



Merycism and Rumination – a comparative view of an evolutionary adaptation and a behavioural disorder



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5. Zürcher Dyphagietagung, 24.-25.01.2014



**University of
Zurich^{UZH}**



Clinic
of Zoo Animals, Exotic Pets and Wildlife



JOH. CONRADI PEYERI

Med. Doct. & Acad. Nat. Cur. Collegæ
cognomento Pythagoræ

MERYCO- LOGIA

SIVE DE
RVMINANTIBVS
ET
RVMINATIONE
COMMENTARIVS.

Quo primùm exponuntur

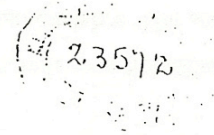
*RVMINANTIVM SPECIES ET DIFFE-
rentie, per omnia animalium genera; deinde organorum
ruminationi inservientium admiranda structura desegitur, & iconibus
ari incisus ante oculos ponitur: denique de ruminatione ipsa
ejusque causis ac utilitate differitur.*

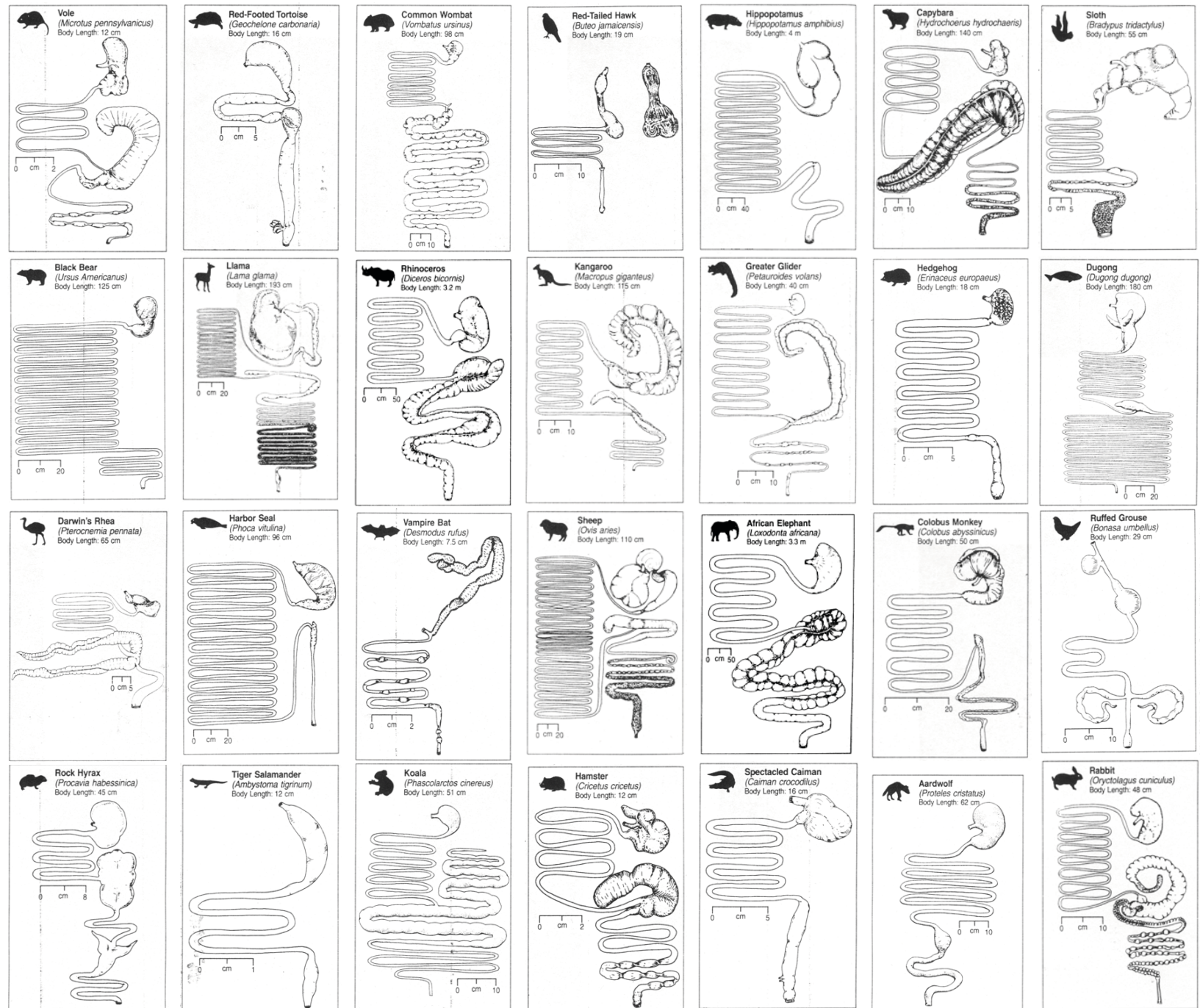


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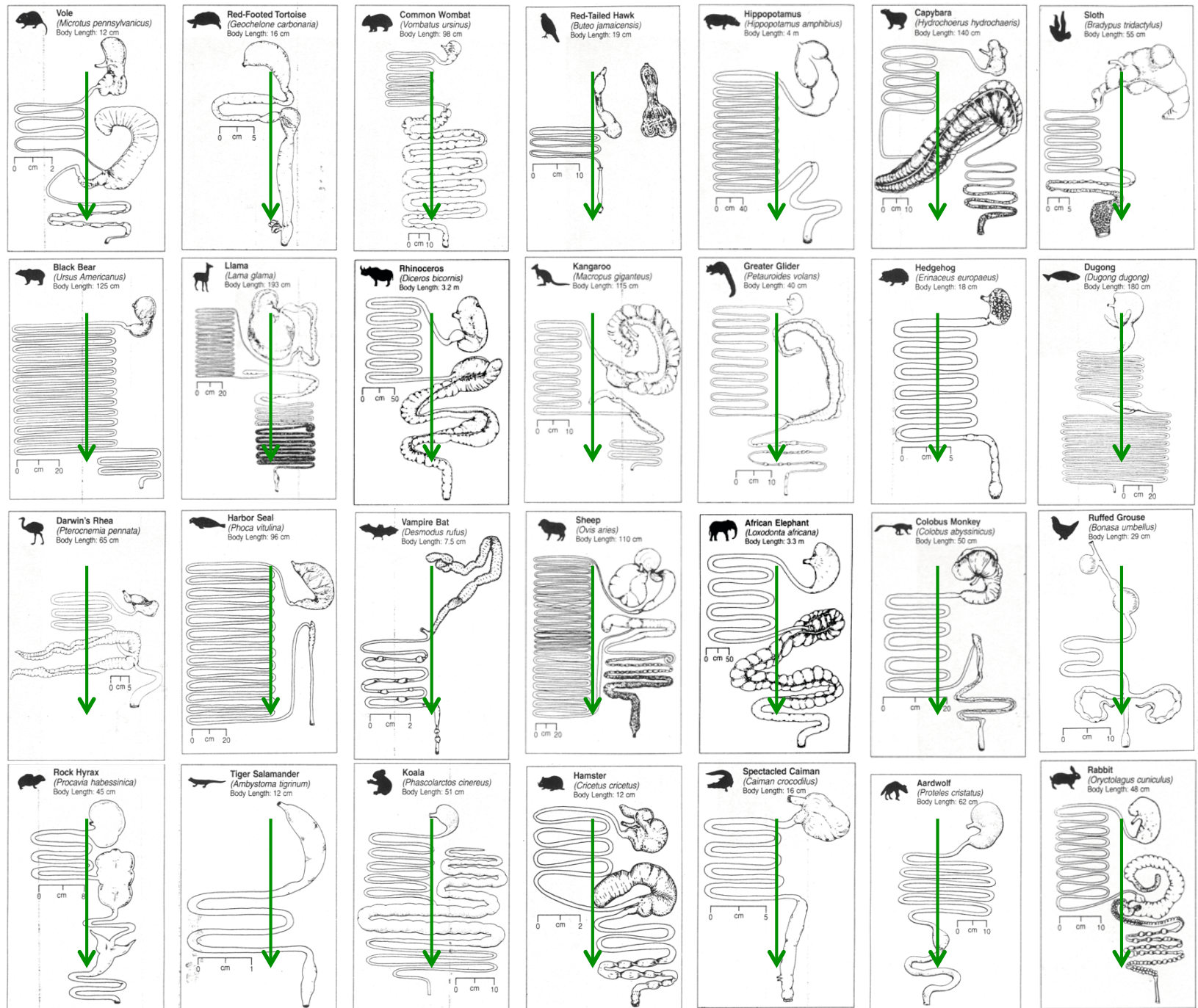
Apud JOH. LUDOVICVM KOENIG
& JOH. BRANDMYLLERVM.

