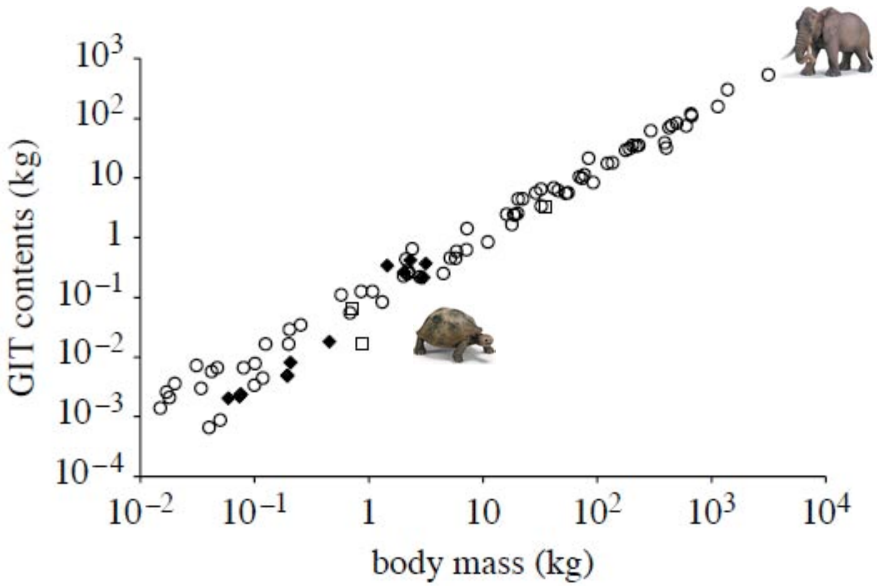
Conceptualizing herbivore diversity

metabolic intensity

Gut capacity is relatively constant across metabolic intensities

Conceptualizing herbivore diversity

Gut capacity is relatively constant across metabolic intensities

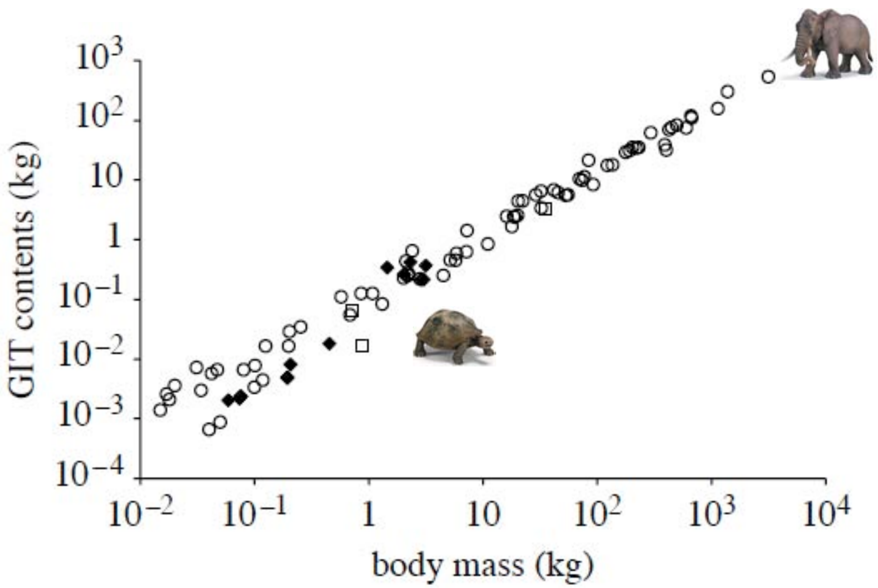


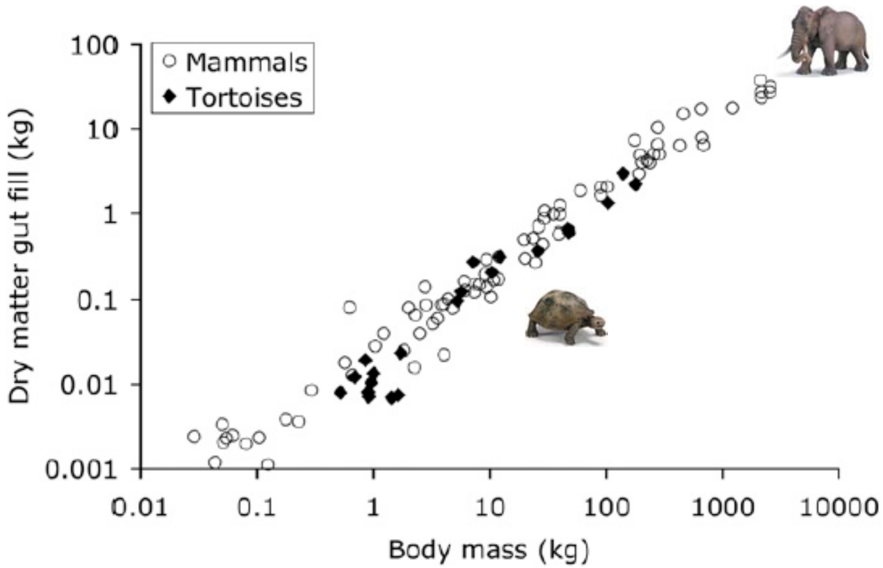
from Franz et al. (2009)

Conceptualizing herbivore diversity

metabolic intensity

Gut capacity is relatively constant across metabolic intensities



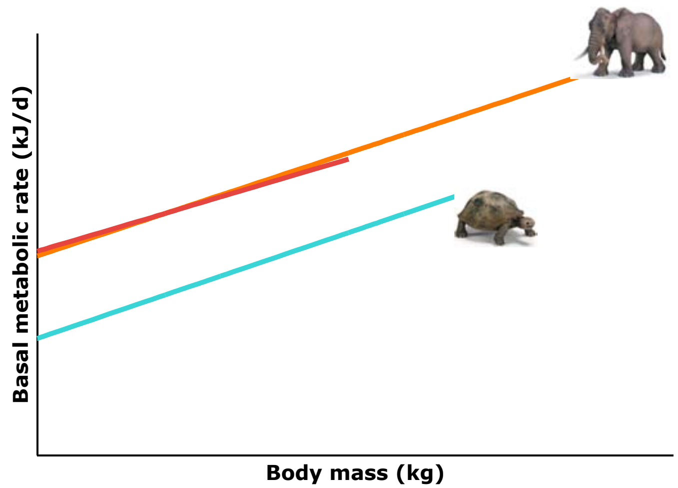


from Franz et al. (2009)

from Franz et al. (2011)

Conceptualizing herbivore diversity

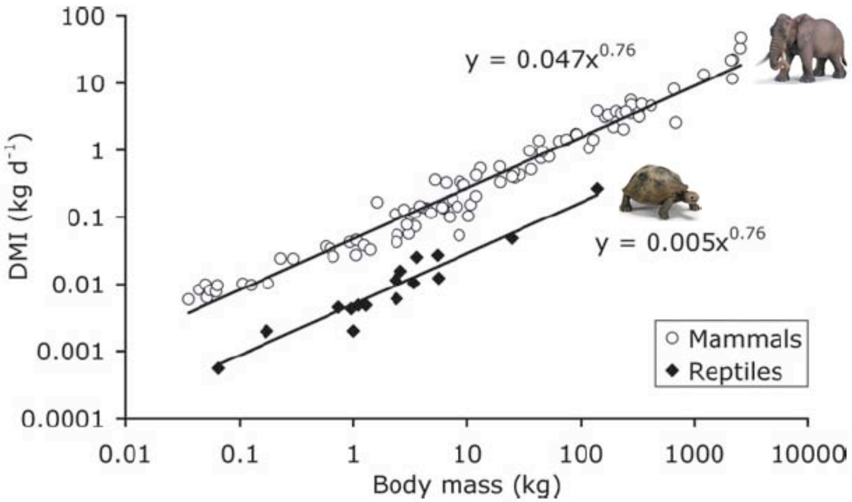
metabolic intensity

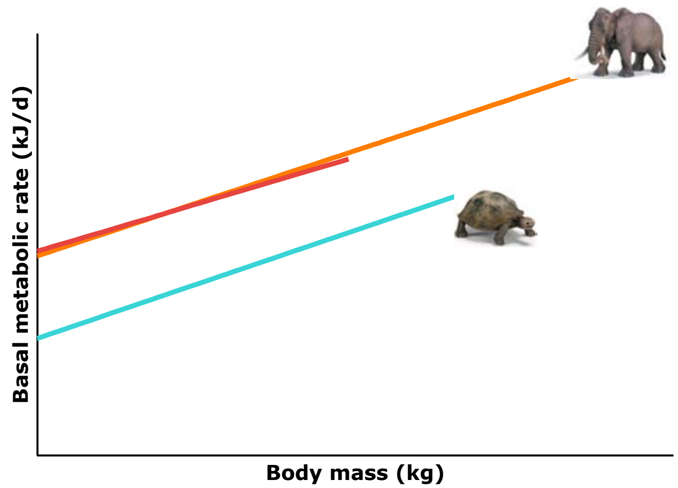


after Kirkwood (1996)

Conceptualizing herbivore diversity

metabolic intensity

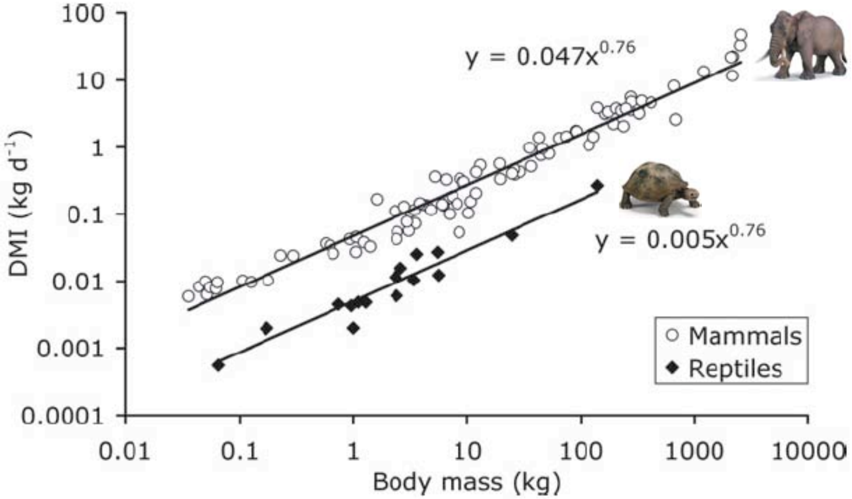




from Franz et al. (2011)

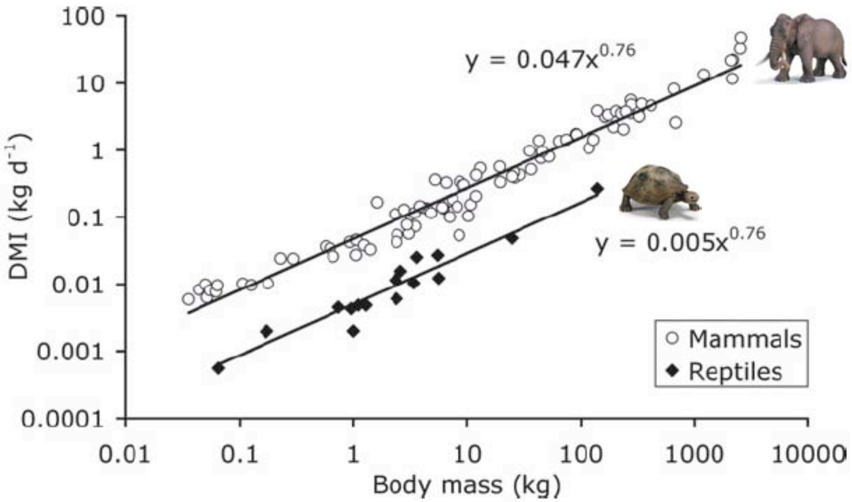
after Kirkwood (1996)

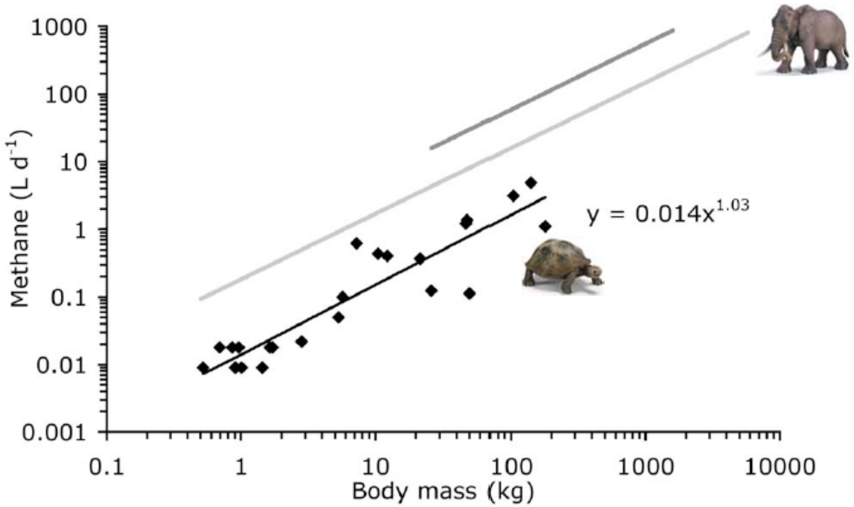
Conceptualizing herbivore diversity



from Franz et al. (2011)

Conceptualizing herbivore diversity



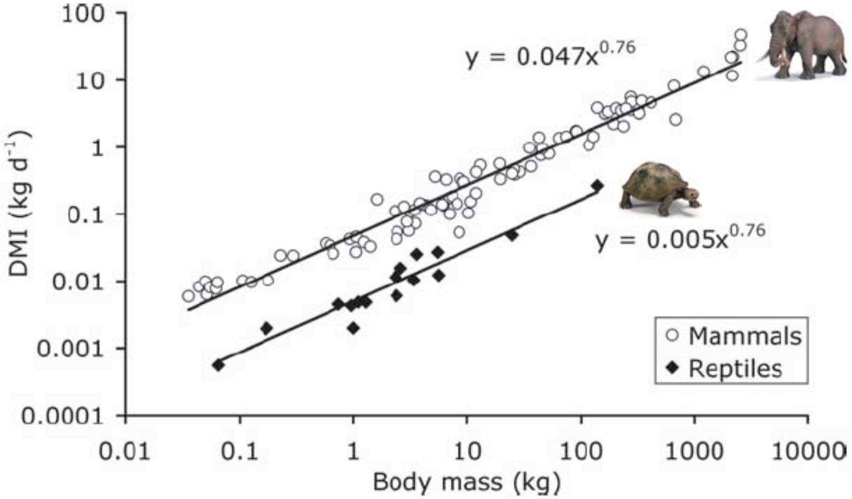


from Franz et al. (2011a)

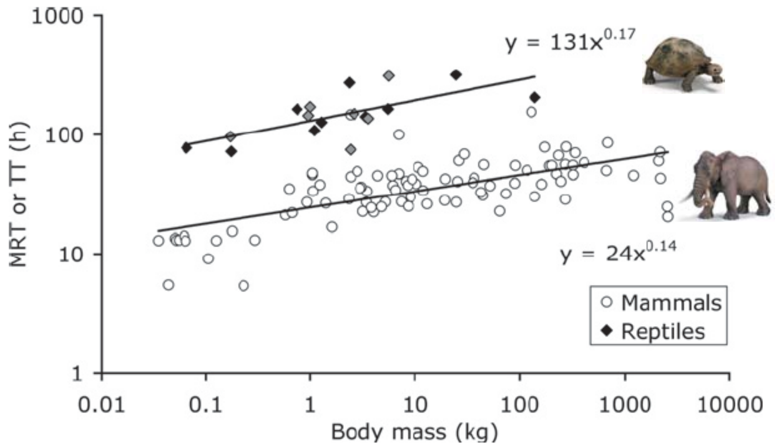
from Franz et al. (2011b)

Conceptualizing herbivore diversity

metabolic intensity

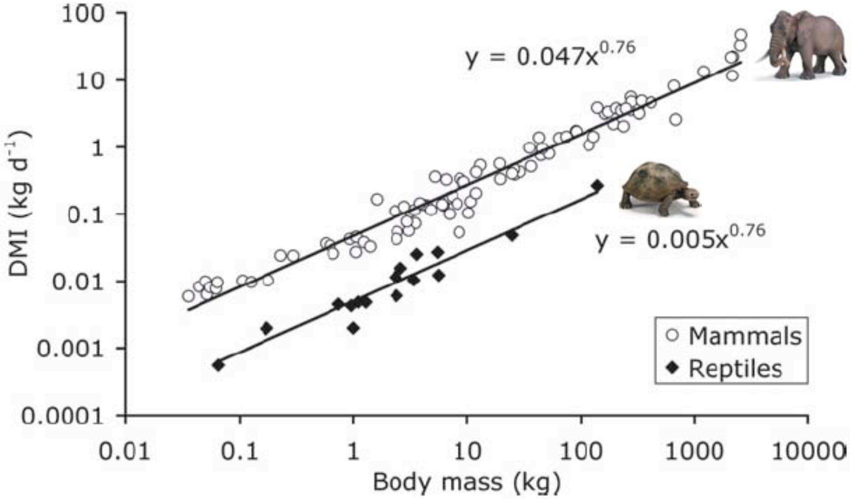


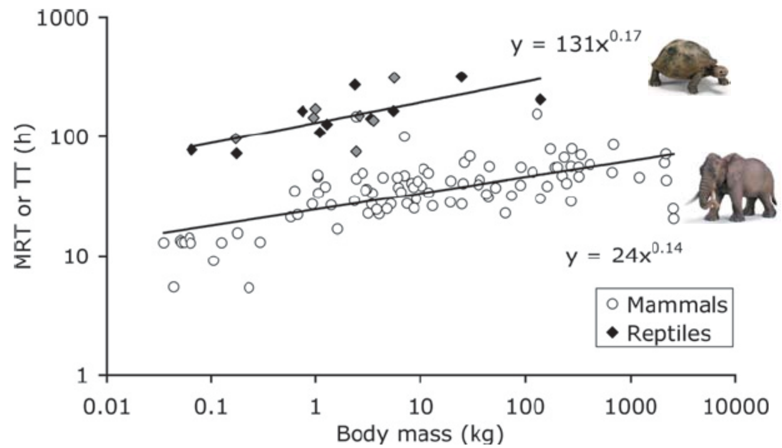
from Franz et al. (2011)

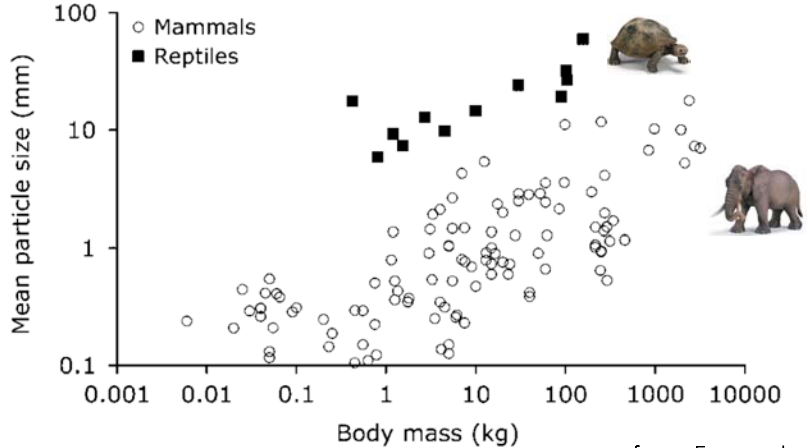


from Franz et al. (2011)

Conceptualizing herbivore diversity



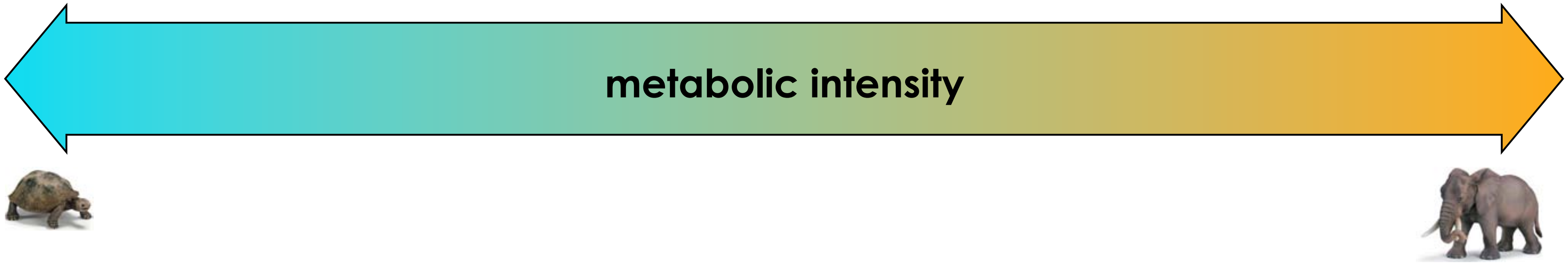




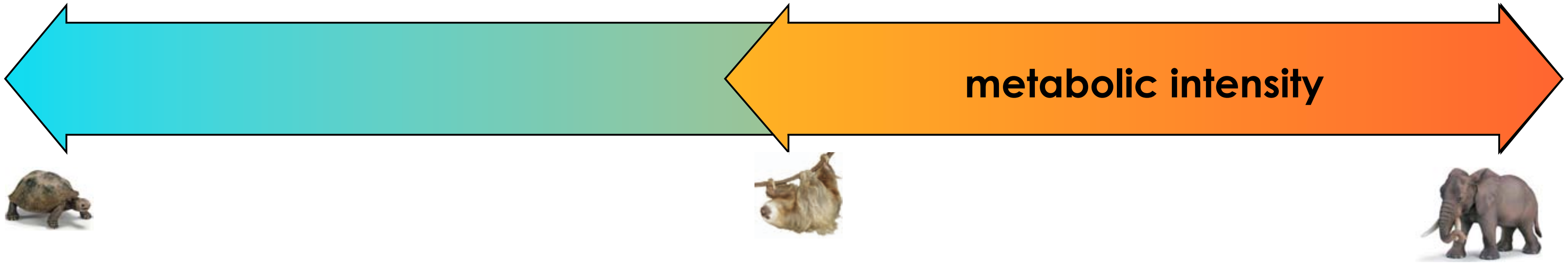
from Franz et al. (2011)

from Franz et al. (2011)
and Fritz et al. (2010)

Conceptualizing herbivore diversity

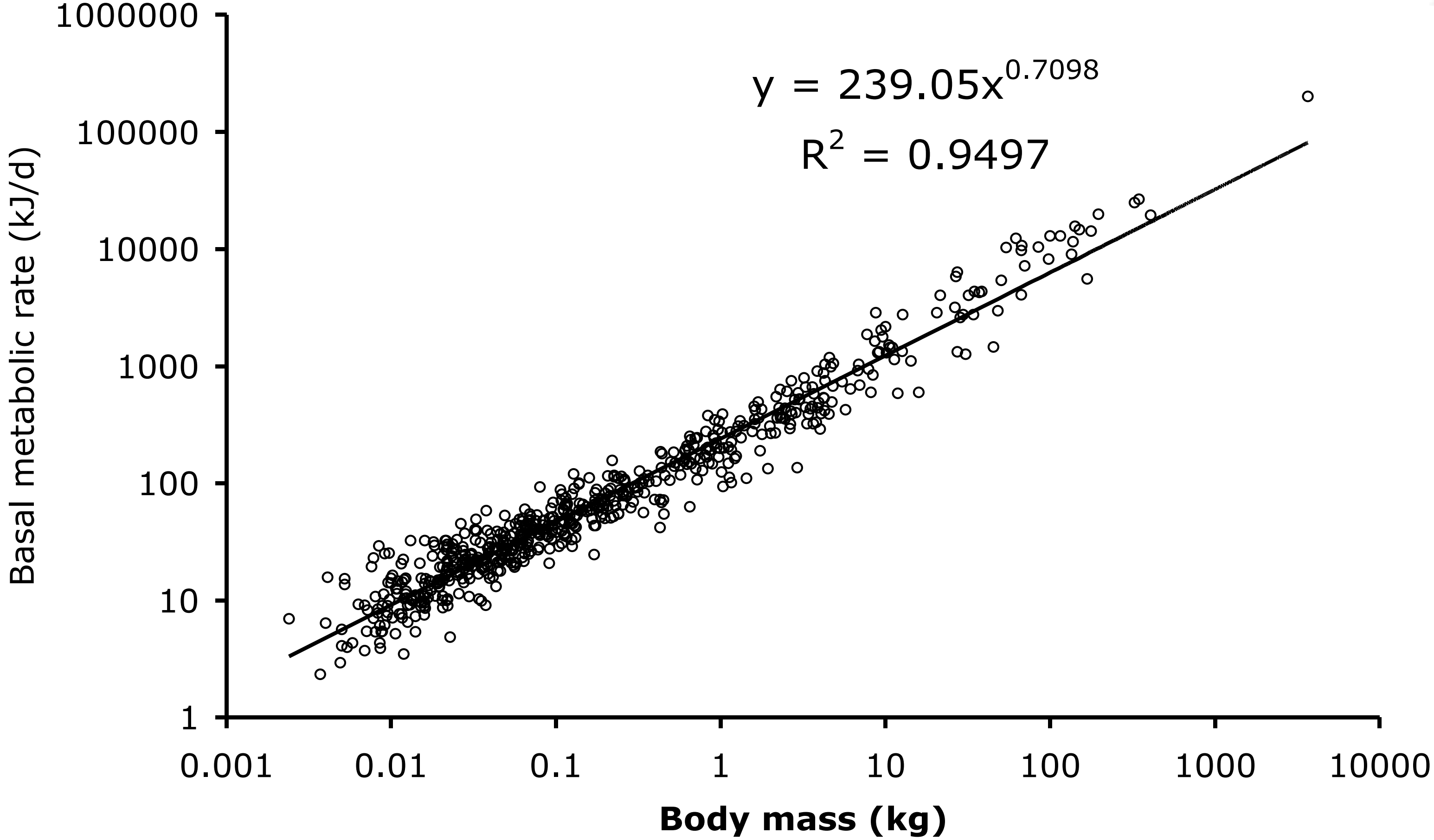


Conceptualizing herbivore diversity



Conceptualizing herbivore diversity

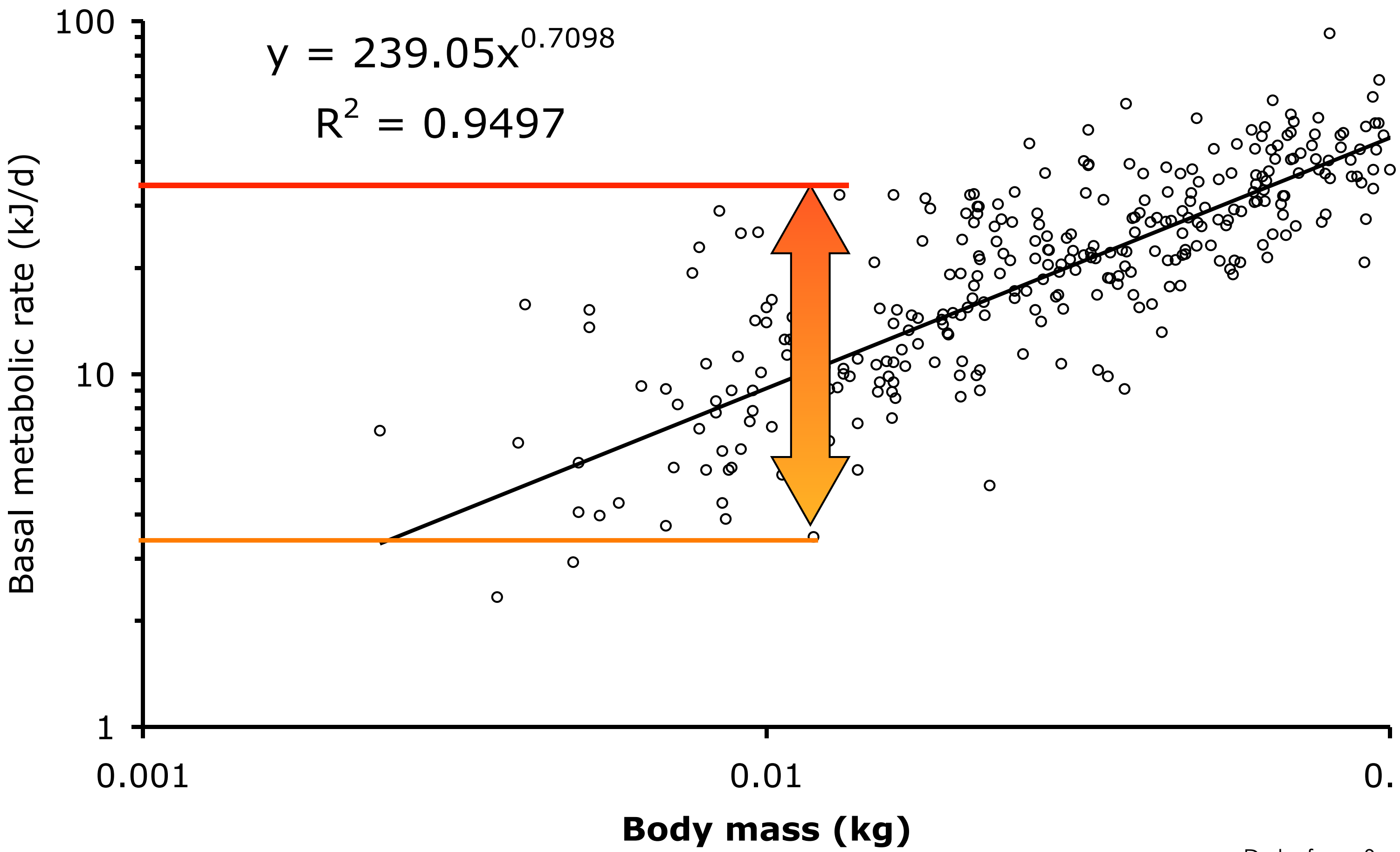
metabolic intensity



Data from Savage et al. (2004)

Conceptualizing herbivore diversity

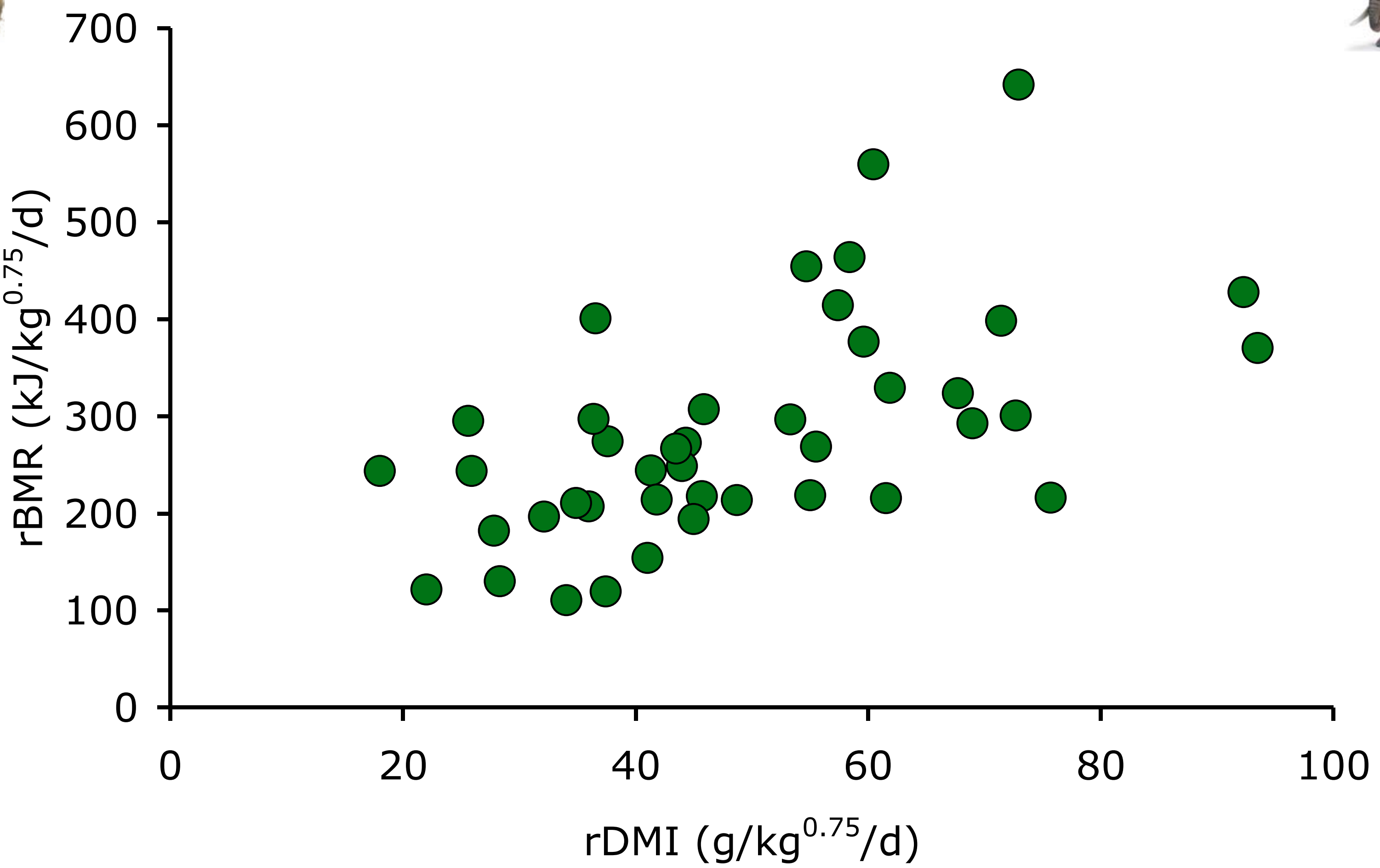
metabolic intensity



Data from Savage et al. (2004)

