



# How can we increase chewing efficiency ?

surprising morphophysiological solutions

Marcus Clauss

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Evolutionary Biology 2021*



**University of  
Zurich<sup>UZH</sup>**



**Clinic**  
of Zoo Animals, Exotic Pets and Wildlife



*Why is chewing important ?*

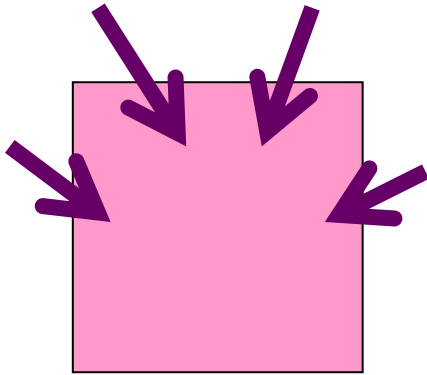


# Digestion takes time ...

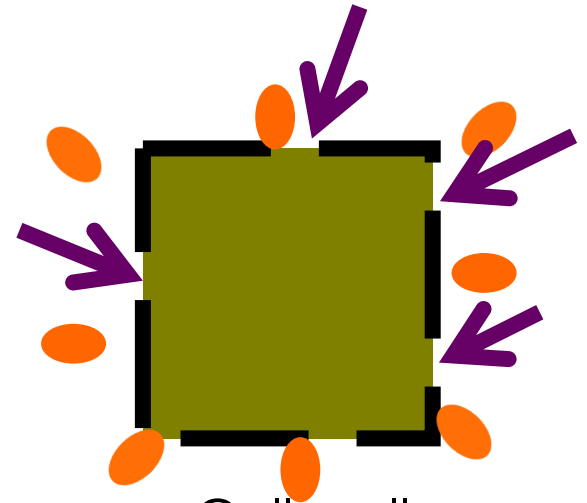
Animal cell

–

Plant cell



Cell membrane



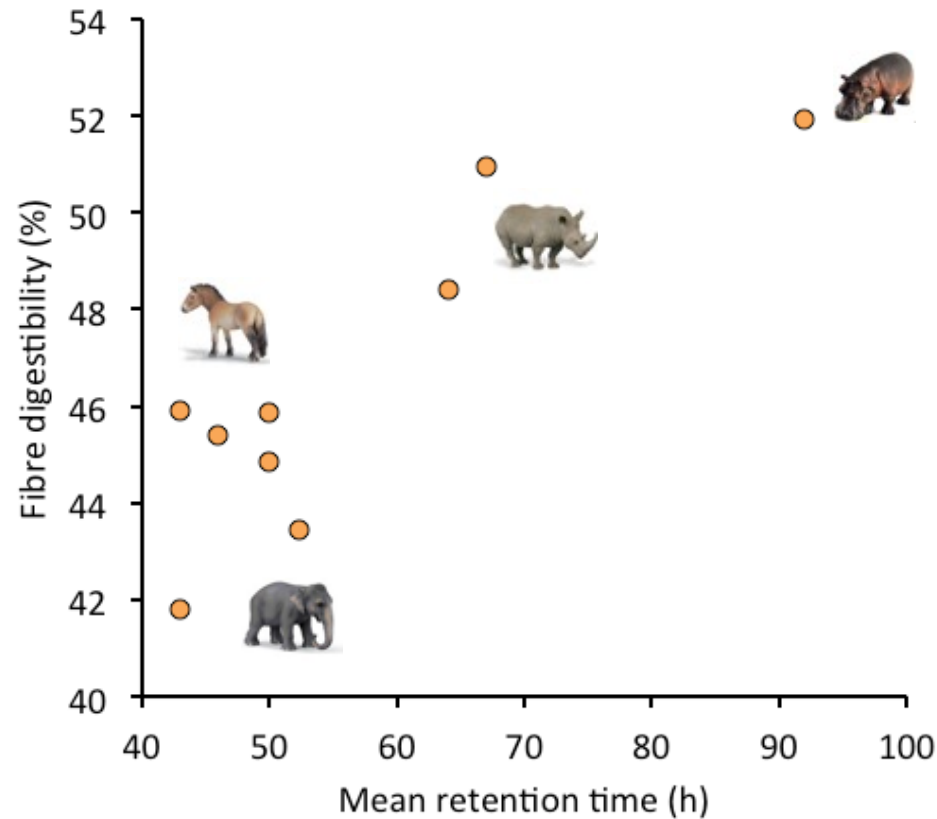
Cell wall



# Evidence for a tradeoff between retention time and chewing efficiency in large mammalian herbivores

Marcus Clauss <sup>a,\*</sup>, Charles Nunn <sup>b,c</sup>, Julia Fritz <sup>d</sup>, Jürgen Hummel <sup>e</sup>

Comparative Biochemistry and Physiology, Part A 154 (2009) 376–382

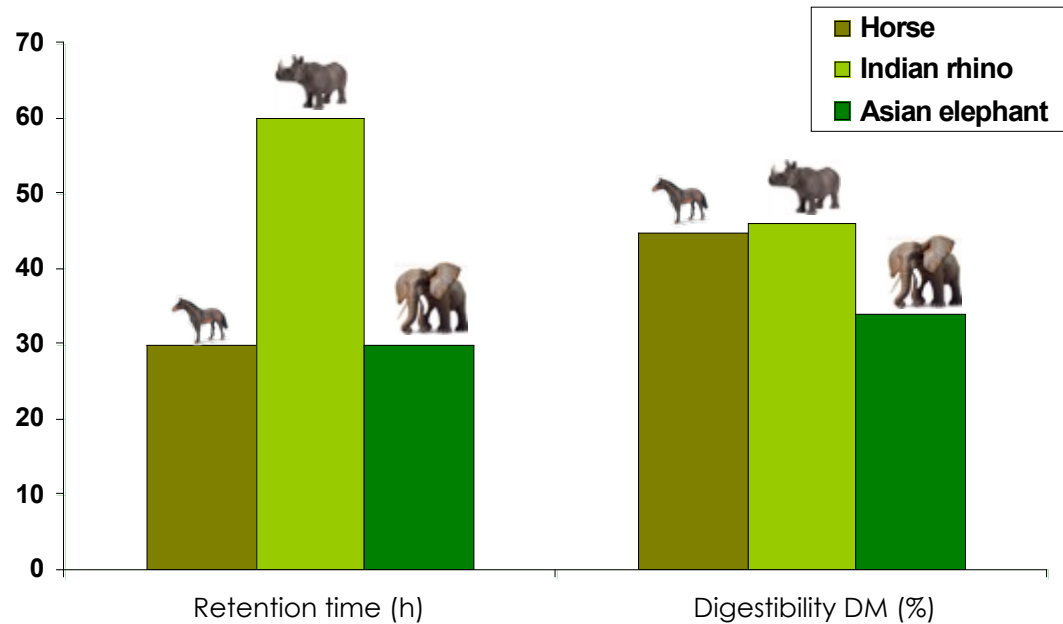




# Studies on digestive physiology and feed digestibilities in captive Indian rhinoceros (*Rhinoceros unicornis*)

M. Clauss<sup>1</sup>, C. Polster<sup>1</sup>, E. Kienzle<sup>1</sup>, H. Wiesner<sup>2</sup>, K. Baumgartner<sup>3</sup>, F. von Houwald<sup>4</sup>, S. Ortmann<sup>5</sup>, W. J. Streich<sup>5</sup> and E.S. Dierenfeld<sup>6</sup>

Journal of Animal Physiology and Animal Nutrition **89** (2005) 229–237



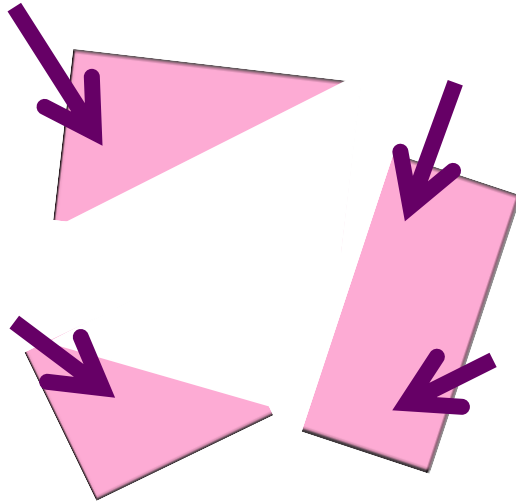


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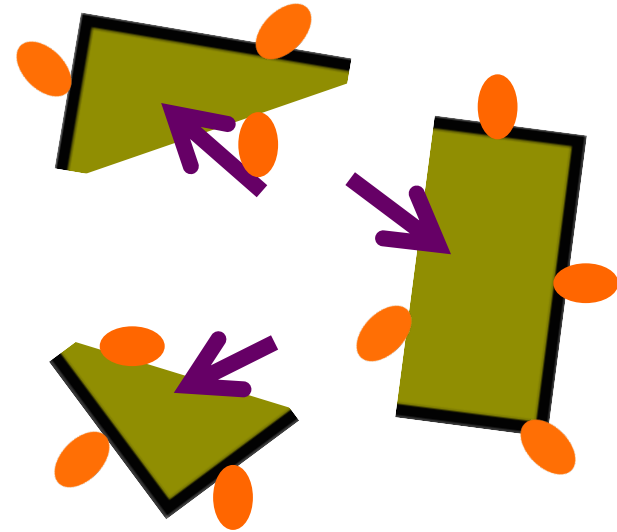
Animal cell

–

Plant cell



Cell membrane



Cell wall



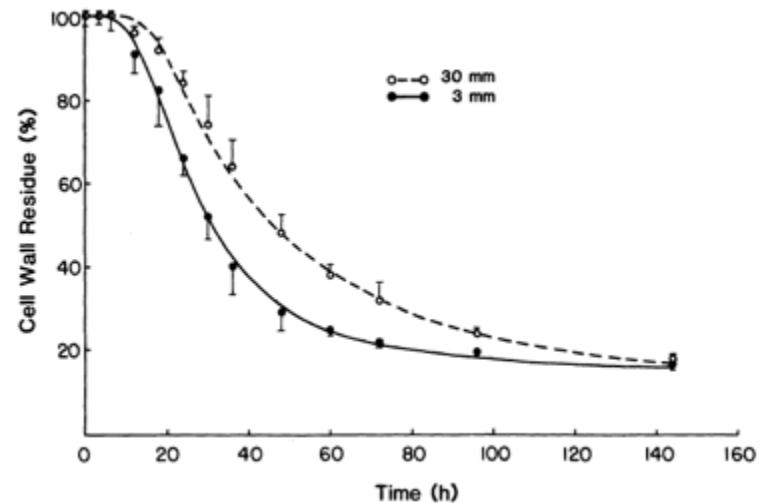
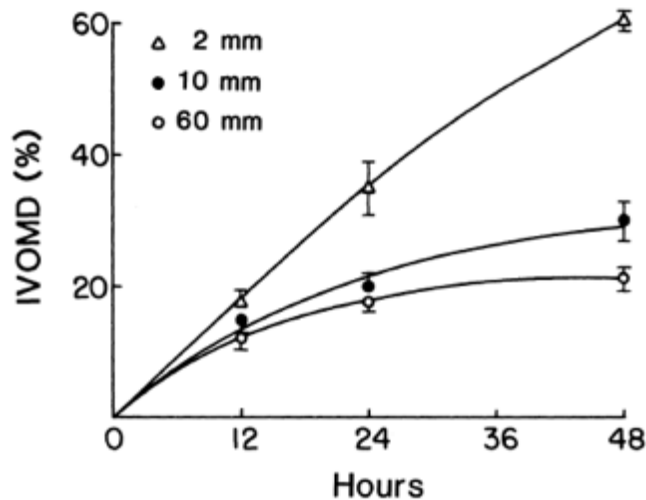
# Digestive Fermentation in Herbivores: Effect of Food Particle Size

*Physiological Zoology* 63(4):710–721. 1990.