M DC LXXXV.





from Stevens und Hume (1995)



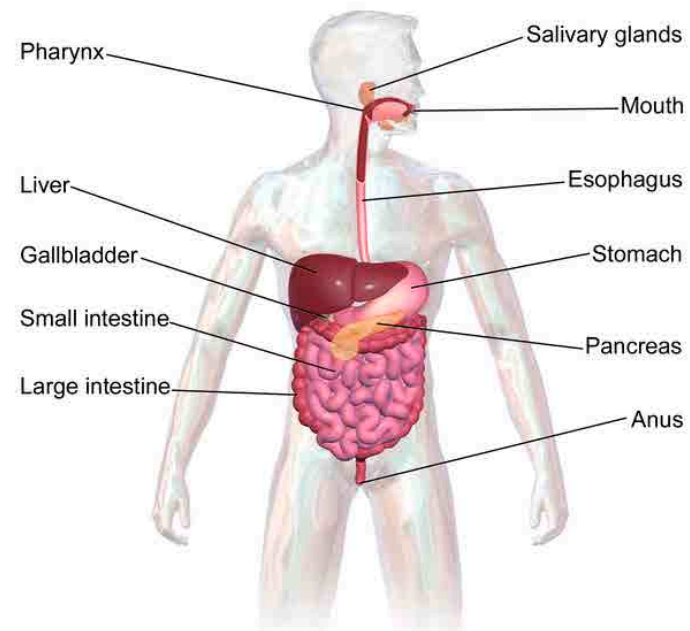
from Stevens und Hume (1995)