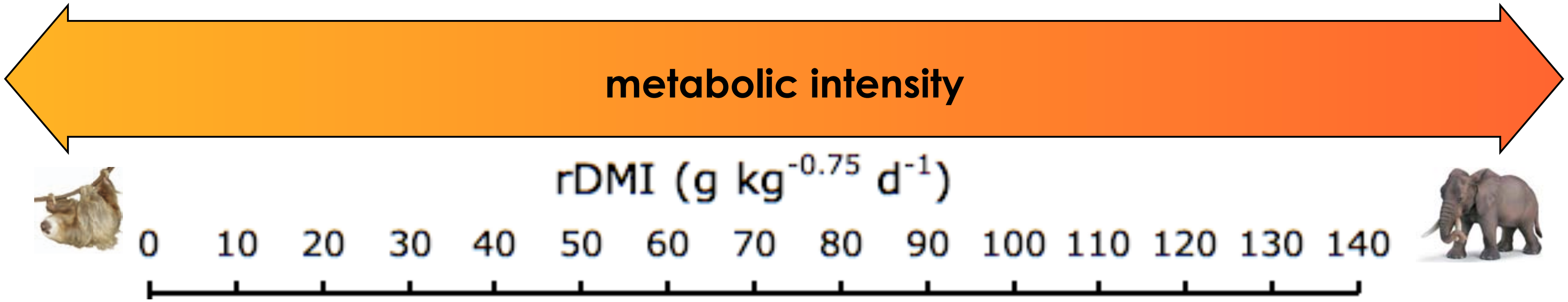
Conceptualizing herbivore diversity

metabolic intensity



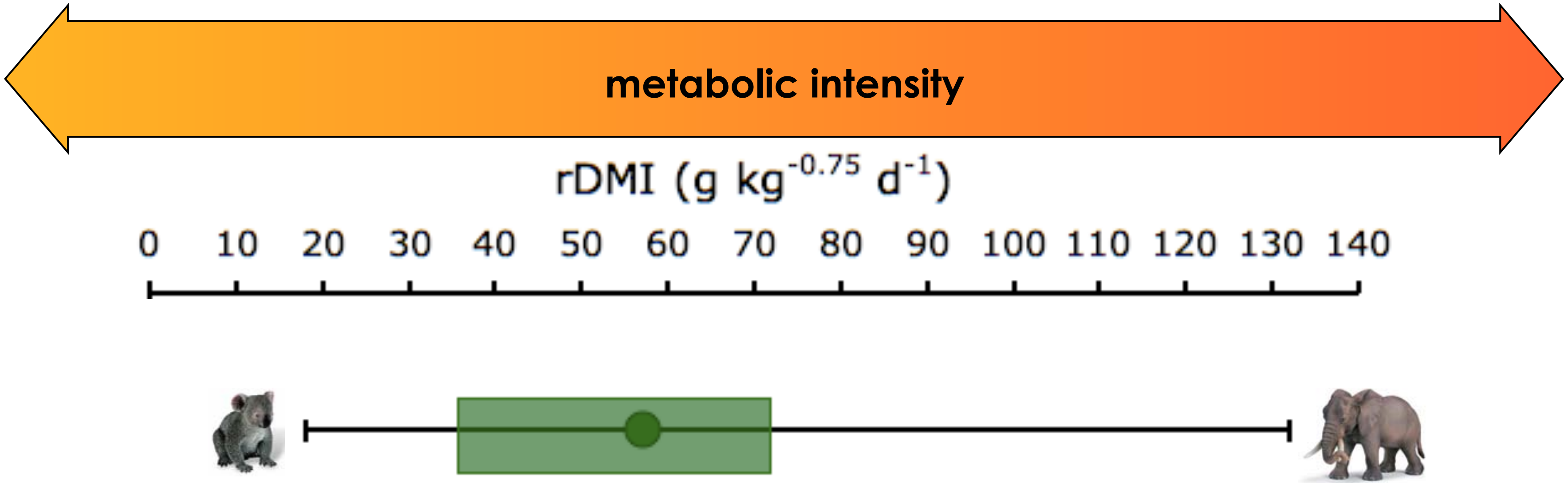
Data overlap from Savage et al. (2004) and Clauss et al. (2007)

Conceptualizing herbivore diversity



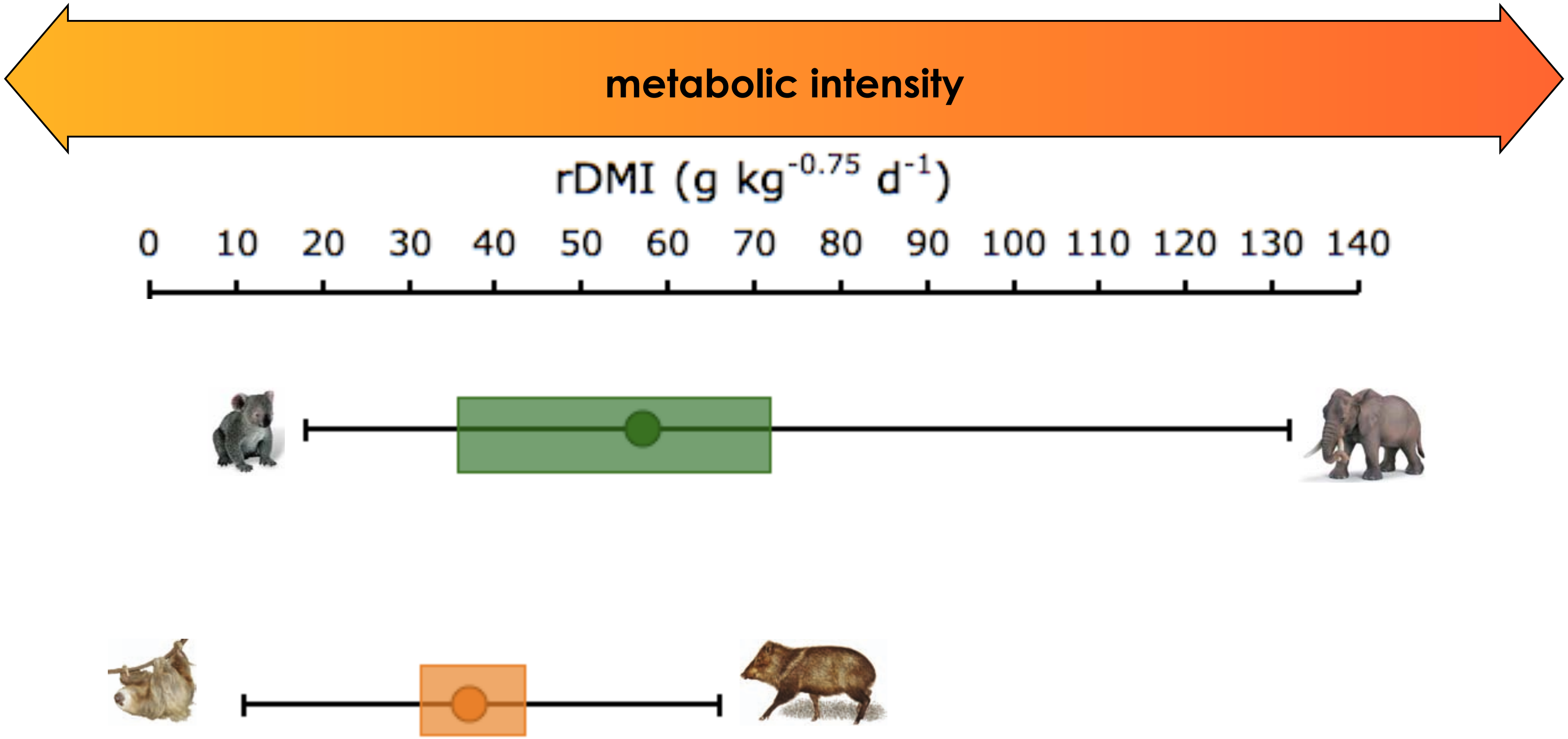
from Clauss et al. (2010)

Conceptualizing herbivore diversity



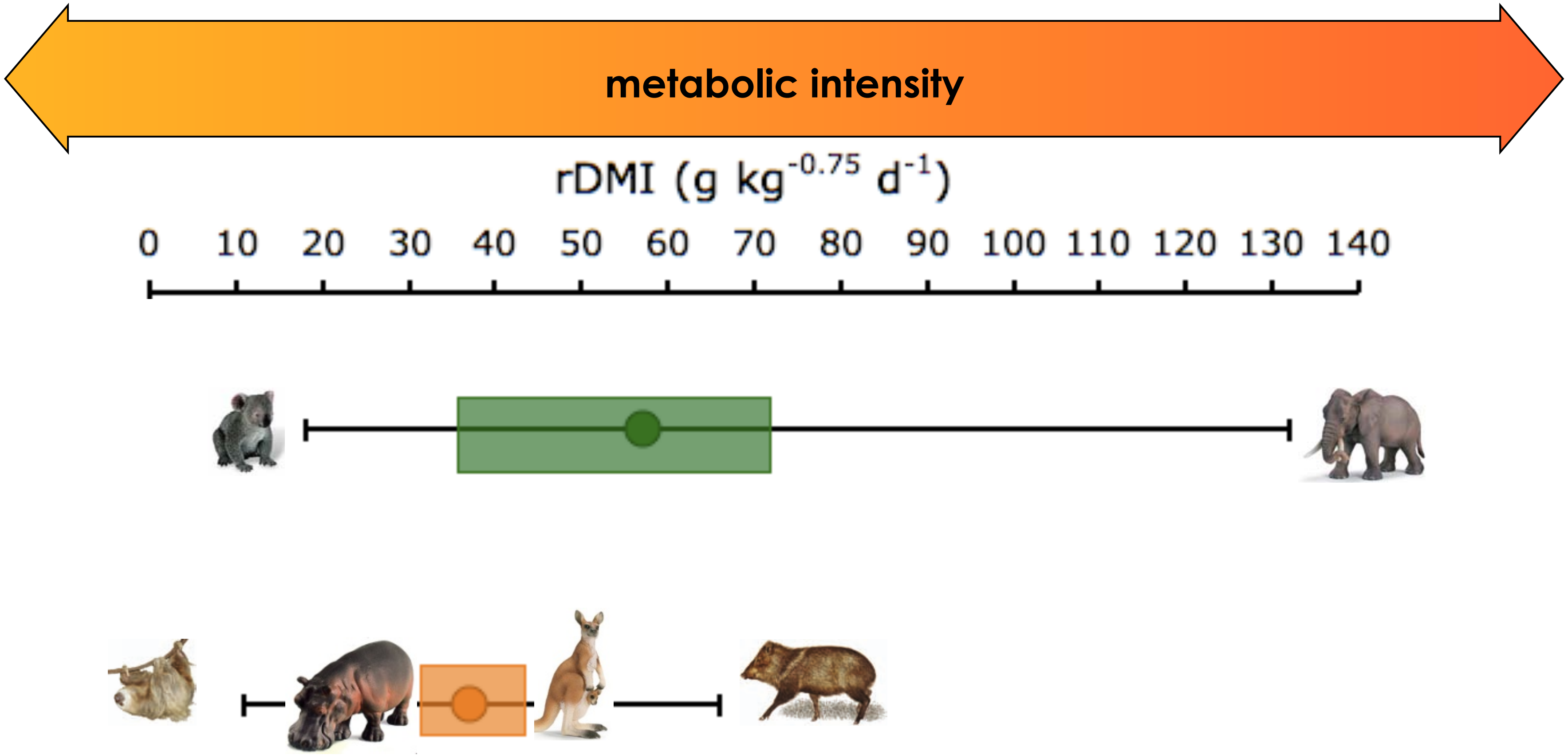
from Clauss et al. (2010)

Conceptualizing herbivore diversity



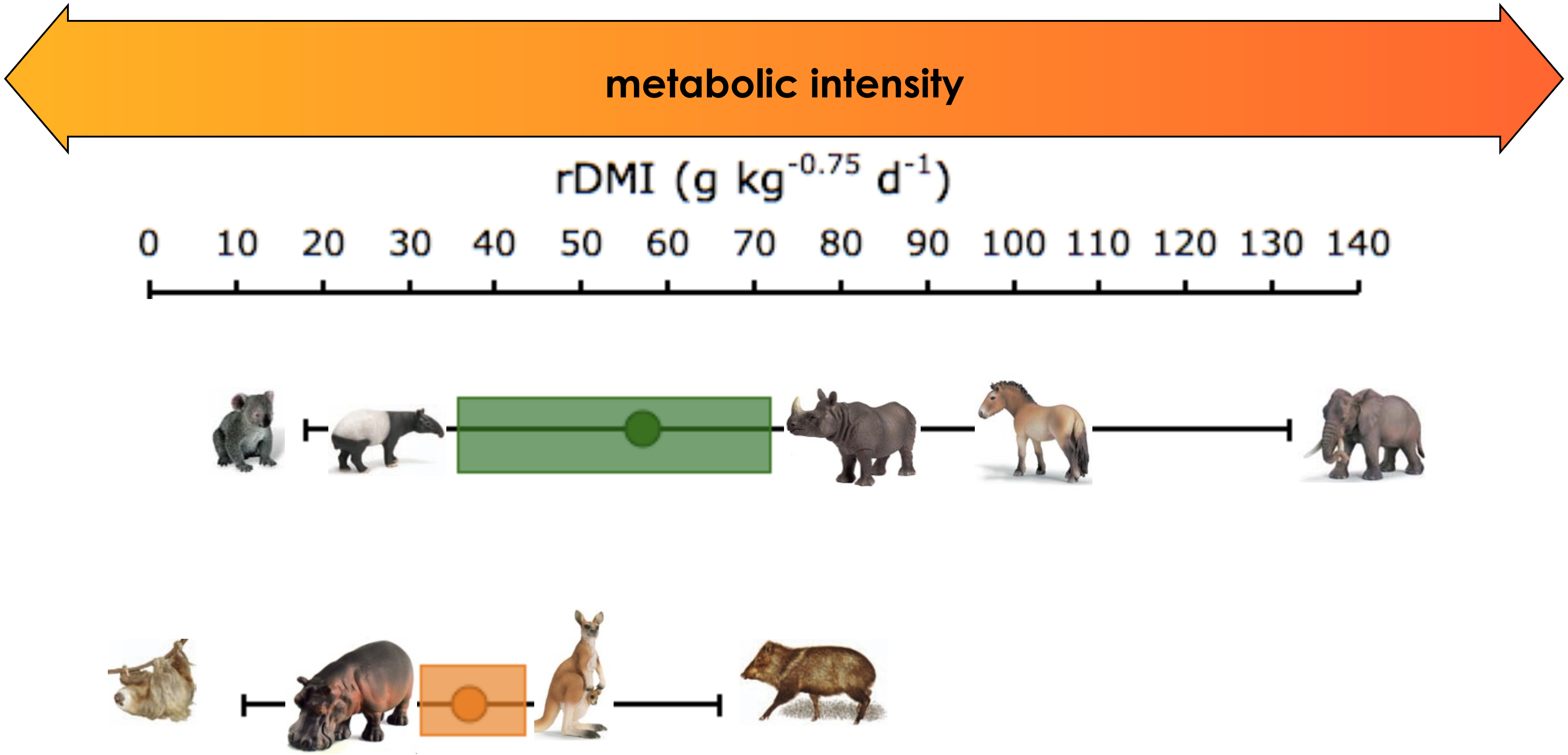
from Clauss et al. (2010)

Conceptualizing herbivore diversity



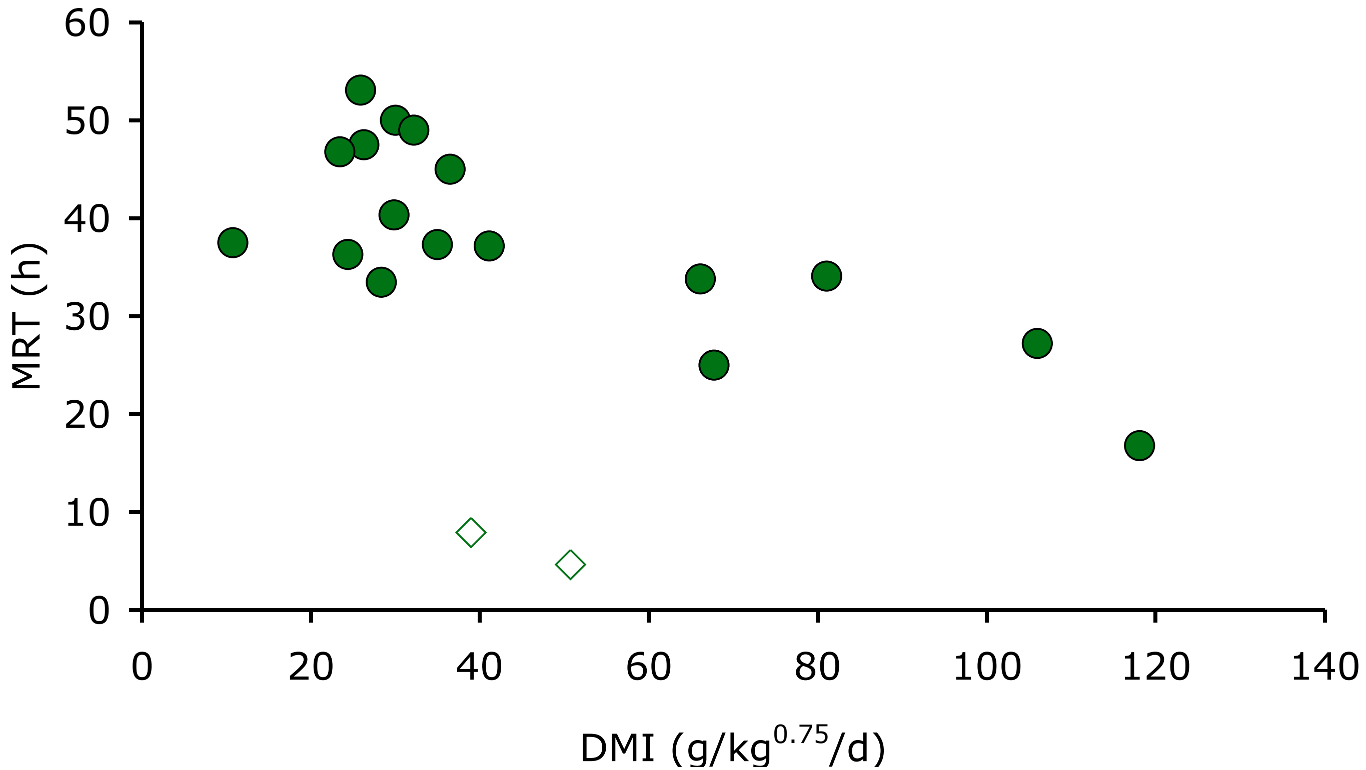
from Clauss et al. (2010)

Conceptualizing herbivore diversity



from Clauss et al. (2010)

Intake and Passage in Primates



from Clauss et al. (2008)

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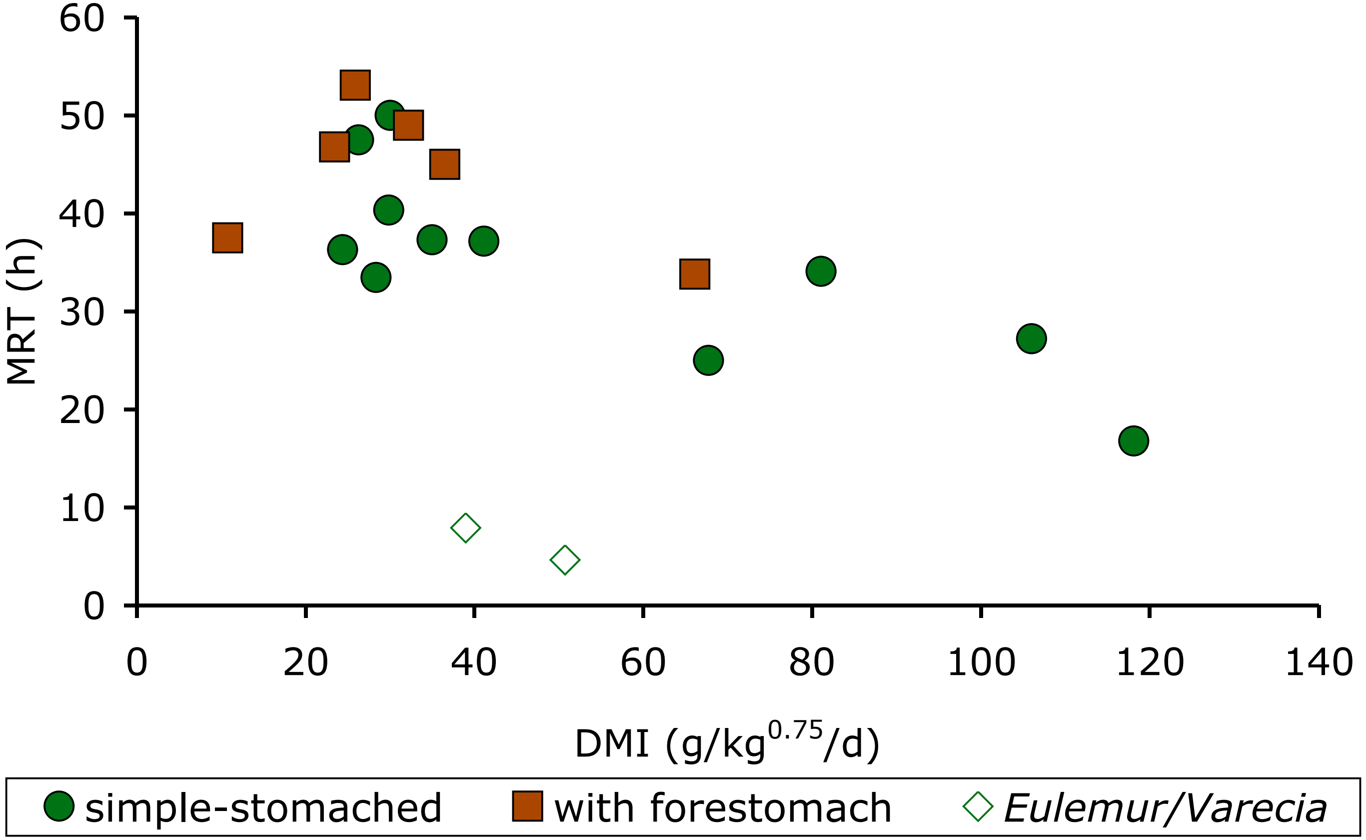
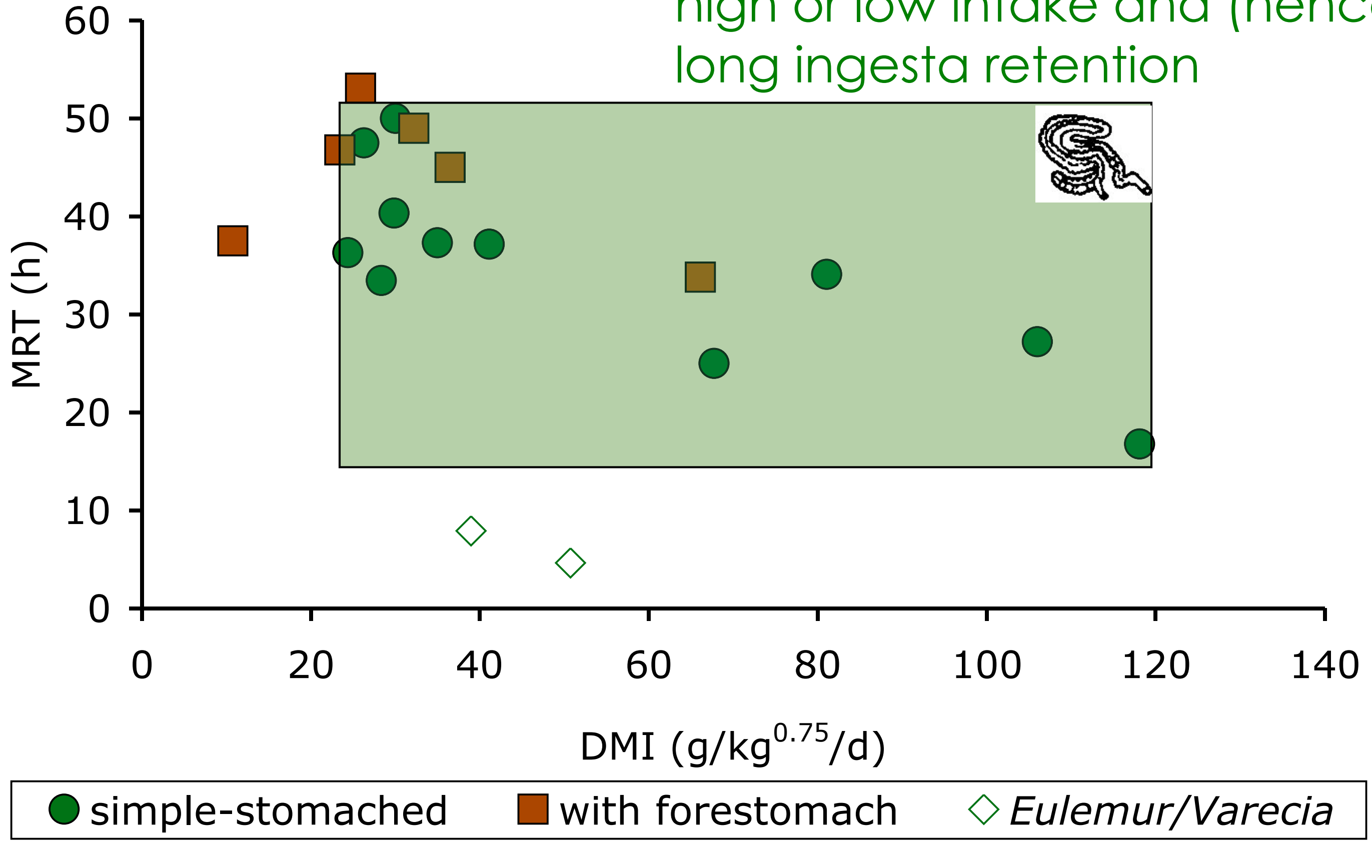


from Clauss et al. (2008)

Intake and Passage in Primates

Hindgut fermenters can have either - high or low intake and (hence) short or long ingesta retention



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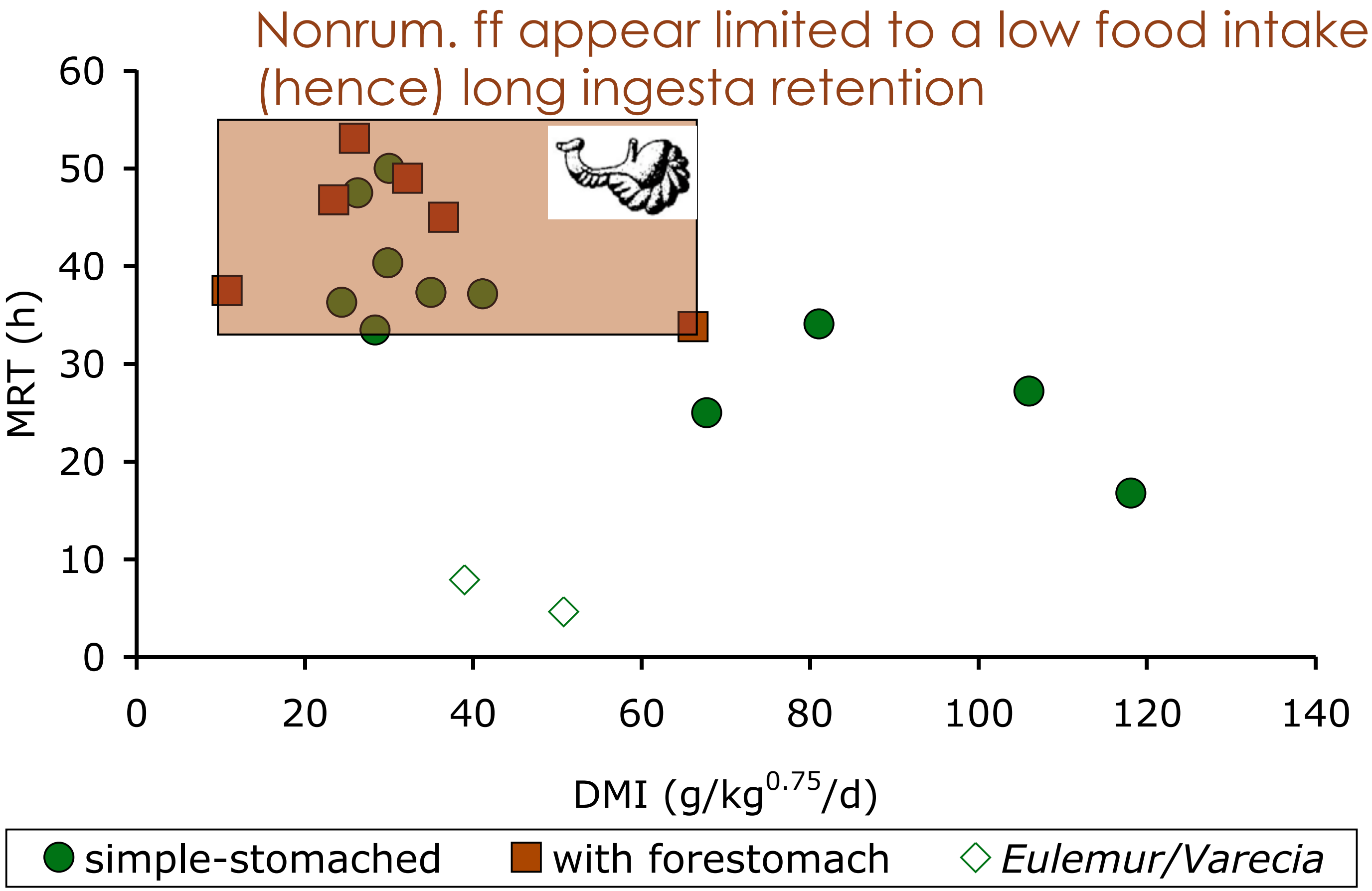
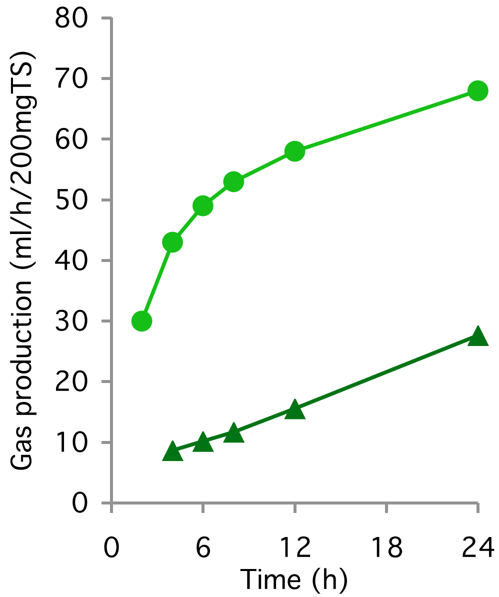
Intake and Passage in Primates



from Clauss et al. (2008)

Two Preconditions

1. It is energetically favourable to digest 'autoenzymatically digestible' components autoenzymatically, not by fermentative digestion.
2. Autoenzymatically digestible components are fermented ***at a drastically higher rate*** than plant fiber.



from Hummel et al. (2006ab)

Digestive Strategies

		
Low intake ⇒ long passage		
High intake ⇒ short passage		

Digestive Strategies

		
Low intake ⇒ long passage	Autoenzymatic digestion followed by thorough fermentative digestion ✓	
High intake ⇒ short passage		

Digestive Strategies

		
Low intake ⇒ long passage	Autoenzymatic digestion followed by thorough fermentative digestion ✓	
High intake ⇒ short passage	Autoenzymatic digestion followed by cursory fermentative digestion ✓	

Digestive Strategies

Low intake ⇒ long passage	Autoenzymatic digestion followed by thorough fermentative digestion ✓	Fermentative digestion followed by autoenzymatic digestion of products (and remains) ✓
High intake ⇒ short passage	Autoenzymatic digestion followed by cursory fermentative digestion ✓	

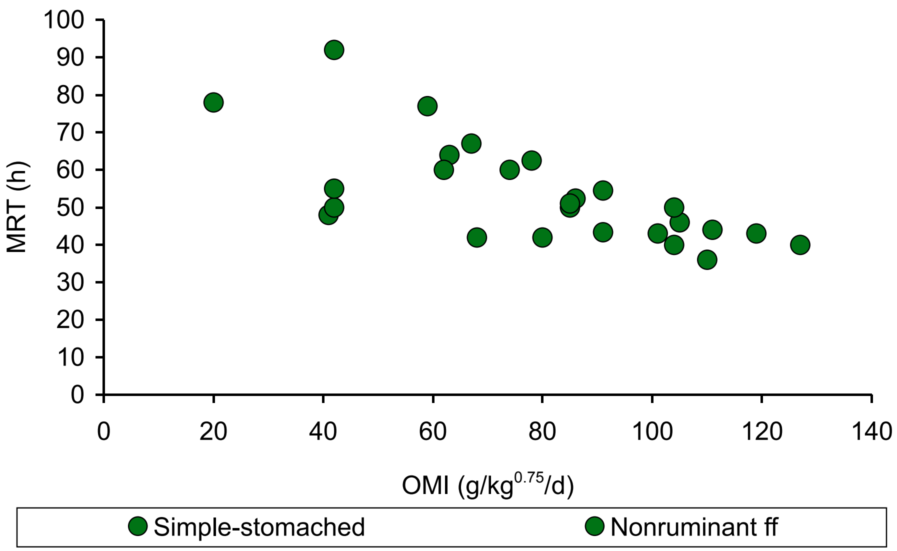
Digestive Strategies

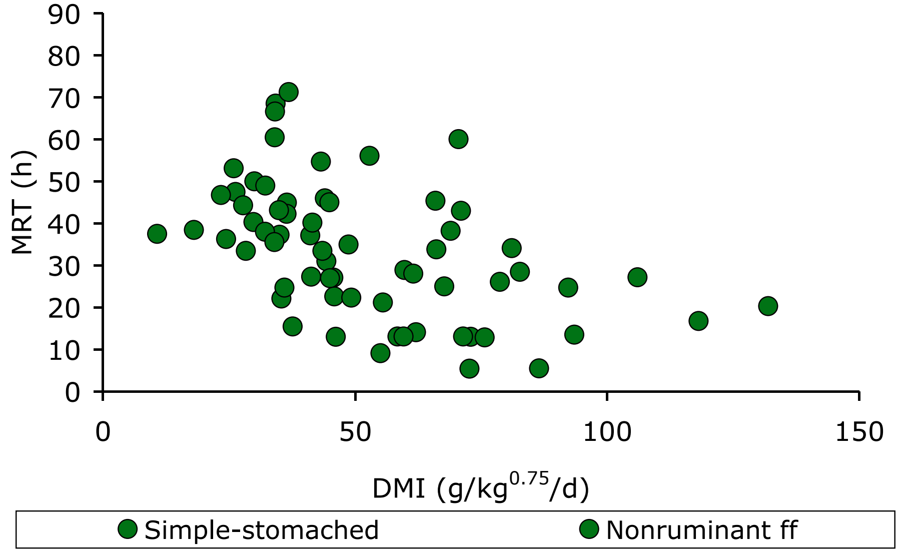
Low intake ⇒ long passage	Autoenzymatic digestion followed by thorough fermentative digestion ✓	Fermentative digestion followed by autoenzymatic digestion of products (and remains) ✓
High intake ⇒ short passage	Autoenzymatic digestion followed by cursory fermentative digestion ✓	*Cursory fermentative digestion mainly of autoenzymatically digestible components followed by ineffective autoenzymatic digestion of undigested fiber?*

Digestive Strategies

		
Low intake ⇒ long passage	Autoenzymatic digestion followed by thorough fermentative digestion ✓	Fermentative digestion followed by autoenzymatic digestion of products (and remains) ✓
High intake ⇒ short passage	Autoenzymatic digestion followed by cursory fermentative digestion ✓	~~*Cursory fermentative digestion mainly of autoenzymatically digestible components followed by ineffective autoenzymatic digestion of undigested fiber?*~~