Karen A. Bjorndal<sup>1</sup>

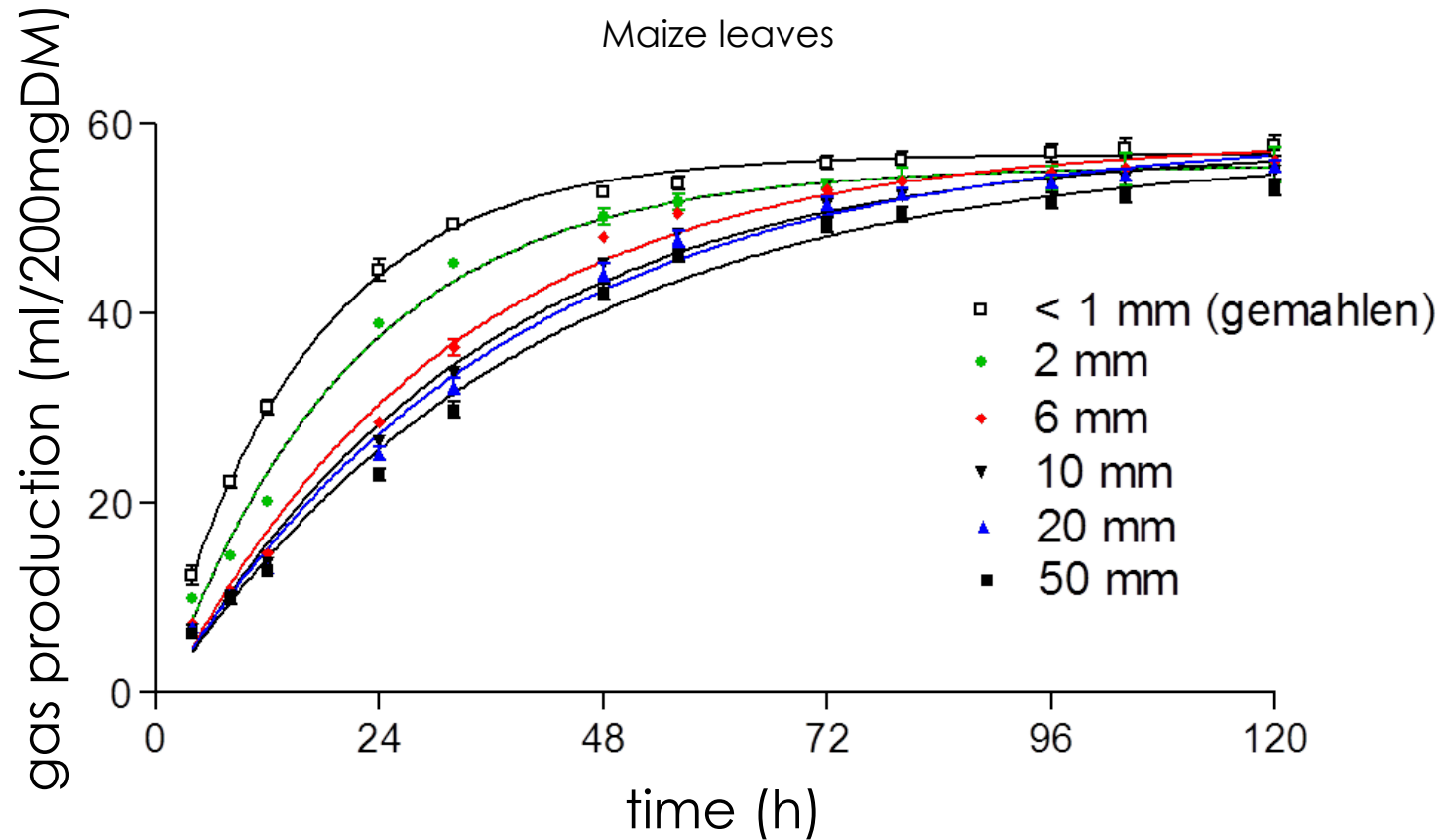
Alan B. Bolten<sup>1</sup>

John E. Moore<sup>2</sup>





# In vitro fermentation and particle size



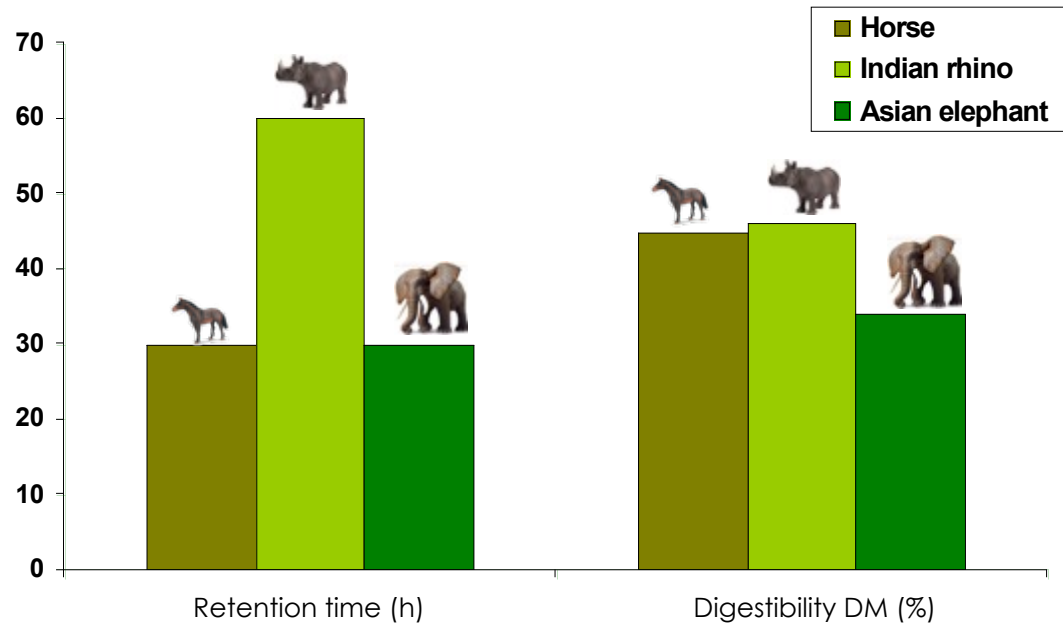




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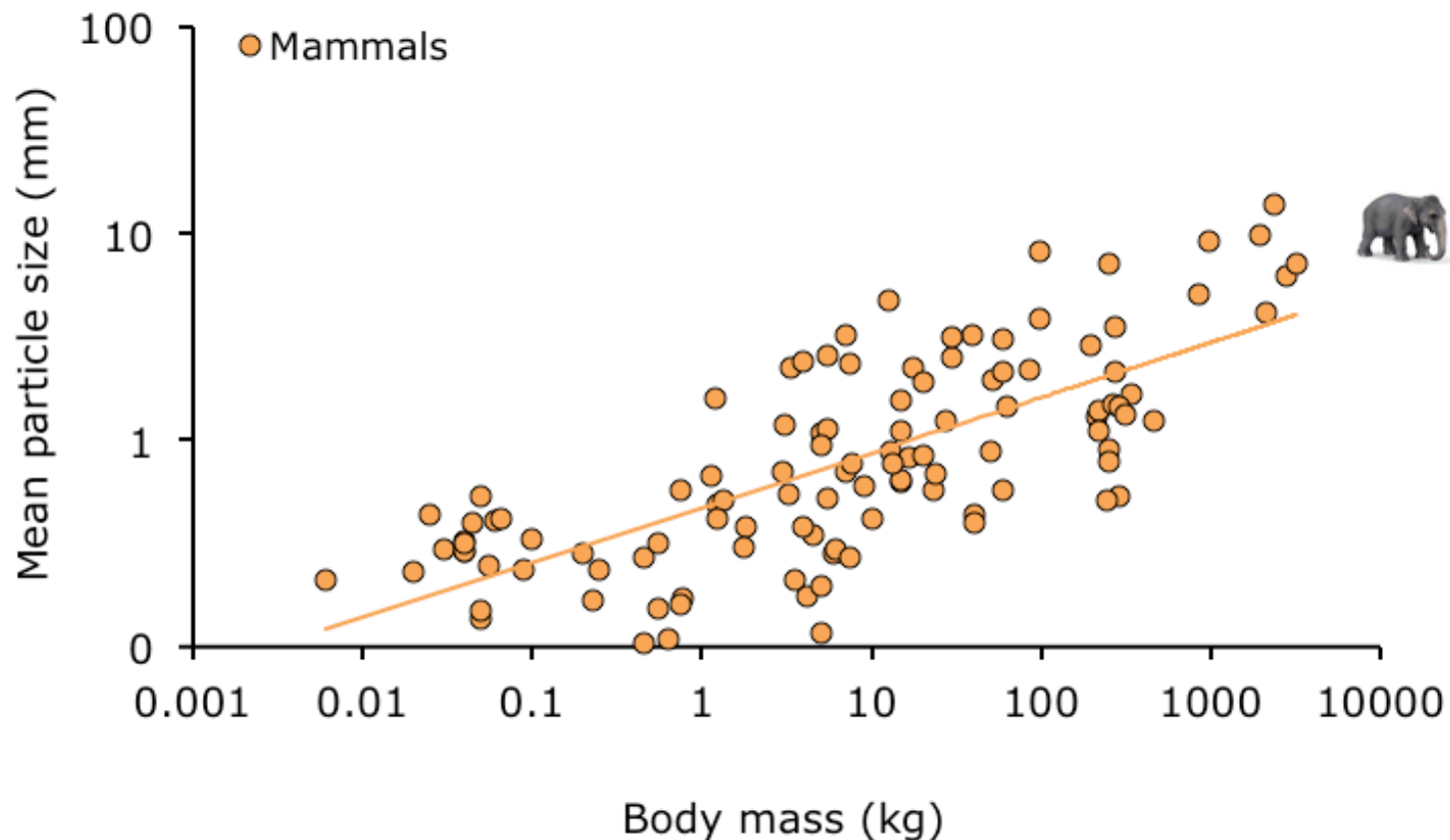
# *Quantifying particle size reduction*



# Comparative chewing efficiency in mammalian herbivores

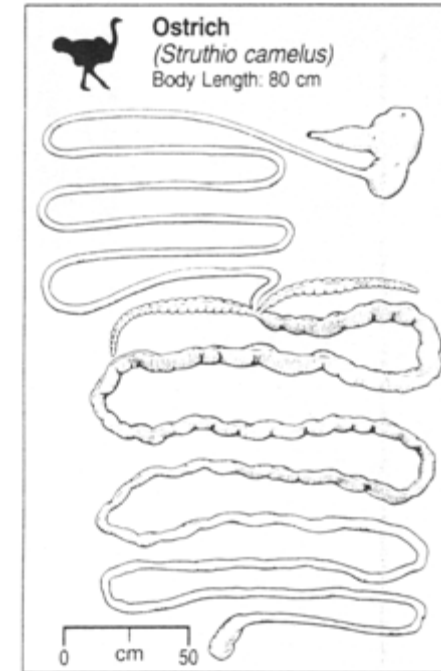
Julia Fritz, Jürgen Hummel, Ellen Kienzle, Christian Arnold, Charles Nunn and Marcus Clauss

*Oikos* 118: 1623–1632, 2009





# Avian herbivores ?



from Stevens und Hume (1995)  
Photo: J. Fritz



# Avian herbivores ?



Photos: J. Fritz



# Gizzard vs. teeth, it's a tie: food-processing efficiency in herbivorous birds and mammals and implications for dinosaur feeding strategies

*Julia Fritz, Jürgen Hummel, Ellen Kienzle, Oliver Wings, W. Jürgen Streich,  
and Marcus Clauss*