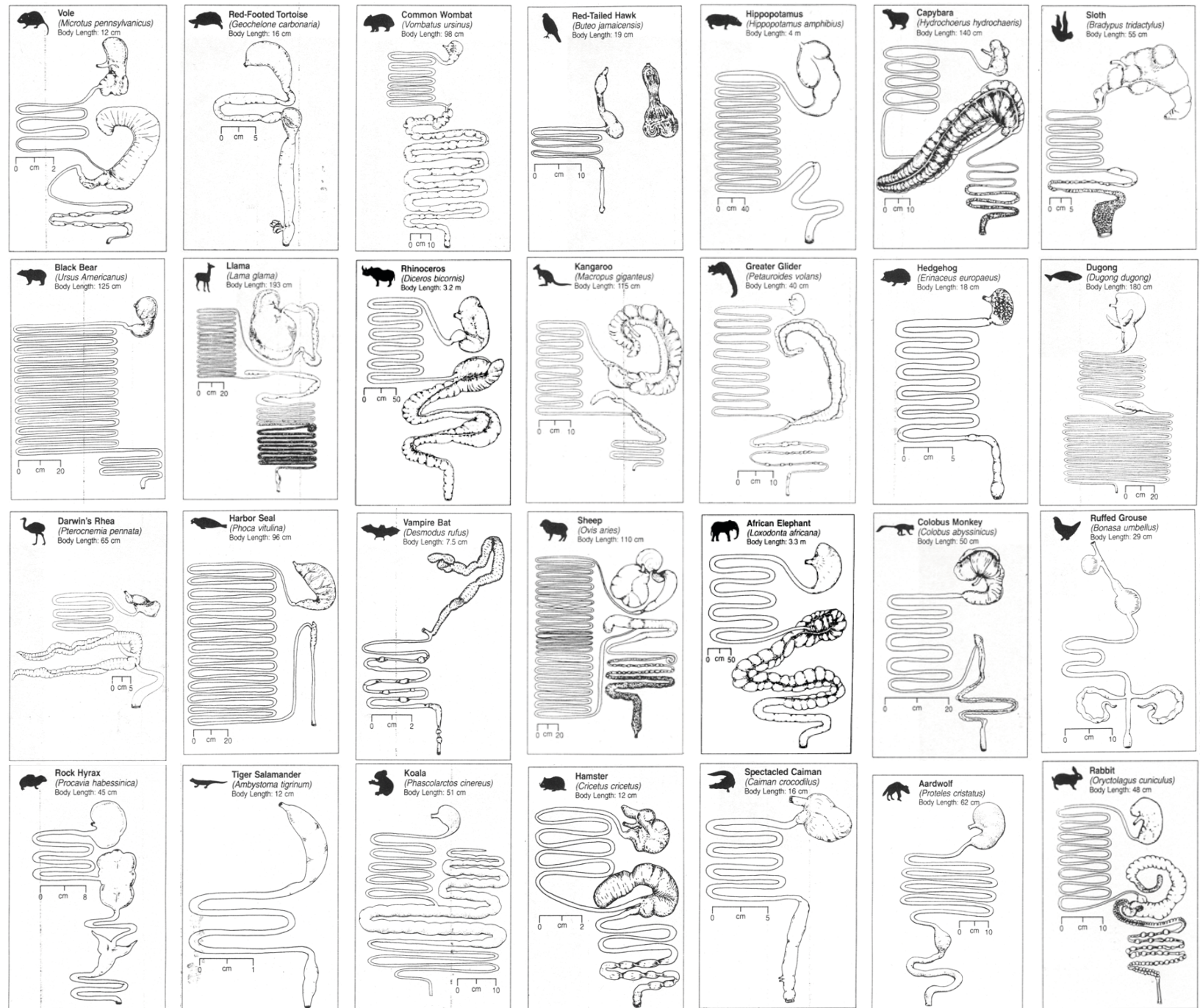


Definitions

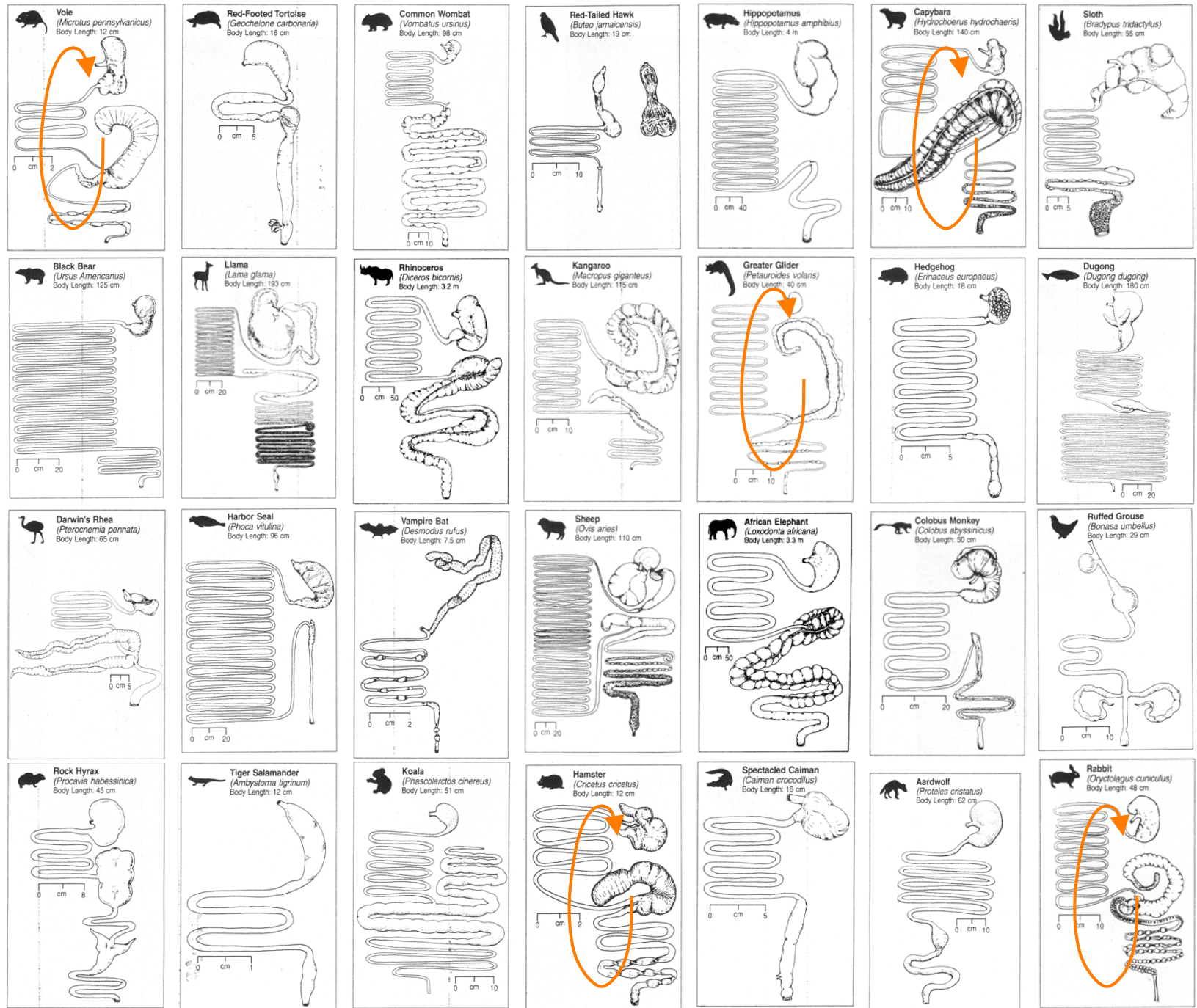
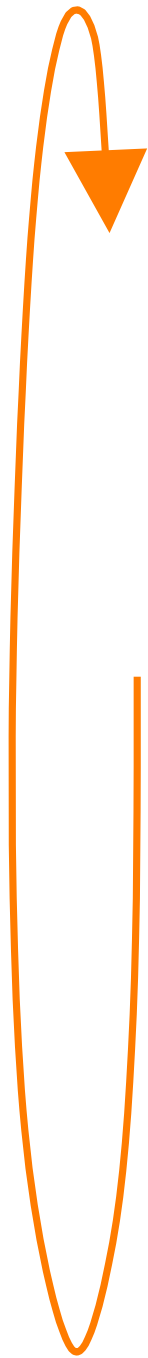
- Digestion

- mechanical and chemical breakdown of food into smaller components that can be absorbed
- takes place during the retention in, and passage through, the digestive tract





from Stevens und Hume (1995)



from Stevens und Hume (1995)