Intake and Passage

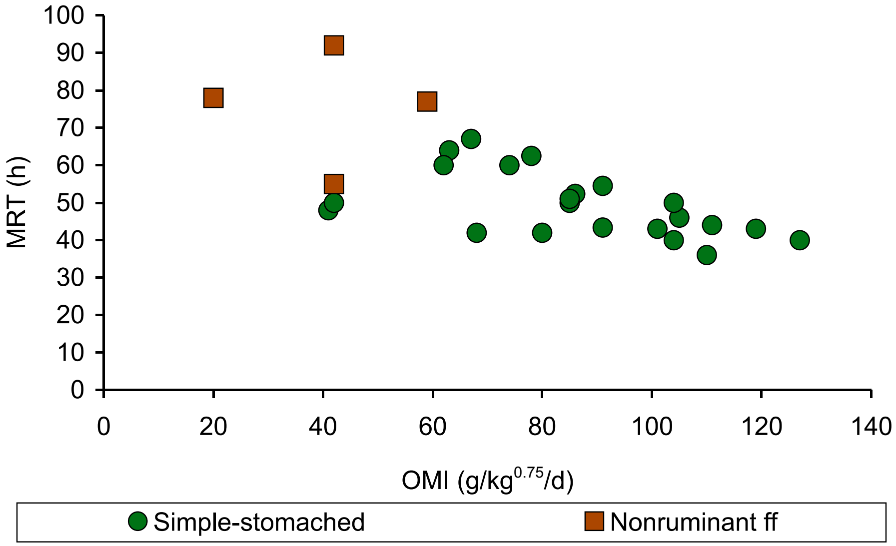


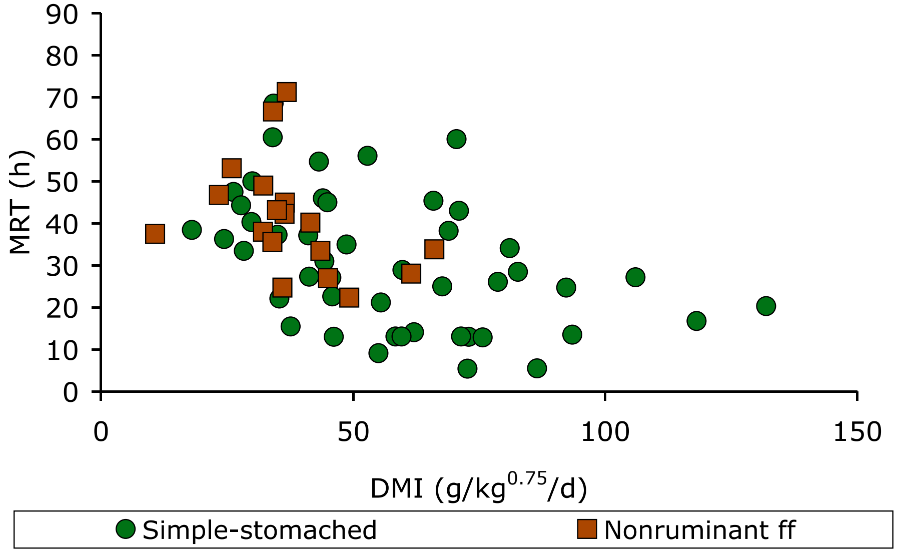


ungulates
from Foose (1982)

mammal herbivores
Clauss et al. (2007)

Intake and Passage





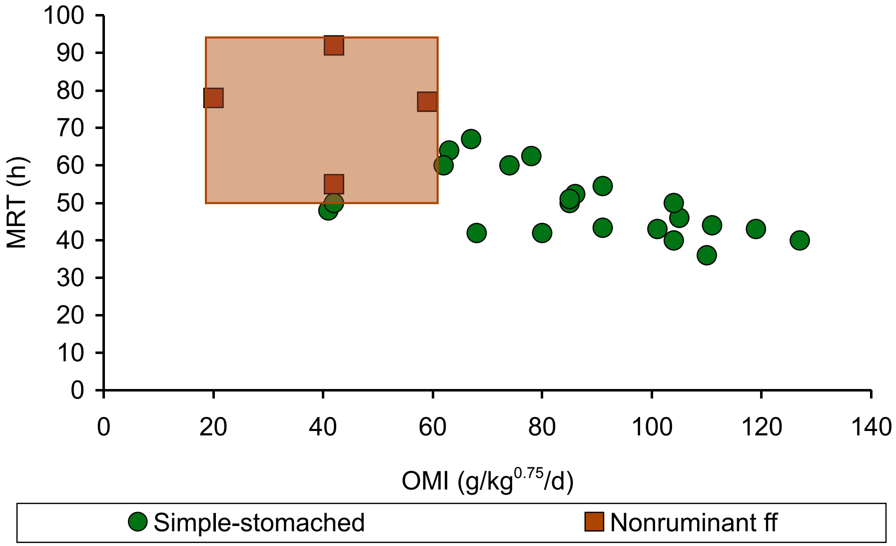
ungulates
from Foose (1982)

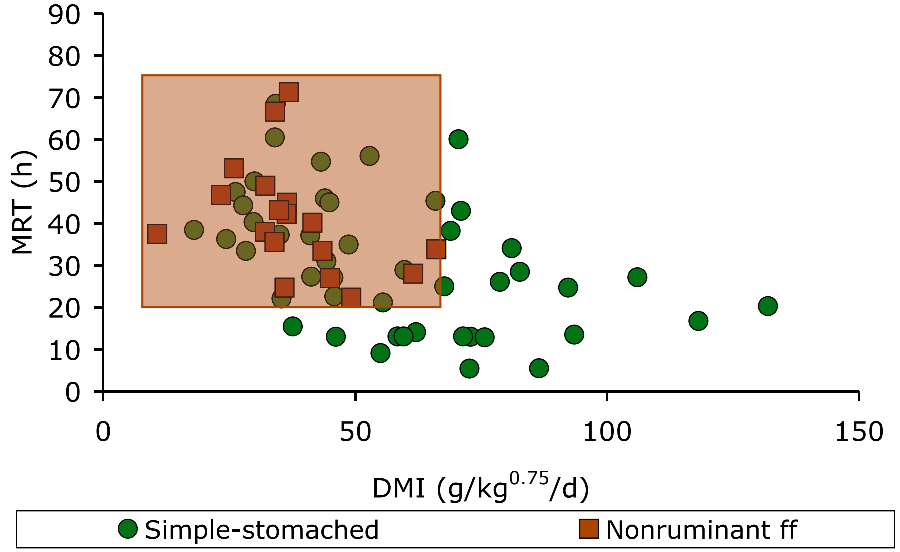
mammal herbivores
Clauss et al. (2007)

Intake and Passage

Nonrum. ff appear limited to a low food intake and (hence) long ingesta retention

while hindgut fermenters can cover the whole range





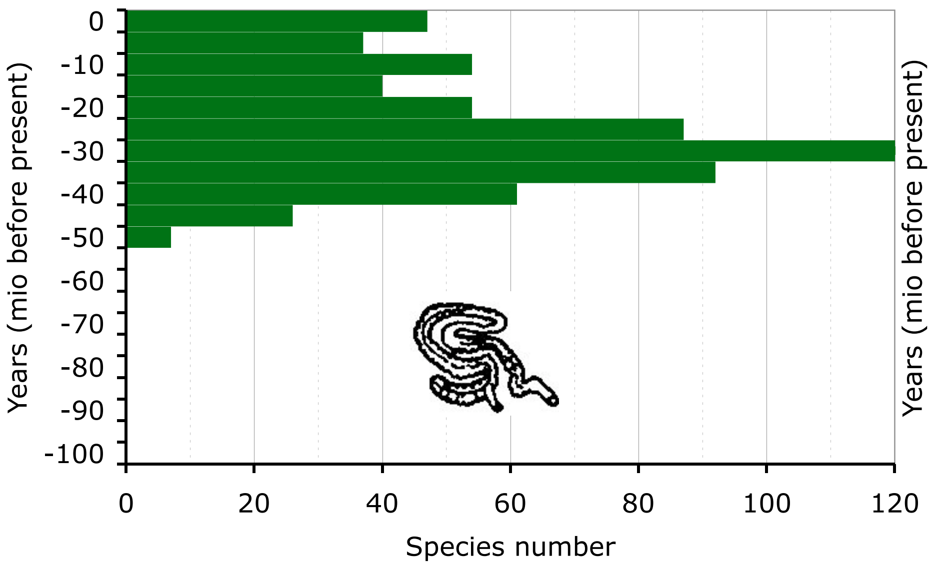
ungulates
from Foose (1982)

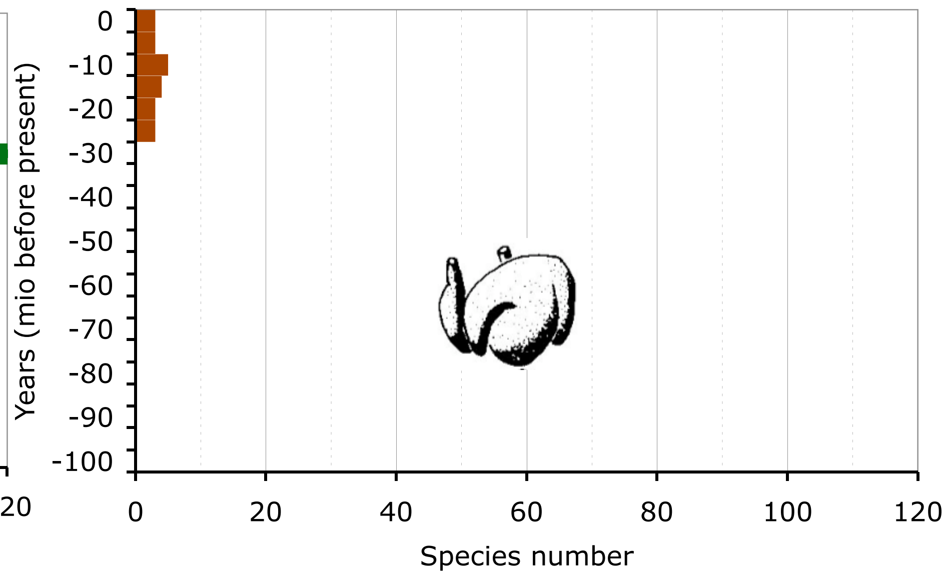
mammal herbivores
Clauss et al. (2007)

From Digestive to Metabolic Strategies

		
Low intake ⇒ long passage ⇒ ***low BMR***	✓	✓
High intake ⇒ short passage ⇒ ***high BMR***	✓	✗

European Mammal Herbivores in Deep Time





from Langer (1991)

How can you increase fermentative digestive efficiency?

- Digestion of plant fibre by bacteria is the more efficient ...
  - the more time is available for it
    = the longer the mean gastrointestinal retention time.
  - the finer the plant fibre particles are
    = the finer the ingesta is chewed.

How can you increase energy intake?

- higher food intake
- higher digestive efficiency

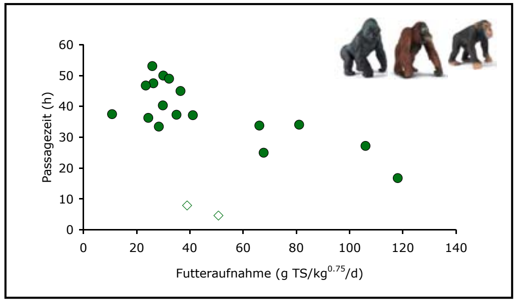
How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing

How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing

?



How can you increase energy intake?

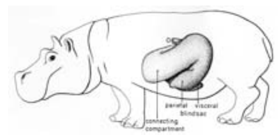
- higher food intake
- longer retention
- finer chewing

higher gut volume

How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing

higher gut volume



How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing

higher gut volume

Higher breathing frequency in bovini - larger rumen - less space for lung - Mortolaa and Lanthier(2005)

How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing

→ higher gut volume

Mortolaa and Lanthier (2005)

wetter faeces in bovini - larger rumen - less space for colon - Clauss et al. (2003)

How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing

→ sorting !

If you do not sort ...

If you do not sort ...

If you do not sort ...

If you do not sort ...

If you do not sort ...

If you do not sort ...

If you do not sort ...

If you do not sort ...

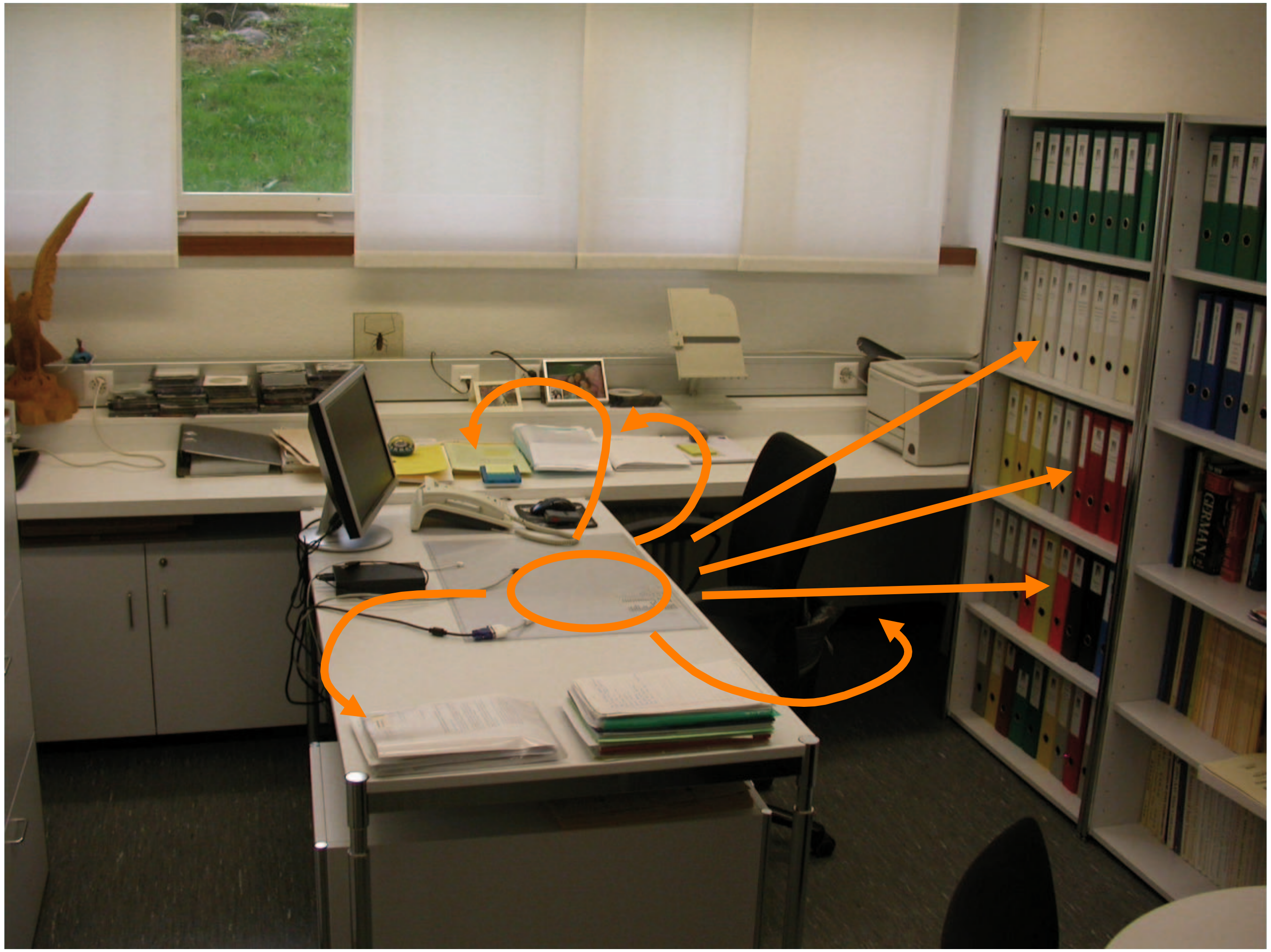
The power of sorting

The power of sorting

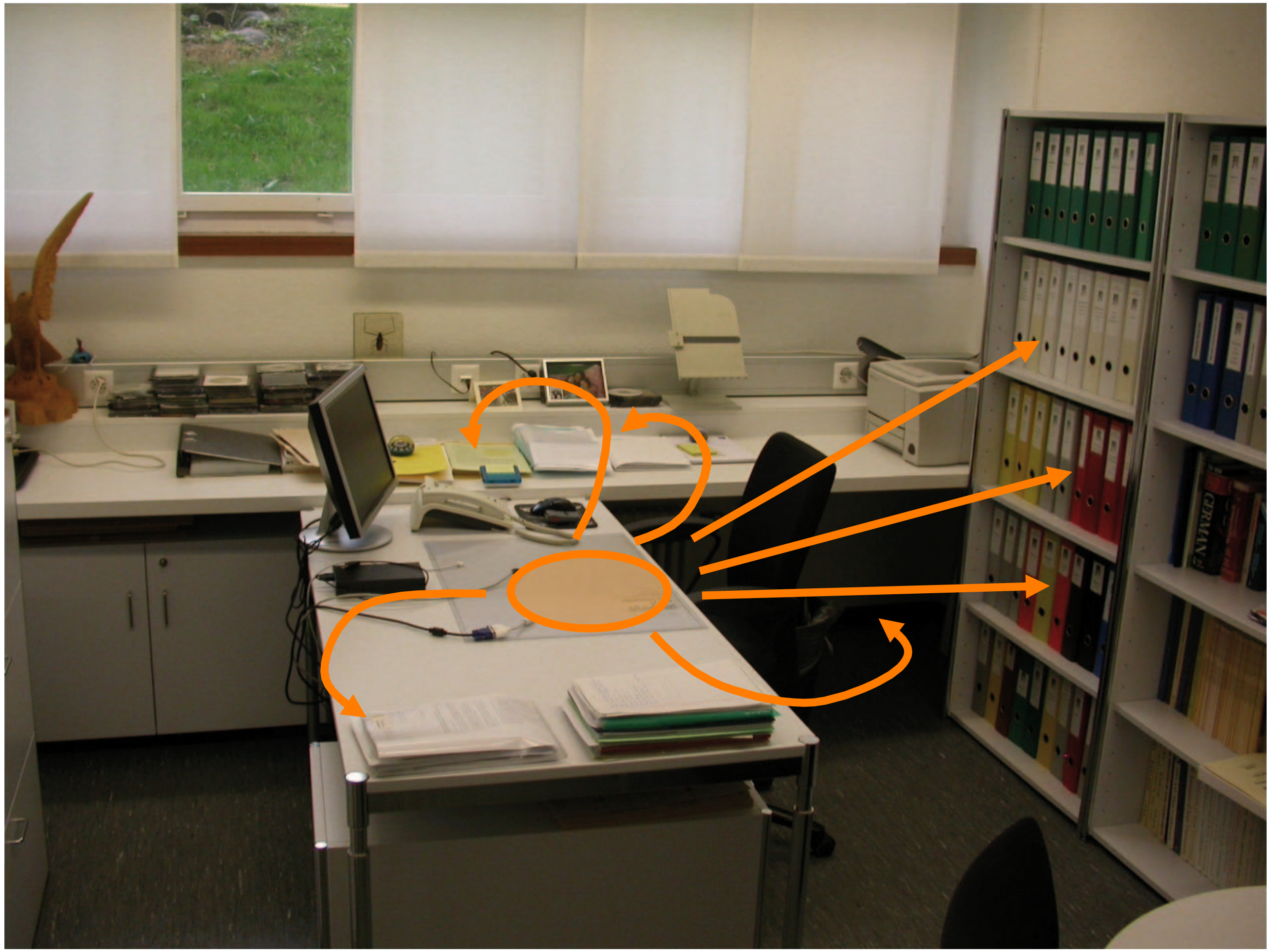
The power of sorting

The power of sorting

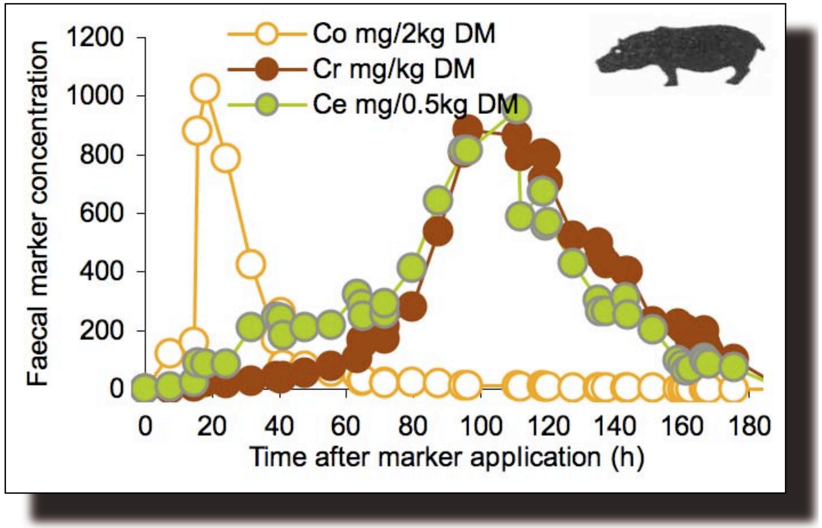
The power of sorting



The power of sorting

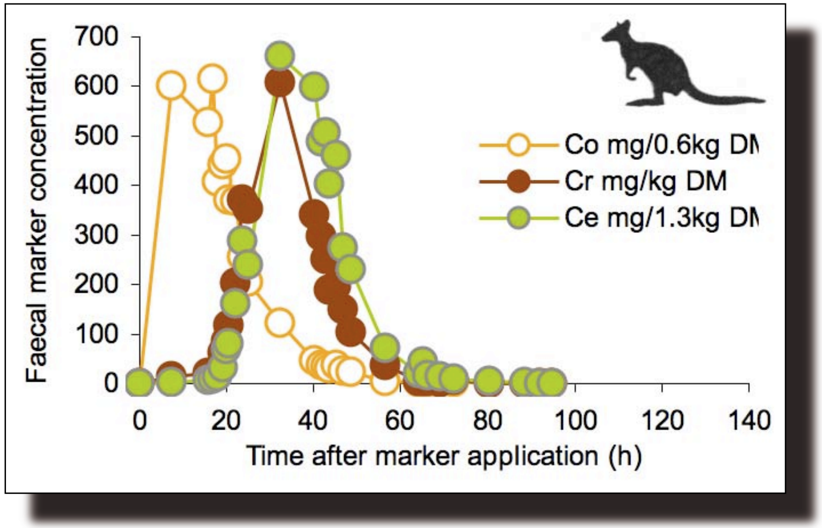


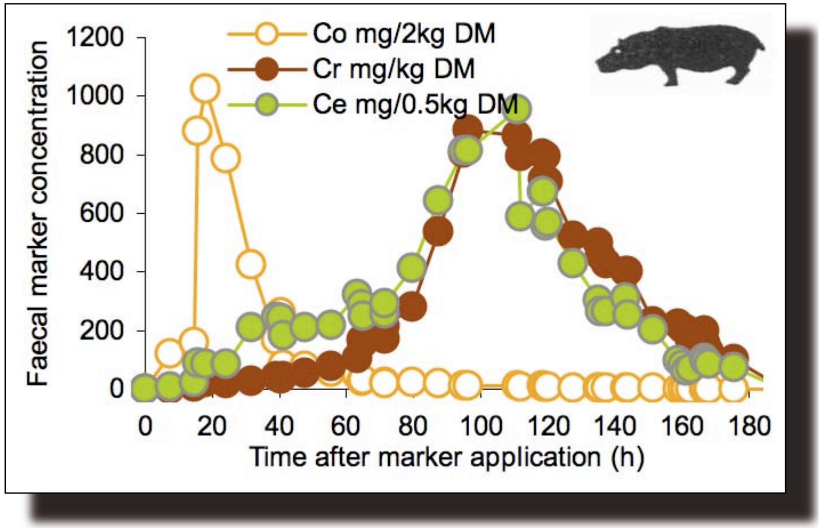
Ruminant vs. Nonruminant Foregut Fermentation



Schwarm et al. (2008)

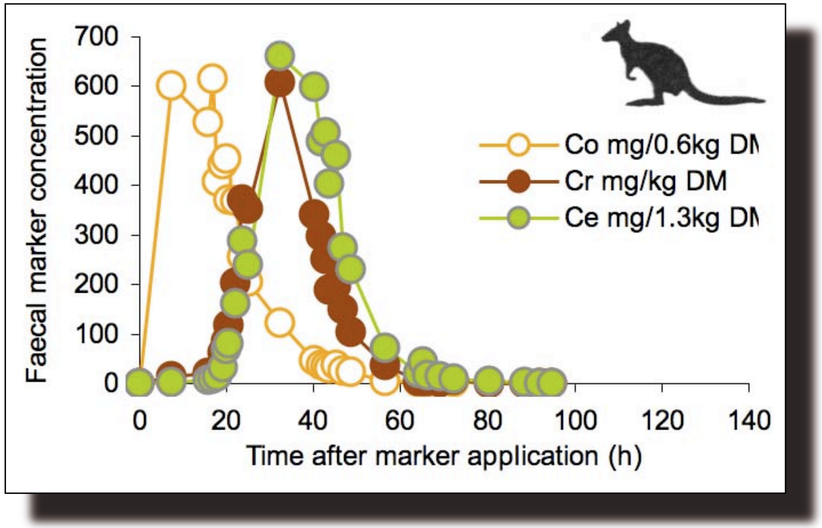
Ruminant vs. Nonruminant Foregut Fermentation

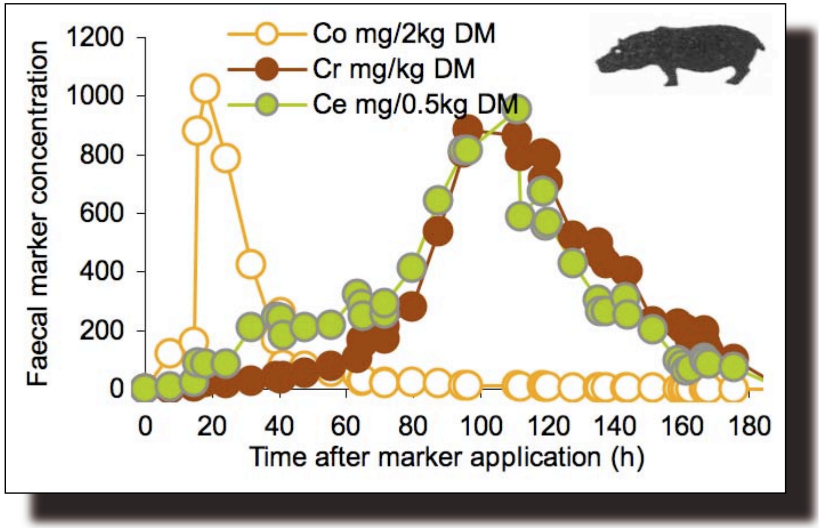




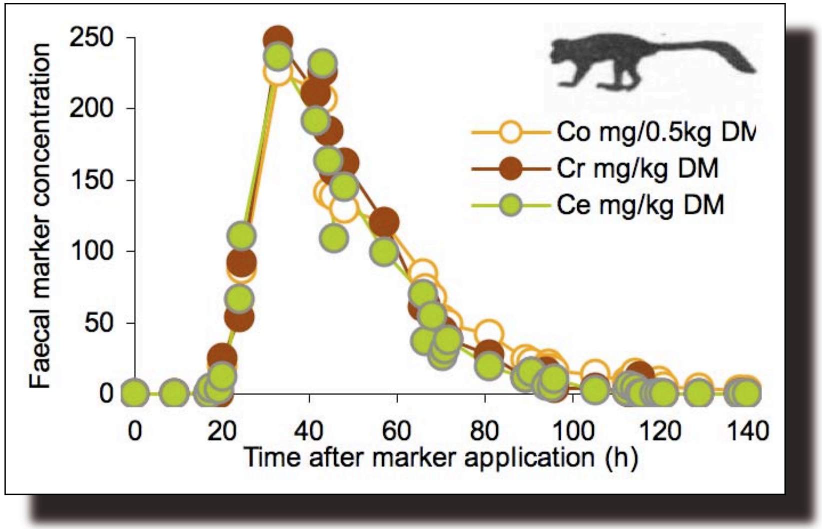
Schwarm et al. (2008,2009)

Ruminant vs. Nonruminant Foregut Fermentation

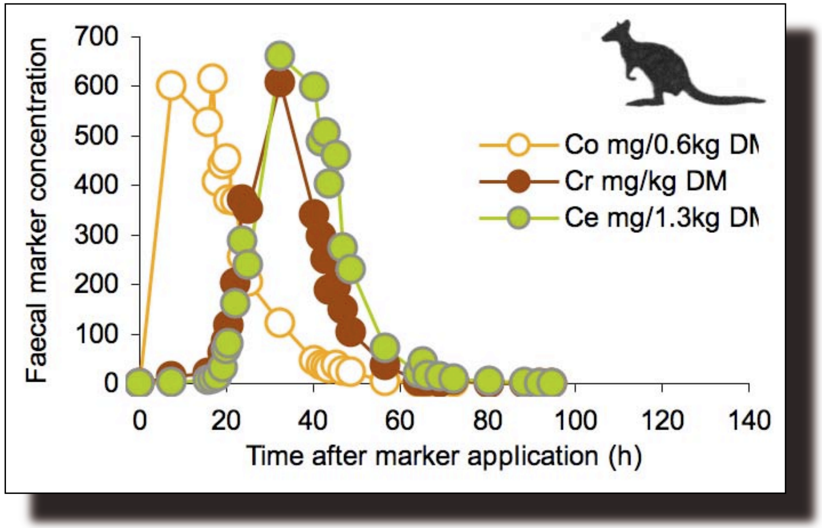


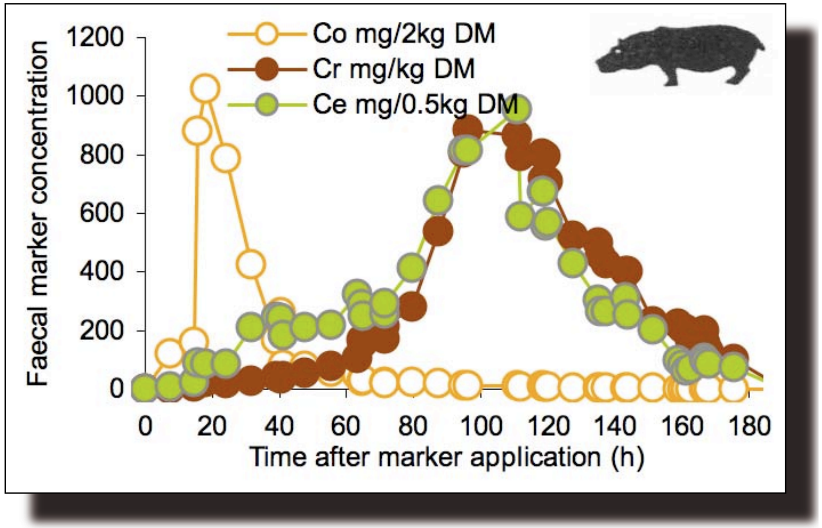


Schwarm et al. (2008,2009)

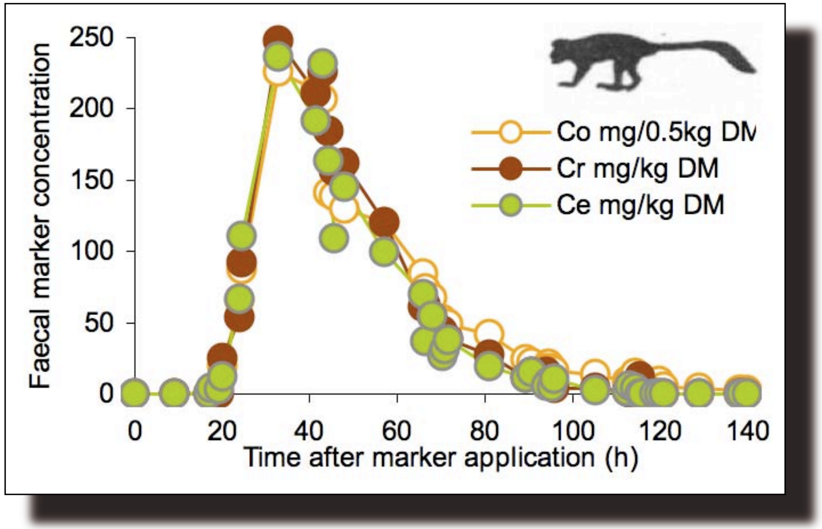


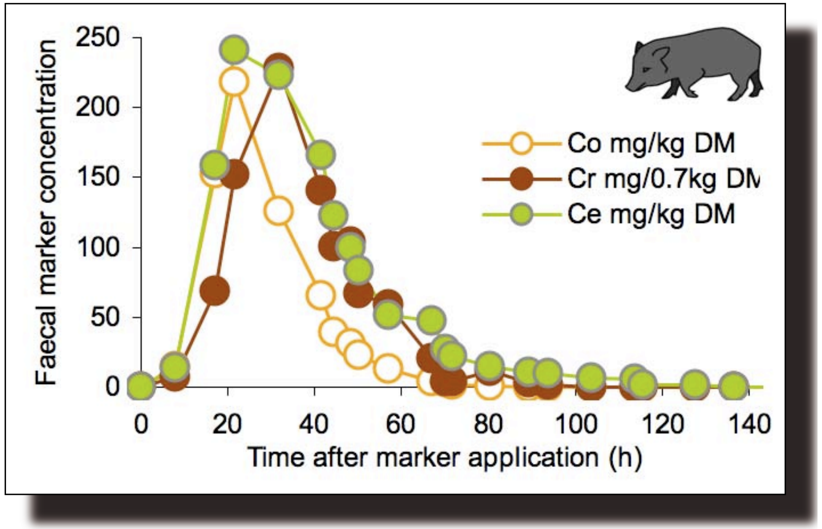
Ruminant vs. Nonruminant Foregut Fermentation



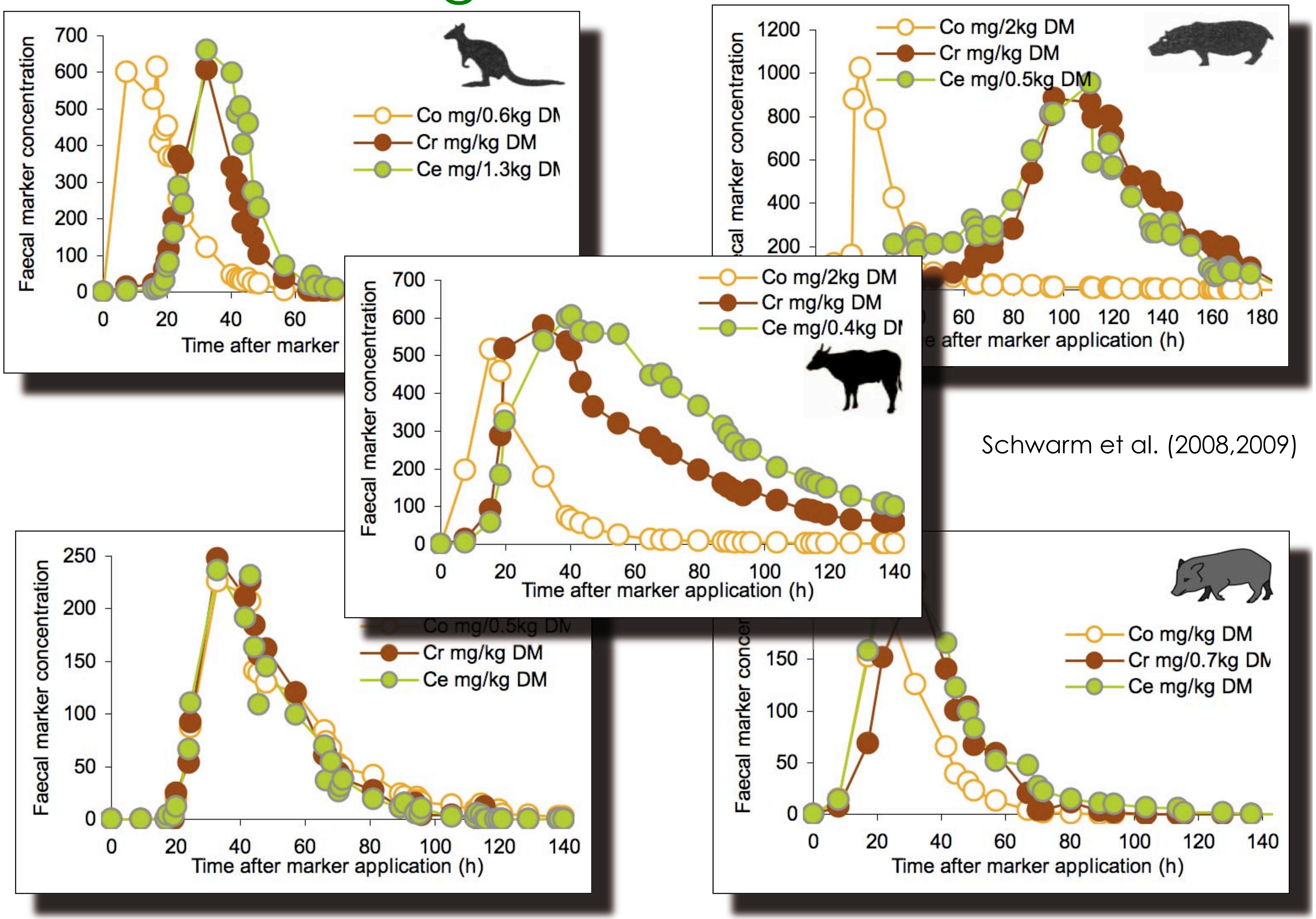


Schwarm et al. (2008,2009)





Ruminant vs. Nonruminant Foregut Fermentation

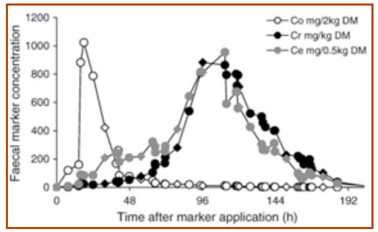


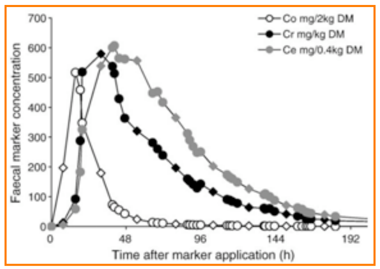
Schwarm et al. (2008,2009)

How can you increase energy intake?