*Paleobiology*, 37(4), 2011, pp. 577–586

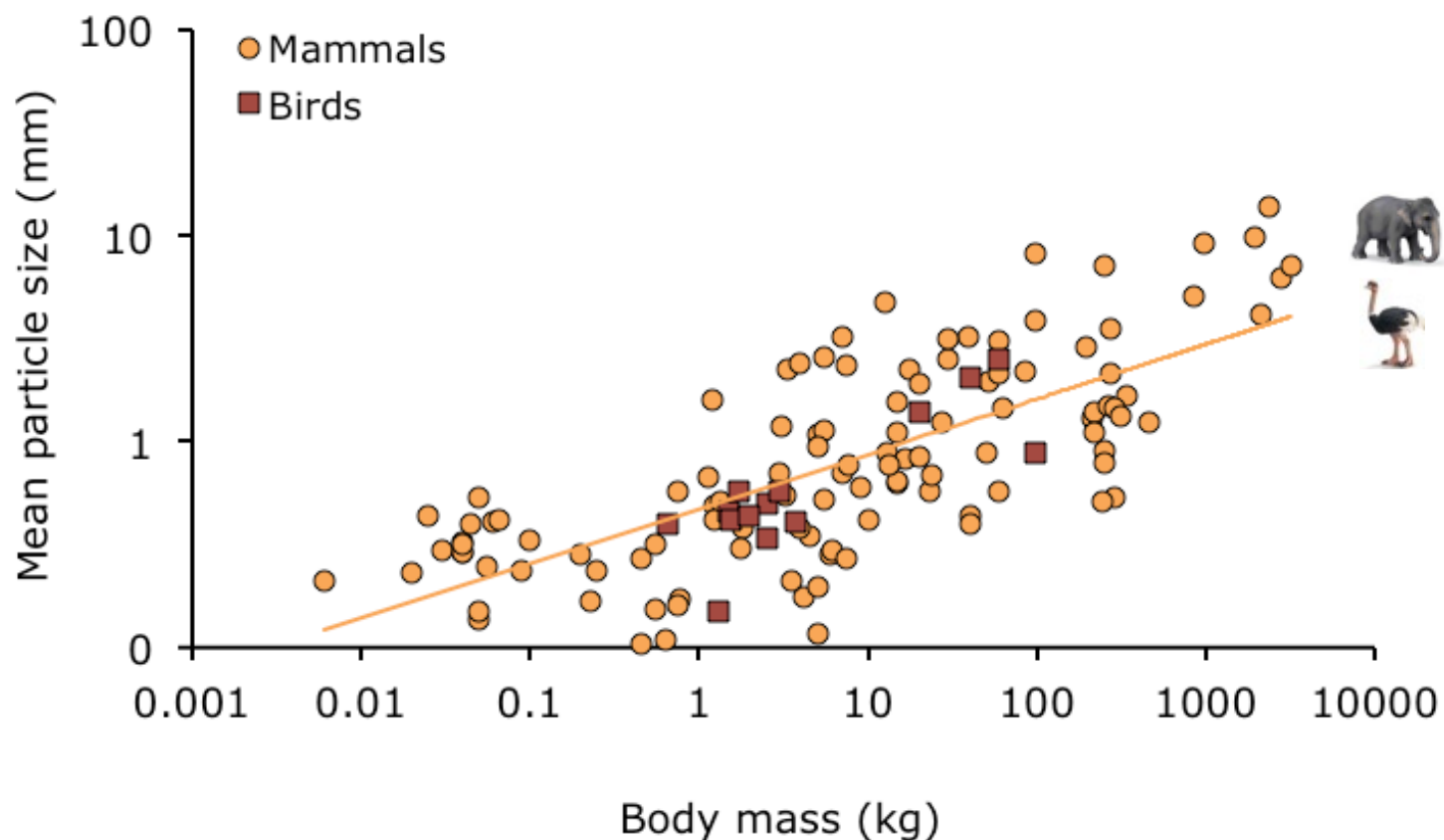




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# To Chew or Not to Chew



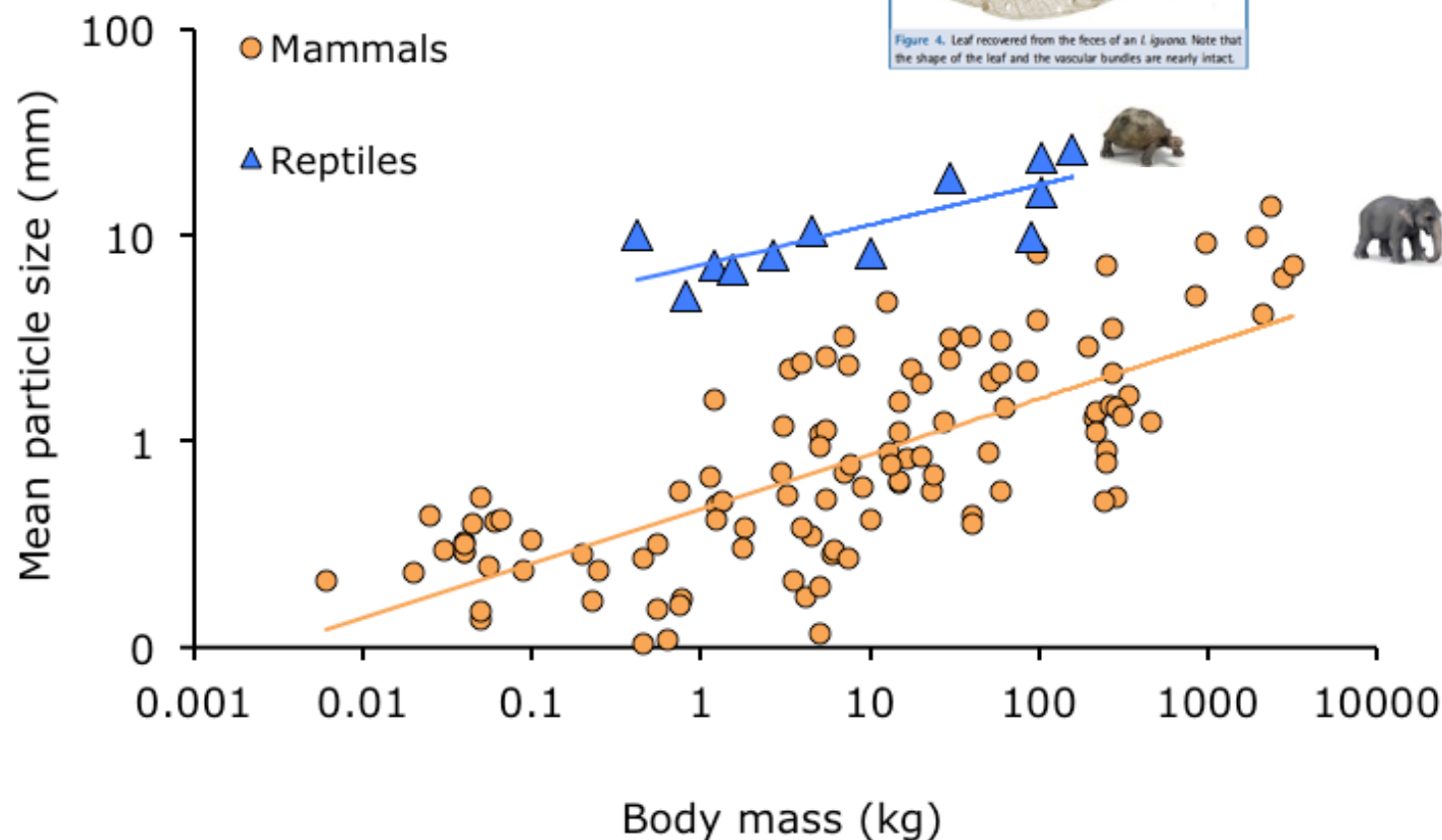




# To Chew or Not to Chew: Fecal Particle Size in Herbivorous Reptiles and Mammals

*J. Exp. Zool.*  
313A:579–586,  
2010

JULIA FRITZ<sup>1\*</sup>, JÜRGEN HUMMEL<sup>2</sup>, ELLEN KIENZLE<sup>1</sup>,  
W. JÜRGEN STREICH<sup>3</sup>, AND MARCUS CLAUSS<sup>4</sup>

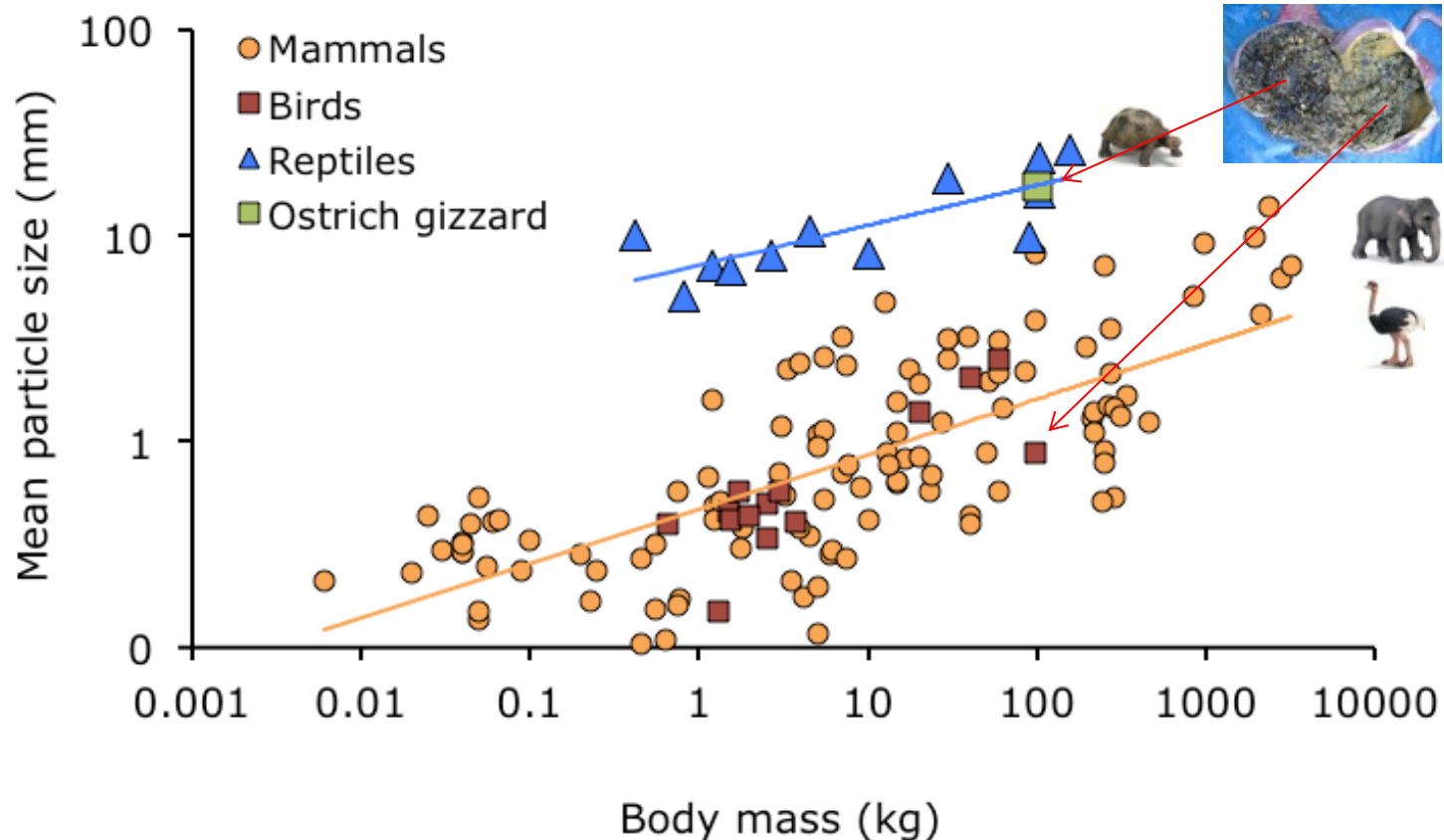




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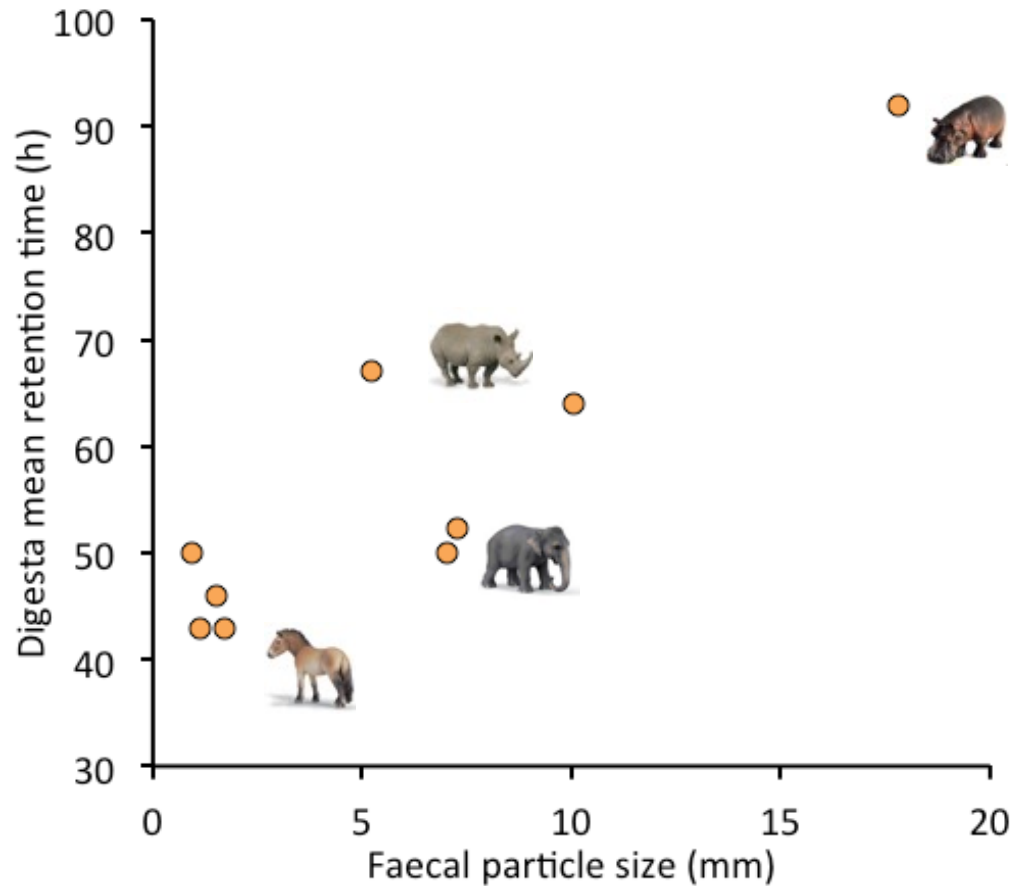




# Evidence for a tradeoff between retention time and chewing efficiency in large mammalian herbivores

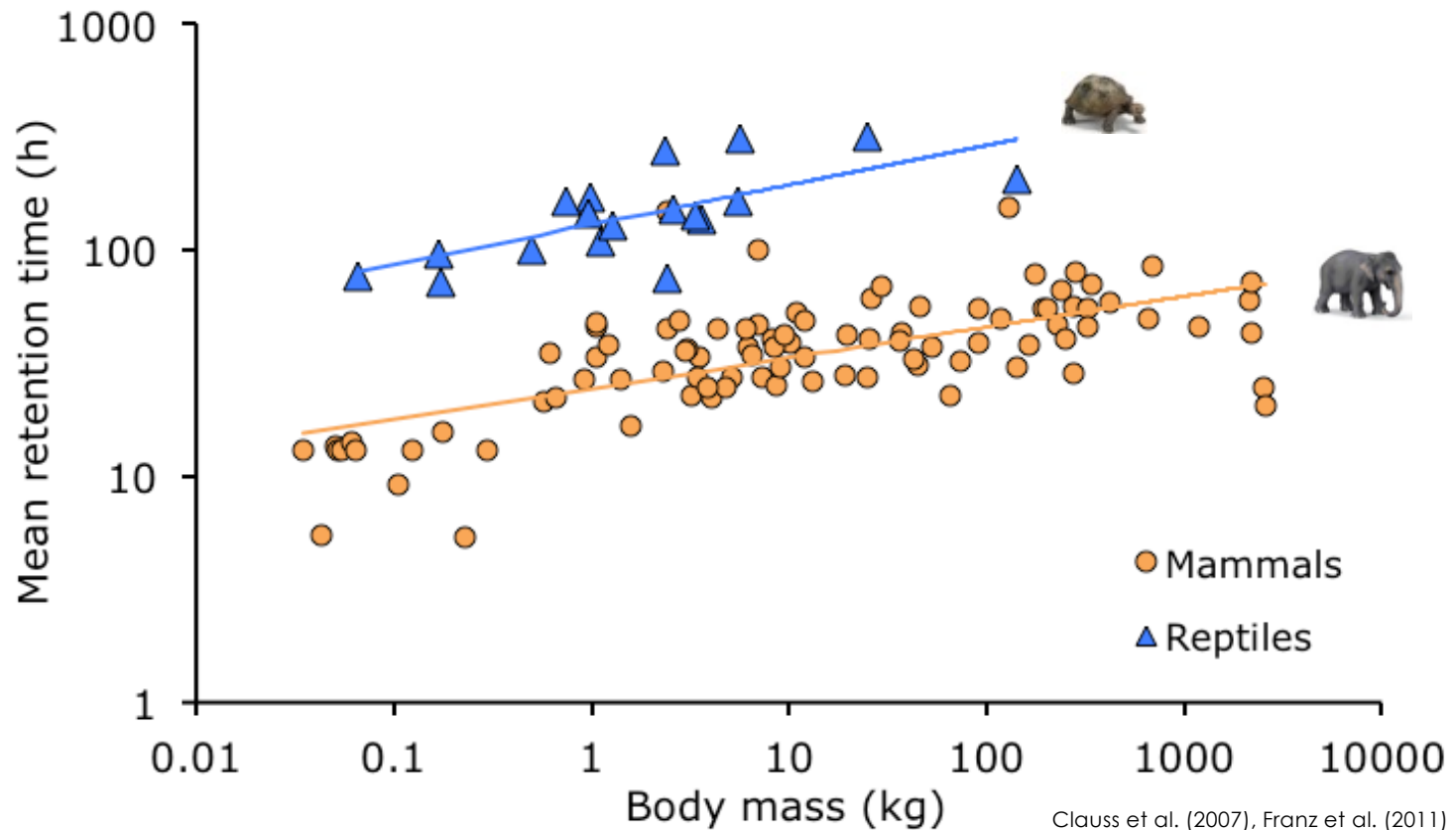
Marcus Clauss <sup>a,\*</sup>, Charles Nunn <sup>b,c</sup>, Julia Fritz <sup>d</sup>, Jürgen Hummel <sup>e</sup>

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# How long does food stay in the gut ?