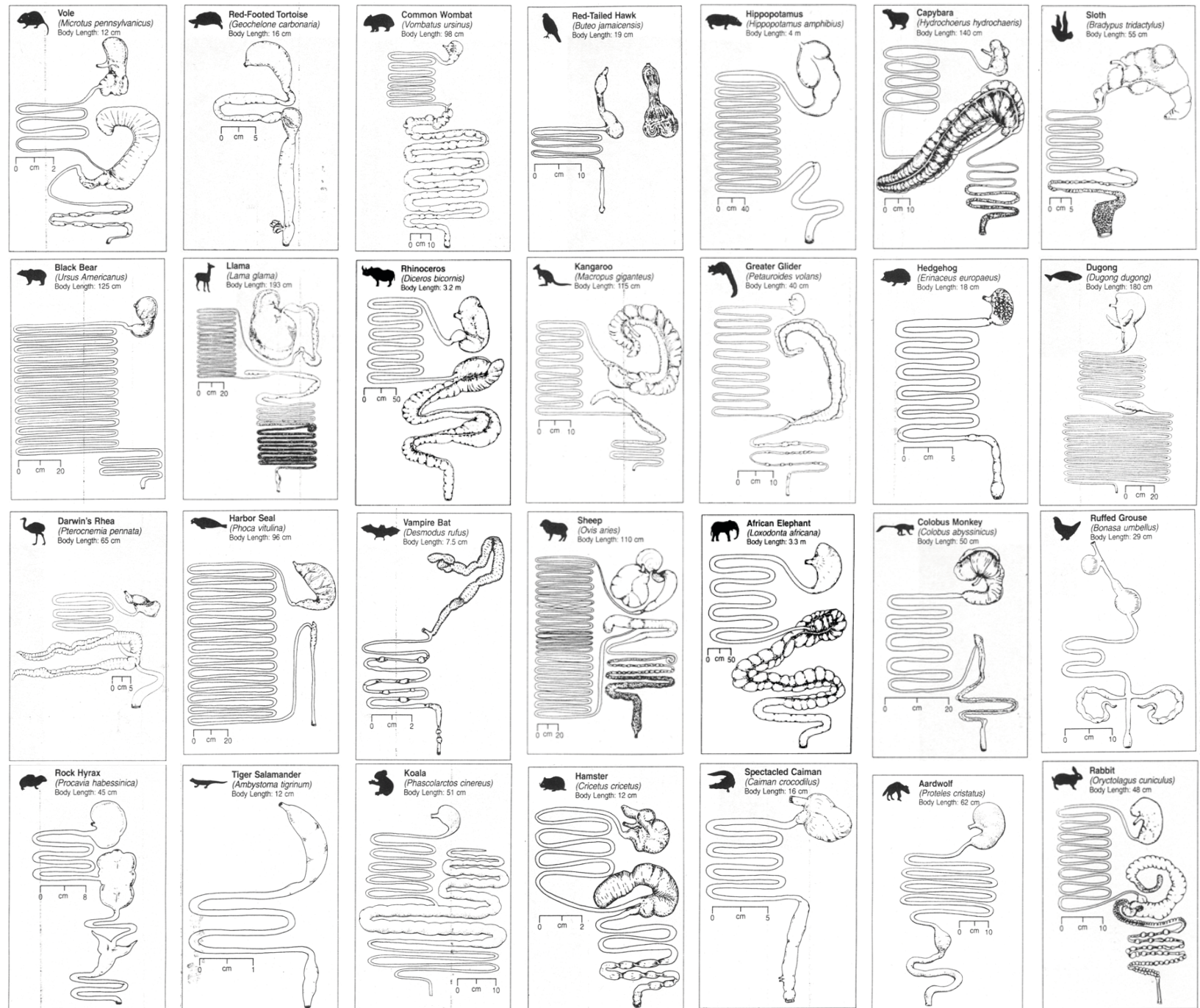
Definitions

- Coprophagy

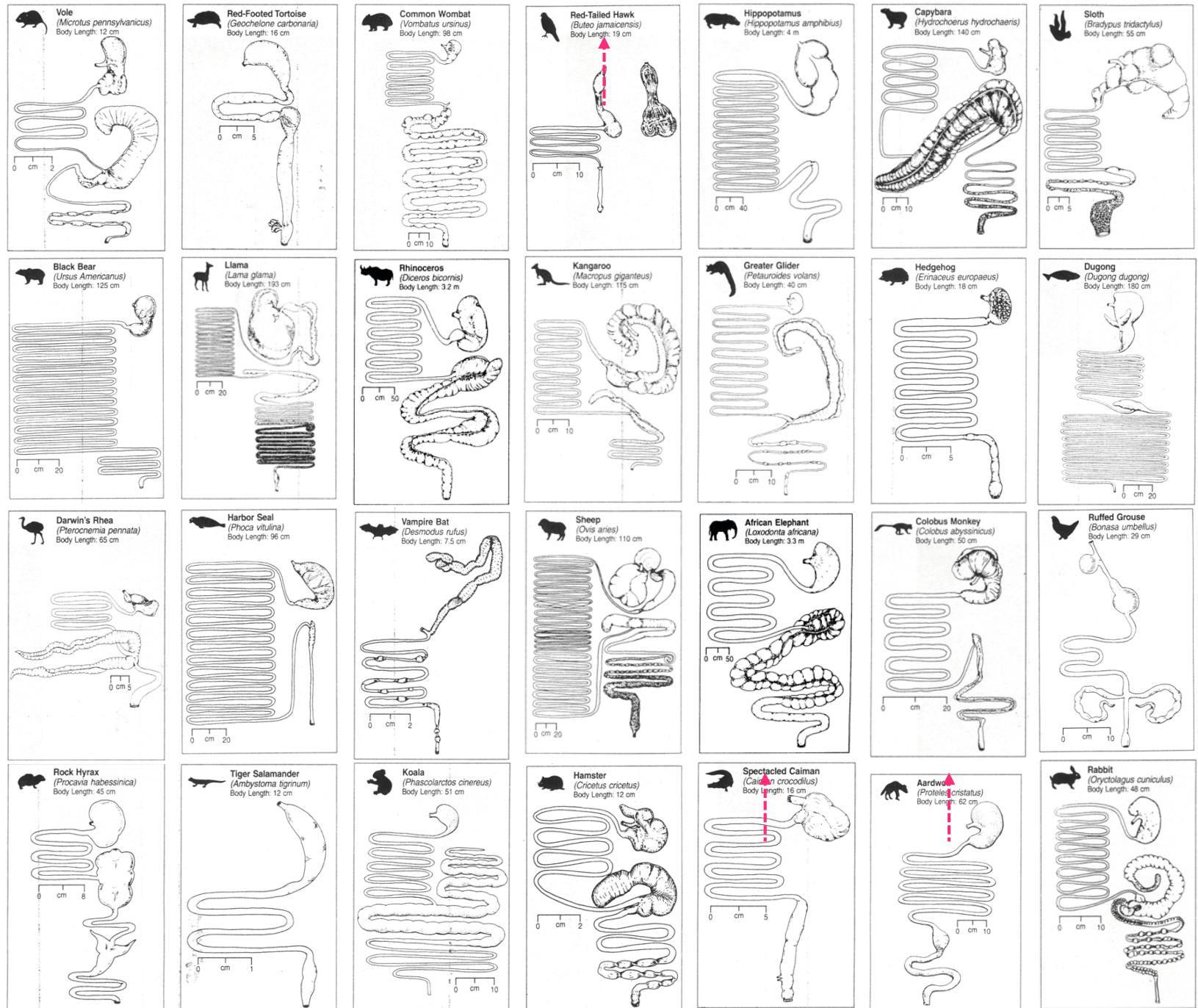
- ingestion of regular faeces
 - => normal feeding behaviour ('detritivores')
 - => behavioural mechanism to ensure inoculation of GIT with symbiotic microbes (rare)
 - => abnormal behaviour
- ingestion of special faeces ('caecotrophs')
 - => separation mechanism in the hindgut
 - => recycling of bacterial protein
 - => near-obligatory in many rodents and



lagomorphs



from Stevens und Hume (1995)



from Stevens und Hume (1995)



Definitions

- Vomiting
 - involuntary (forceful) expulsion of stomach contents
 - => linked to aversive condition (gastritis, poisoning)
 - => 'does not stop in the mouth'



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- voluntary/intentional expulsion of material from mouth/pharynx/esophagus/stomach
 - => transport: feeding young/sharing food
 - production of special products in GIT (crops milk in pigeons, bee honey)
 - => elimination: indigestible products (pellets/'casting' in carnivorous/piscivorous birds; stomach eversion in sharks)

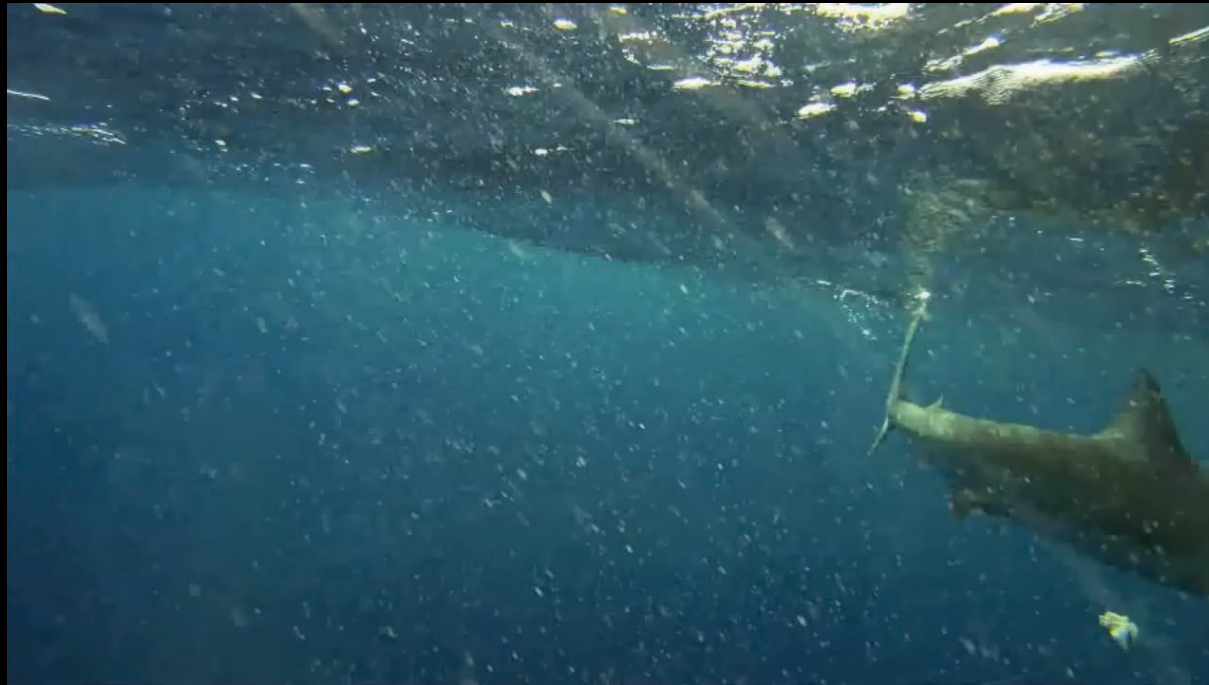


Crocodile regurgitating





Shark stomach eversion





Eagle pellet





Shrike pellet





Owl pellet





Owl pellet





Owl pellet





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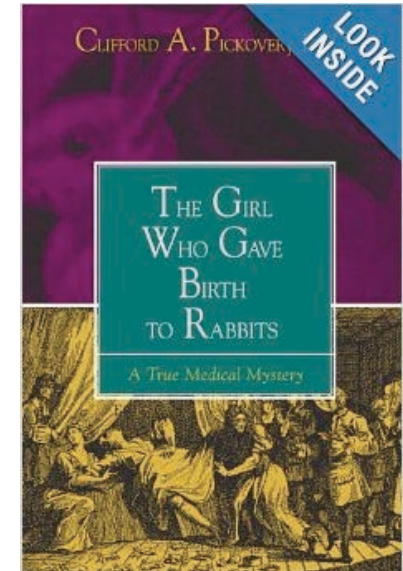
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 - => 'regurgitating artists'