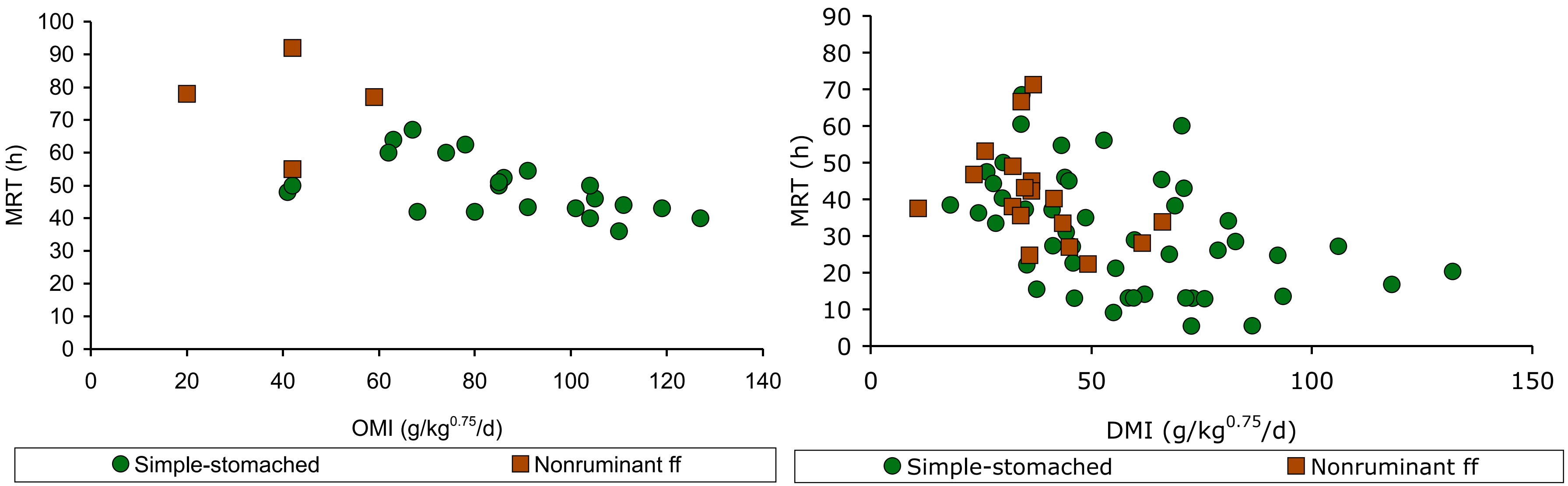
- higher food intake
- longer retention
- finer chewing

→ sorting !





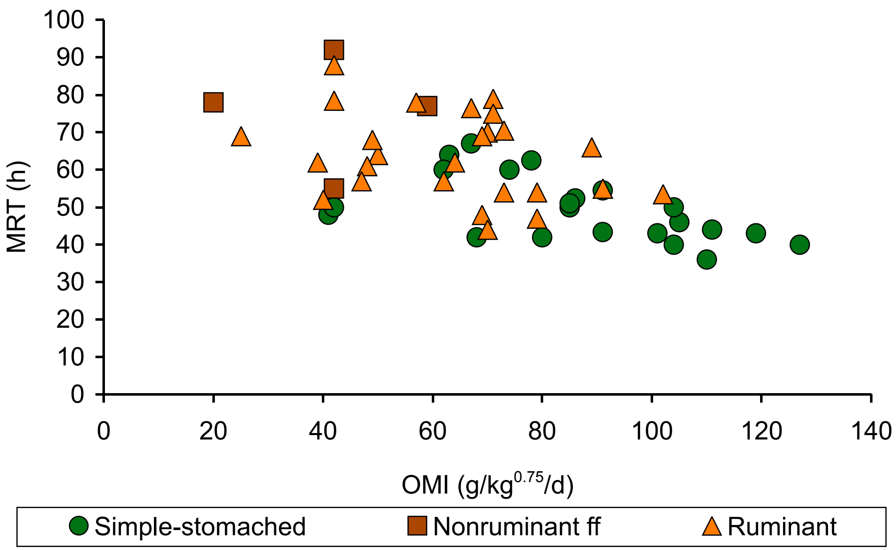
Intake and Passage

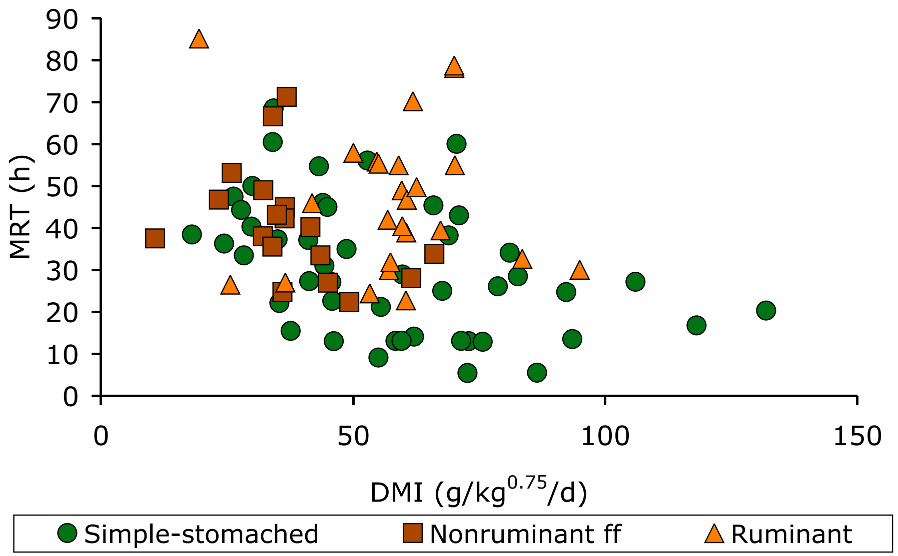


ungulates
from Foose (1982)

mammal herbivores
Clauss et al. (2007)

Intake and Passage





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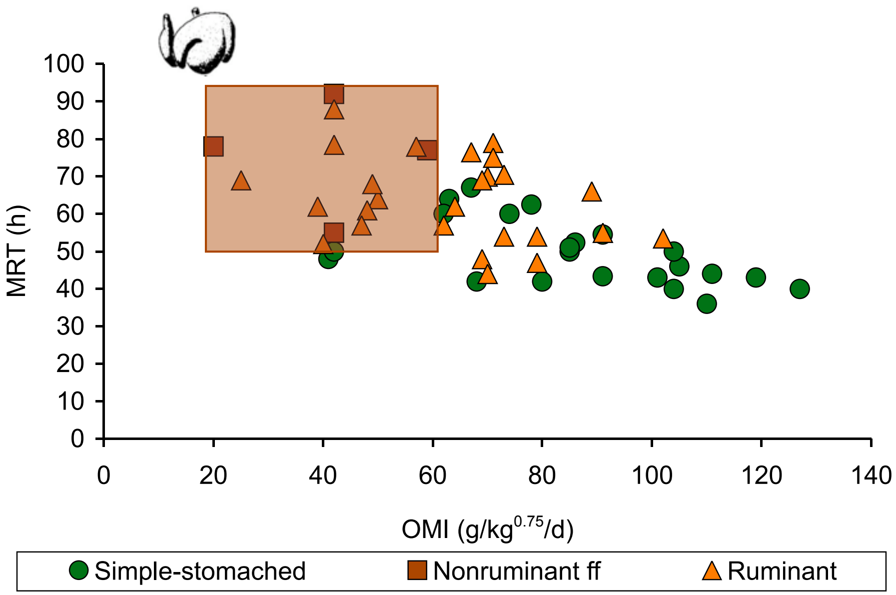
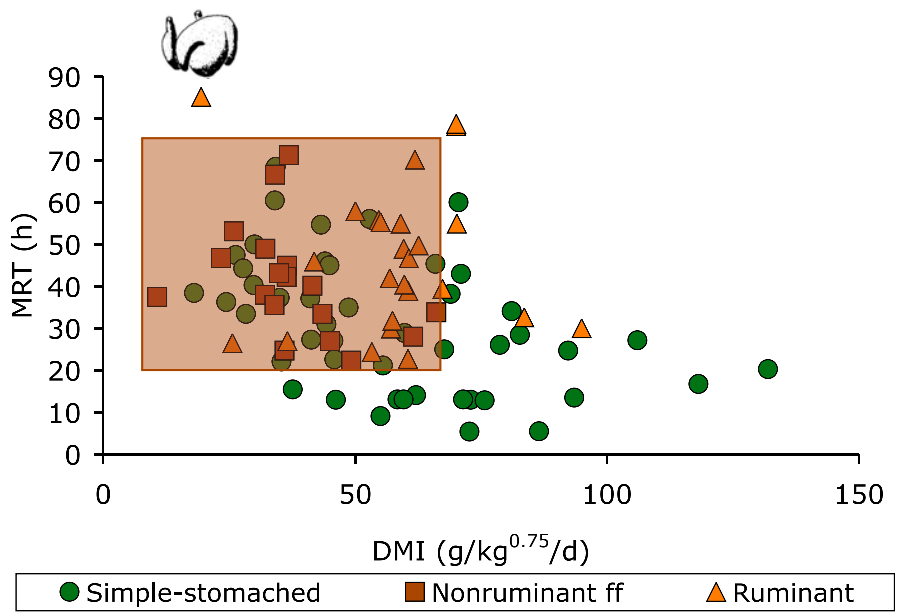
Intake and Passage



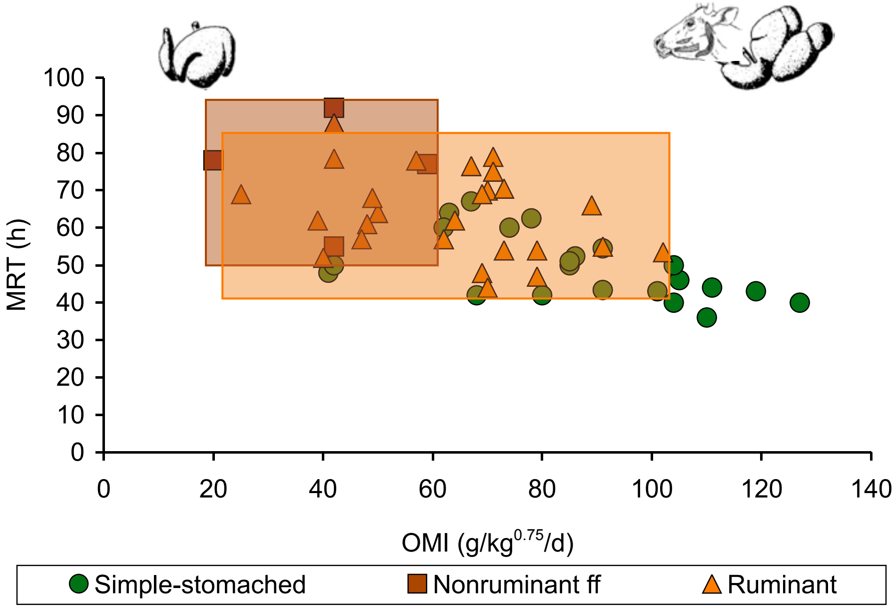


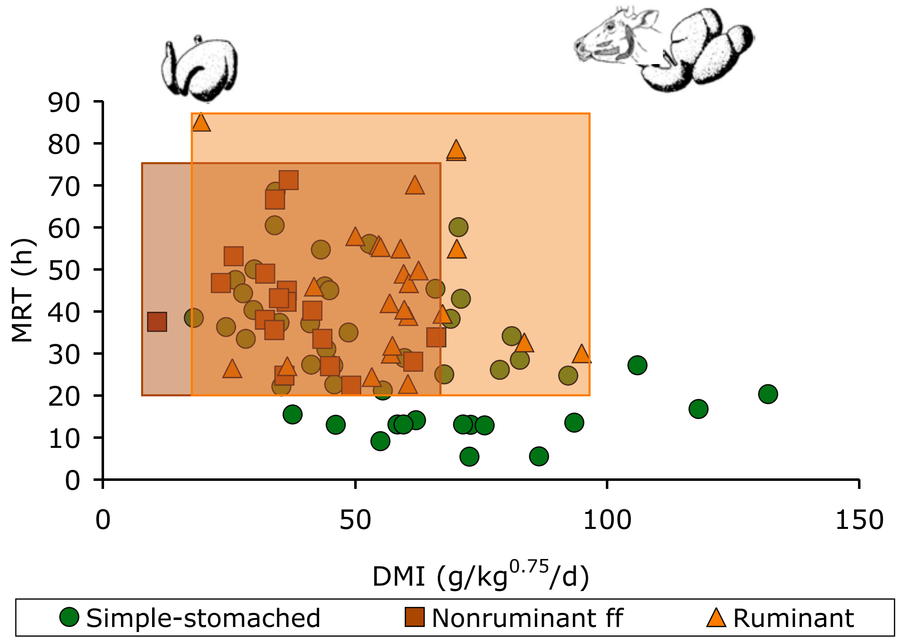
ungulates
from Foose (1982)

mammal herbivores
Clauss et al. (2007)

Intake and Passage

Ruminants expand the intake range of foregut fermenters (while retaining long retention times)





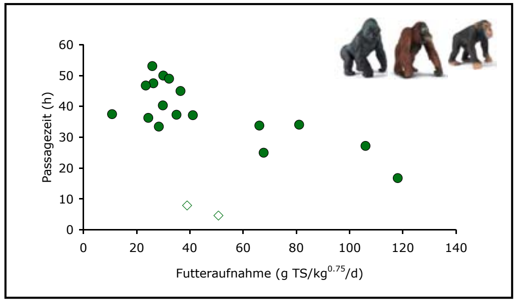
ungulates
from Foose (1982)

mammal herbivores
Clauss et al. (2007)

How can you increase energy intake?

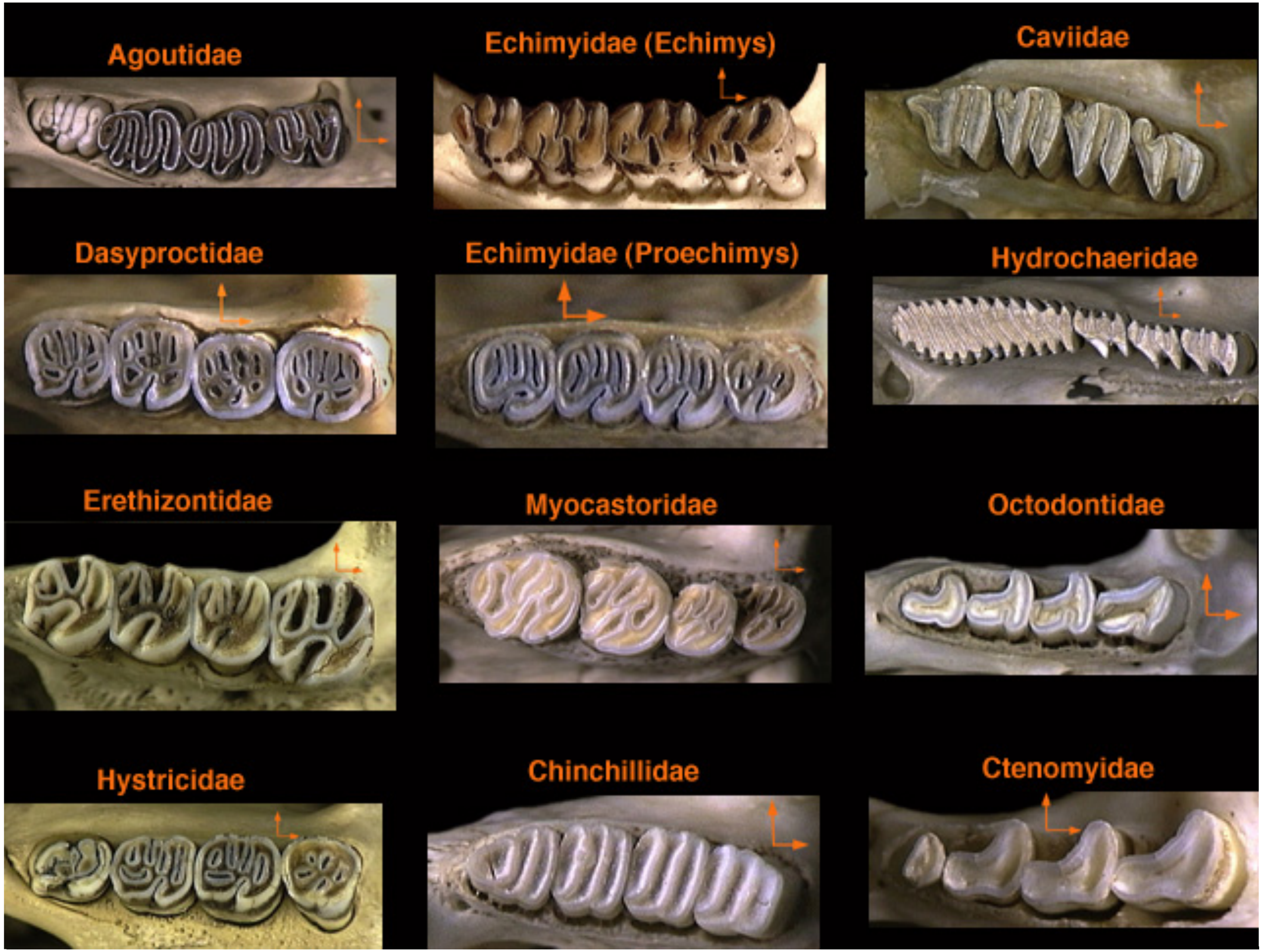
- higher food intake
- longer retention

?



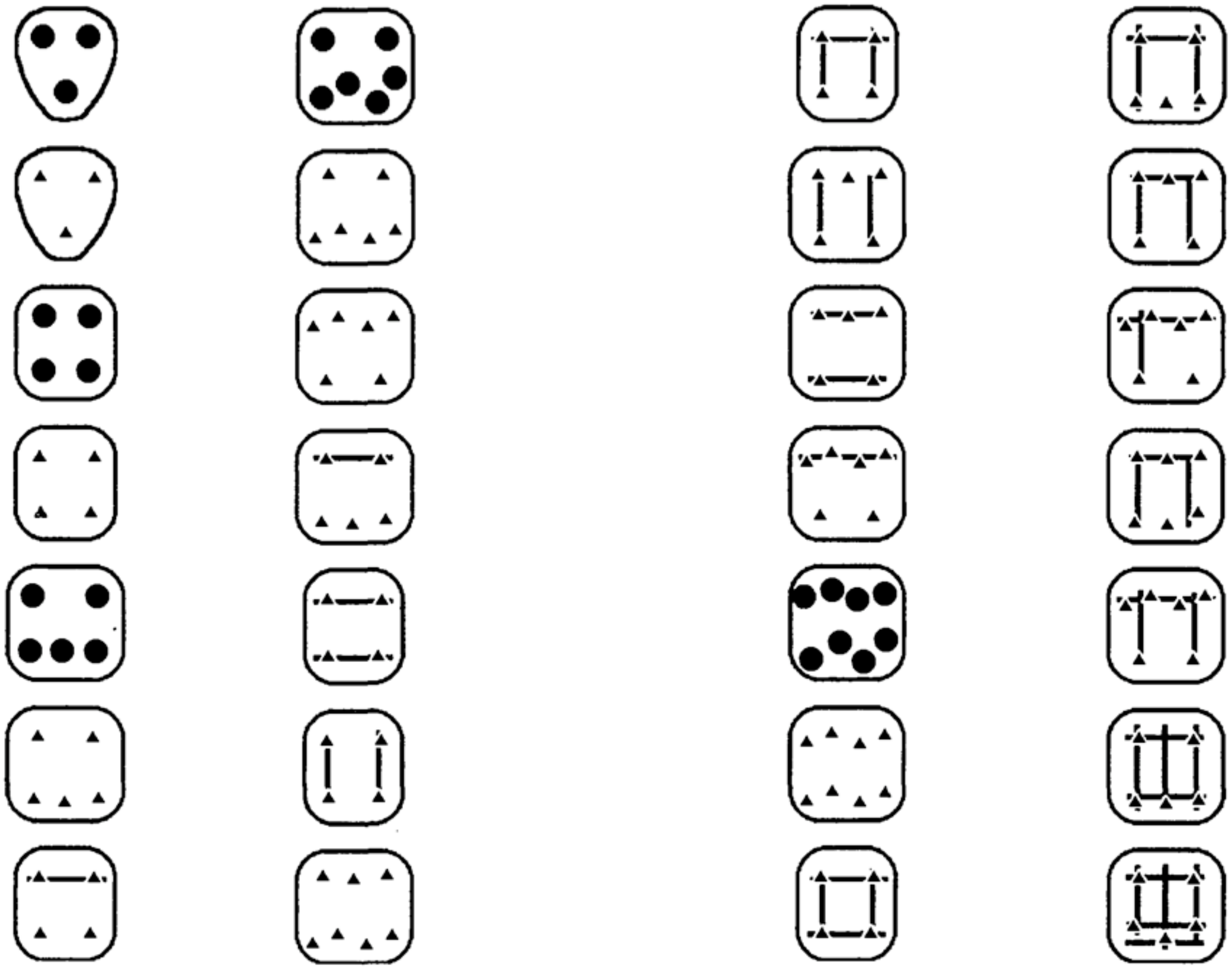
- finer chewing

“Mammals are the definite chewers”



aus The Animal Diversity Web - http://animaldiversity.org

“Mammals are the definite chewers”



aus Jernvall et al. (1996)

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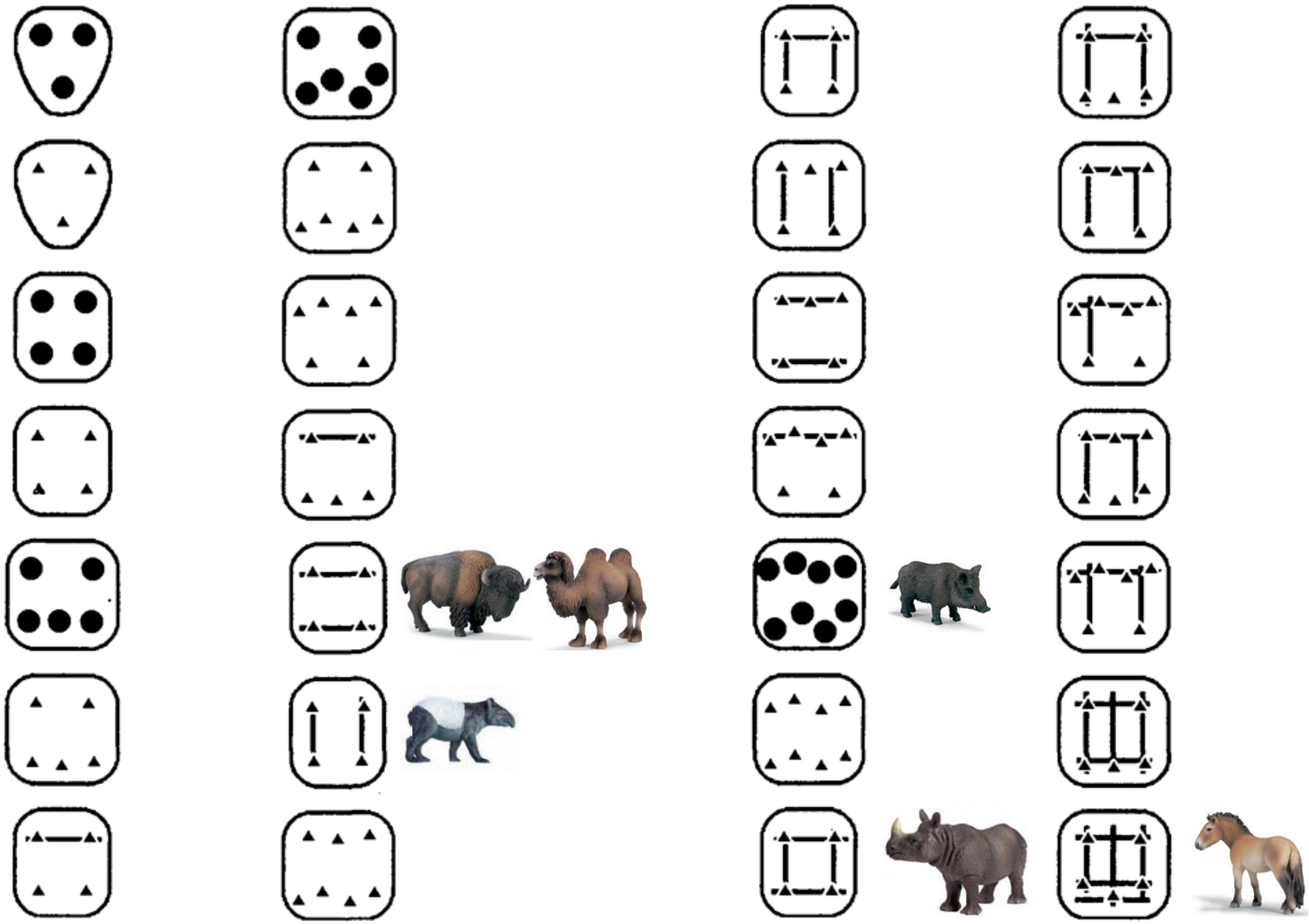

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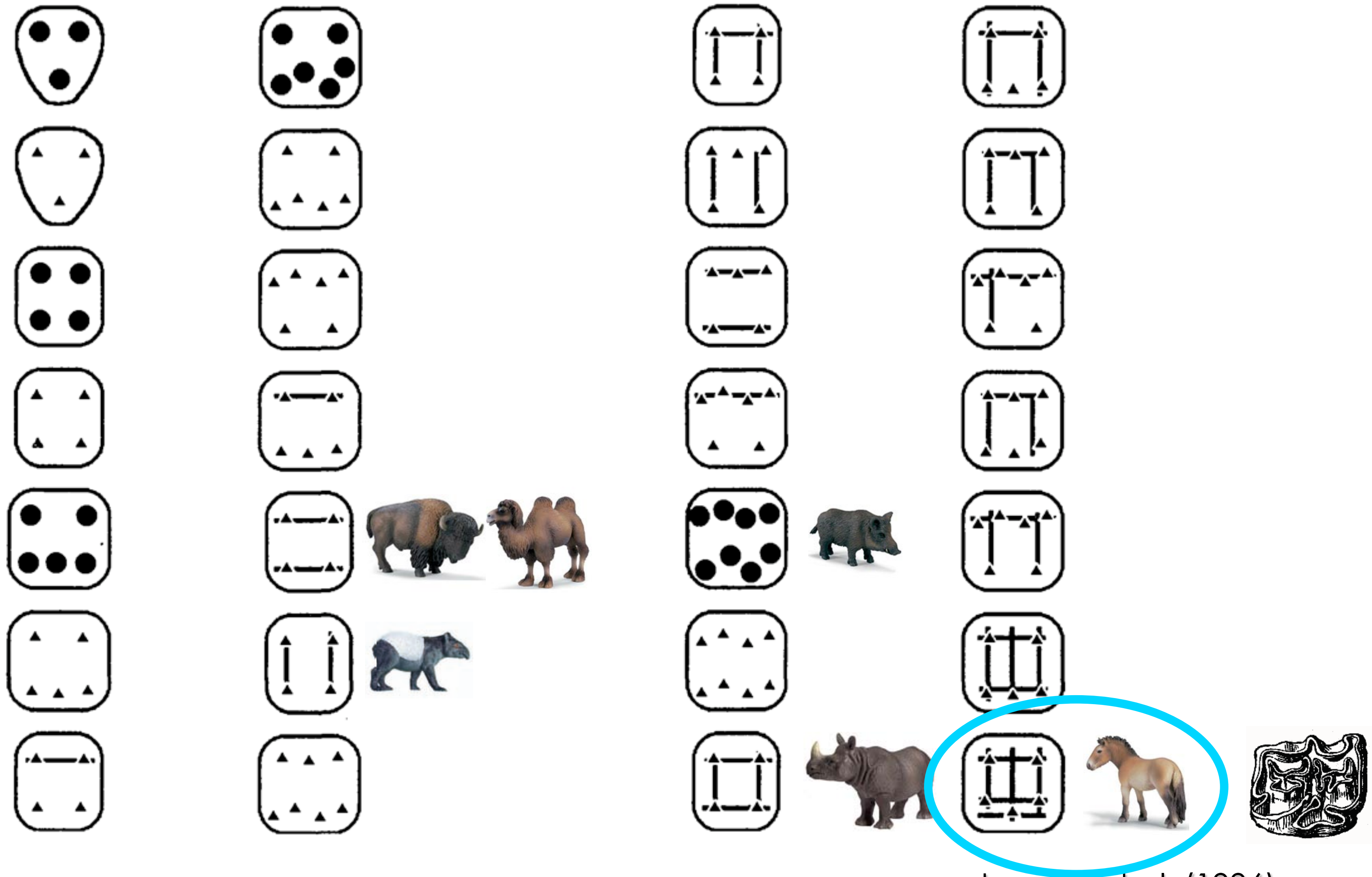
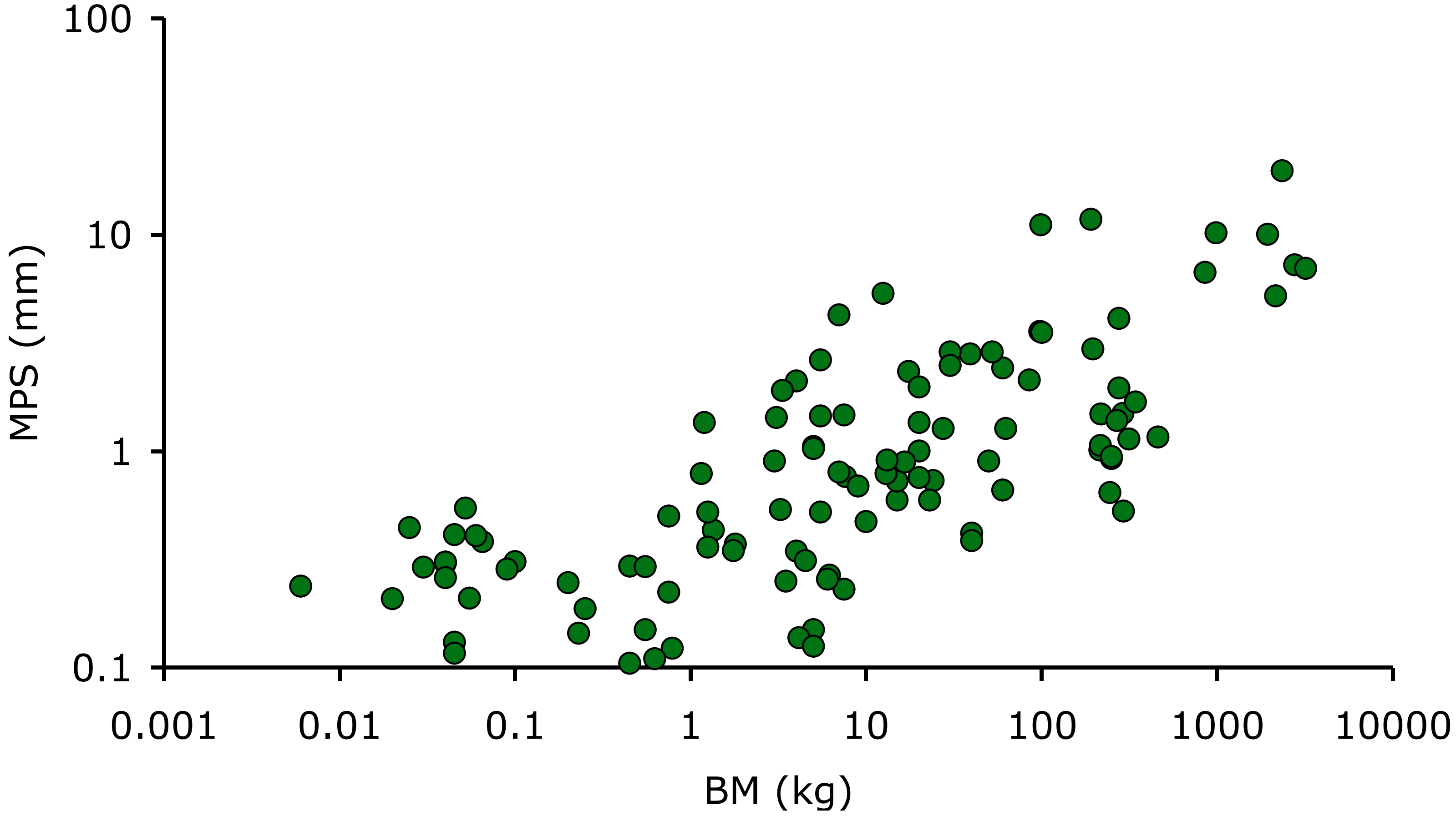


aus Jernvall et al. (1996)

Ingesta particle size (chewing efficiency)



from Fritz (2007)