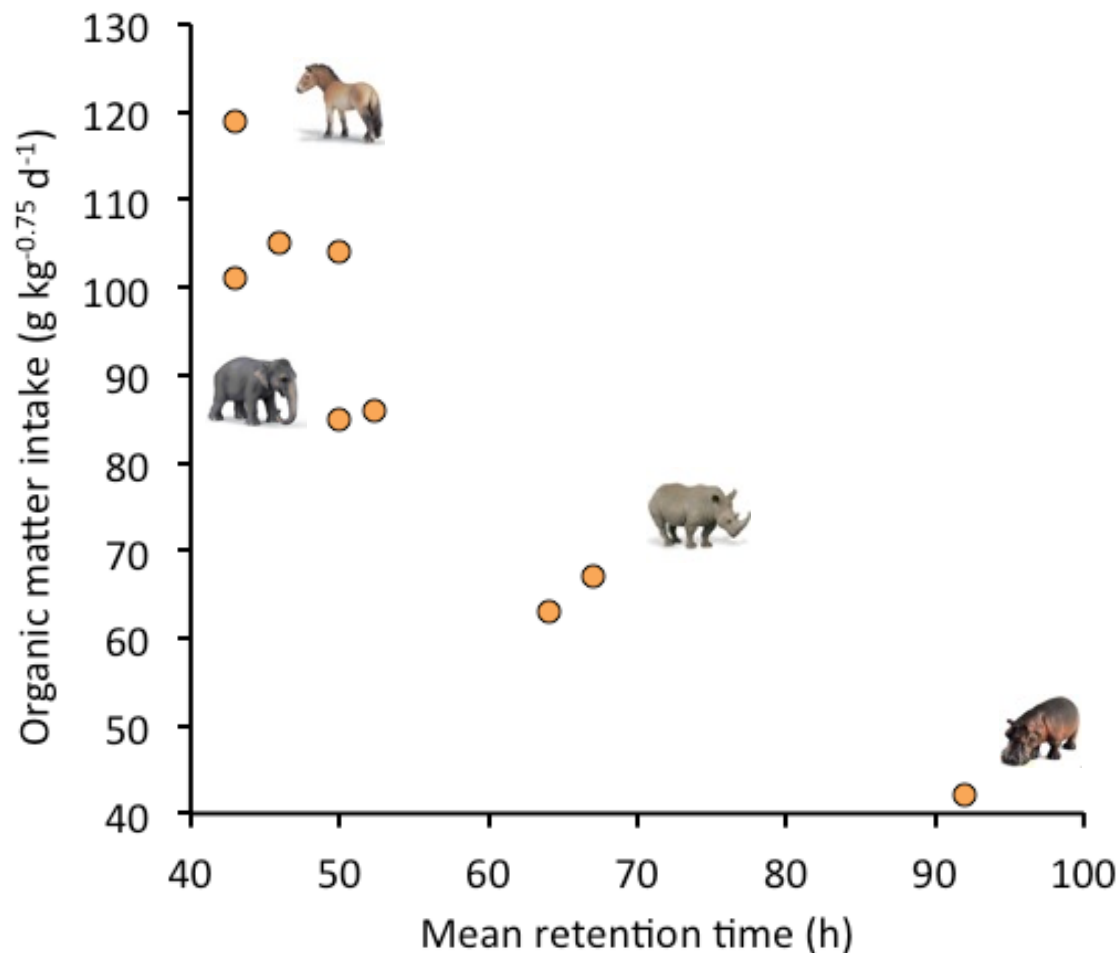




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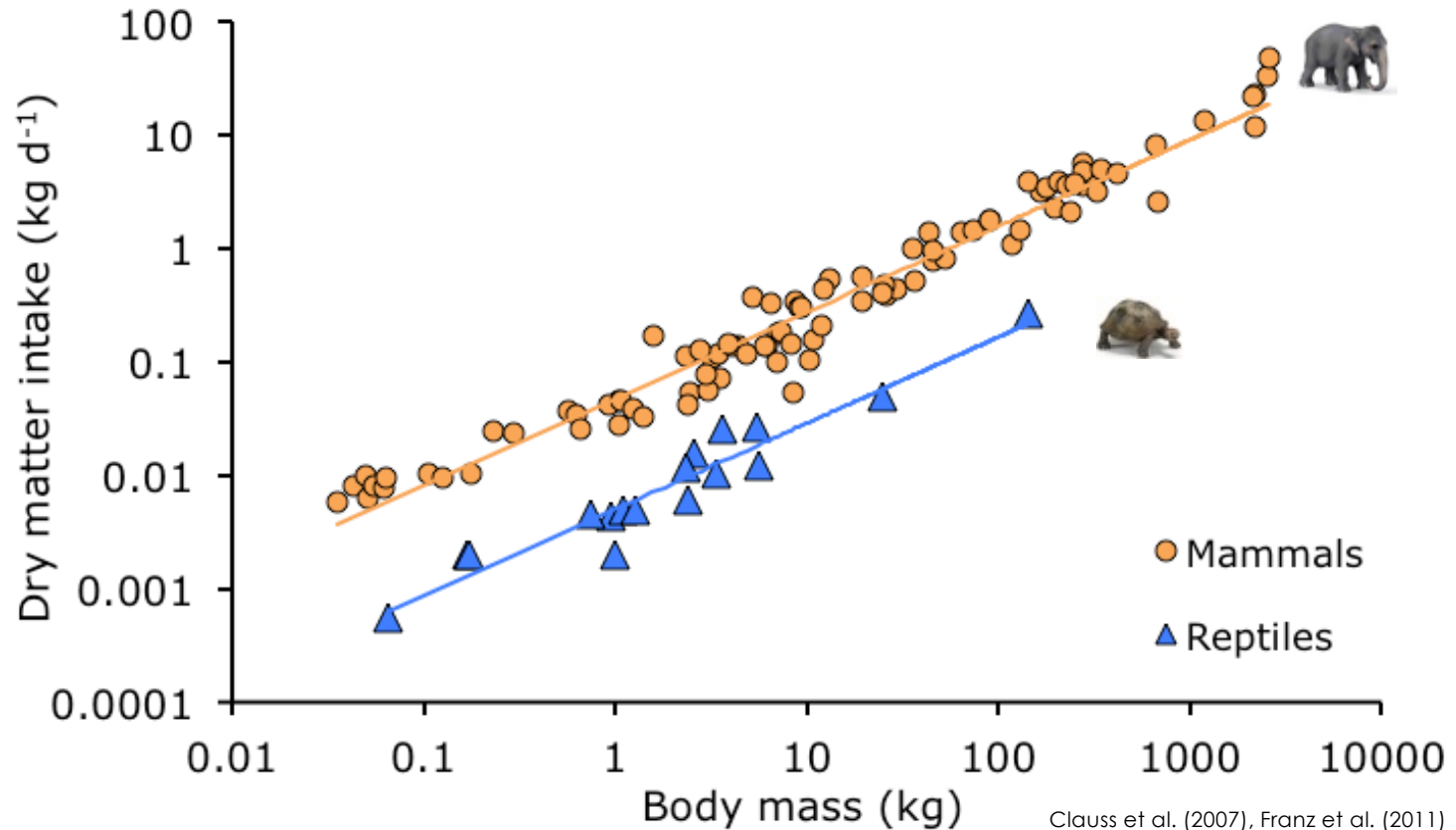
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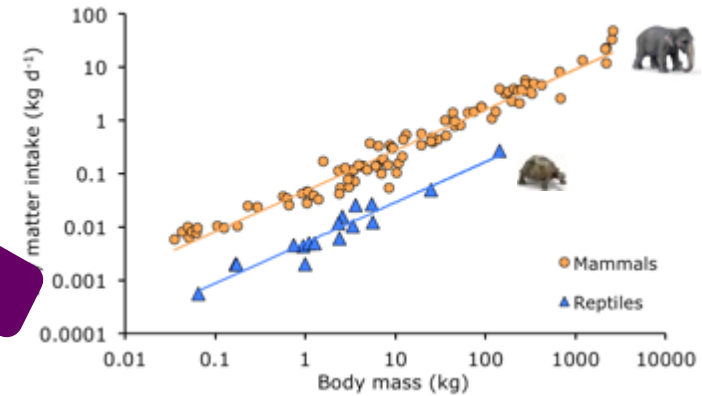
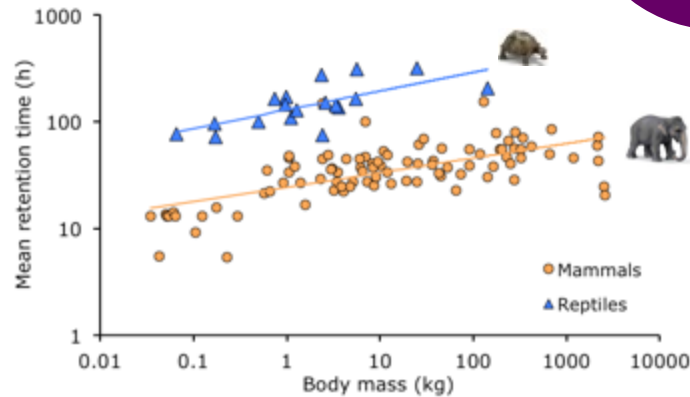
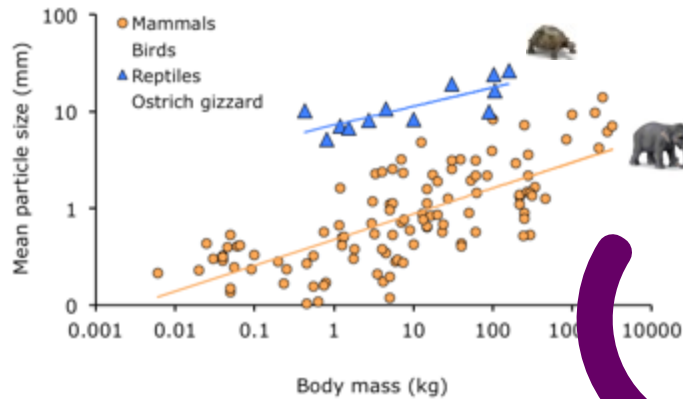


# Food intake





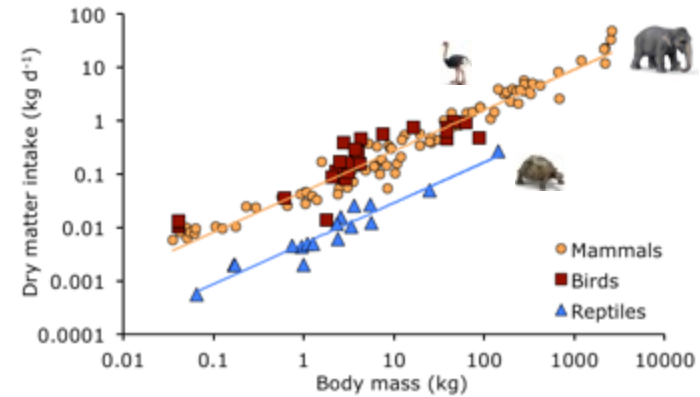
# Chewing ... facilitates higher intake





# Particle size reduction ... facilitates higher intake

*in herbivores, particle size reduction is a prerequisite for endothermy*



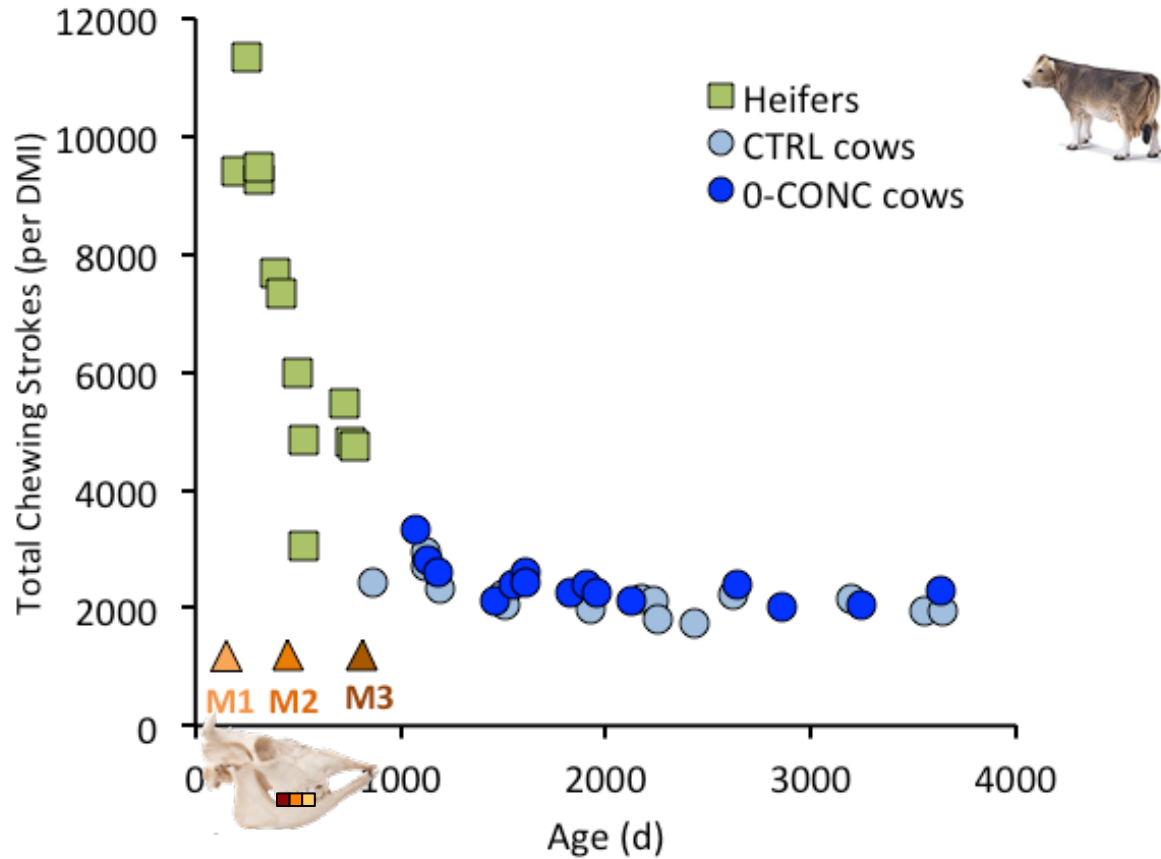




# Quiz



# Chewing surface matters



Age effect on chewing intensity  
(due to molar eruption)

from Grandl et al. (2019)

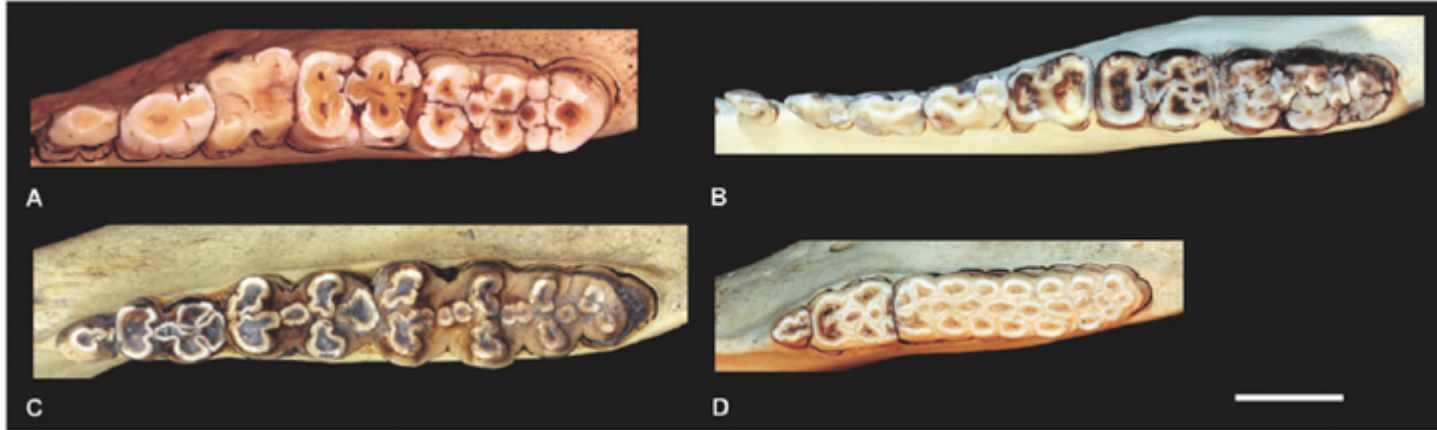


# How can we increase chewing efficiency?

more chewing surface



# Third molar prolongation suids





## 'Molarisation' or premolars



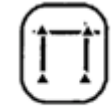
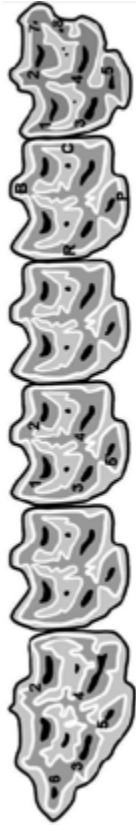