Regurgitators

- 1621 'nail-vomiting boy of Boston'
- 1642 Catharina Geisslerin, the 'toad-vomiting woman of Germany'
- 1694 Theodorus Döderlein (vomiting newts and frogs)
- 1834 Henriette Pfenning (vomiting frogs)
- compulsive swallows (1927 patient with toothbrushes and disposable razor handles in his stomach)
- Stevie Starr – the 'professional regurgitator'





Regurgitators

Stevie Starr★ The Regurgitator Unofficial Fan Site

Stevie Starr Swallows and Then
Regurgitates Things in the Most
Amazing Way



Stevie Starr

**Stevie Starr on Czech and
Slovak Got Talent (October
2011)!**

Stevie is in another "Got
Talent" competition, this time
in the Czech and Slovak
Republics. He is in the first
round and "everyone loves
him," according to fan Václav C.

In 2010, Stevie made it to the
semi-finals on "Britain's Got Talent" as
well as on "Das Supertalent," Germany's
version of the show.

About The Regurgitator

I first saw "The Regurgitator" (Stevie
Starr) on a rerun of the Tonight Show
with Jay Leno in 2005, and I decided I
needed to make a fan site for him.

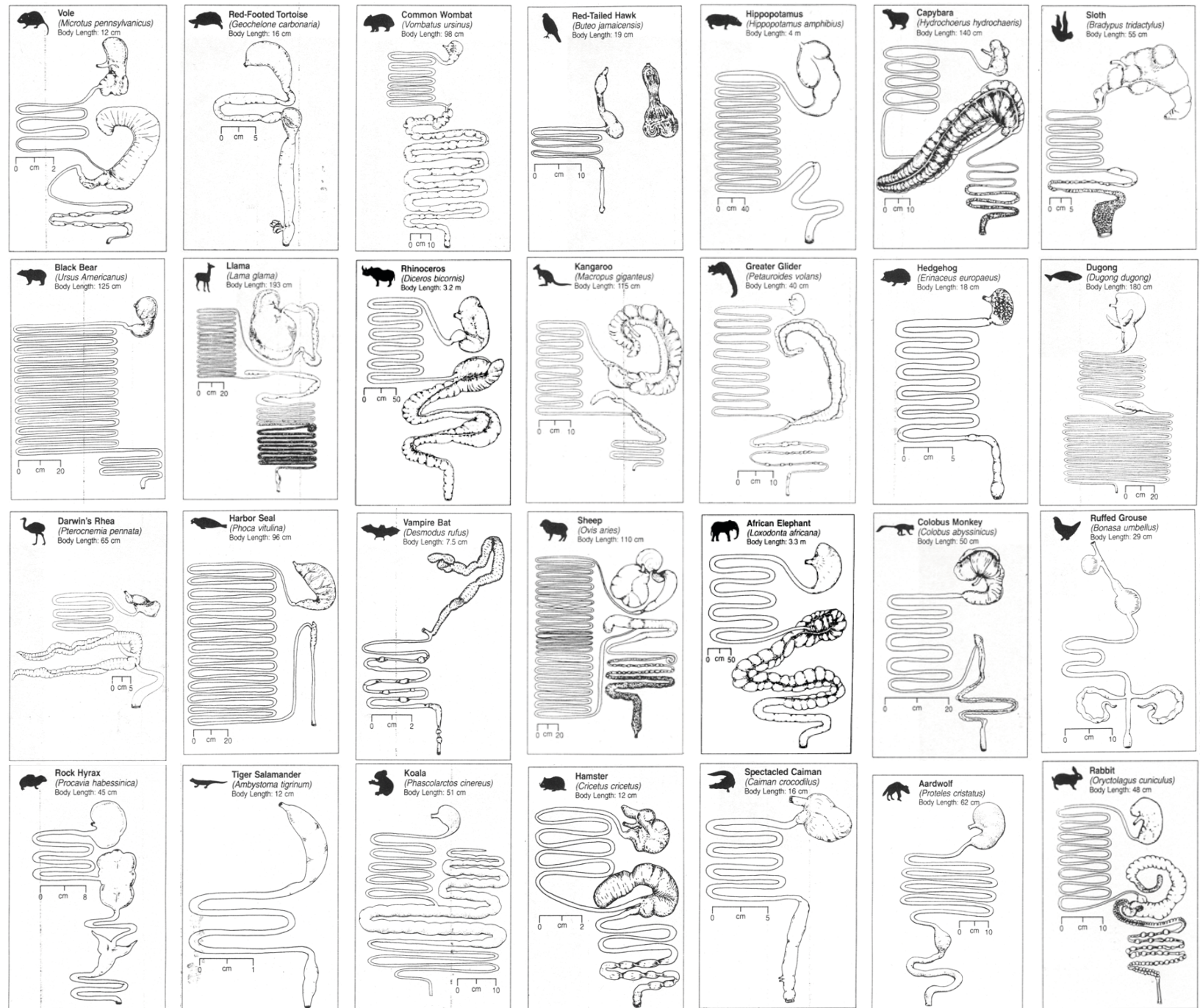
Stevie Starr is amazing. I have no idea
how he does it and I couldn't find out
any more information in a google
search.