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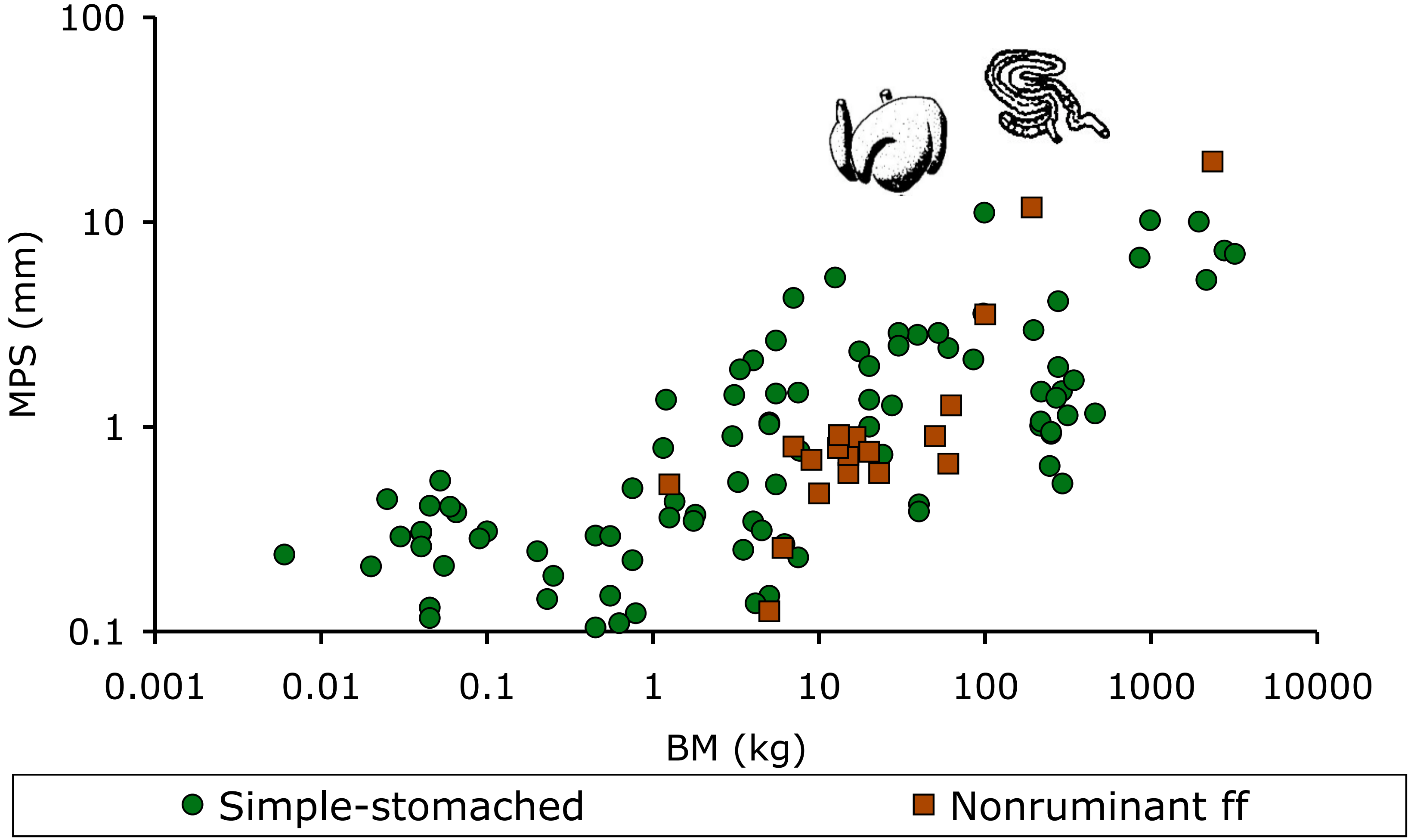

from Fritz (2007)

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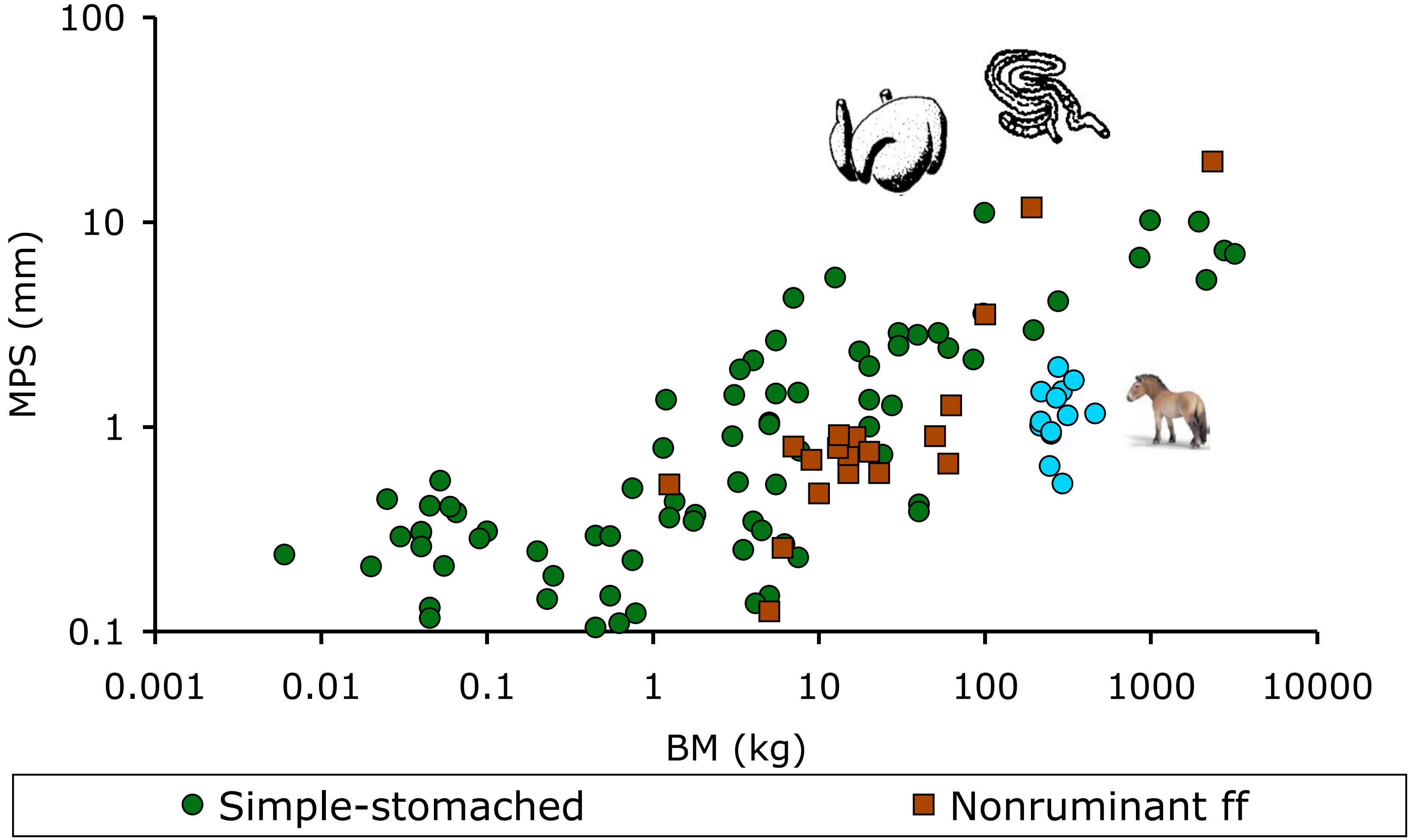

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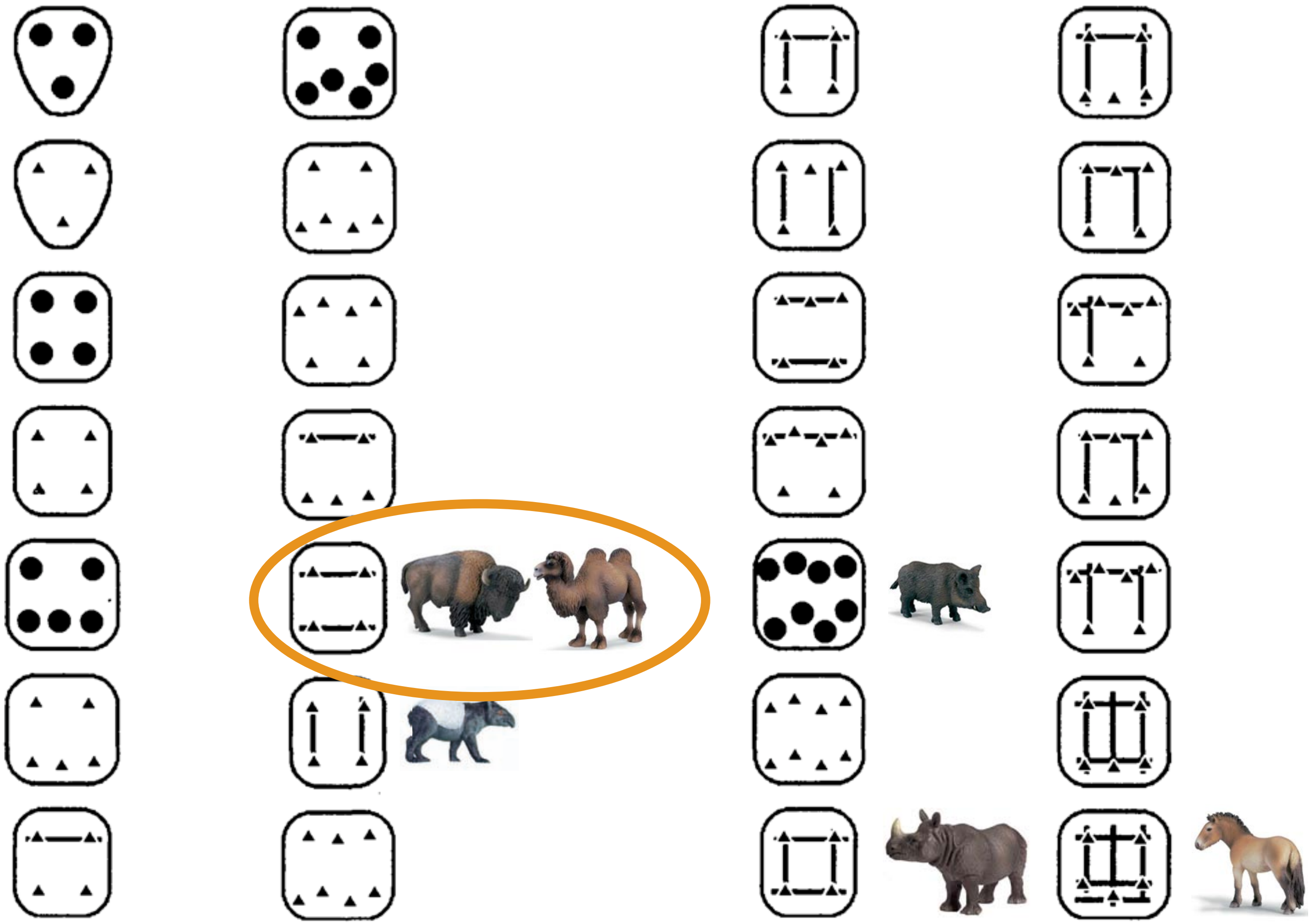

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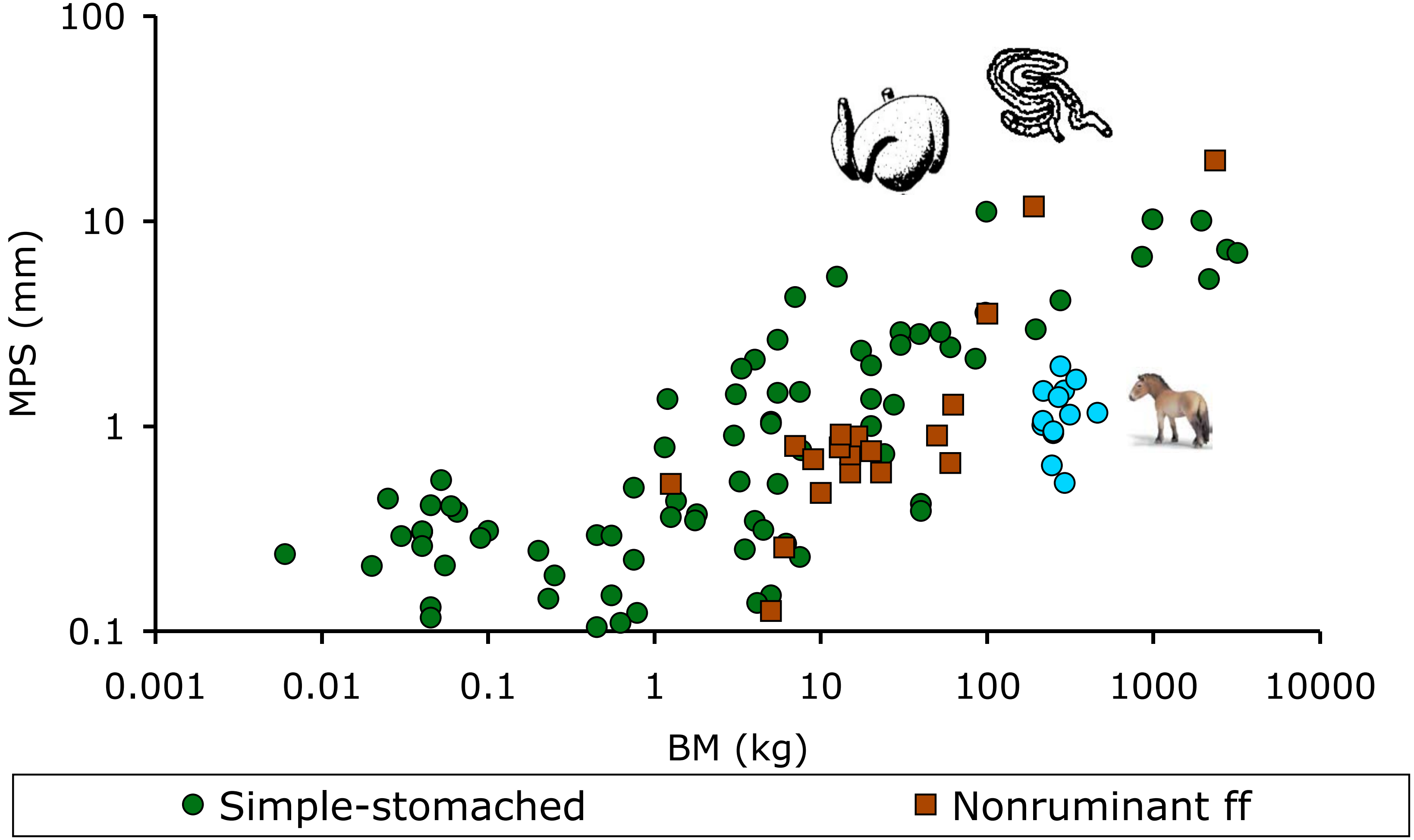
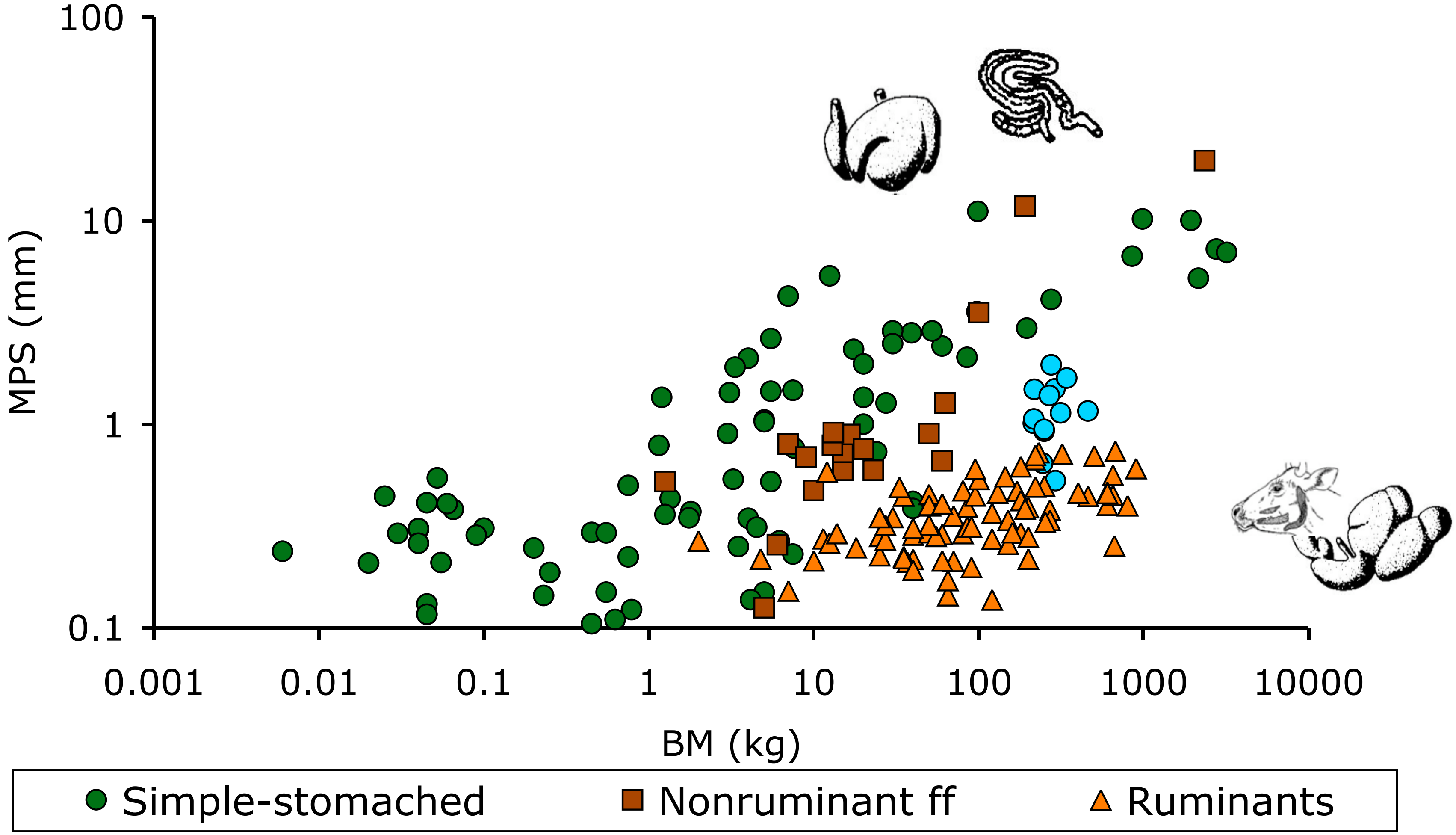


from Fritz (2007)

Ingesta particle size (chewing efficiency)



from Fritz (2007)

Why can't everyone just chew more?

Chewing in ruminants and nonruminants

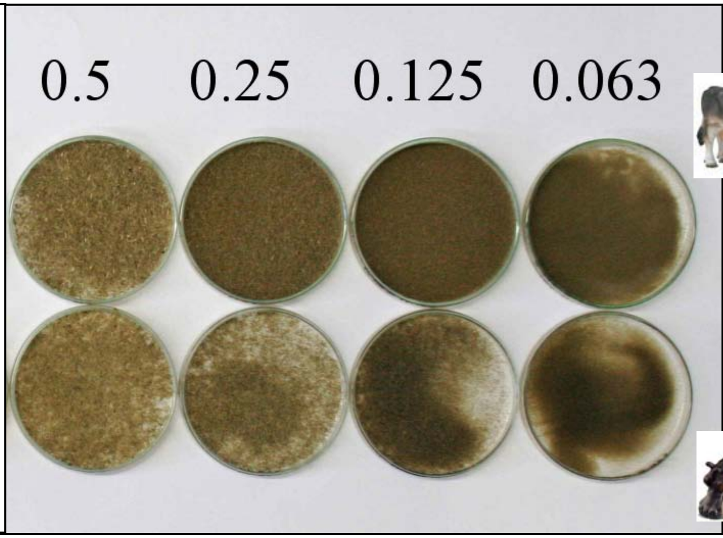


Photo A. Schwarm

Chewing in ruminants and nonruminants

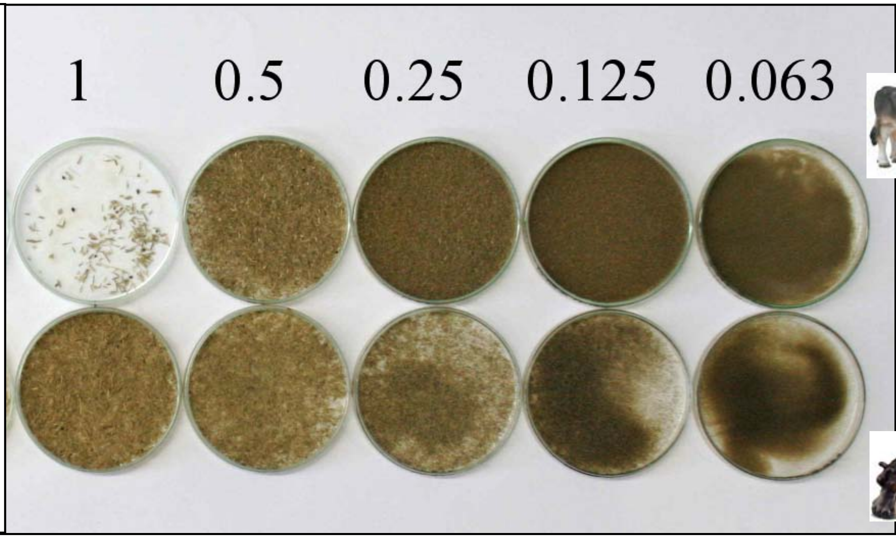


Photo A. Schwarm

Chewing in ruminants and nonruminants

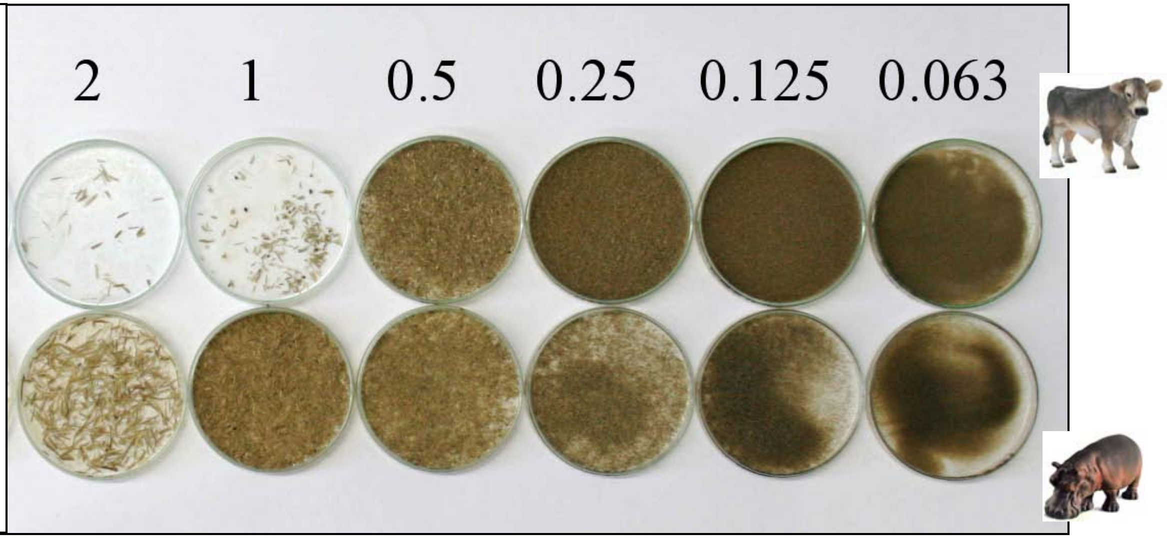


Photo A. Schwarm

Chewing in ruminants and nonruminants

Photo A. Schwarm

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Photo A. Schwarm

Chewing in ruminants and nonruminants

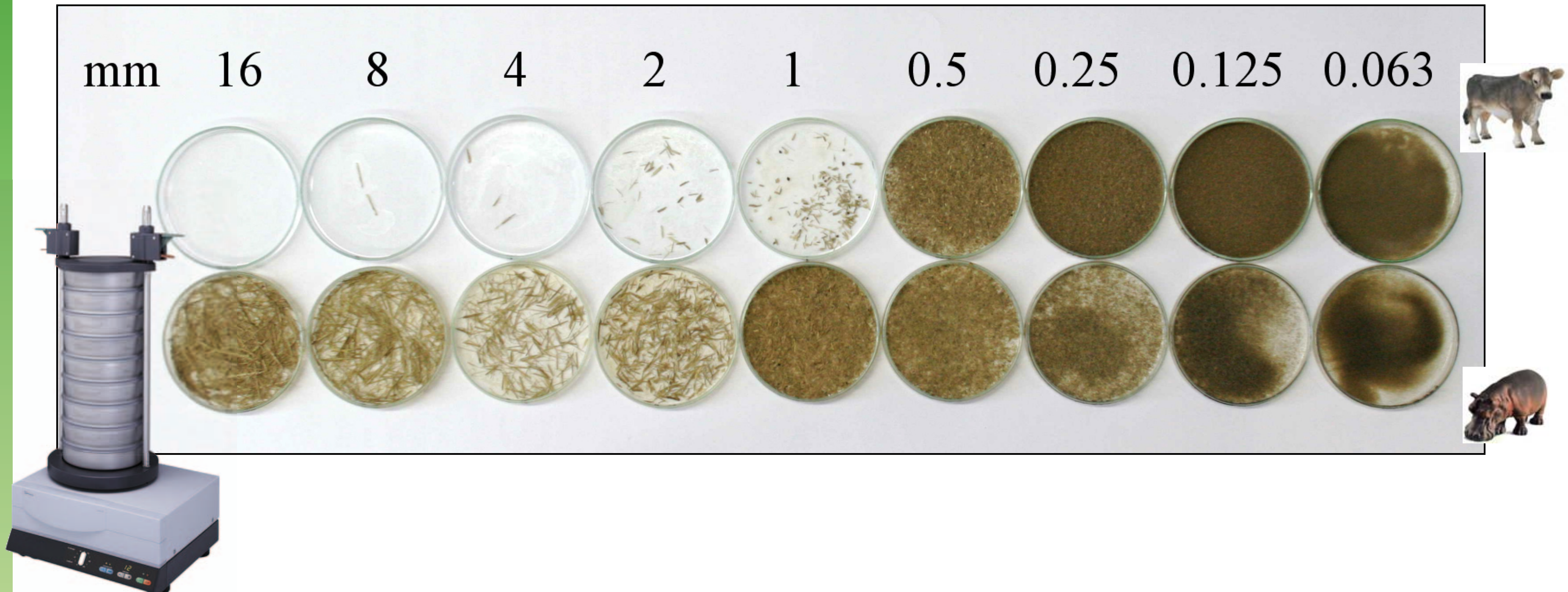
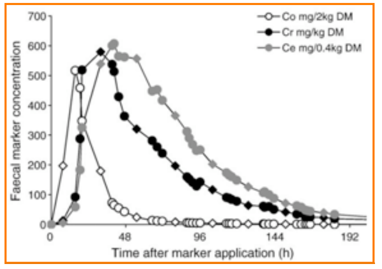


Photo A. Schwarm

How can you increase energy intake?

- higher food intake
- longer retention

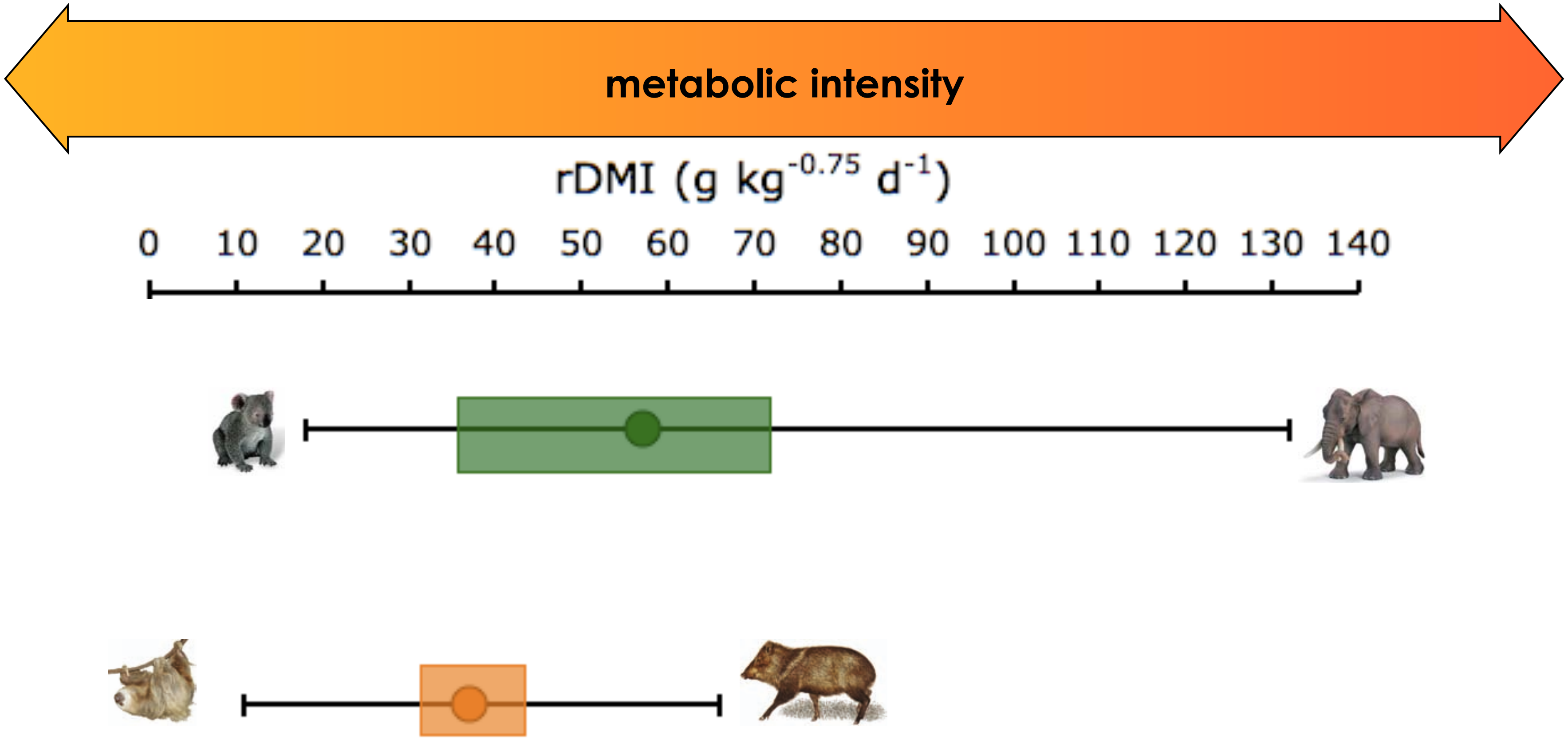
→ sorting !



- finer chewing

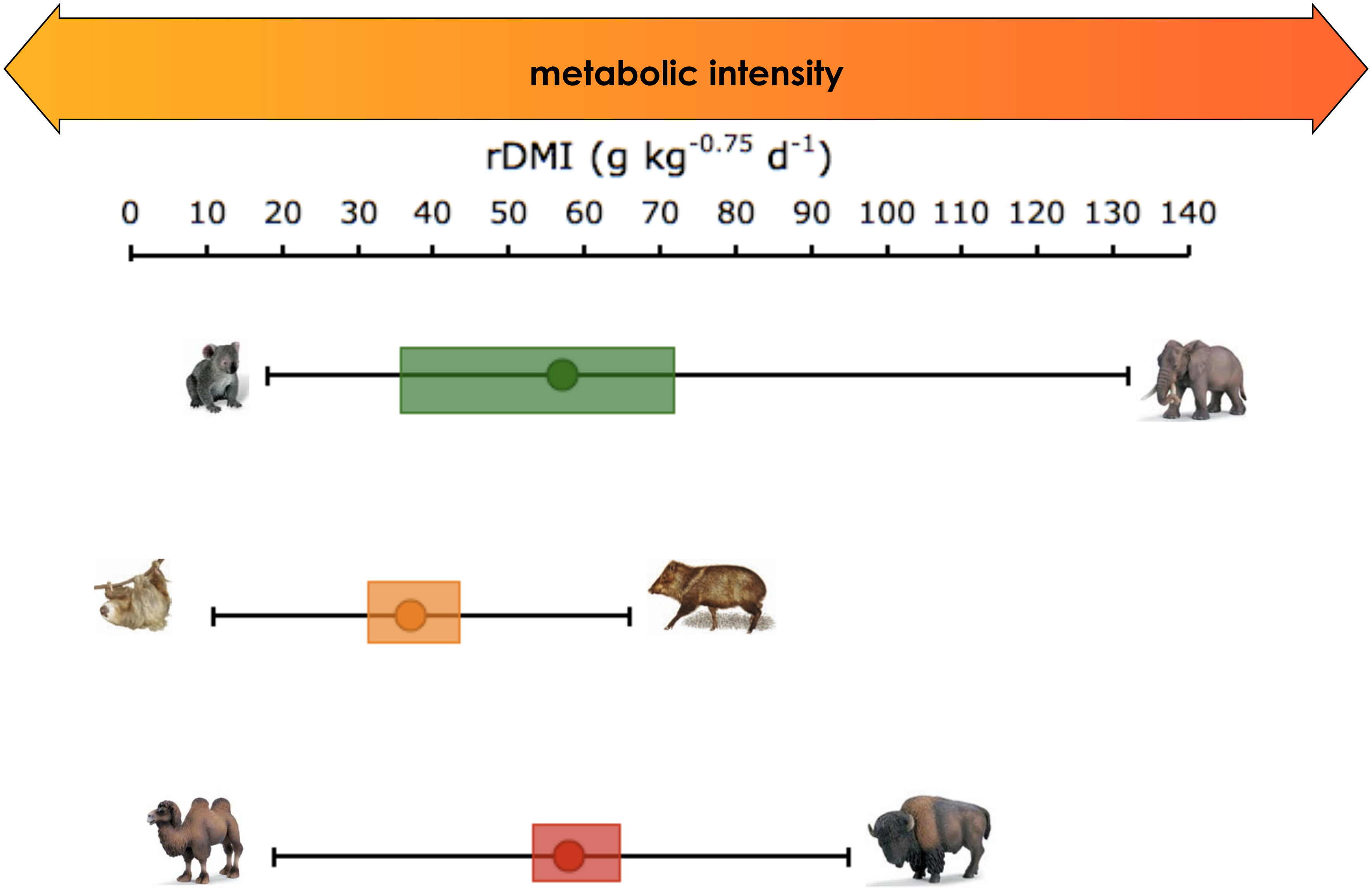
→ Sorting !