# How can we increase chewing efficiency?

dental design



# Chewing surfaces – enamel ridges



aus Jernvall et al. (1996)



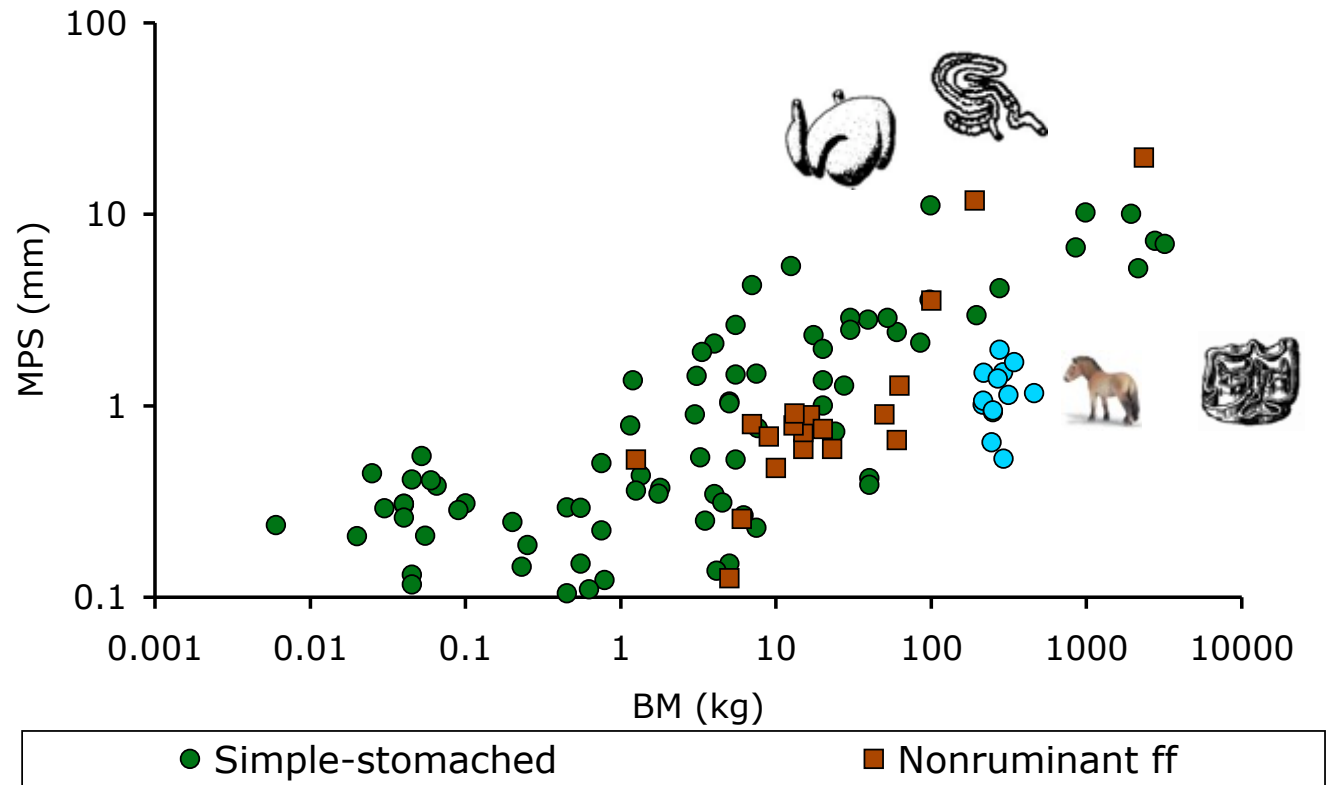




# Comparative chewing efficiency in mammalian herbivores

Julia Fritz, Jürgen Hummel, Ellen Kienzle, Christian Arnold, Charles Nunn and Marcus Clauss

*Oikos* 118: 1623–1632, 2009





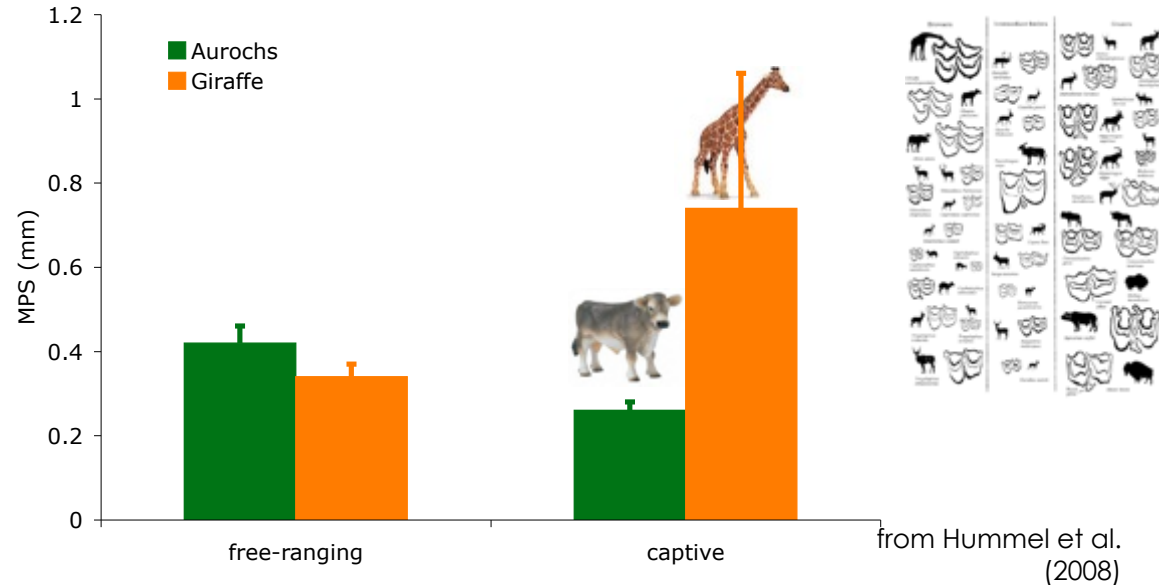
# Chewing surfaces – enamel ridges





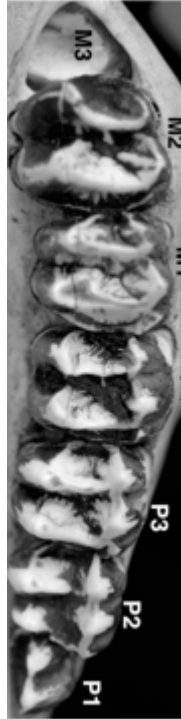
# Chewing surfaces – enamel ridges

- We expect captive herbivores to have finer faecal particles than free-ranging conspecifics (due to pellet feeding)
- This is confirmed in Aurochs but not in giraffes!
- Indication that giraffe teeth are adapted to chewing something else - not the diets offered in captivity.





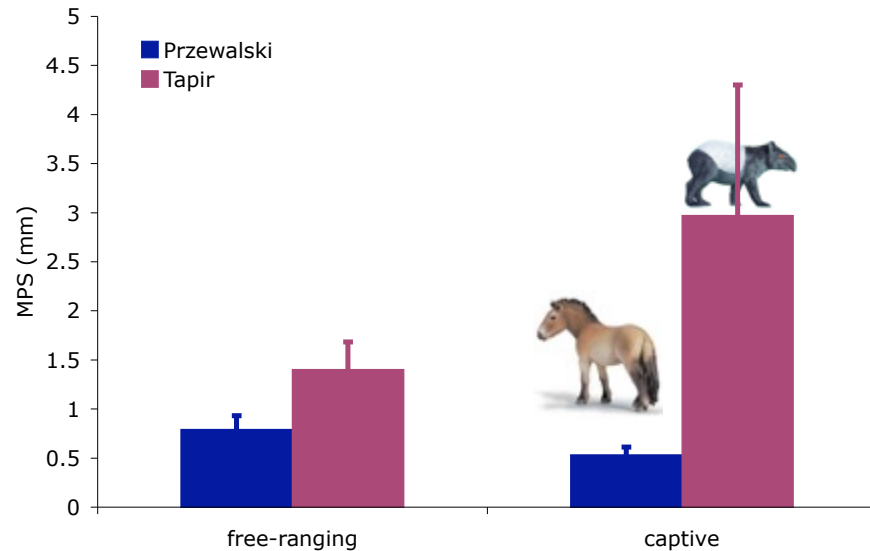
# Chewing surfaces – enamel ridges





# Chewing surfaces – enamel ridges

- We expect captive herbivores to have finer faecal particles than free-ranging conspecifics (due to pellet feeding)
- This is confirmed in Przewalski horse but not in tapirs!
- Indication that tapir teeth are adapted to chewing something else - not the diets offered in captivity.



from Hummel et al.  
(2008)



# How can we increase chewing efficiency?

something completely different

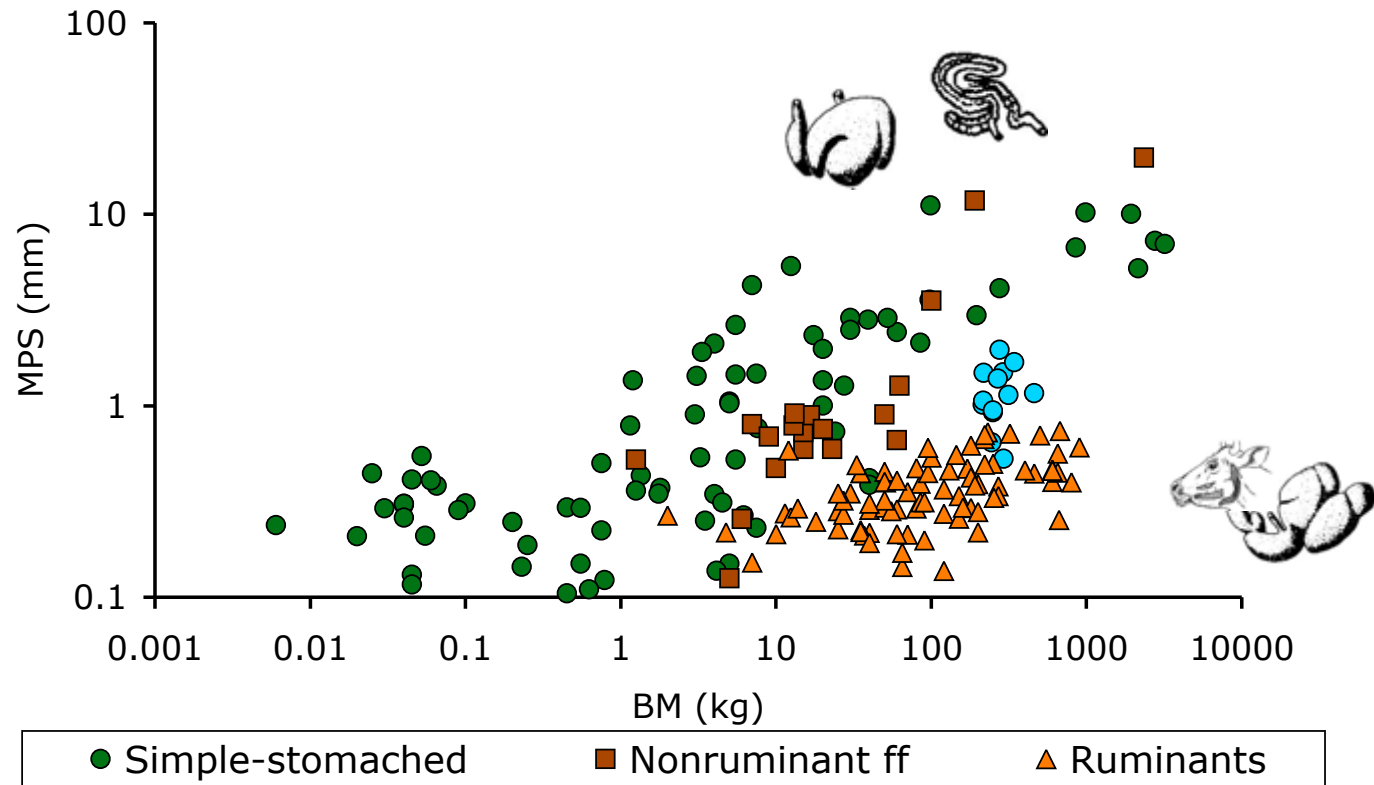




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*... just chew more ... ?*





# Faecal particles in a ruminant and a nonruminant

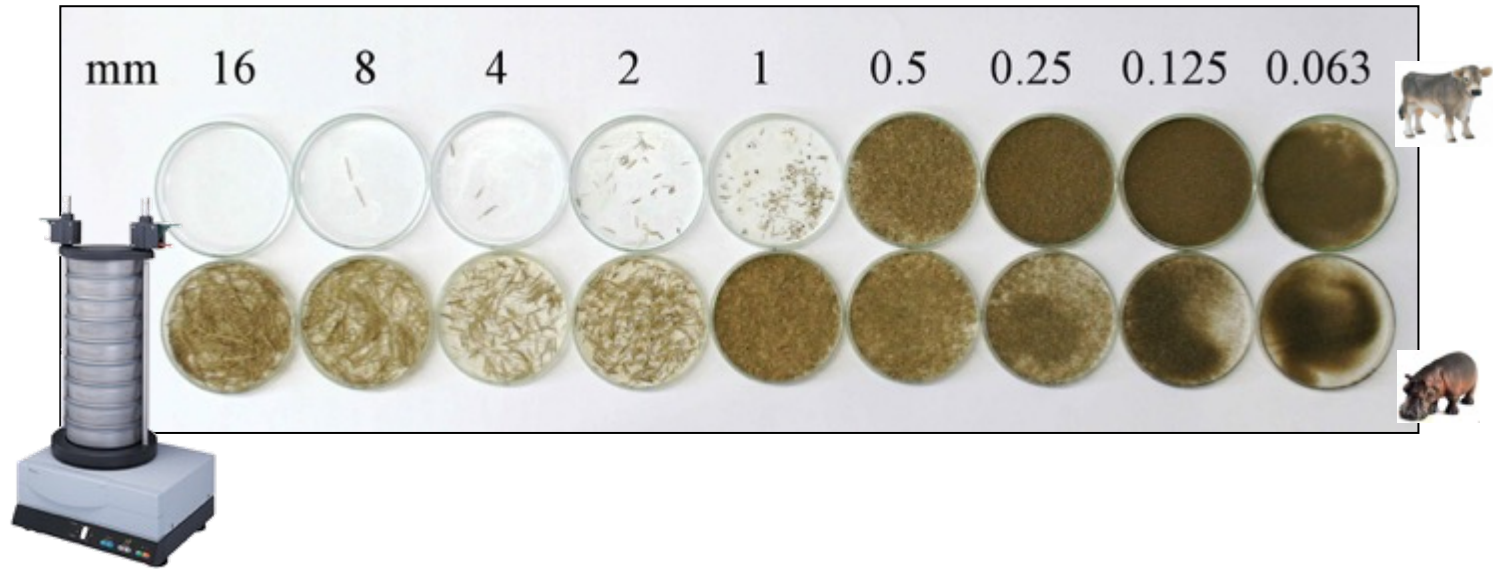


Photo A. Schwarm



# Why rumination ?

- Anti-predation strategy
  - “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

## Life cycle period and activity of prey influence their susceptibility to predators

A. Molinari-Jobin, P. Molinari, A. Loison, J.-M. Gaillard and U. Breitenmoser  
ECOGRAPHY 27: 323–329, 2004



We found more chamois predated when feeding, whereas roe deer were predated mainly when ruminating.