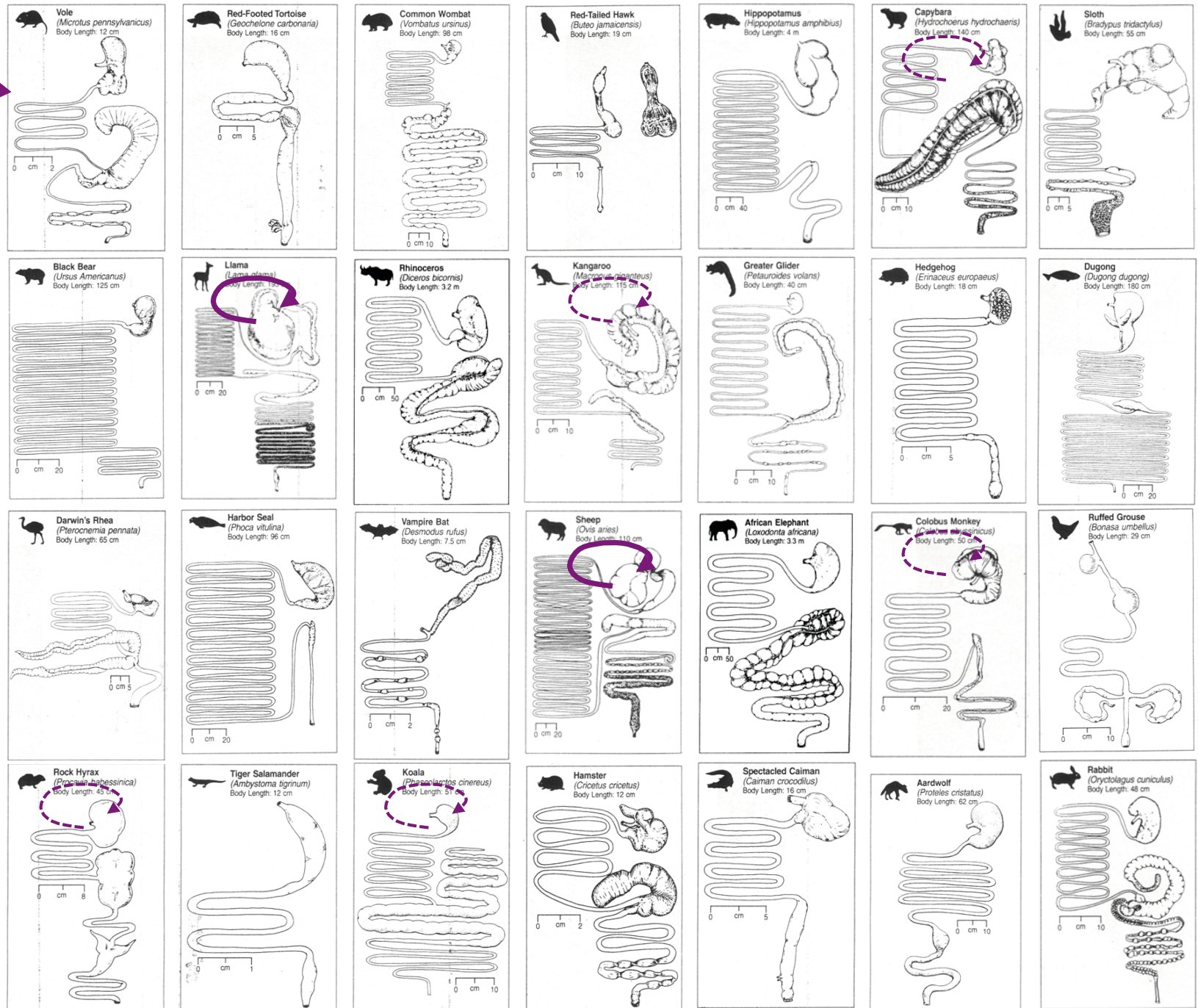


Human regurgitators





from Stevens und Hume (1995)



from Stevens und Hume (1995)



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 - “to turn over in the mind”
 - “to chew the cud”
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Gorilla R/R





Gorilla R/R





A review of nutritional and motivational factors contributing to the performance of regurgitation and reingestion in captive lowland gorillas (*Gorilla gorilla gorilla*)

Kristen E. Lukas *

Applied Animal Behaviour Science 63 (1999) 237–249

Despite findings that provision of browse and removal of fruit from the diet reduces R/R (Loeffler, 1982; Gould and Bres, 1986a; Ruempler, 1992; Wiard, 1992; Velderman, 1997), no one has yet documented the elimination of this behavior from an individual's repertoire. Ruempler (1992), however, reported that one gorilla's R/R had completely ceased for over a year after removing all but huge portions of vegetables and browse (18 kg per adult animal per day) from the diet at Cologne Zoo in Germany. For comparison, an adult male gorilla consumes approximately 6 kg/day at Zoo Atlanta (G. Hamor, personal communication), 13 kg/day at Brookfield Zoo (C. Demitros, personal communication), and 30 kg/day in the wild (*G.g. beringei*, Goodall, 1977). Unfortu-



Removing Milk from Captive Gorilla Diets: The Impact on Regurgitation and Reingestion (R/R) and Other Behaviors

Kristen E. Lukas,^{1,2,3*} Gloria Hamor,³ Mollie A. Bloomsomsmith,^{2,3}
Charles L. Horton,³ and Terry L. Maple^{2,3}

Zoo Biology 18:515 - 528 (1999)

TABLE 6. Comparisons of gorilla behavior between conditions in Phase 2

	Baseline (32 oz milk)	Treatment 32 oz diluted (fruit juice)	Baseline (32 oz milk)	Hypothesis test: baselines vs. treatment	Probability ($\alpha = 0.05$)
Scan data (percentage of time)					
R/R	5.9%	3.7%	6.3%	F = 8.508	P = 0.010
Eat hay	1.3%	1.6%	0.3%	F = 0.767	ns
Inactive	45.5%	46.6%	46.3%	F = 0.115	ns
Drink water	3.4%	3.3%	2.9%	F = 0.011	ns
Social (affiliative)	8.4%	8.0%	11.7%	F = 1.221	ns
Other undesirable	1.0%	1.2%	2.0%	F = 0.594	ns
Self-directed behavior	17.1%	17.5%	13.9%	F = 1.681	ns
Social (agonistic)	0.1%	0.3%	0.4%	F = 0.136	ns
Other active behavior	16.0%	16.7%	15.0%	F = 0.605	ns
All-occurrence data (no. per 5 - min)					
R/R attempts	0.022	0.017	0.011	F = 0.000	ns
R/R bouts	0.428	0.256	0.422	F = 4.684	P = 0.045
Feed on another's regurgitant	0.061	0.061	0.072	F = 0.239	ns
Examine another engaging in R/R	0.056	0.056	0.072	F = 0.221	ns
Agonistic behavior	0.089	0.111	0.233	F = 1.342	ns



Chimpanzee R/R





Chimpanzee R/R





An analysis of regurgitation and reingestion in captive chimpanzees

Kate C. Baker^{a,*}, Stephen Phillip Easley^b

Applied Animal Behaviour Science 49 (1996) 403–415

of cagemates or housing history; nor were sex differences detected. Meal composition was not found to effect the time devoted to R/R. Statistical tests did show a strong positive relationship between rates of R/R and elapsed time since feeding. These results suggest that increasing meal frequency or providing consistently available edible material may prove more broadly effective than altering meal composition. Temporal distributions of R/R differed from those of abnormal

old male) (Morgan et al., 1993). That study found that R/R occurred within minutes of each meal, and was most frequent following meals consisting of fruit. Reductions in R/R occurred during behavioral training sessions and when more browse was provided.



Orangutan R/R





Orangutan R/R

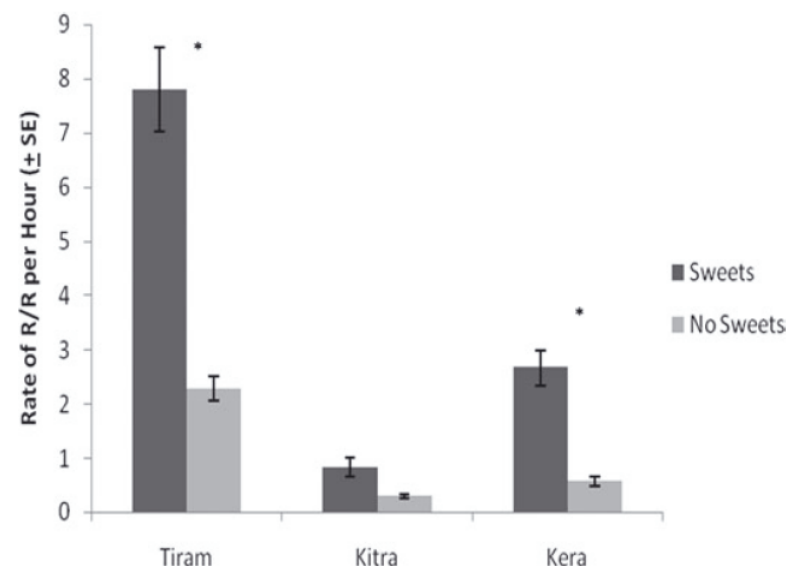
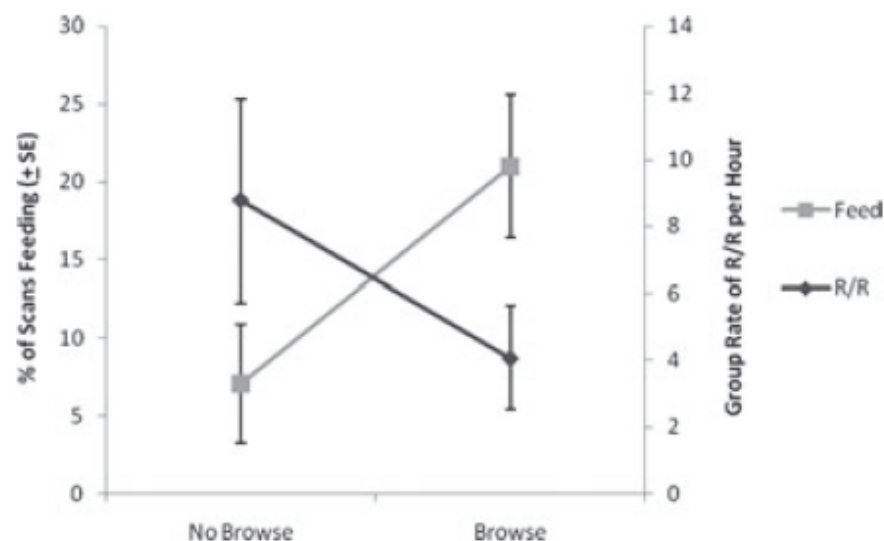