Conceptualizing herbivore diversity



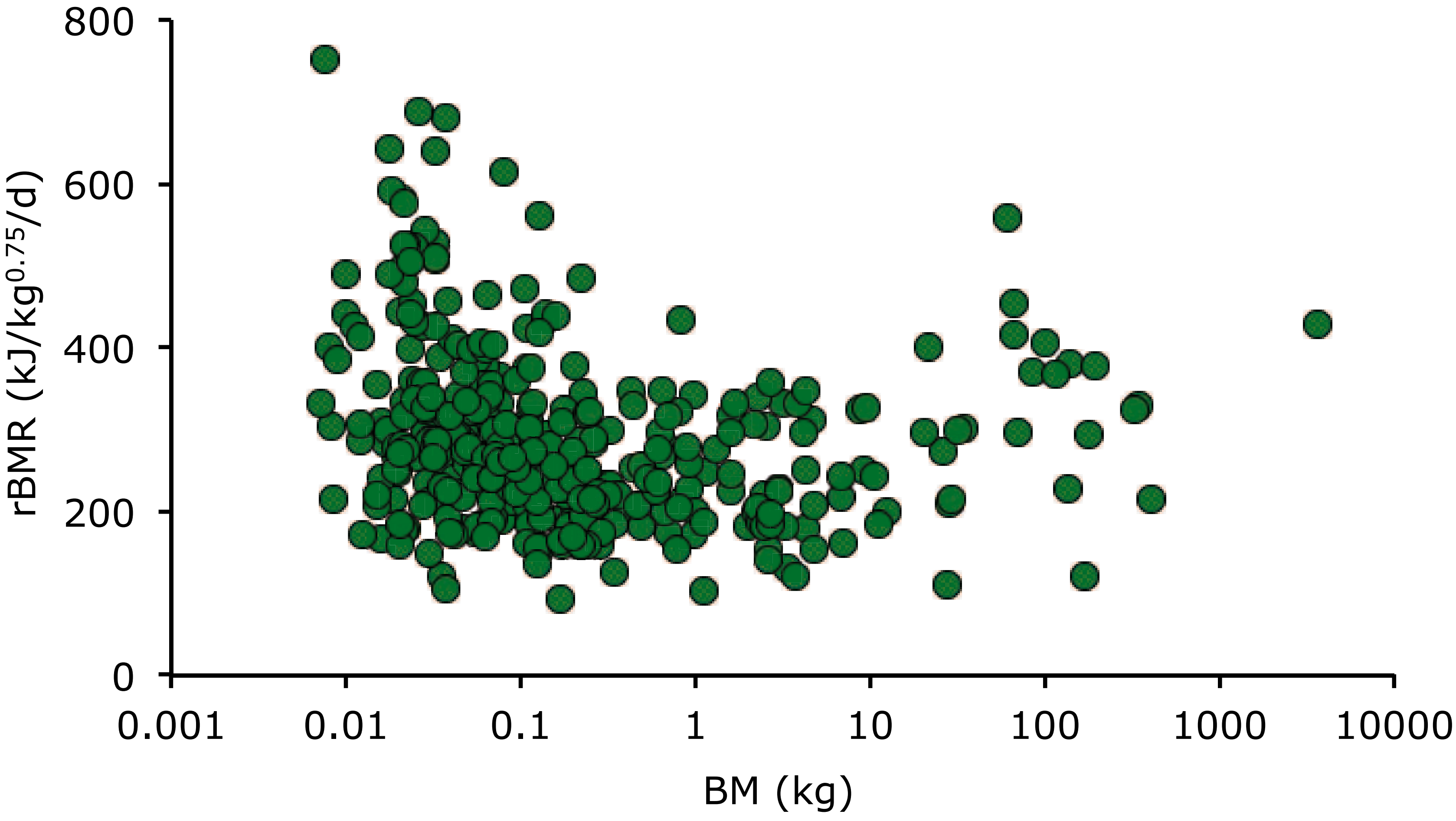
from Clauss et al. (2010)

Conceptualizing herbivore diversity



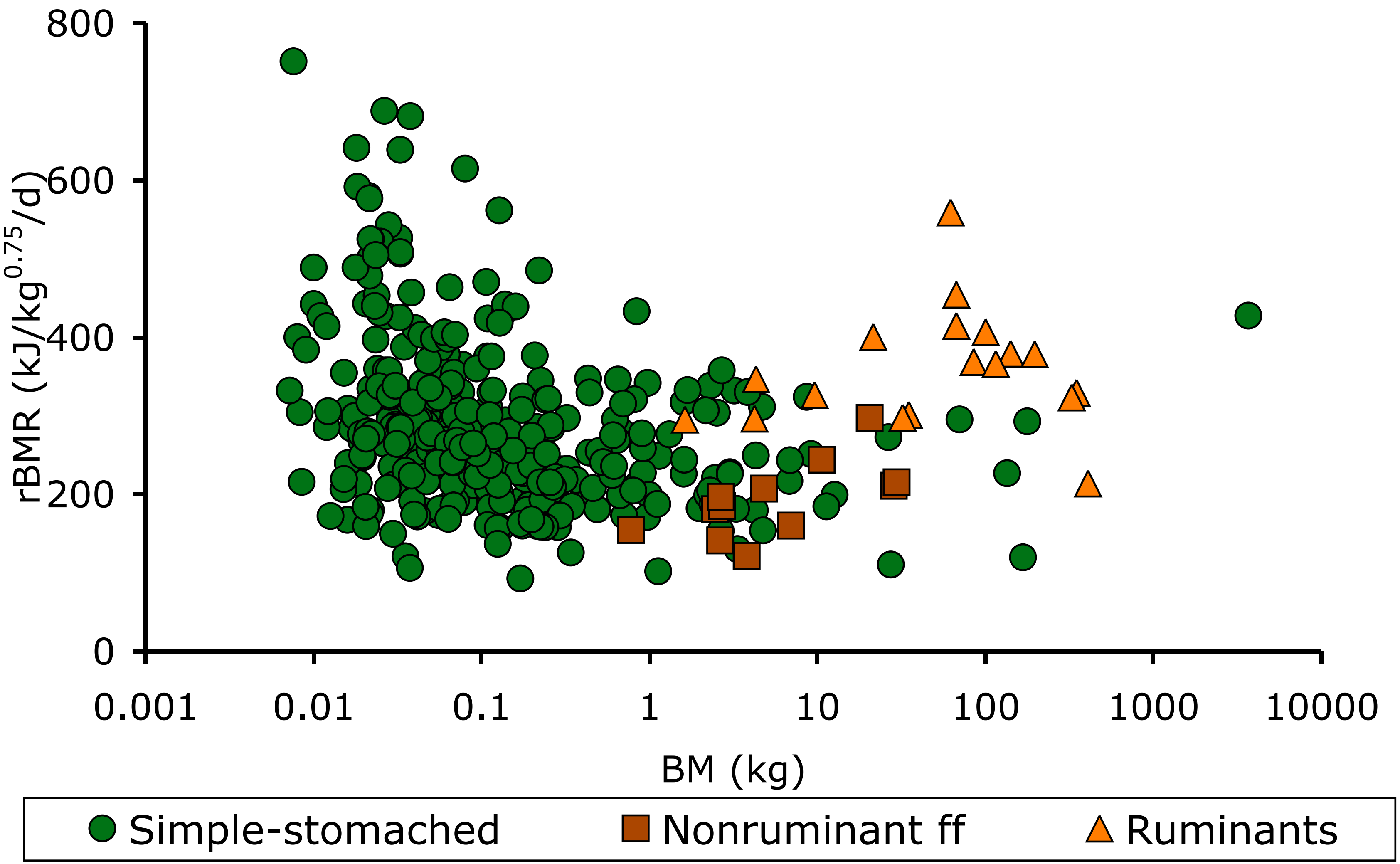
from Clauss et al. (2010)

Comparative Herbivore BMR



data from Savage et al. (2004)

Comparative Herbivore BMR



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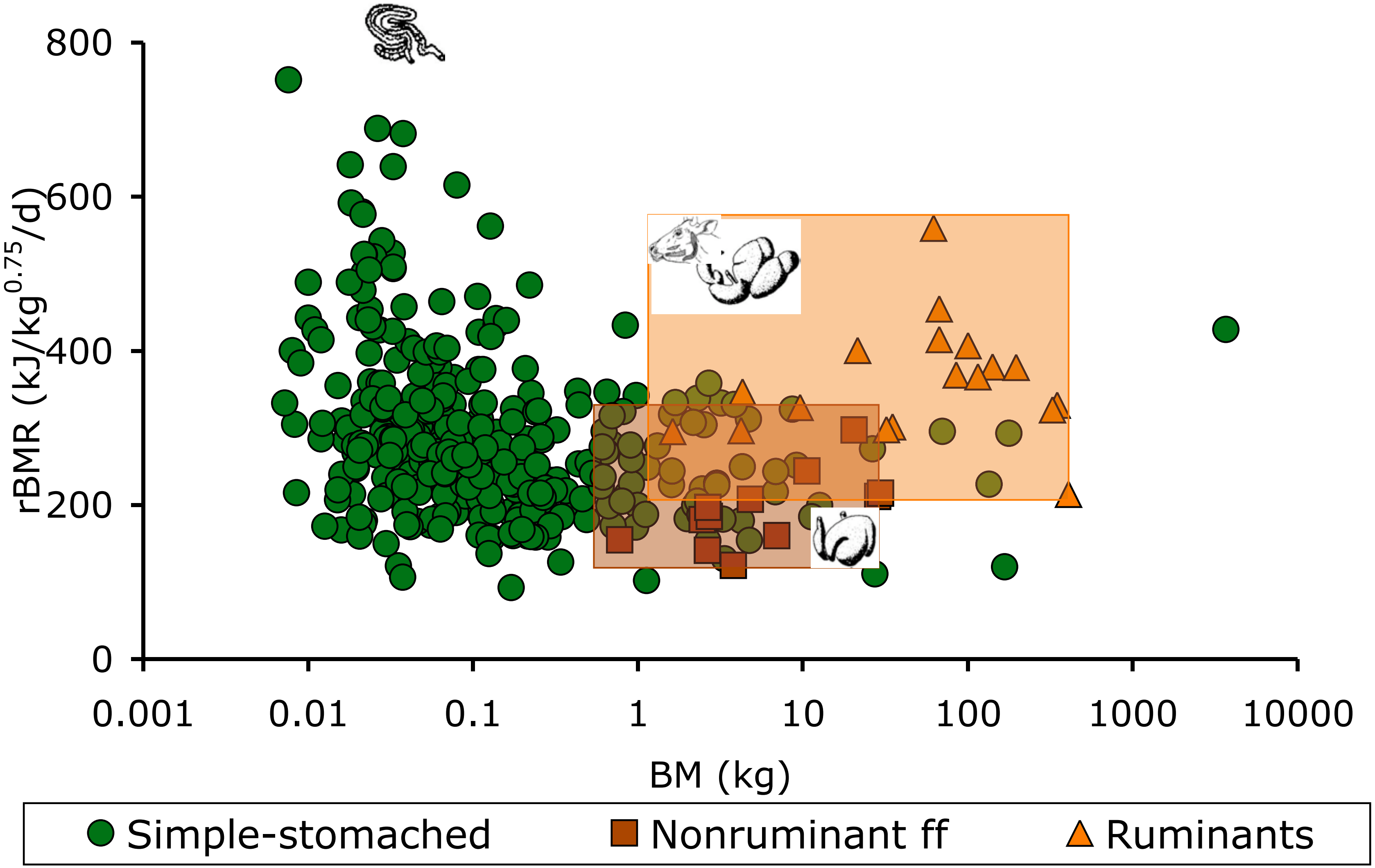
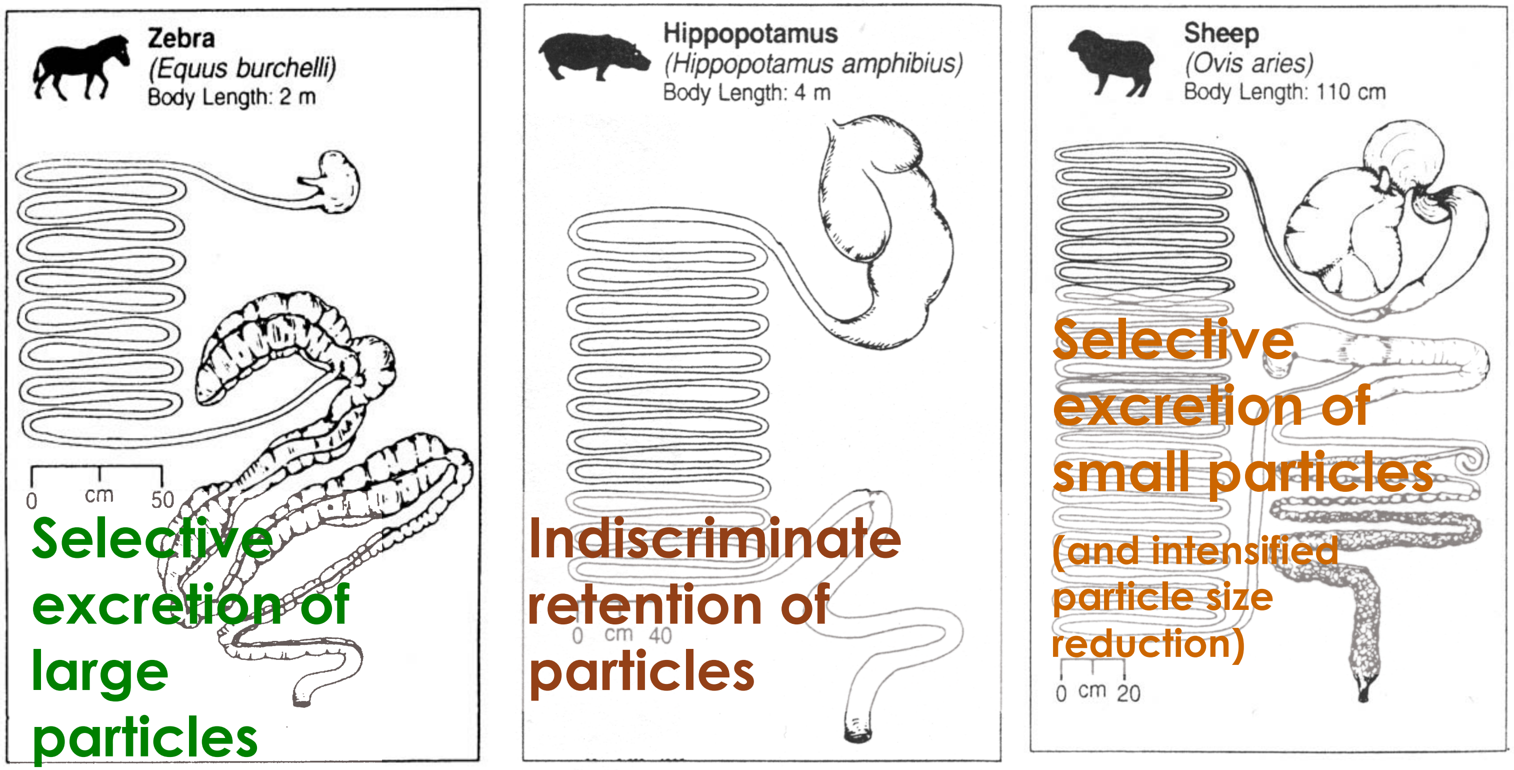
Comparative Herbivore BMR



data from Savage et al. (2004)

Foregut vs. Hindgut Fermentation



Selective excretion of large particles

Indiscriminate retention of particles

Selective excretion of small particles
(and intensified particle size reduction)

"no intake limitation"

"severe intake limitation"

"lessened intake limitation"

from Stevens und Hume (1995)

Digestive and Metabolic Strategies

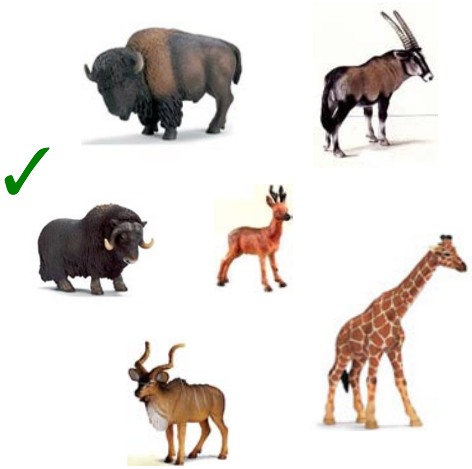
  

Low intake ⇒ long passage ⇒ ***low metabolism***	✓	✓	
High intake ⇒ differentiated passage ⇒ ***high metabolism***	✓	✗	

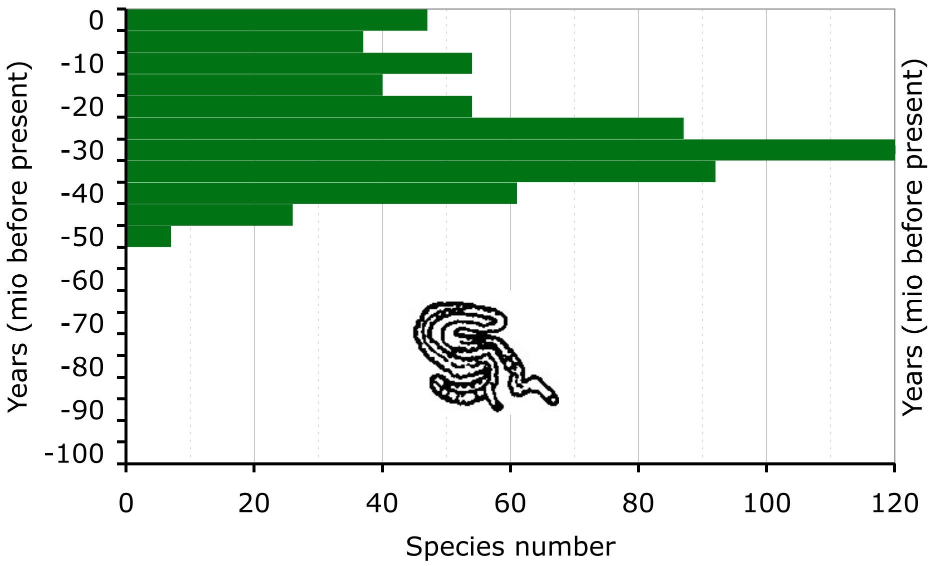
Digestive and Metabolic Strategies

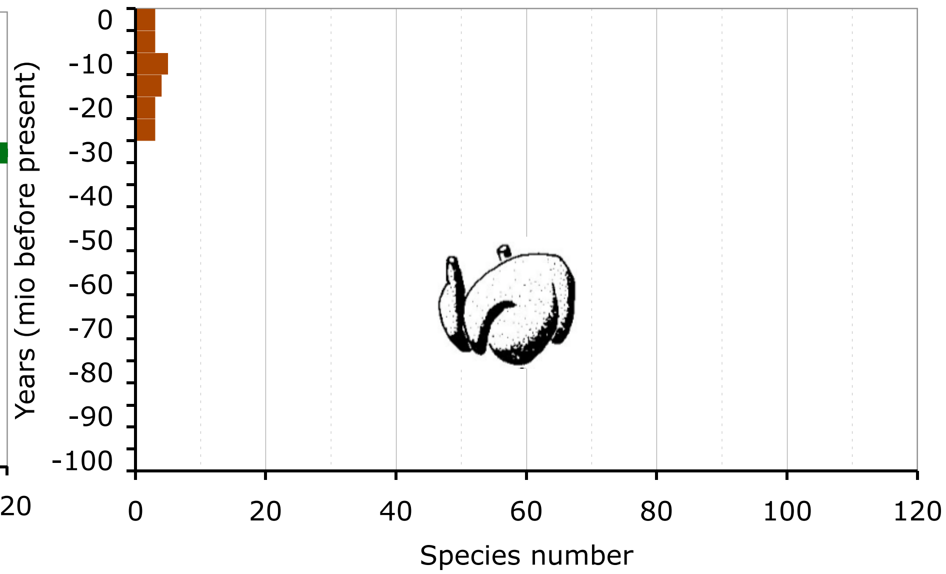
			
Low intake ⇒ long passage ⇒ ***low metabolism***	✓	✓	✓ 
High intake ⇒ differentiated passage ⇒ ***high metabolism***	✓	✗	

Digestive and Metabolic Strategies

				
Low intake $\Rightarrow$ long passage $\Rightarrow$ ***low metabolism***	✓	✓	✓	
High intake $\Rightarrow$ differentiated passage $\Rightarrow$ ***high metabolism***	✓	✗	✓	

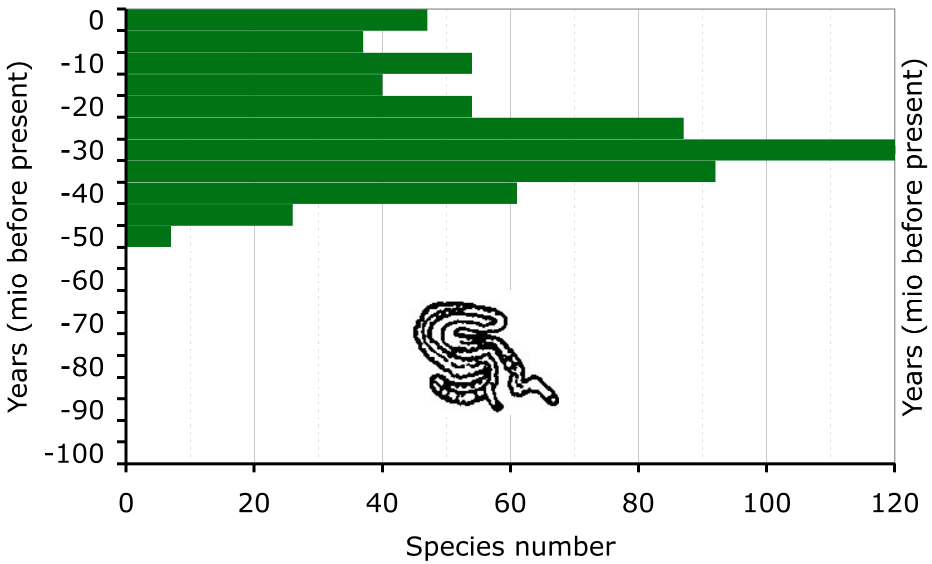
European Mammal Herbivores in Deep Time

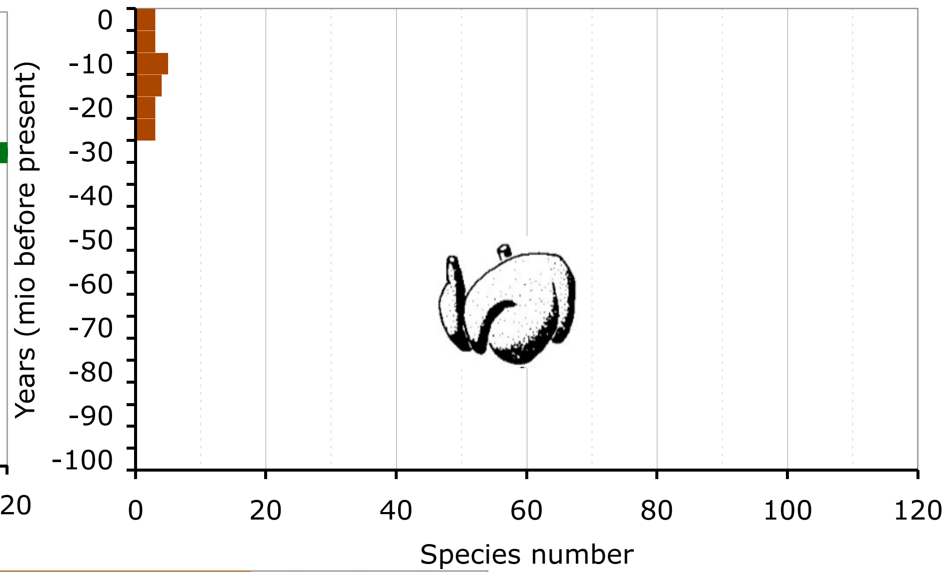


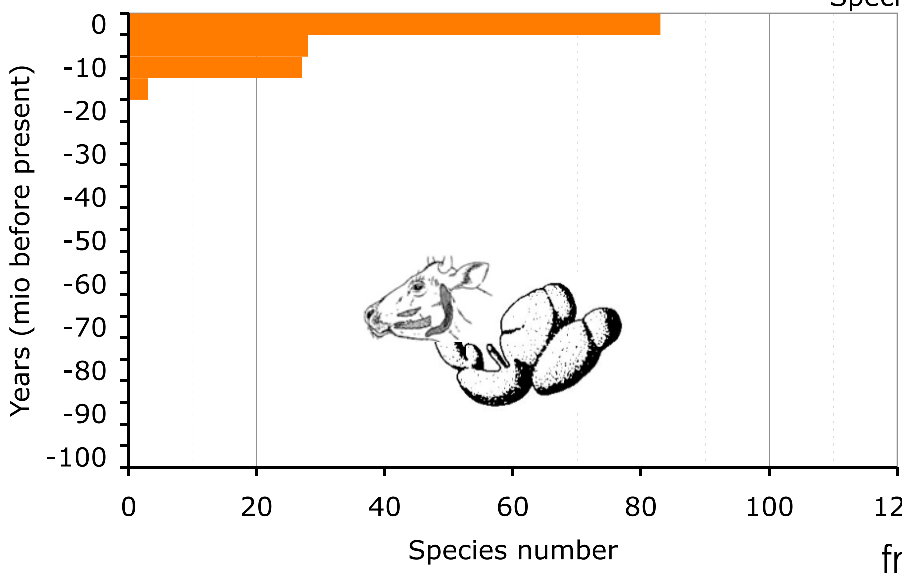


from Langer (1991)

European Mammal Herbivores in Deep Time

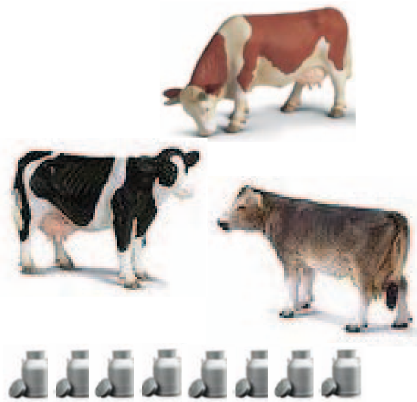




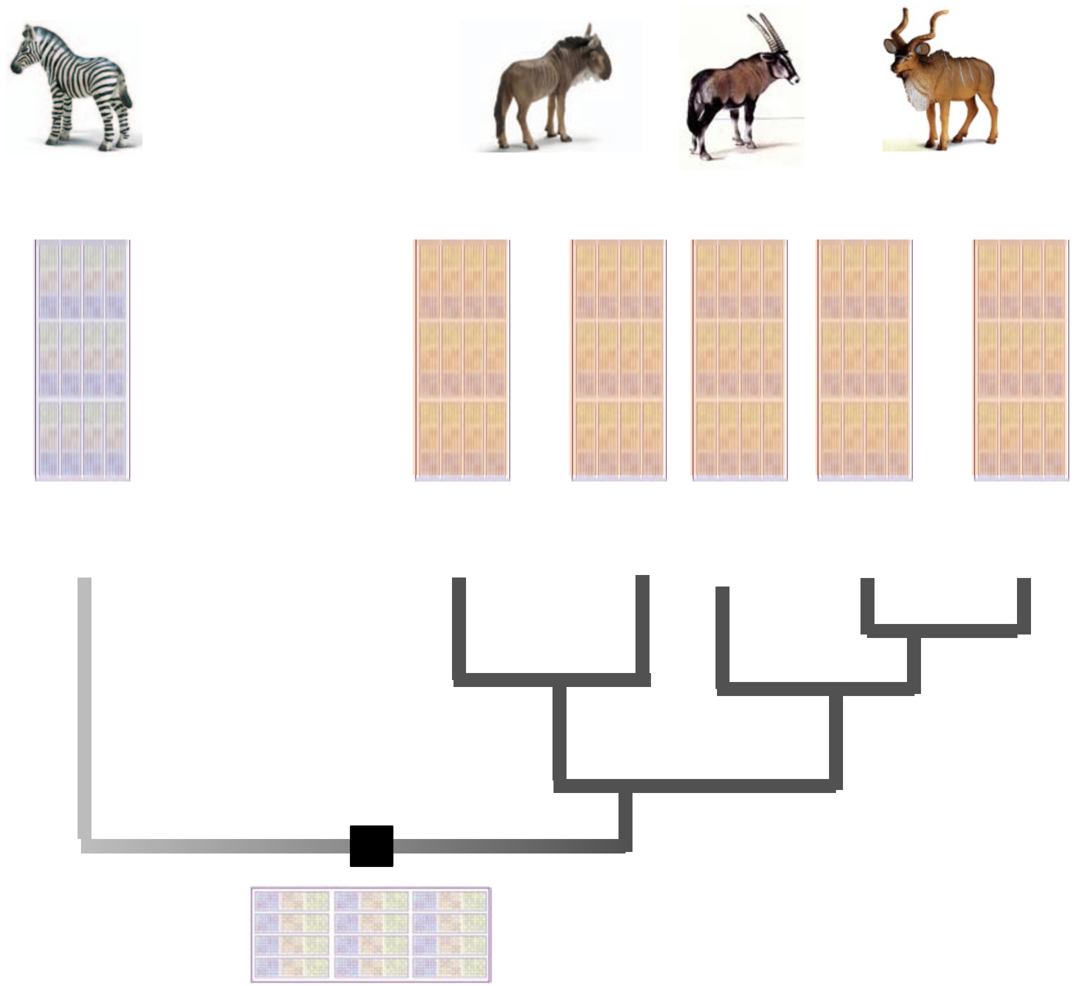


from Langer (1991)

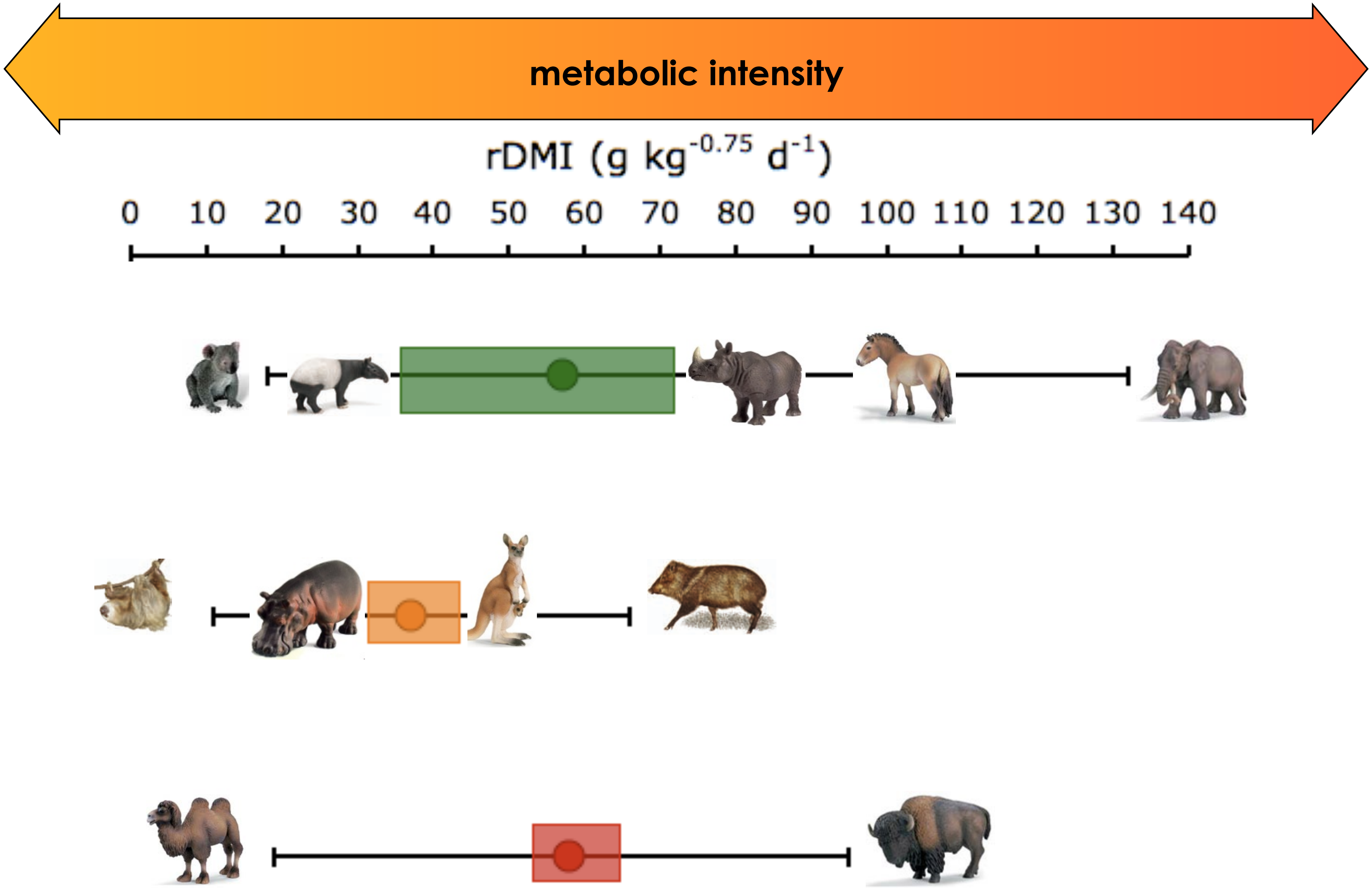
Digestive and Metabolic Strategies

				
Low intake ⇒ long passage ⇒ ***low BMR***	✓	✓	✓	
High intake ⇒ differentiated passage ⇒ ***high BMR***	✓	✗	✓	

Detailed function: solutions of different efficiency



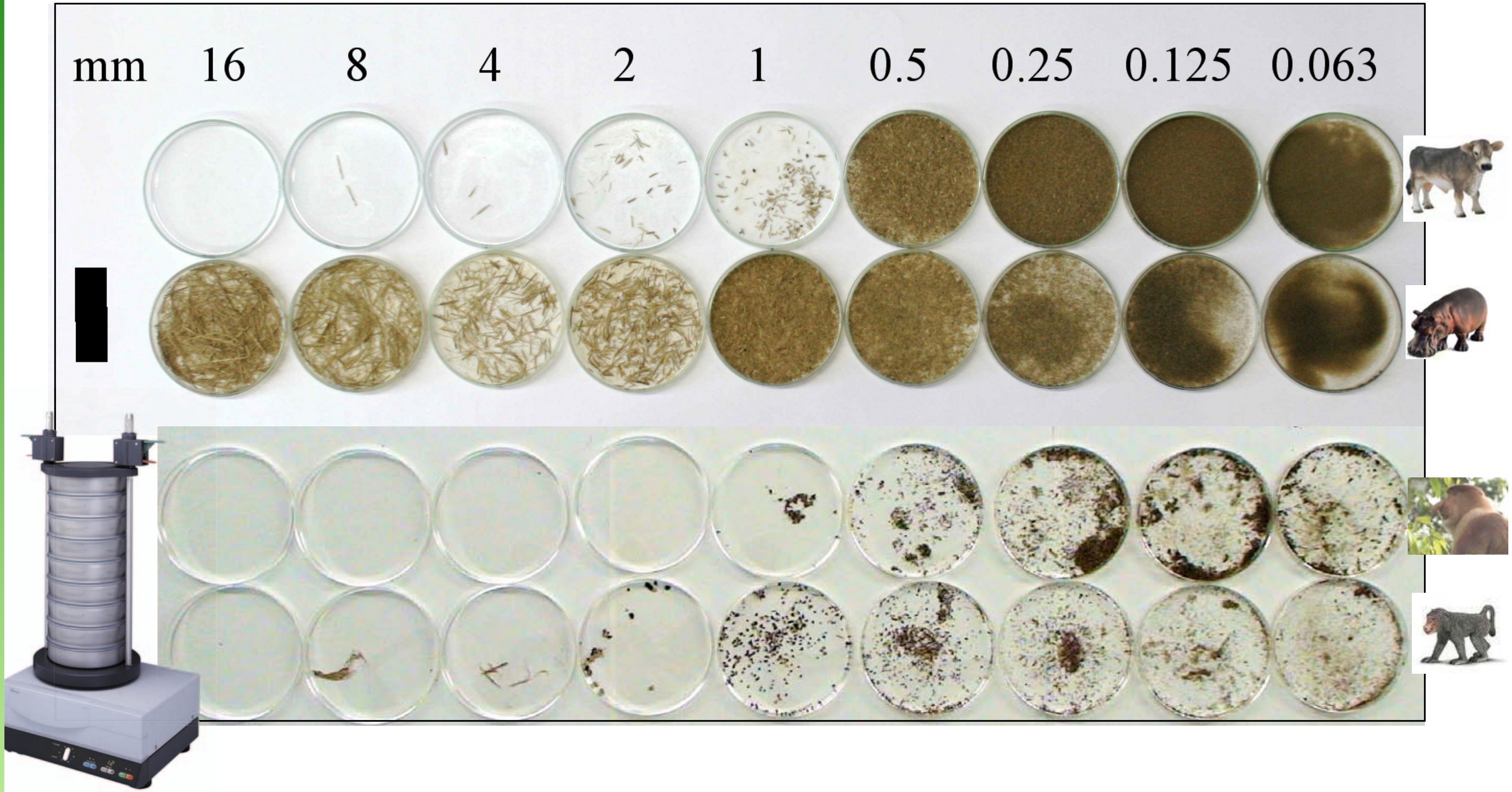
Conceptualizing herbivore diversity



from Clauss et al. (2010)

Matsuda et al. (2011)