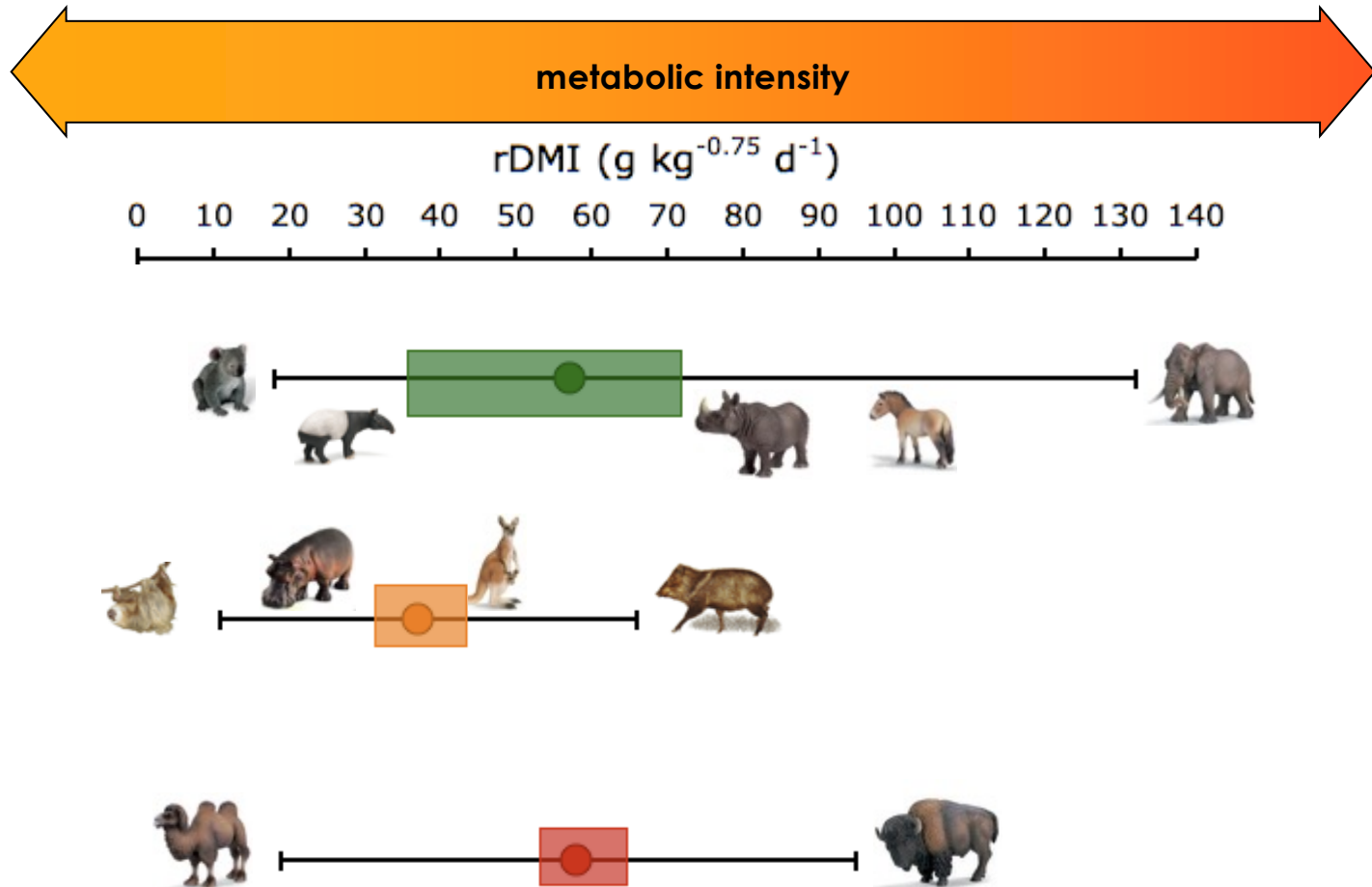


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- Energy-saving mechanism
  - Rumination occurs in a state of ‘drowsiness’ similar to rest; may represent an energy-saving strategy - less time spent ‘wide awake’ (Gordon 1968)
    - => Ruminants should have lower energy requirements/higher productivity than other herbivores
- Enhancement of digestive efficiency and intake
  - Rumination reduces particle size and hence allows faster digestion at constant intake
    - => Ruminants should have smaller digesta particle sizes (and higher intakes) than other herbivores



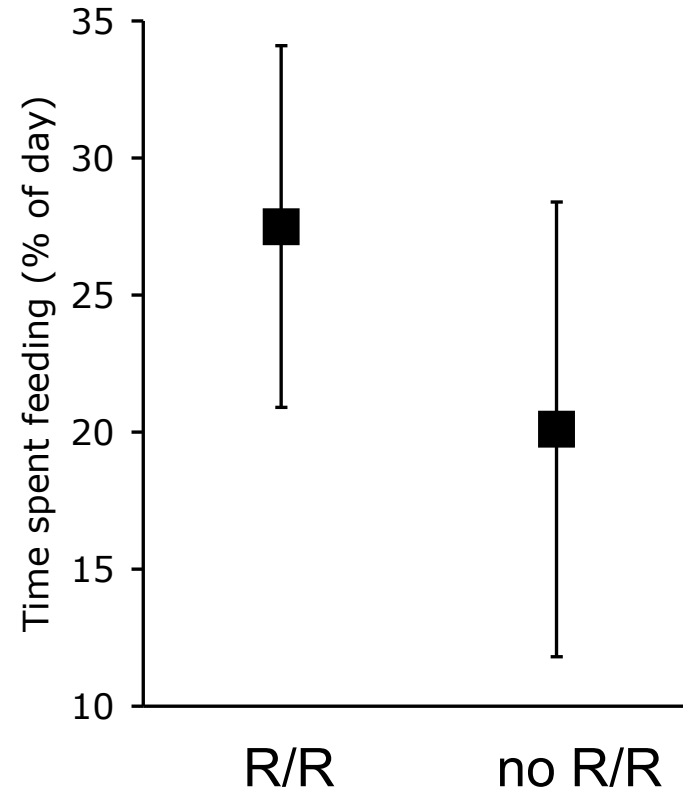
# Herbivore diversity





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

Ikki Matsuda<sup>1,\*</sup>, Tadahiro Murai<sup>1</sup>,  
Marcus Clauss<sup>2</sup>, Tomomi Yamada<sup>3</sup>,  
Augustine Tuuga<sup>4</sup>, Henry Bernard<sup>5</sup>  
and Seigo Higashi<sup>6</sup>



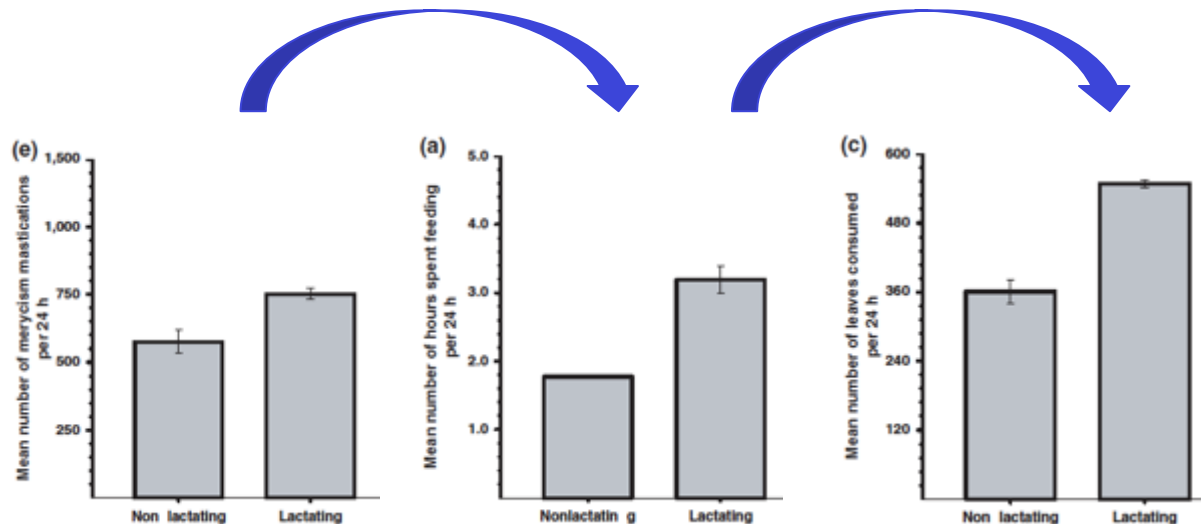


# The example of the koala

## The effects of lactation on the feeding behaviour and activity patterns of free-ranging female koalas (*Phascolarctos cinereus* Goldfuss)

*Australian Journal of Zoology*, 2003, **51**, 415–428

*M. Logan and G. D. Sanson*





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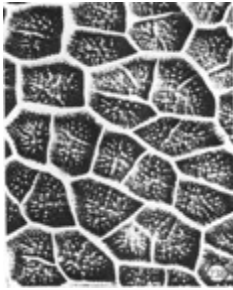
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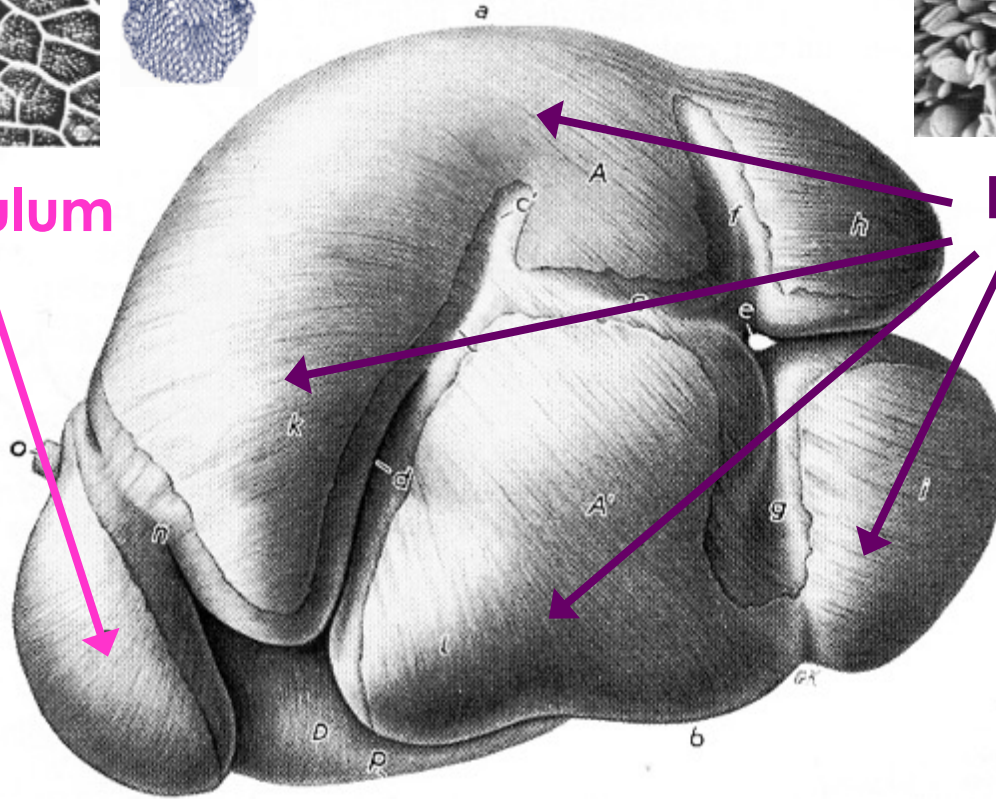
# Sorting in the forestomach

an interplay of fermentation characteristics,  
anatomy, and gravity



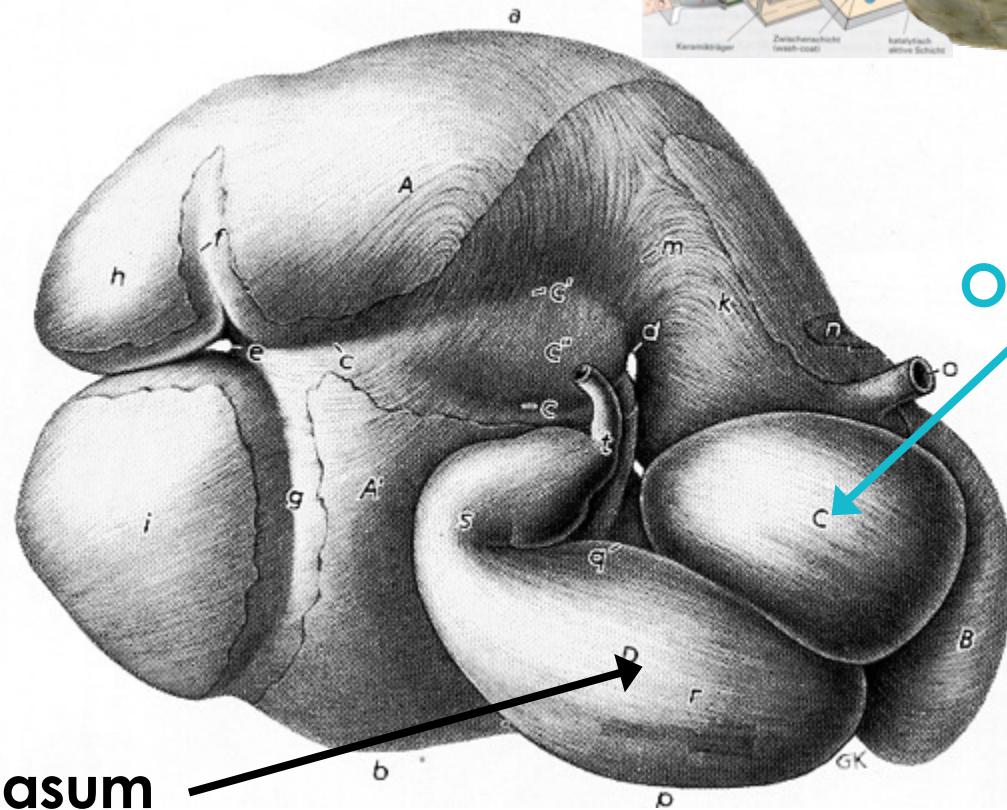
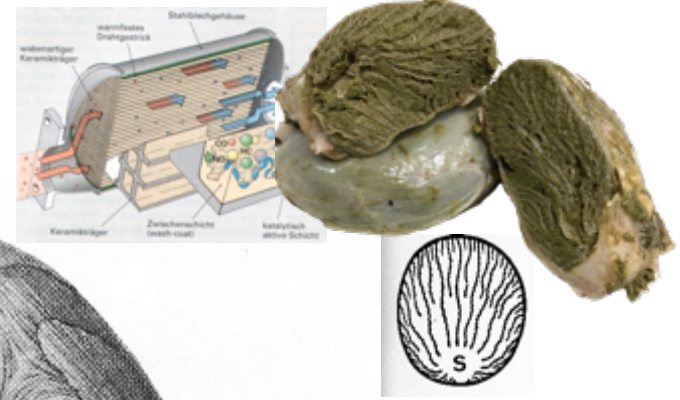
Reticulum