Prevalence of Regurgitation and Reingestion in Orangutans Housed in North American Zoos and an Examination of Factors Influencing its Occurrence in a Single Group of Bornean Orangutans

Zoo Biology 31: 609–620 (2012)

Christine M. Cassella,^{1,2*} Alyssa Mills,¹ and Kristen E. Lukas^{1,2}





Special Articles

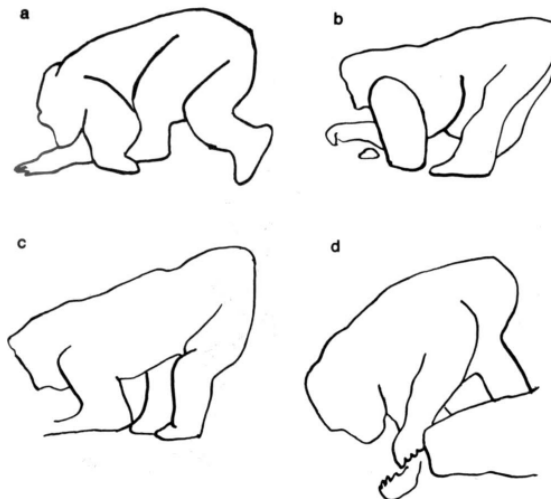
Regurgitation in Gorillas: Possible Model for Human Eating Disorders (Rumination/Bulimia)

EDWIN GOULD, PH.D.

Department of Mammalogy, National Zoological Park, Smithsonian Institution, Washington, D.C.

MIMI BRES, M.S.

Department of Biological Sciences, The George Washington University, Washington, D.C.





Rumination disorder in man

MAY 4, 1907.]

MEMORANDA.

[THE BRITISH
MEDICAL JOURNAL 1053]

MERYCISM OR RUMINATION IN MAN.

BY J. GRANT MILLAR, M.B., CH.B. GLASG.,

BRITISH MEDICAL JOURNAL VOLUME 287 23 JULY 1983

Habitual rumination: a benign disorder

D F LEVINE, D L WINGATE, J M PFEFFER, P BUTCHER

British Journal of Psychiatry (1994), 165, 303–314

Review Article

Merycism or Rumination Disorder A Historical Investigation and Current Assessment

BRENDA PARRY-JONES



Rumination disorder in man

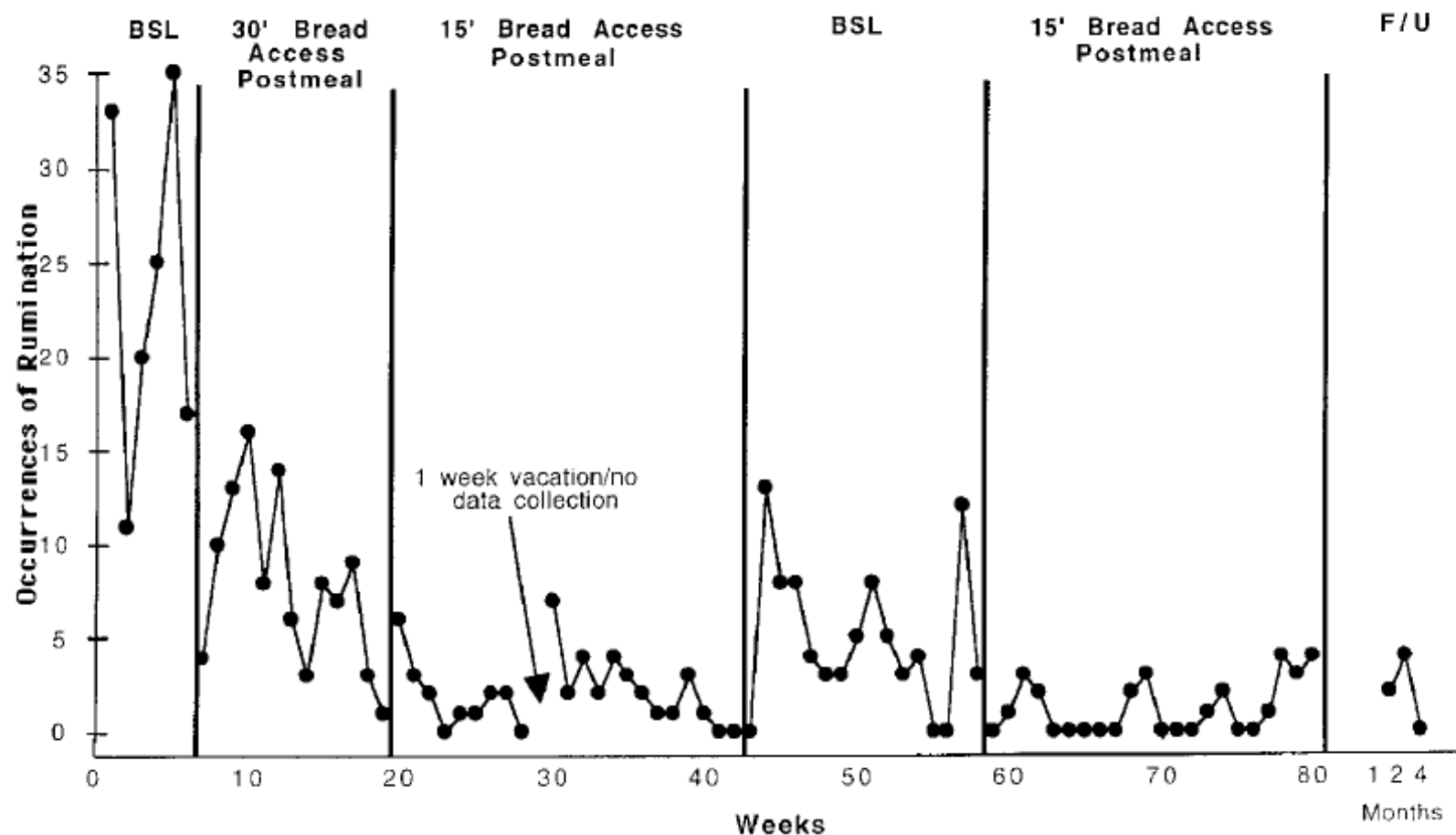
- historically: linking to bovine ancestry (incl. autopsies to check for chambered forestomach)
 - => 'the mark of the beast' (primitive impulse)
- 6-10 % of institutionalized persons with severe mental retardation
- complications: malnutrition, weight loss, aspiration/choking
 - => aspiration cause of death 5-10% of ruminators
- social isolation
- treatment option: ad libitum feeding/satiety