Chewing in ruminants and nonruminants

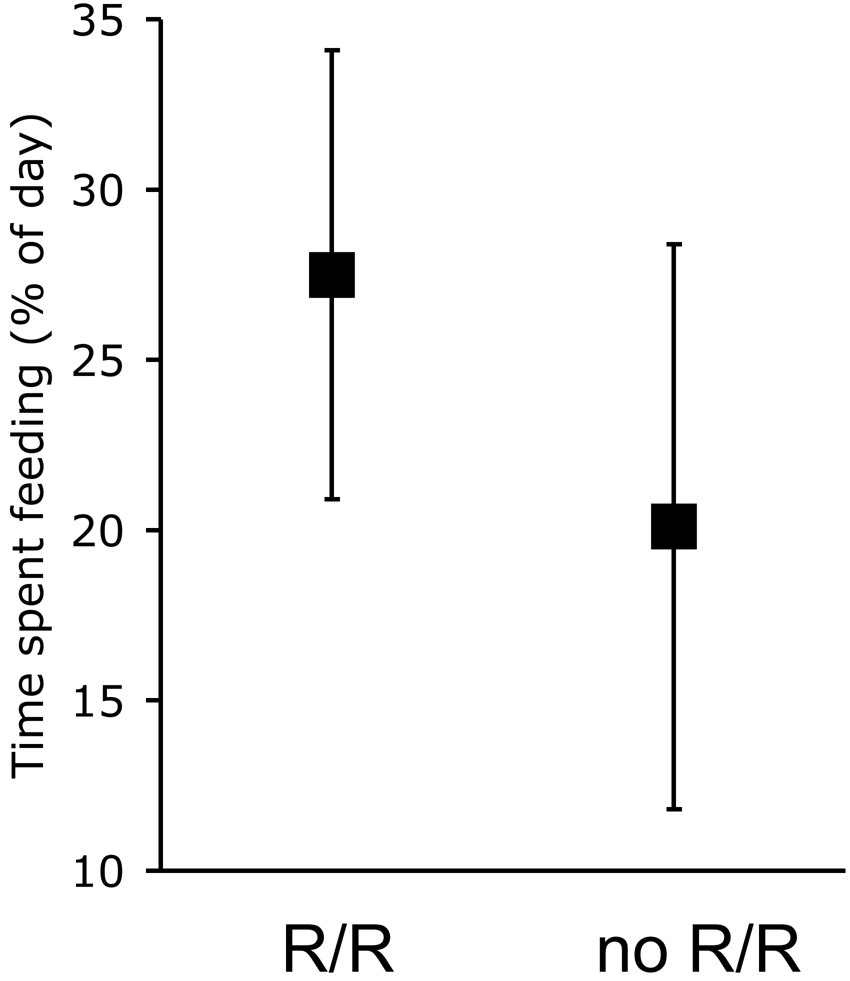


Matsuda et al. (subm.)

biology
letters
Physiology

Regurgitation and remastication in the foregut-fermenting proboscis monkey (*Nasalis larvatus*)

Ikki Matsuda[1,*], Tadahiro Murai[1], Marcus Clauss[2], Tomomi Yamada[3], Augustine Tuuga[4], Henry Bernard[5] and Seigo Higashi[6]



Matsuda et al. (2011)

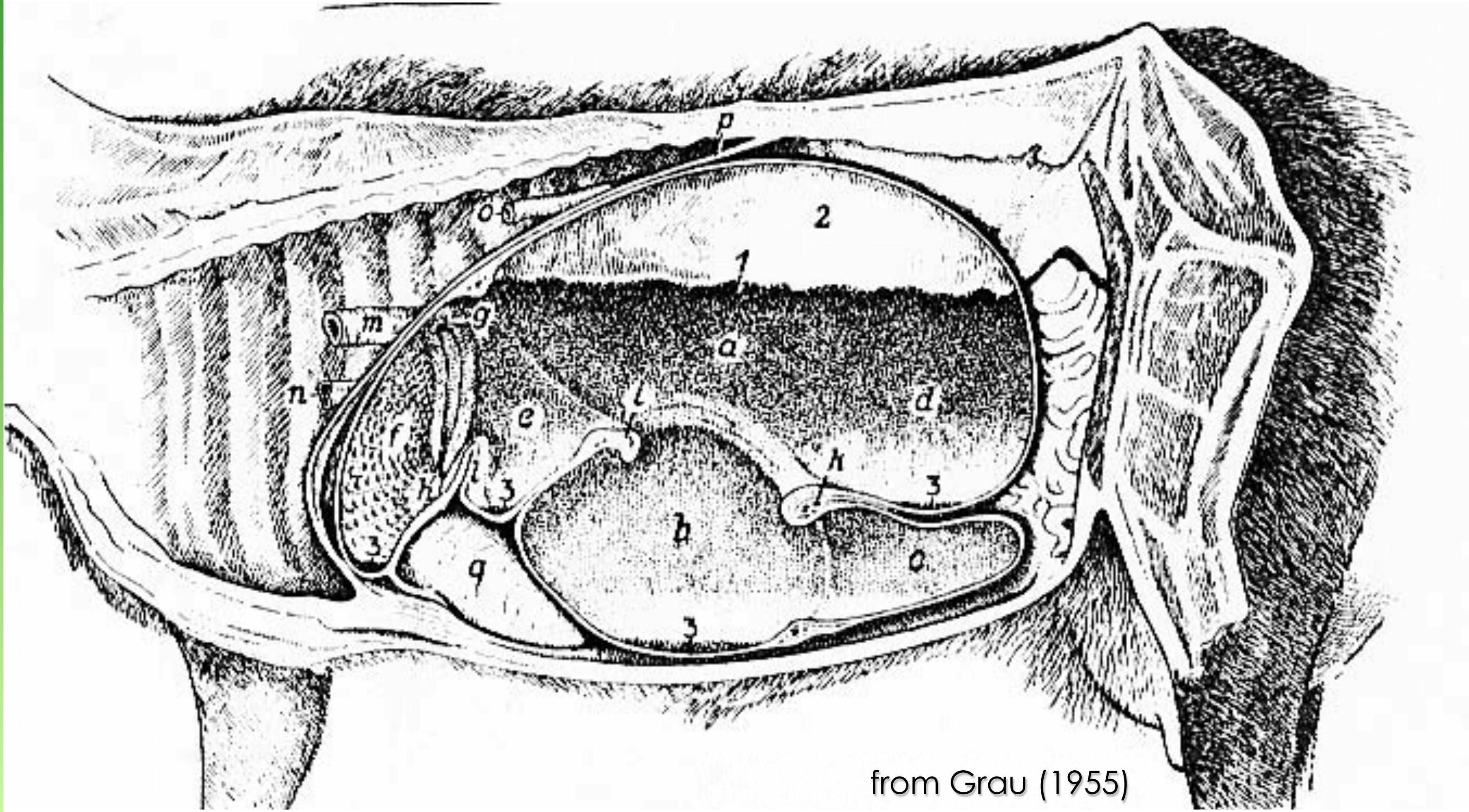
Summary I

1. Fibre digestion with the help of symbiotic microbes is widespread in the animal kingdom
2. So is the direct use of microbial biomass - either via coprophagy, farming, or foregut fermentation
3. Reasons for different proportions of acetogenic and methanogenic hydrogen sinks in ruminants and nonruminants remain unclear
4. Due to its relevance for food encounter rates, harvesting mechanisms and surface/volume geometry, body size has an important influence on foraging strategies and digestive morphophysiology

Summary II

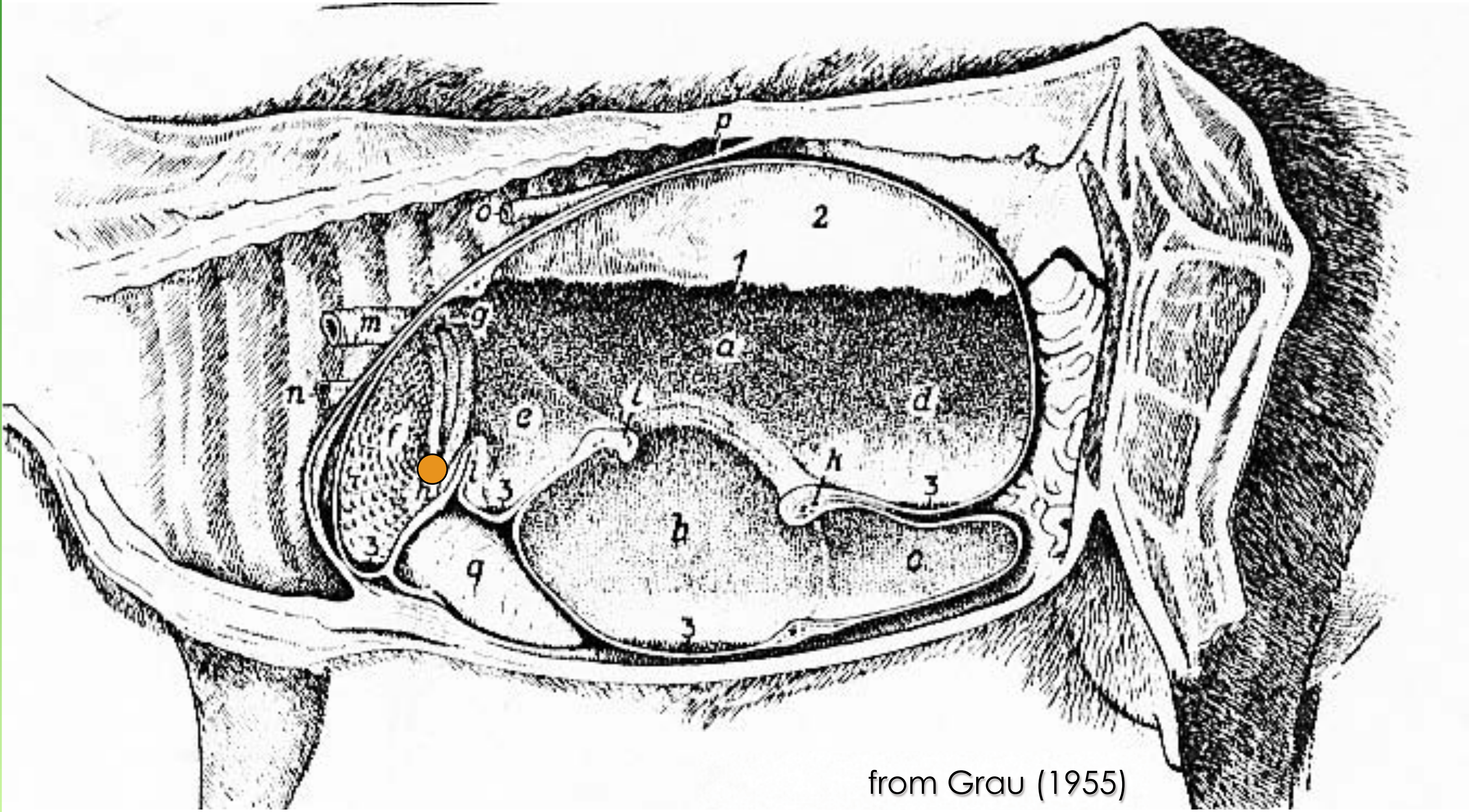
6. Different merits of foregut and hindgut fermentation (at similar metabolic intensity) remain to be fully elucidated
7. Rather than classifying herbivores according to body size or digestion type, classifying herbivores according to metabolic intensity is a promising novel approach
8. Whereas the hindgut fermenter system allows a large range of metabolic intensities, the (nonruminant) foregut fermenter system appears to restrict animals to the low metabolic intensity side of the spectrum

The rumen sorting mechanism



from Grau (1955)

The rumen sorting mechanism



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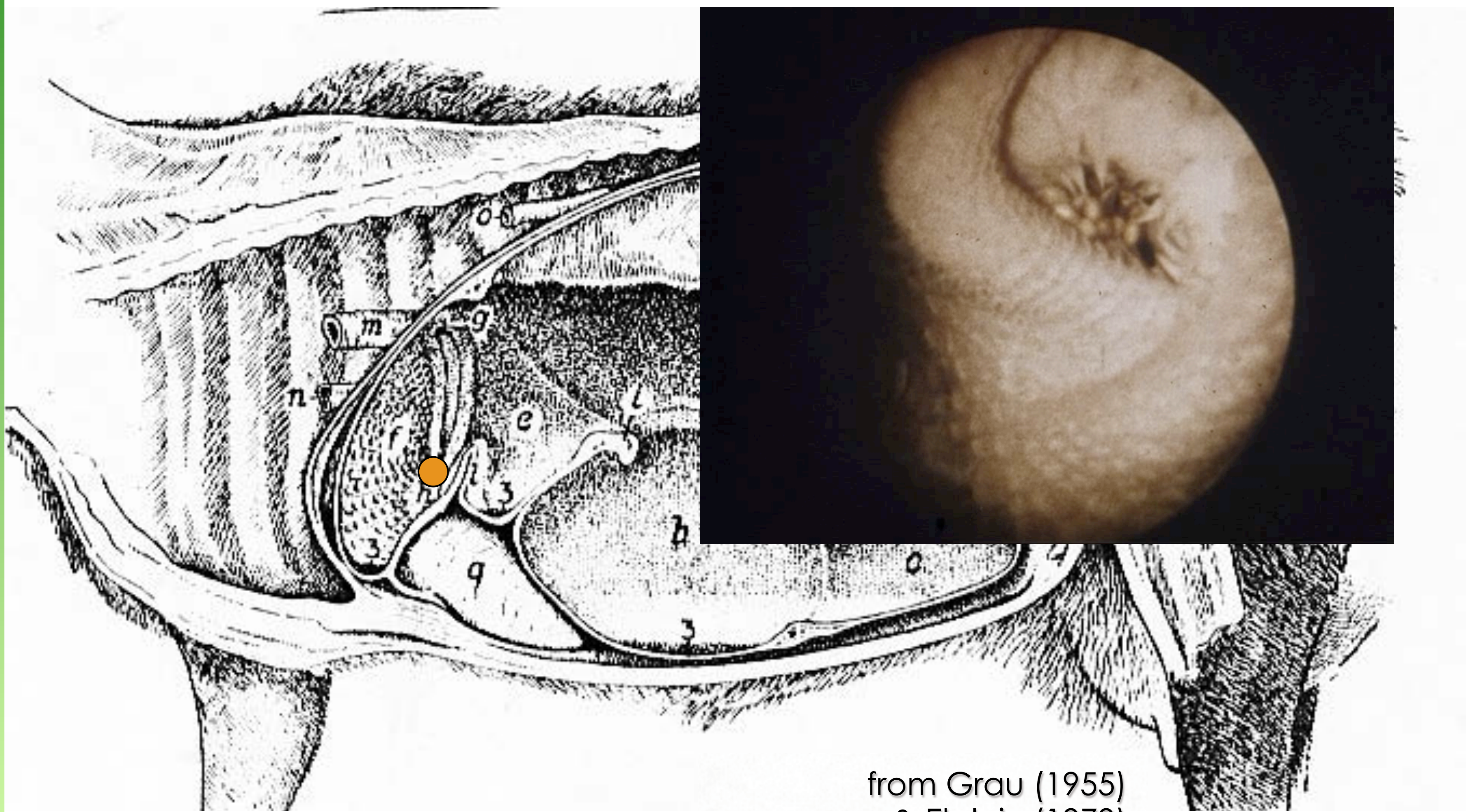
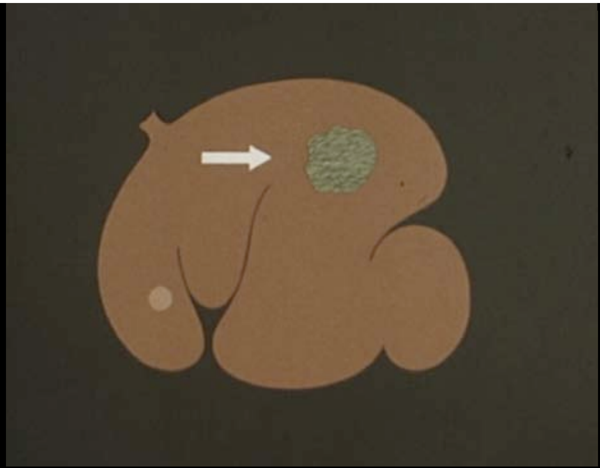
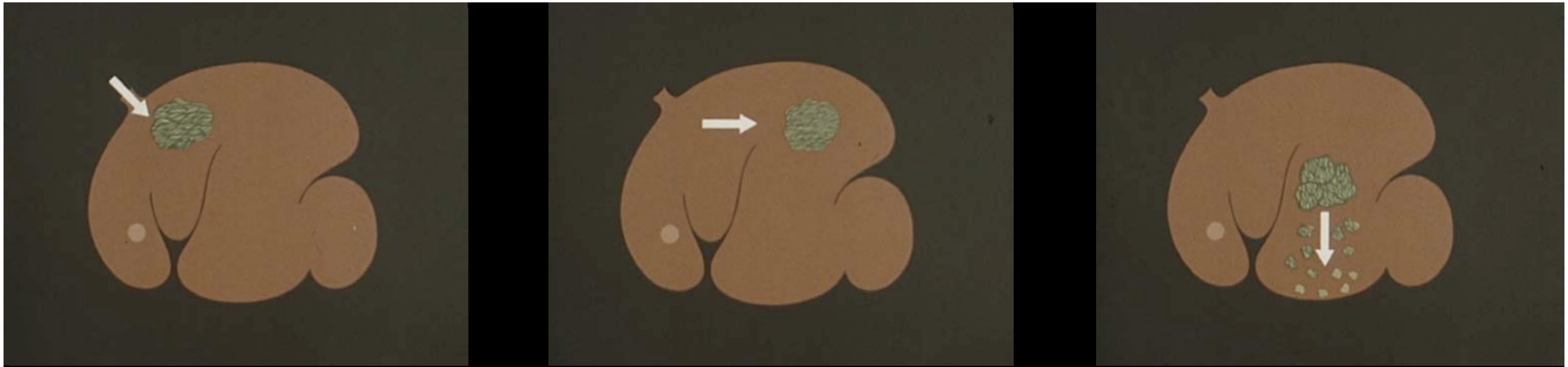


from Grau (1955)
& Ehrlein (1979)

(from Ehrlein 1979)



(from Ehrlein 1979)



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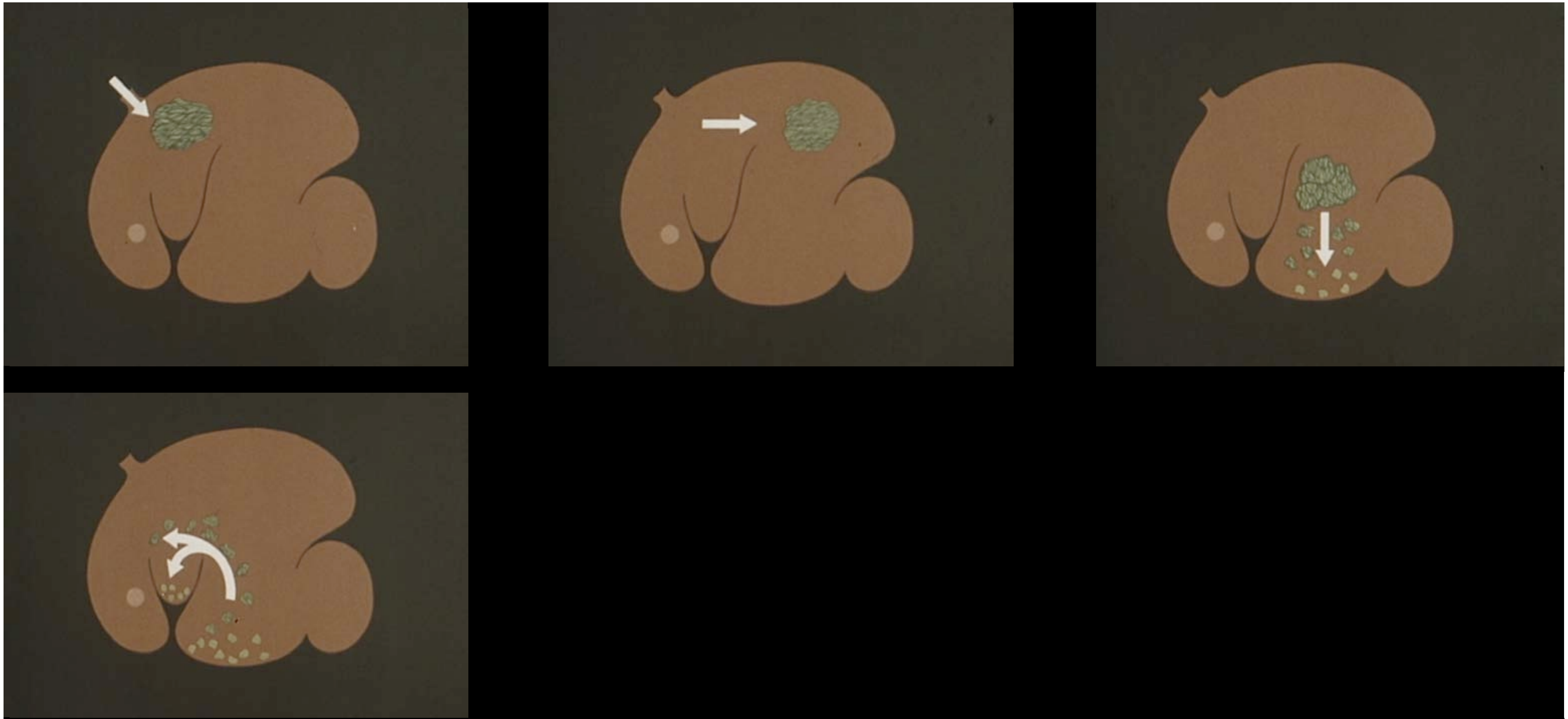
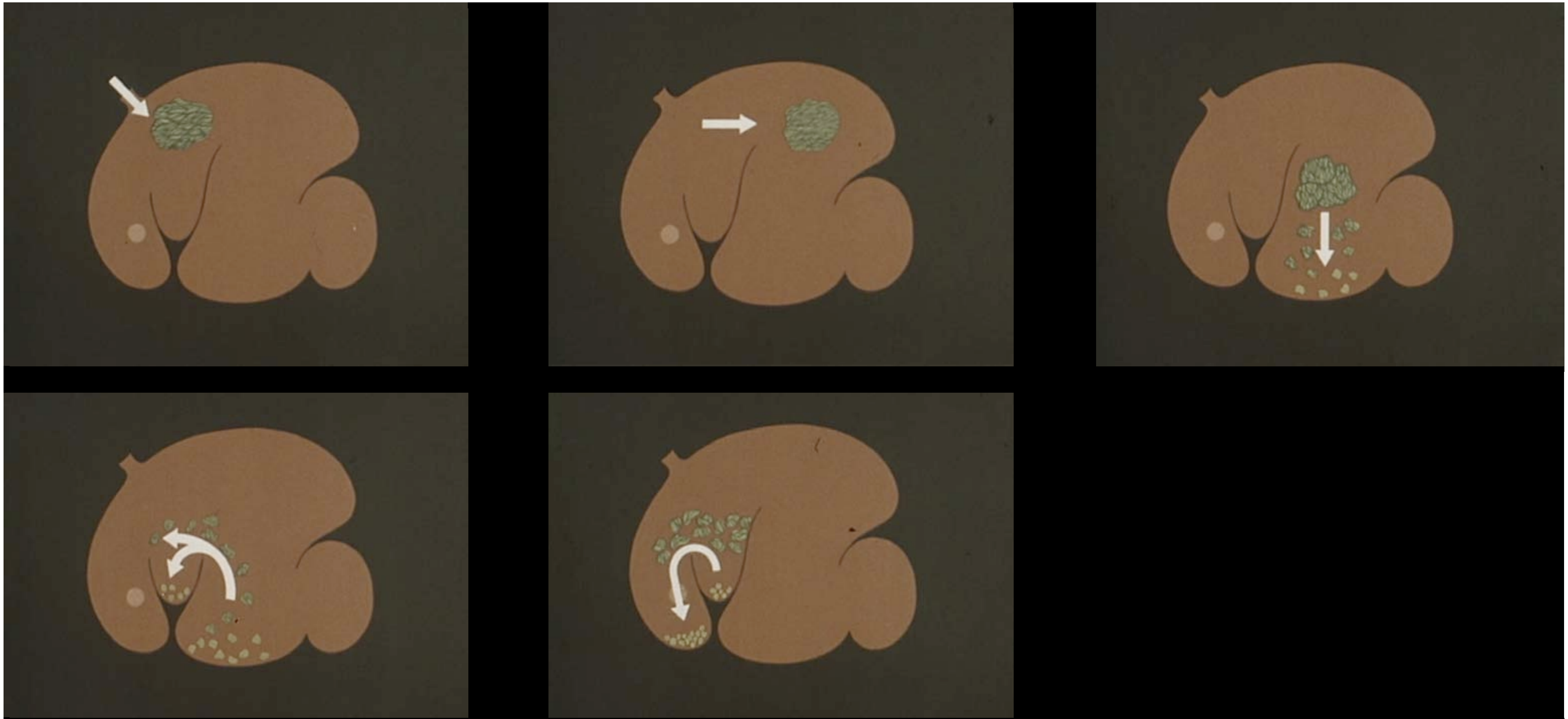


(from Ehrlein 1979)



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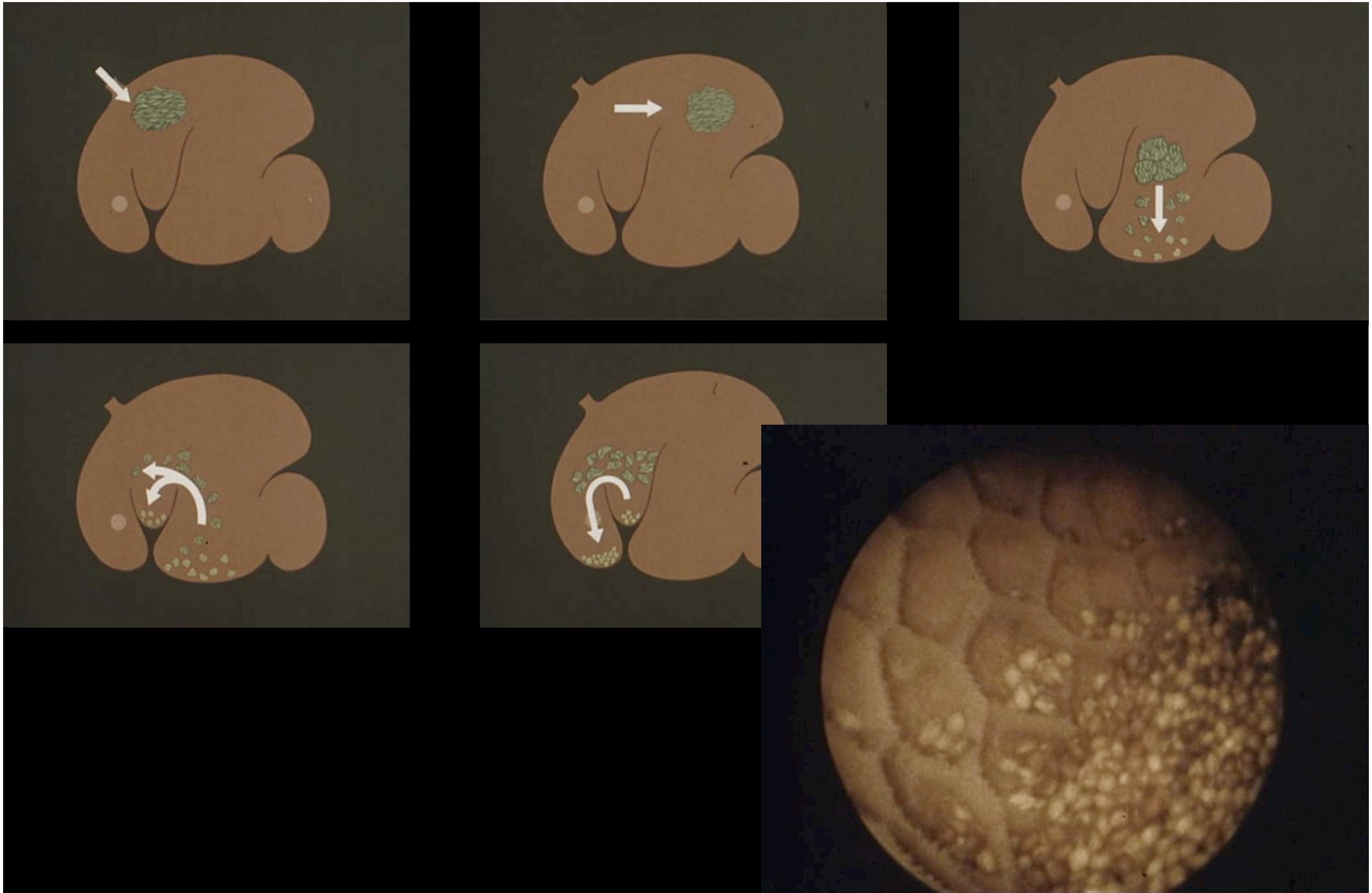

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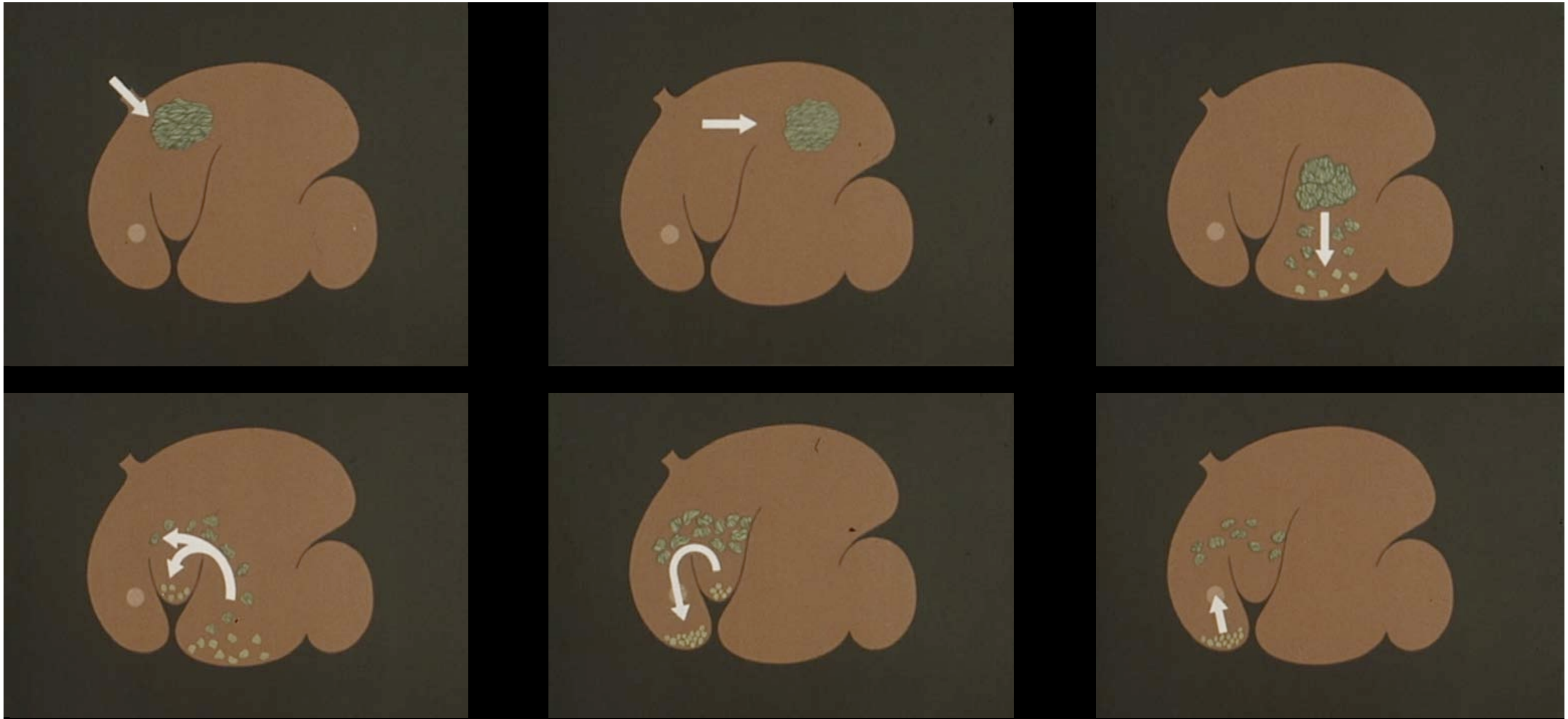

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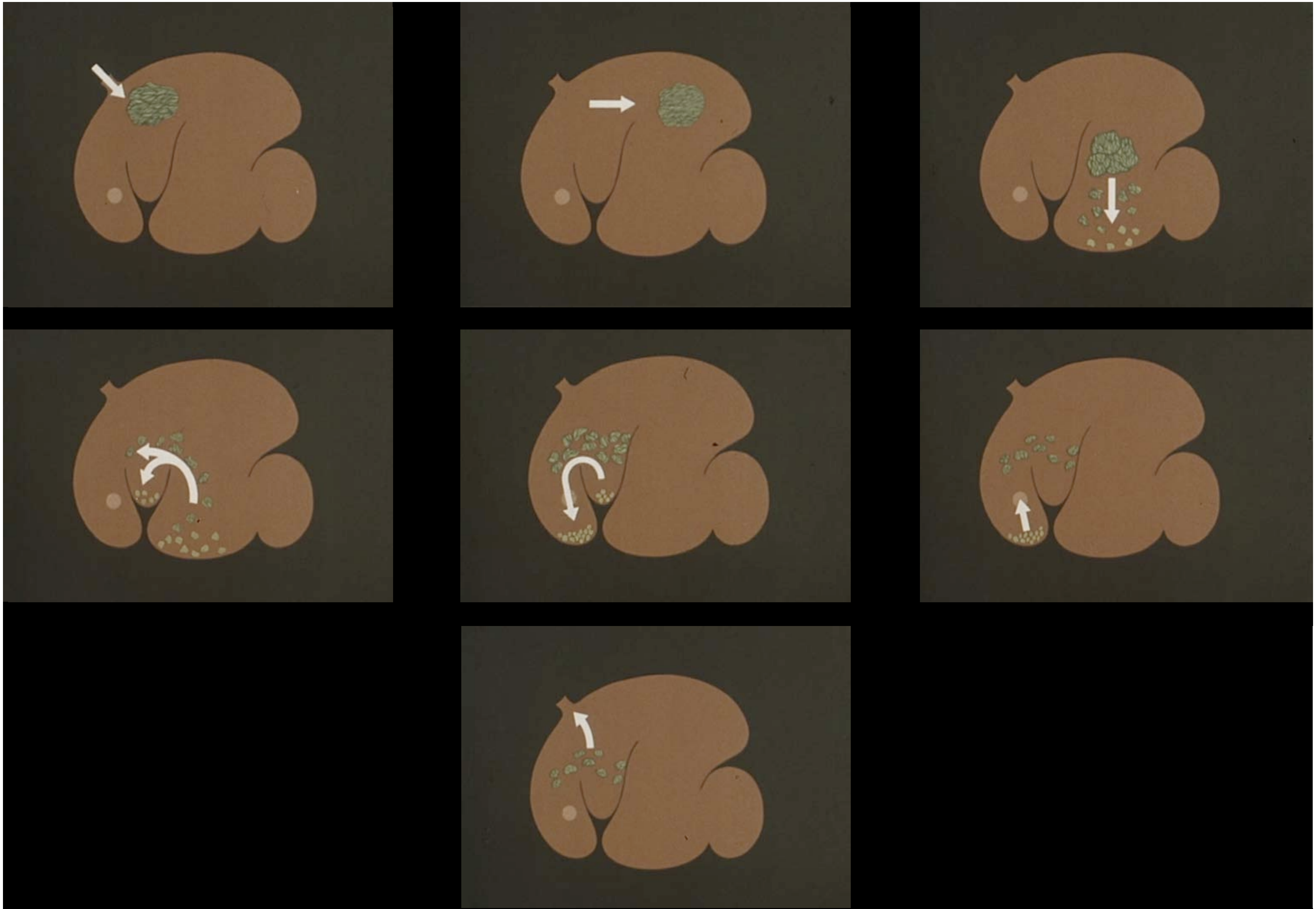
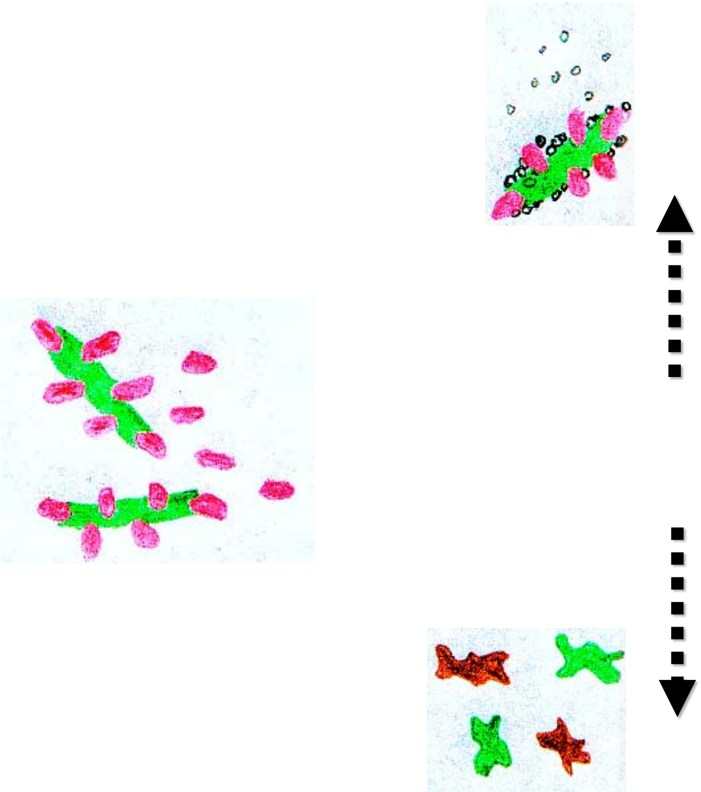