Rumen



(Nickel-Schummer-Seiferle 1967)



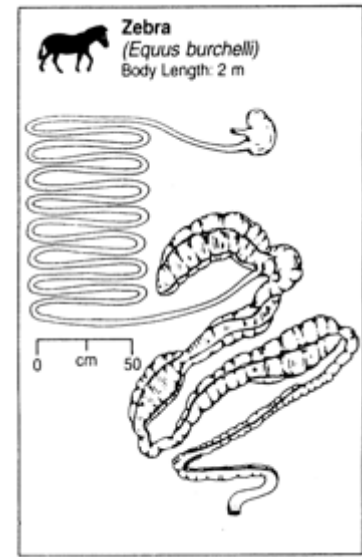
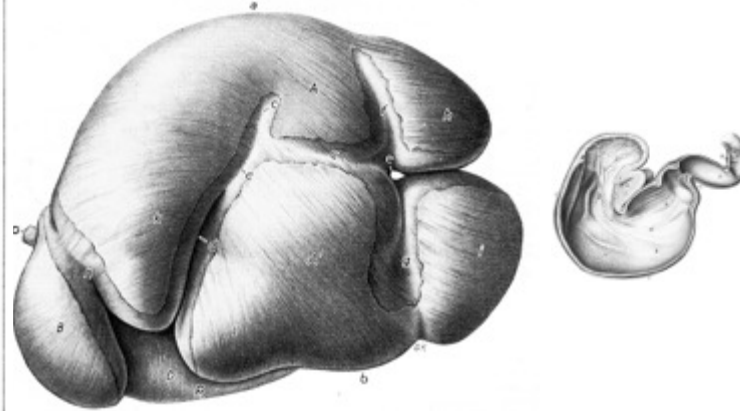
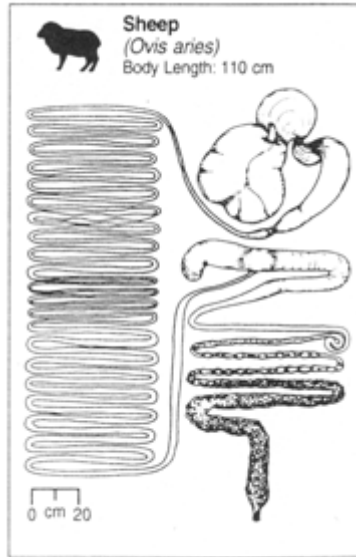


Omasum

# Abomasum

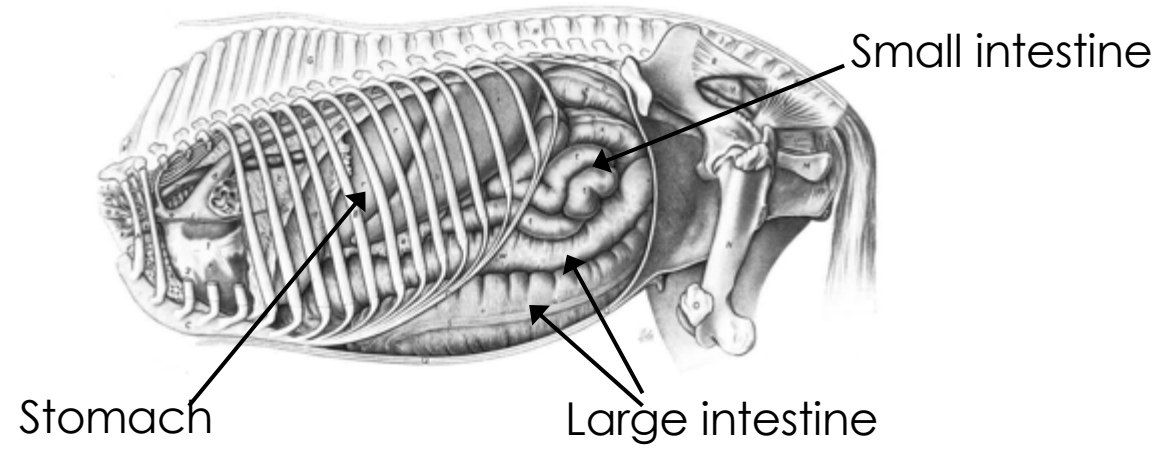
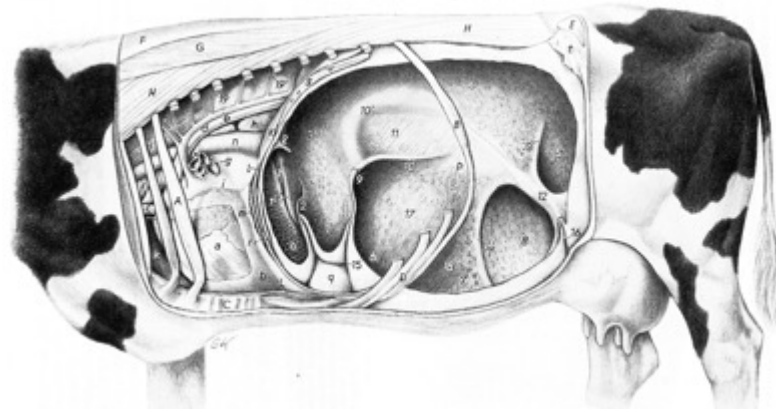
(Nickel-Schummer-Seiferle 1967)





(Nickel-Schummer-Seiferle 1967, Stevens & Hume 1995)

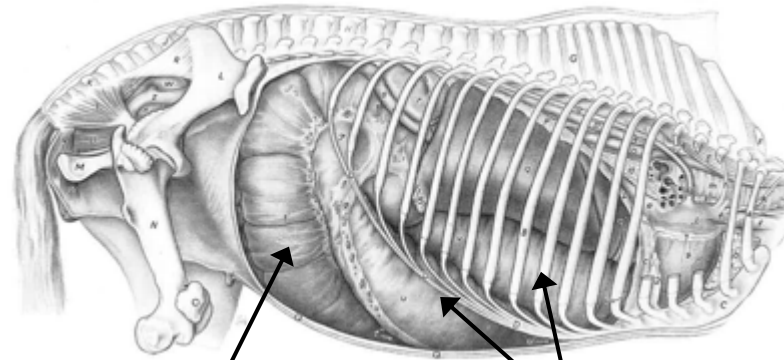
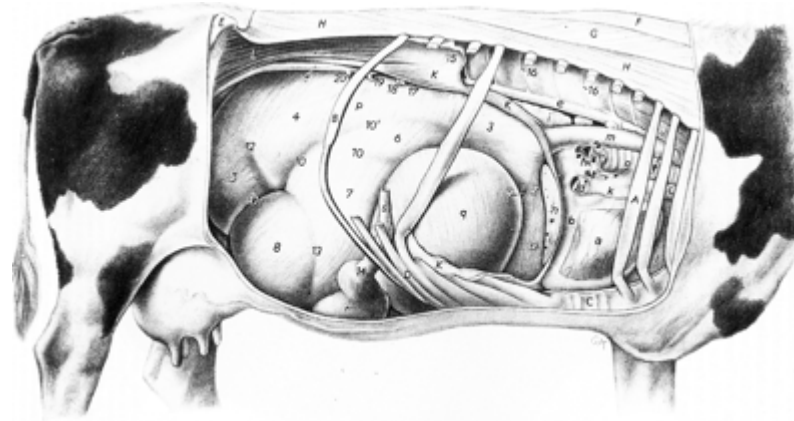




(Nickel-Schummer-Seiferle 1967)







Caecum

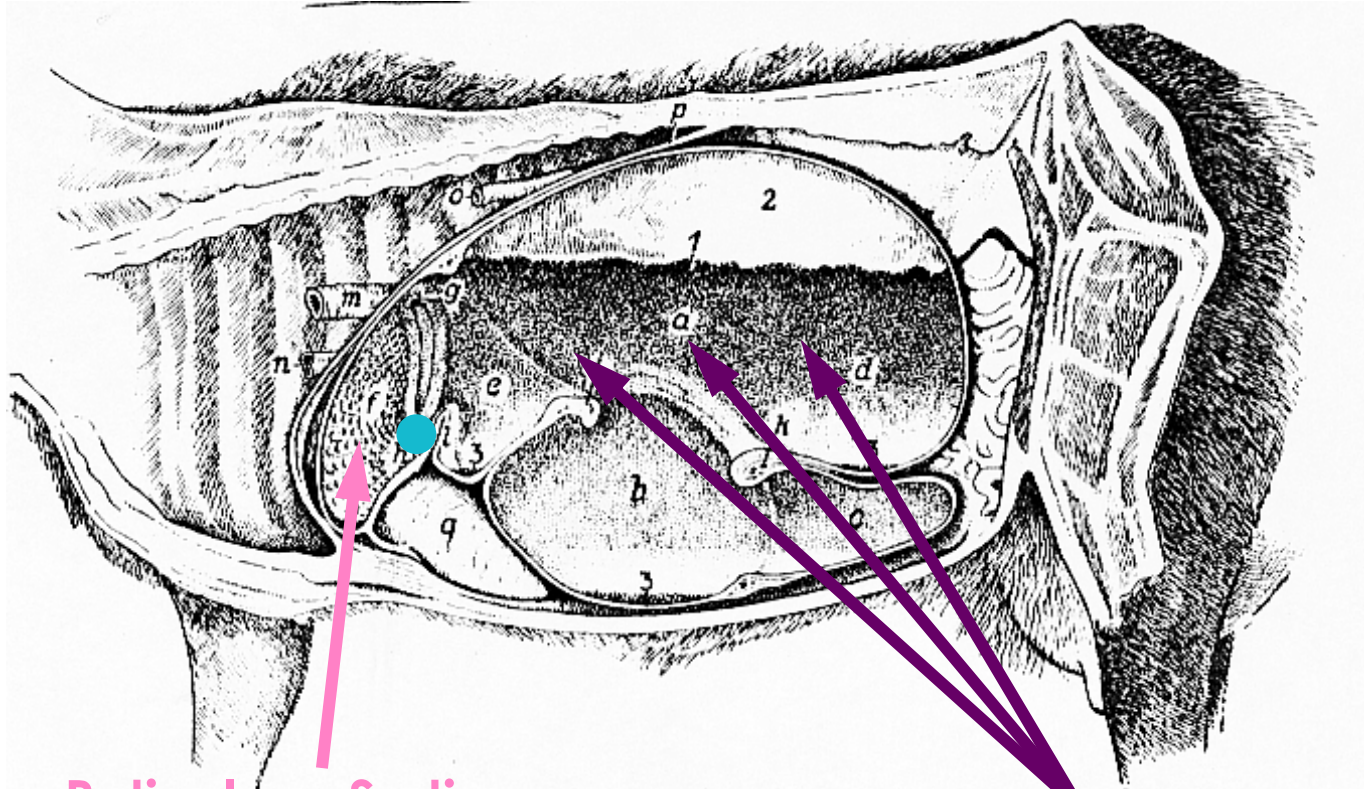
Large intestine



(Nickel-Schummer-Seiferle 1967)



# Digest and sort !



**Reticulum: Sorting**



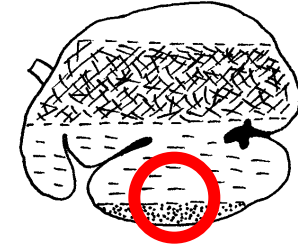
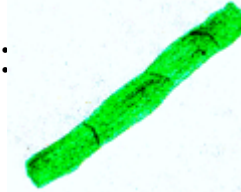
**Rumen:  
Bacteria ferment**

(from Grau 1955)

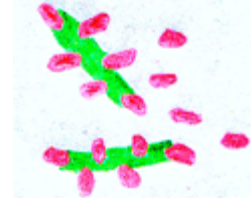


# Functional density

un-fermented ingesta particle:  
entangles in fibre mat



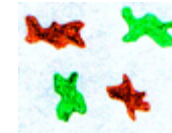
size reduction by rumination/  
attachment of bacteria



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



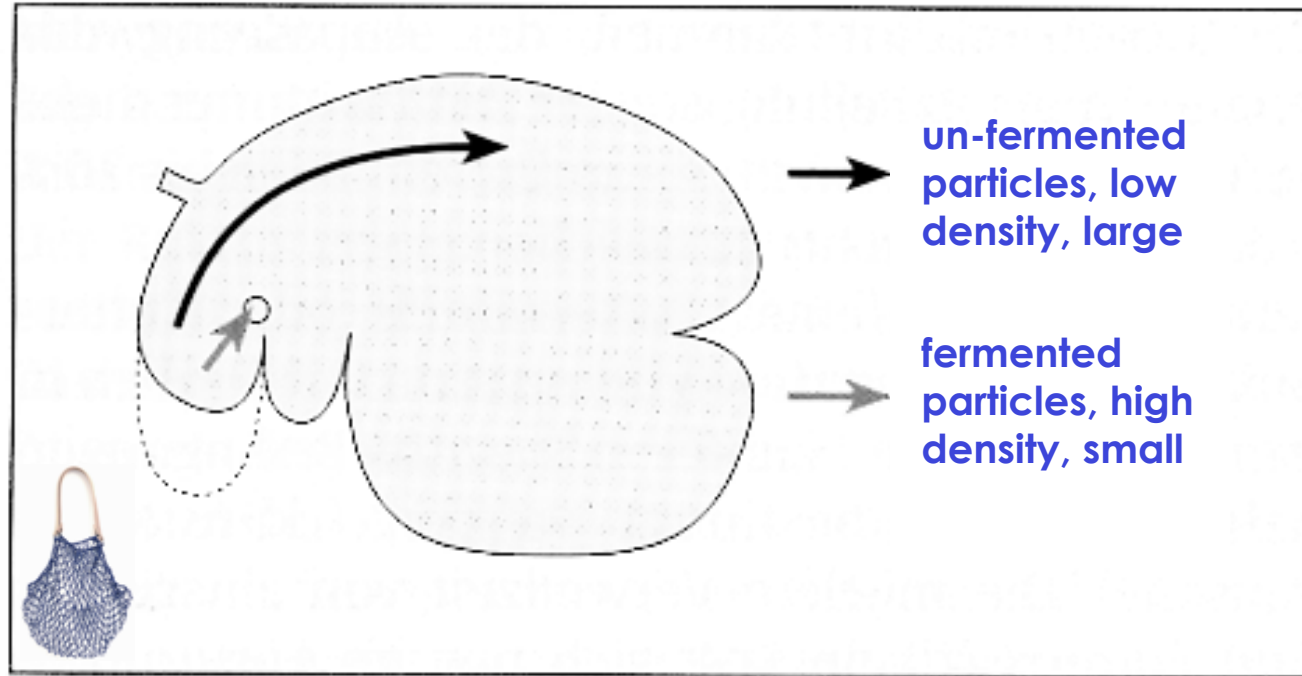
fermented particles:  
high density







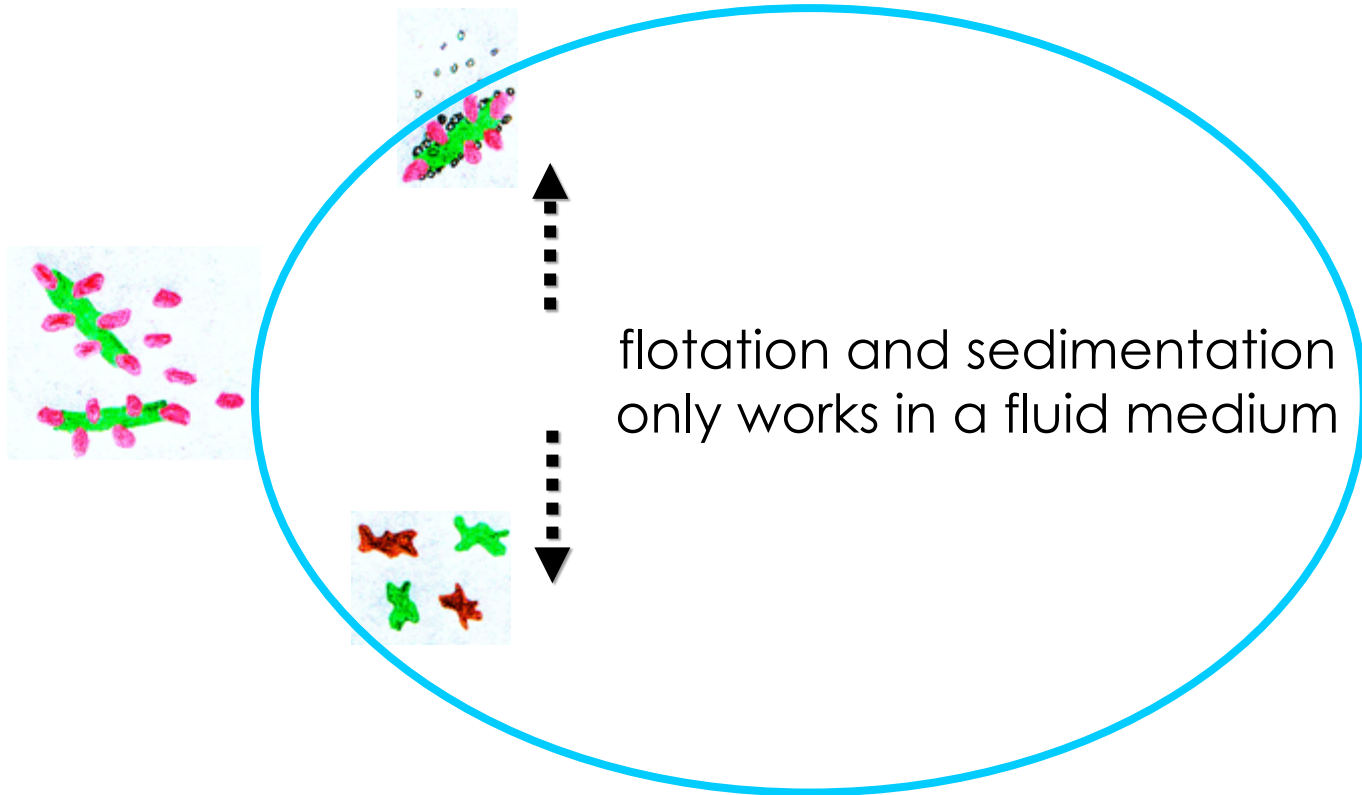
# Sorting in the reticulum



(from von Engelhardt & Breves 2000)



# Sorting by density





# Sorting by density





# Ruminants rest in sternal recumbency





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





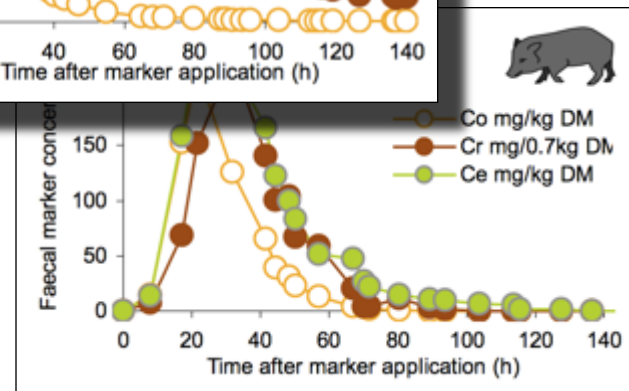
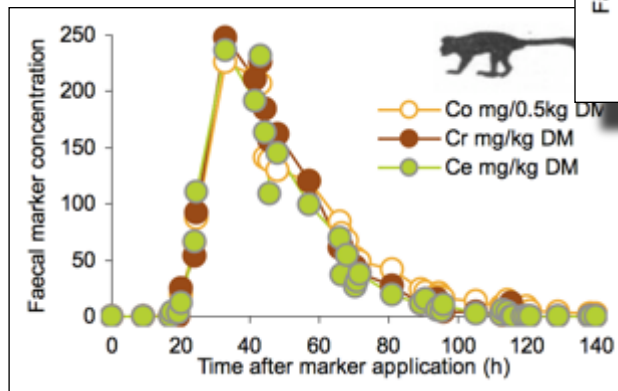
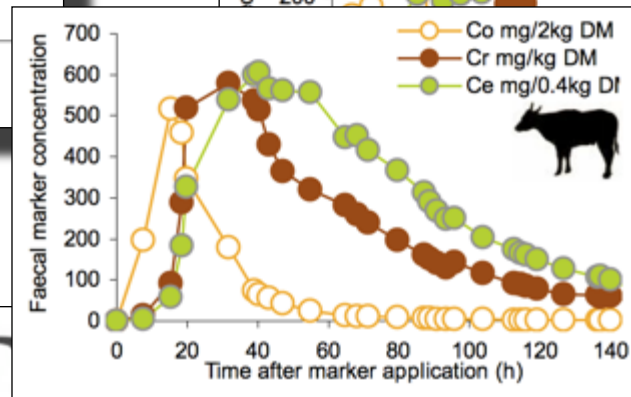
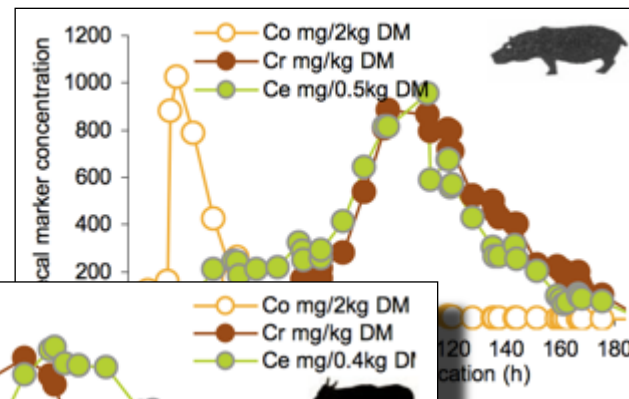
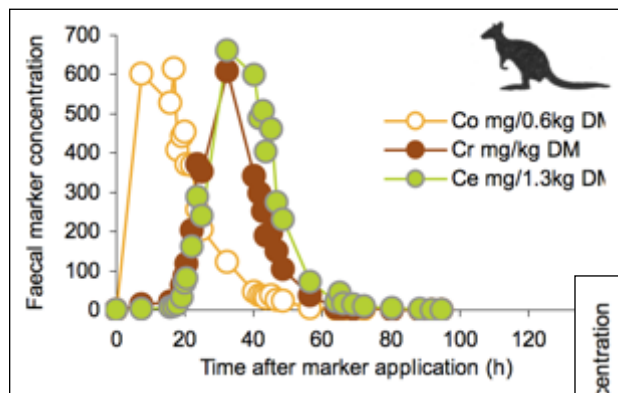
# Demonstration of sorting







# Demonstration of sorting

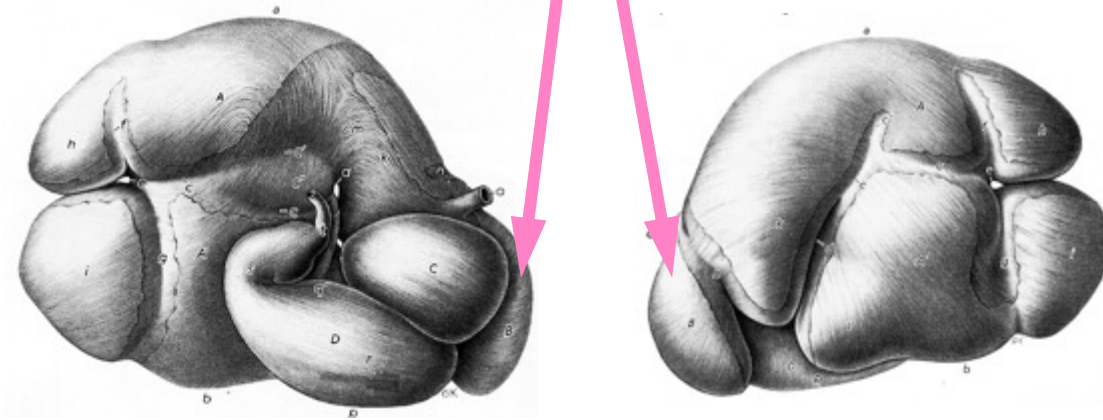


Schwarm et al.  
(2008,2009),



# Fluid is a problem

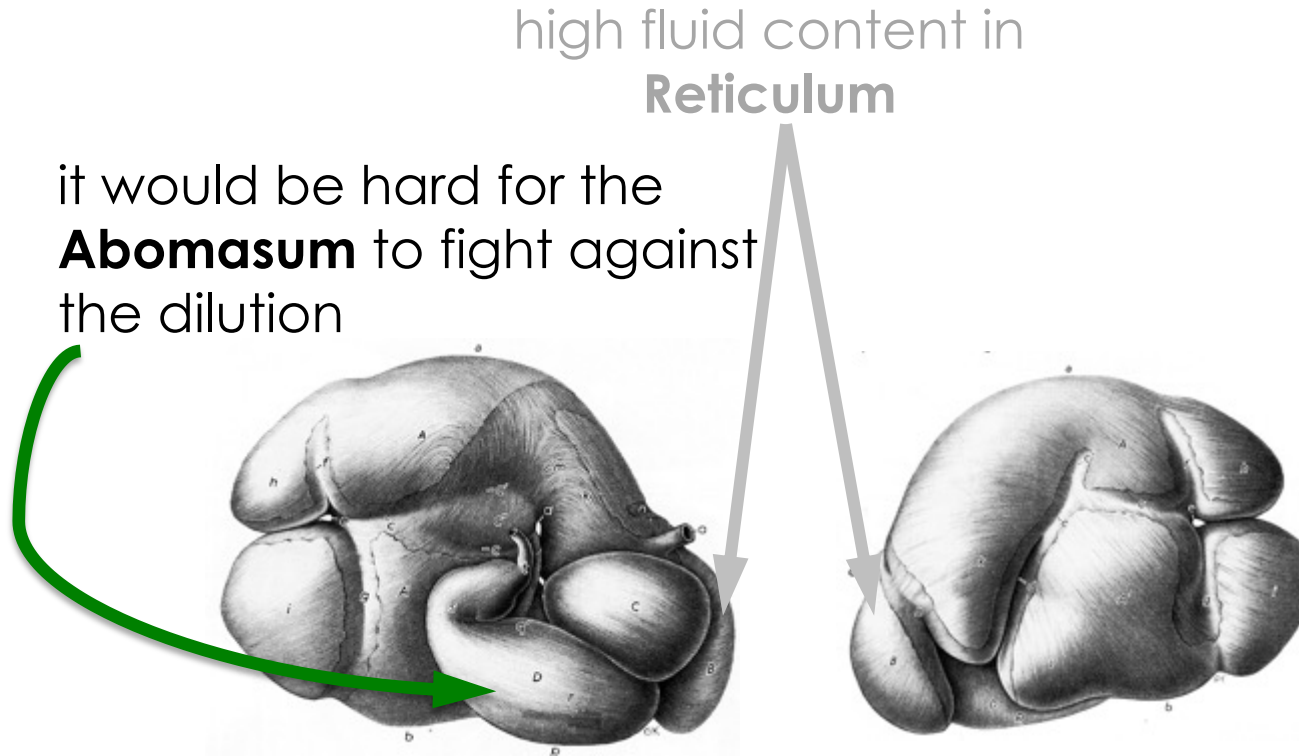
high fluid content in  
**Reticulum**







# Fluid is a problem





# Fluid is a problem