(from Ehrlein 1979)

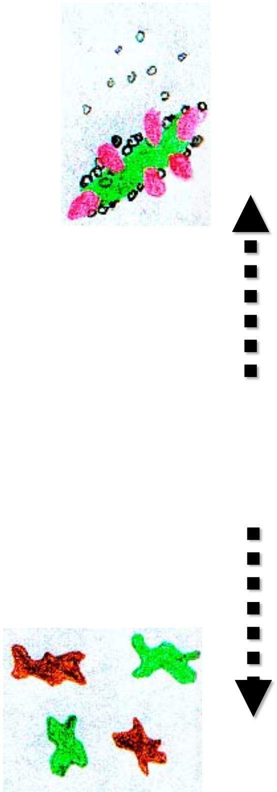
Sorting by density

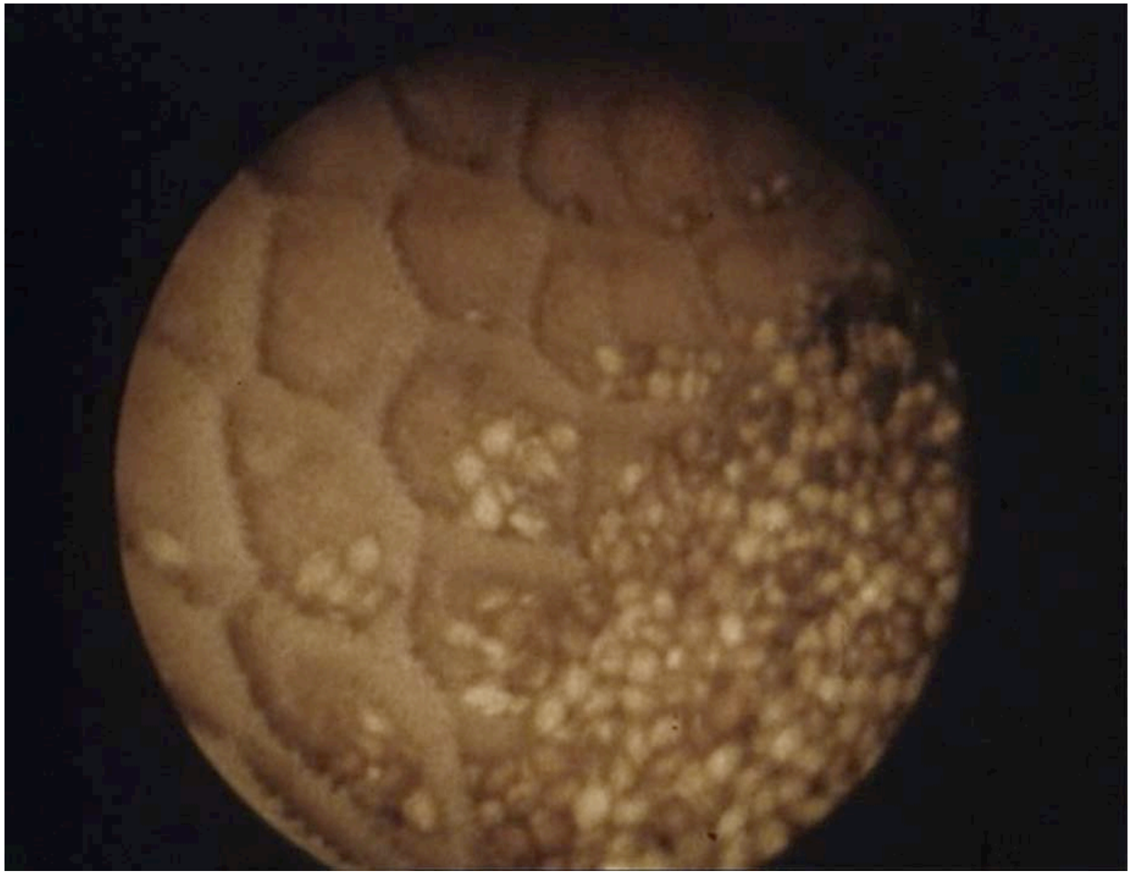


fermentation = gas production
gas bubbles = updrift

fermented particles
no gas bubbles = high density

Sorting by density





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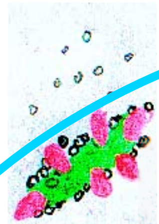
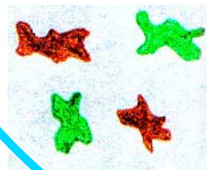
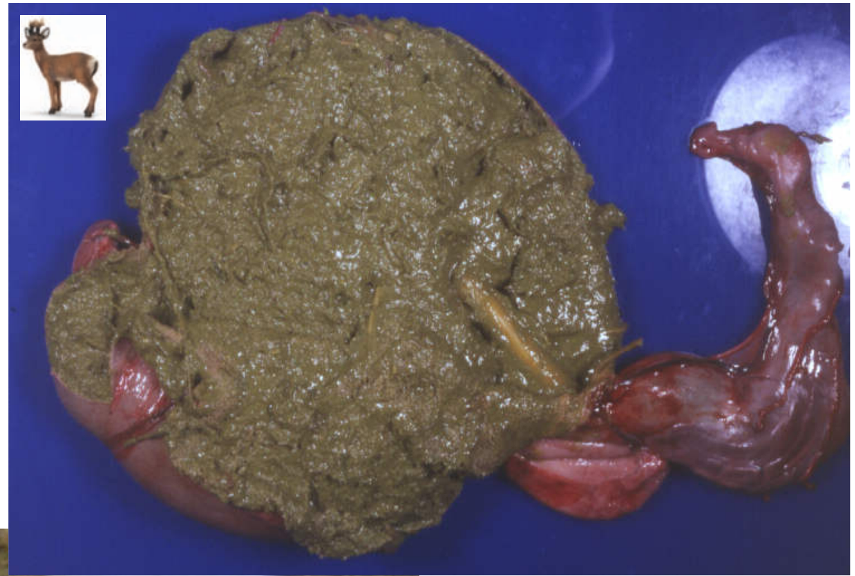


Flotation and Sedimentation
only works in a fluid medium

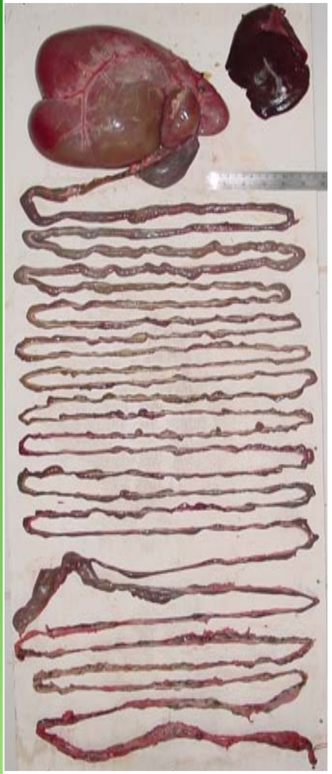


Ruminants have moist forestomach contents



Photos A. Schwarm &
M. Lechner-Doll

Ruminants must eliminate the moisture from their GIT content



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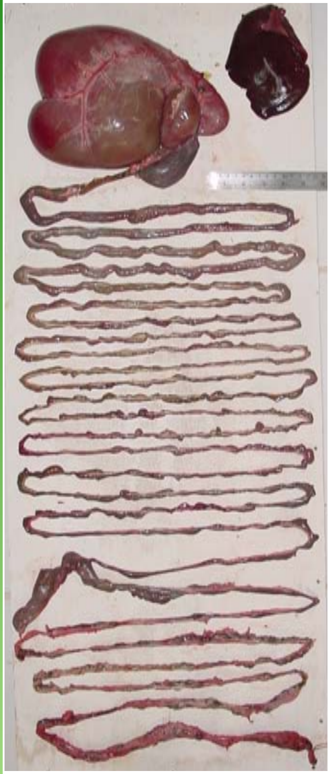
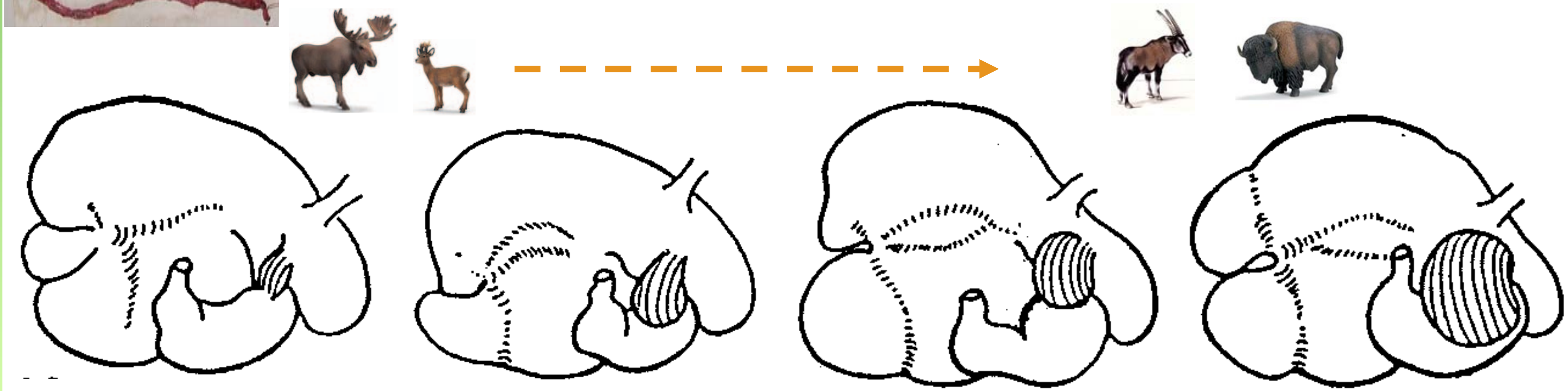


from Hofmann (1973)



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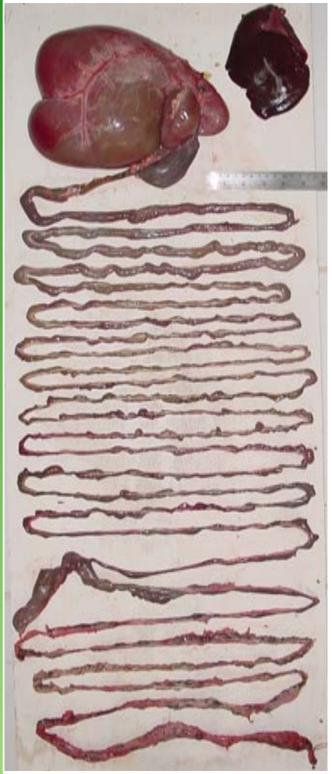
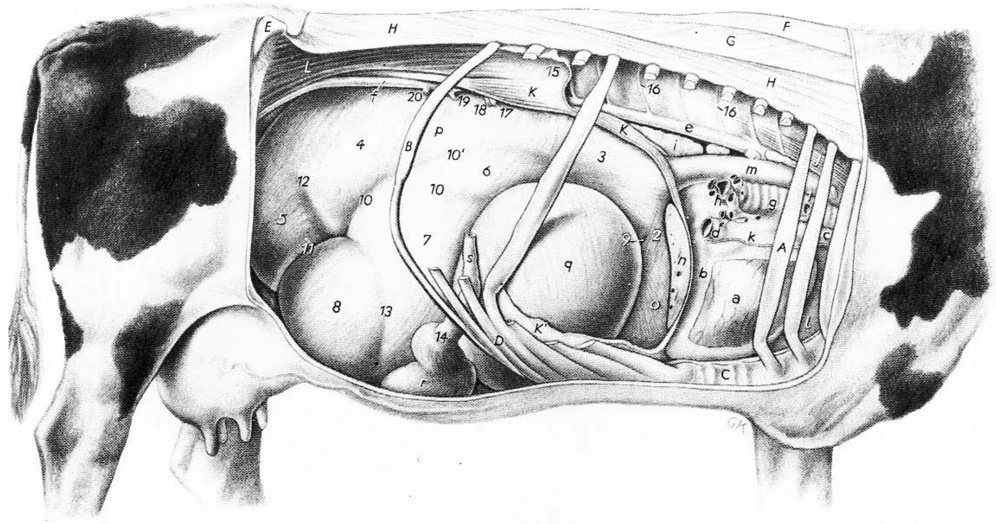
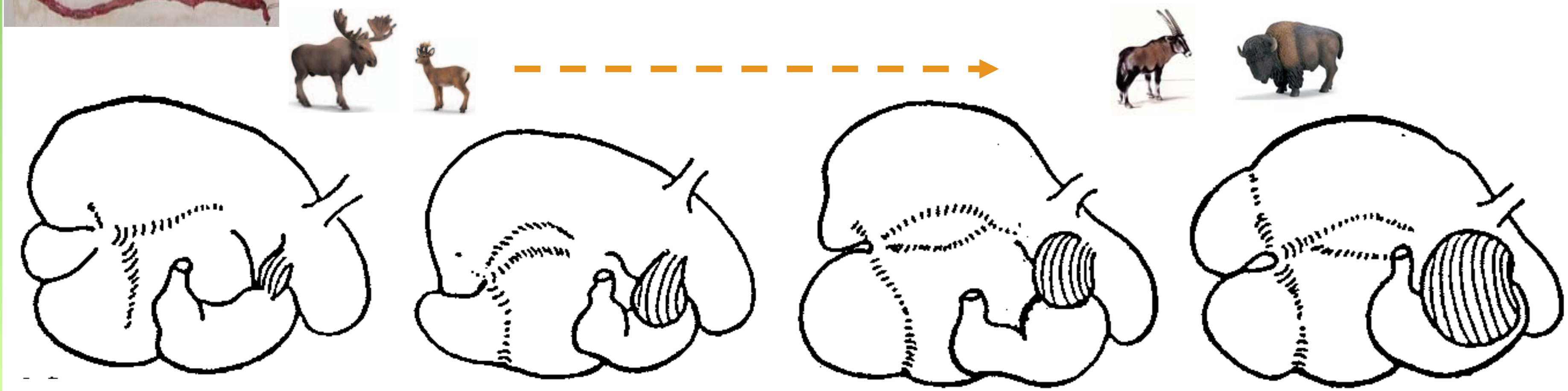


from Hofmann (1973)
& Nickel et al. (1967)





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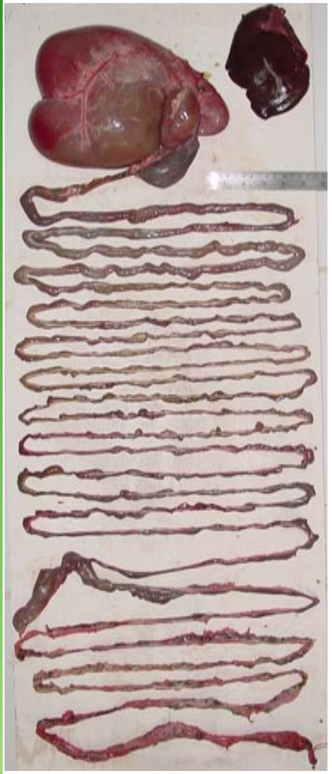

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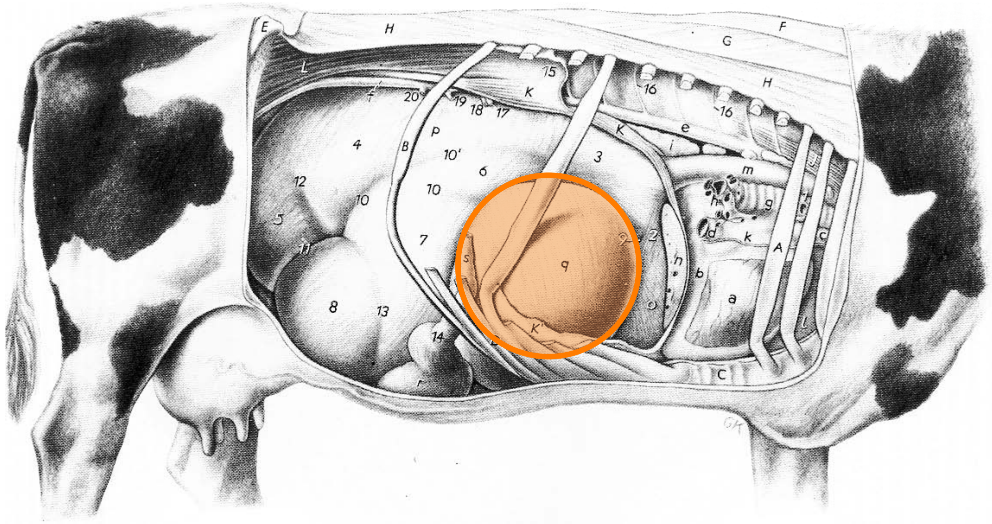
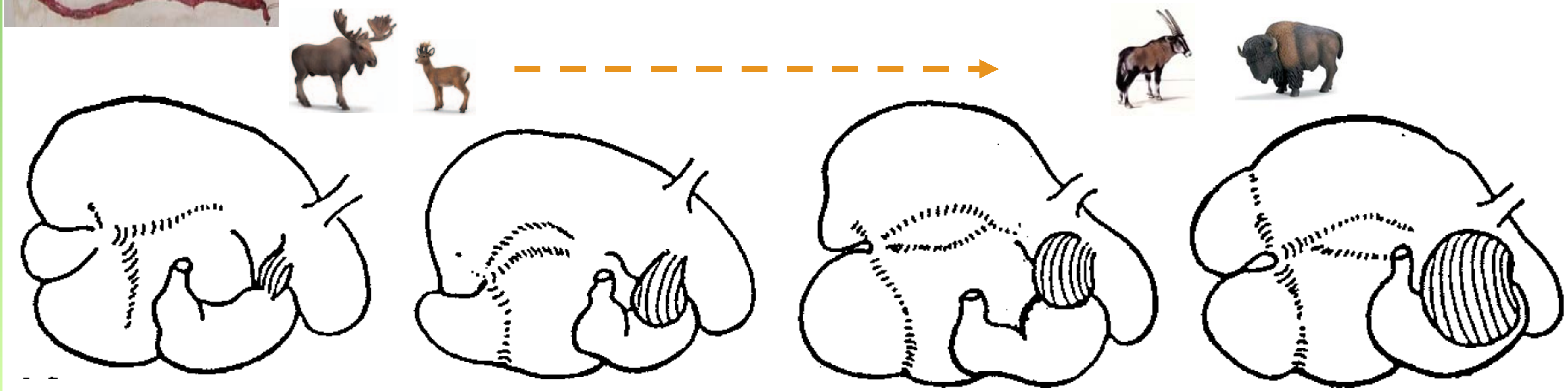
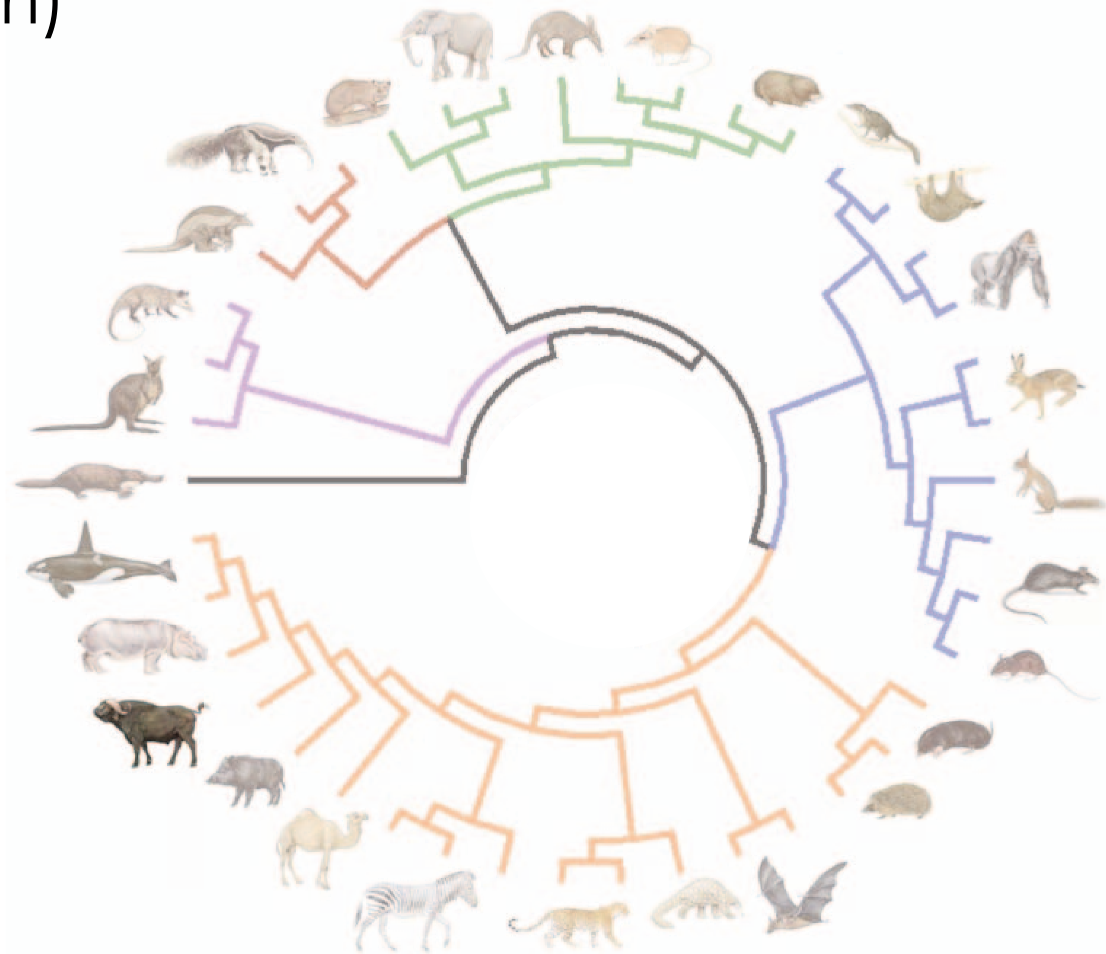


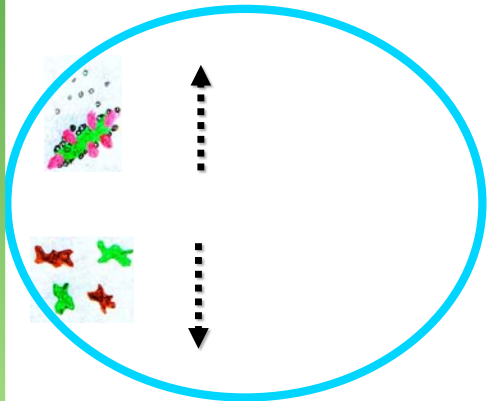


Conclusion: ruminants and fluids

- Ruminants increase energy uptake by means of a sorting mechanism (that requires a fluid medium)



Everything comes at a prize ...



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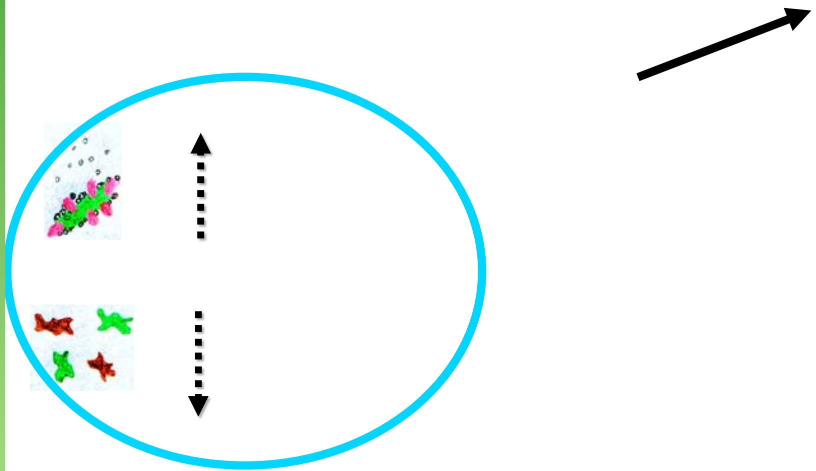

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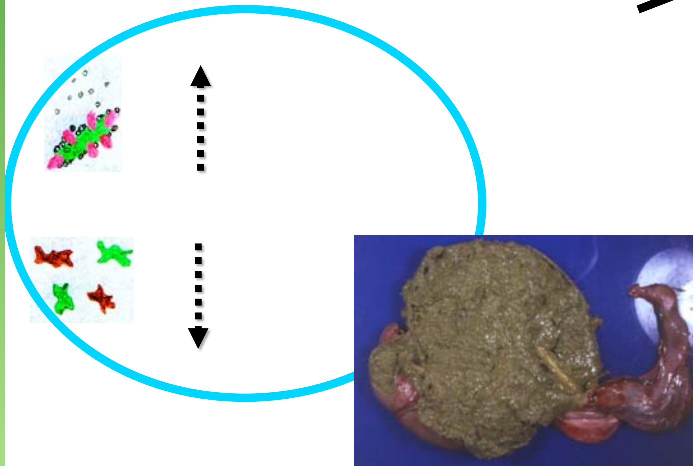

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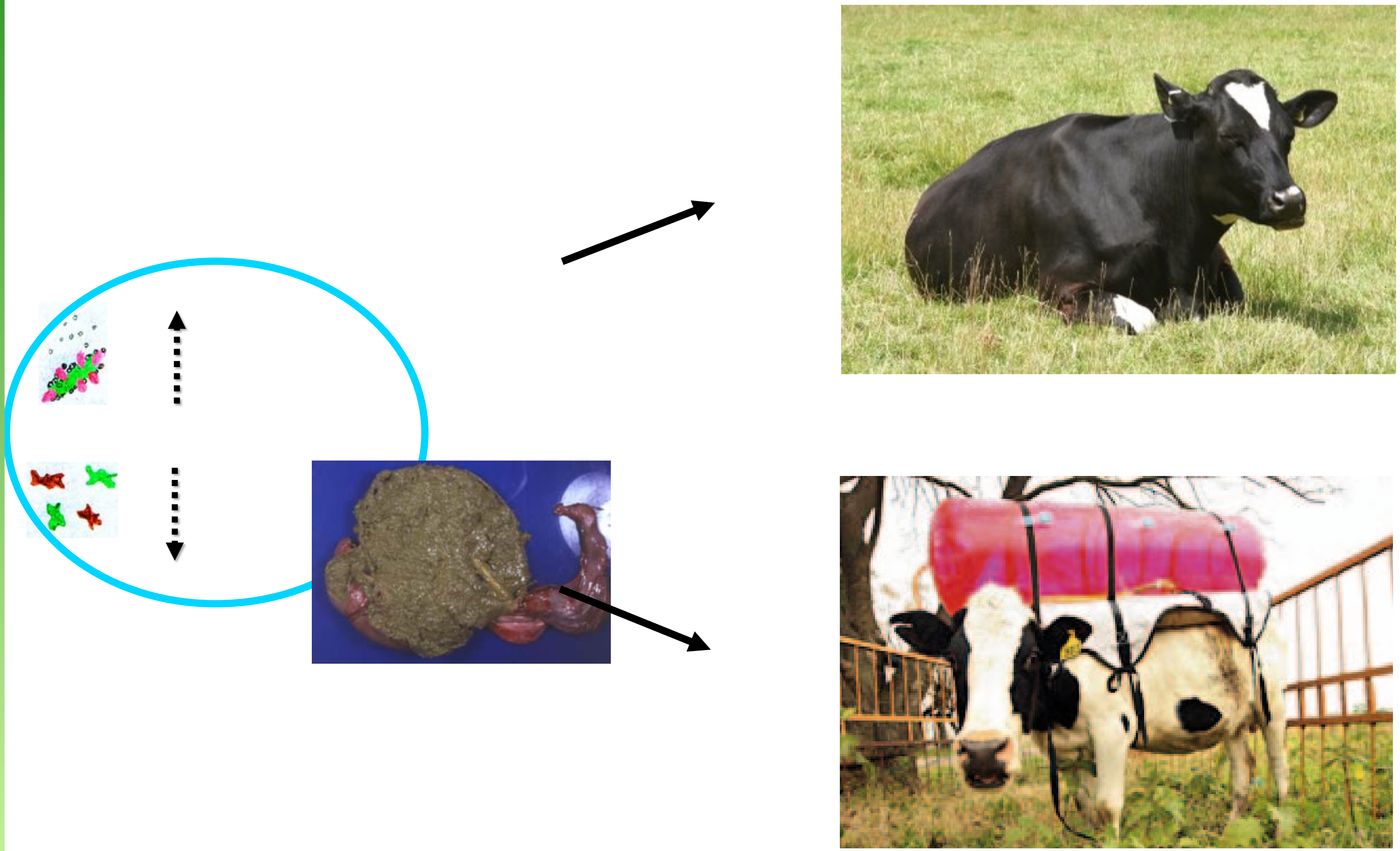

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Why Rumination?

"Rumination seems to allow herbivores to ingest in haste and masticate at leisure" (Karasov & Del Rio 2007)

⇒ *Ruminants should ingest similar amounts of food as other herbivores and just 'chew later' - or become time-constrained in intake*

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Because rumination occurs in a state of 'drowsiness' similar to rest, it may represent an energy-saving strategy (less time spent 'wide awake', Gordon 1968)

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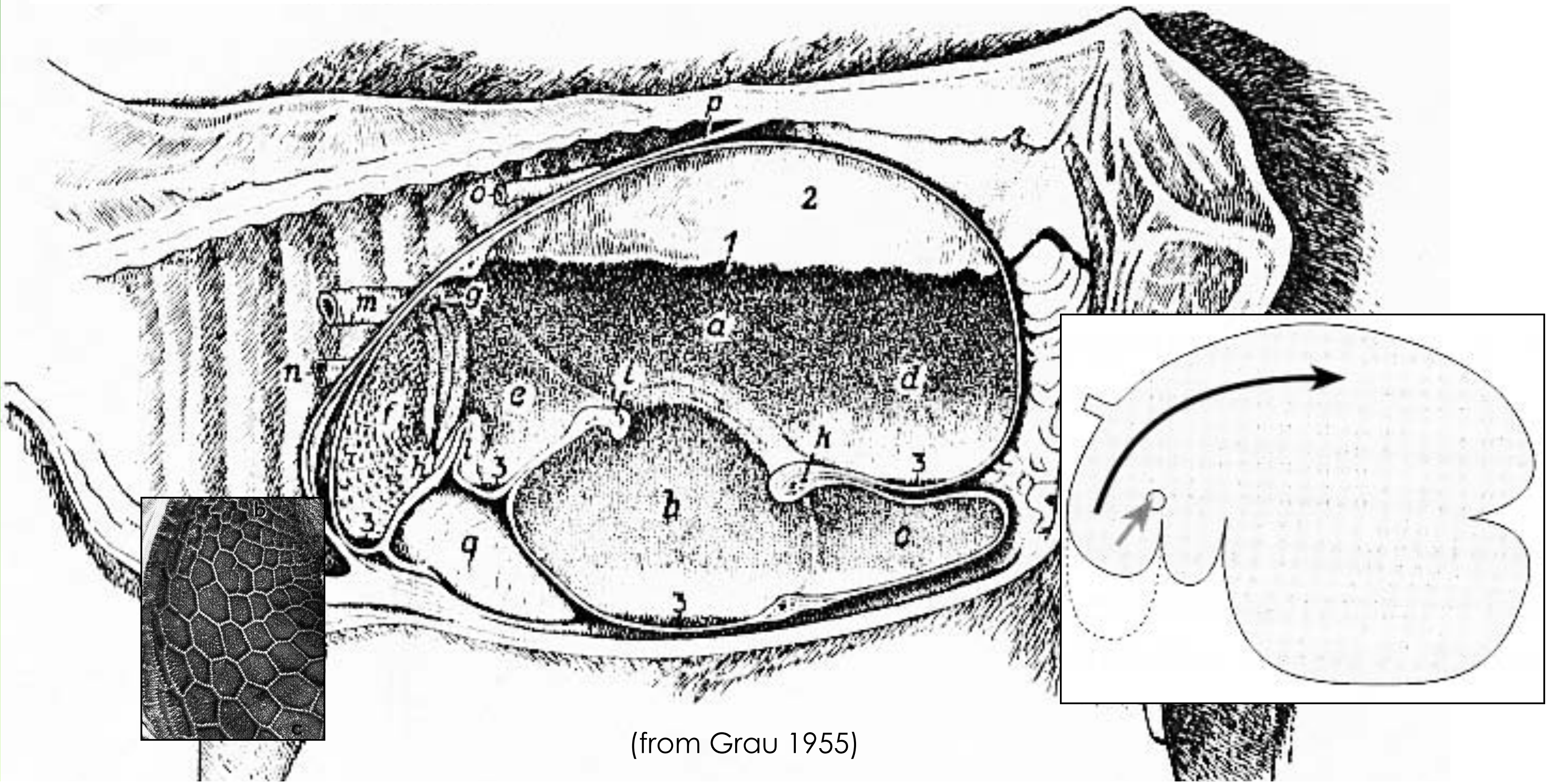

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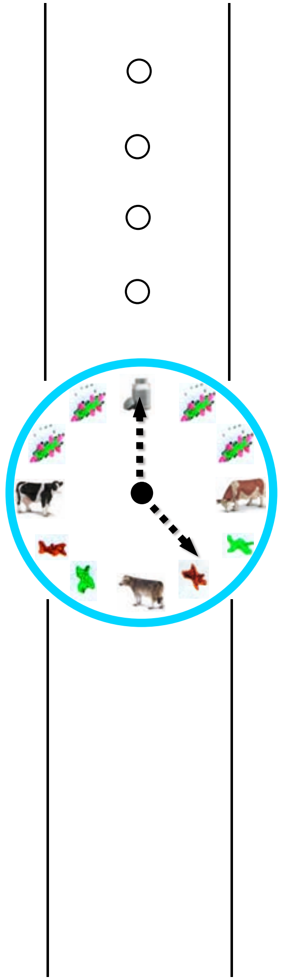
*=> The ruminant way of digestion is a strategy to **shorten** passage as compared to other foregut fermenters*

Fine mechanics at highest level



thank you
for your attention