BRIEF REPORT: EFFECTS OF SUPPLEMENTAL FEEDINGS OF WHITE BREAD ON CHRONIC RUMINATION

Behavioral Interventions
Behav. Intervent., 13, 227-233 (1998)

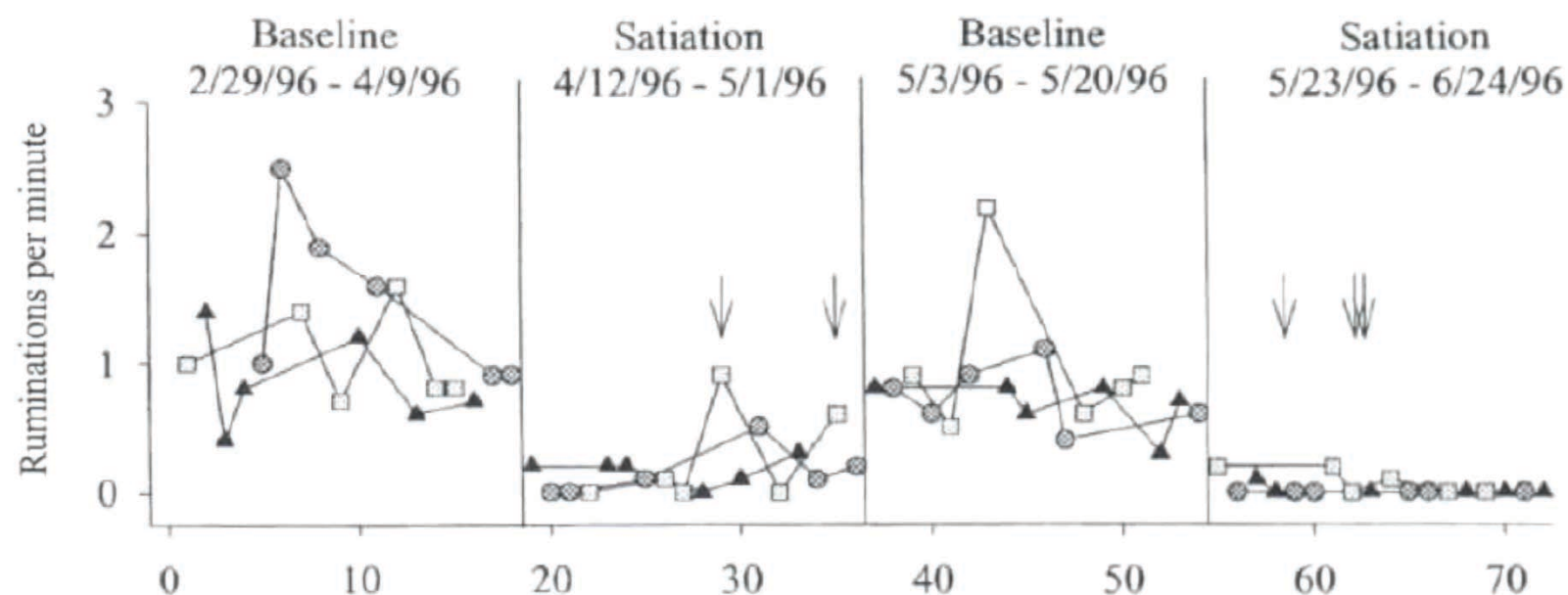
Christopher J. Masalsky* and James K. Luiselli





DECREASING RUMINATION USING A STARCHY FOOD SATIATION PROCEDURE

Laura L. Dudley^{1,2*}, Cammarie Johnson^{1,2*} and R. Scott Barnes¹





Special Articles

Regurgitation in Gorillas: Possible Model for Human Eating Disorders (Rumination/Bulimia)

EDWIN GOULD, Ph.D.

Department of Mammalogy, National Zoological Park, Smithsonian Institution, Washington, D.C.

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Department of Biological Sciences, The George Washington University, Washington, D.C.

TABLE 1. Comparison of Regurgitation and Reingestion with Two Human Disorders

	Bulimia	Rumination	r/r Gorilla
Ontogeny			
Failure to engage mother to interact	O	X ⁱ 36,43	X
Age at onset	11–22 yr ⁴⁶	3–6 mo ^{42,43}	> 5 yr
Parental separation	X ⁴⁶	O	X
Lacks control of eating	X ^{46,50}	O	X
Motor pattern			
Neck swelling	—	X ³	X
Chews	O	X ^{3,7}	X
Mouth fills	O	X ⁷	X
Reingest	O	X ^{7,47–49}	X
Valsalva maneuver	X ⁱ	X ²	X ⁱ
Mueller maneuver	X ⁱ	X ⁵	X ⁱ
Rhythmic chest, neck movement	O	X ³⁶	X
Induced with finger	X ^{46,41}	X ³⁶	X
No effort required	X ⁴⁶	O	X
Bends deeply prior to vomit ejection	X ⁱ	O ^{47,48}	X
Timing			
Interval between eating and regurgitation	> 1 min ⁴⁶	0–30 min ^{47,48,49}	0–8.3 hr
Interval between regurgitations	O	2–4 min ³	1.5–3 min
Duration of bouts	—	30–60 min ³	2 min–6 hr
Frequency/day	1 ⁴⁶	15–20/30–60 ⁴³	1–175
Context			
Do it alone	X	O	X
Favorite foods	O	X	X
Enjoy the taste	O	X ^{2,49}	X
Treatment			
Reduced if more food	O ⁴⁶	X (one study) ³⁵	X (browse)
Increased mother contact	—	X ³⁶	X ⁱ

Definitions: X_i, inferred; X, observed; —, unknown; O, doesn't occur.



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 - => implies regurgitation, chewing, re-swallowing

=> maladaptive in humans as well as certain zoo animals
‘rumination syndrome’ / ‘RR’



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=> ‘bubbling’ in certain flies



Fly bubbling





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=> ‘bubbling’ in certain flies

=> obligatory mechanism in functional ruminants

=> probably facultative mechanism in several herbivores



Rumination in ruminants





Rumination in ruminants





Rumination in camelids





Why rumination?



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



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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

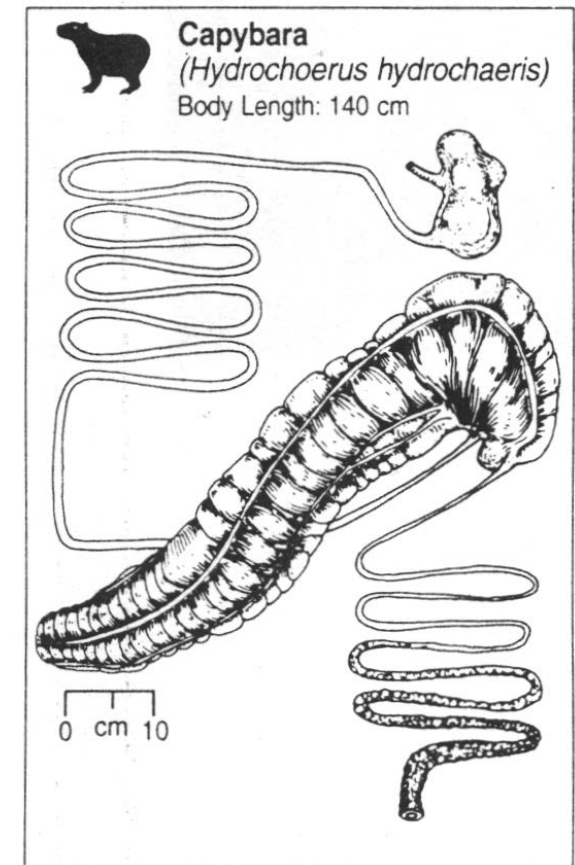
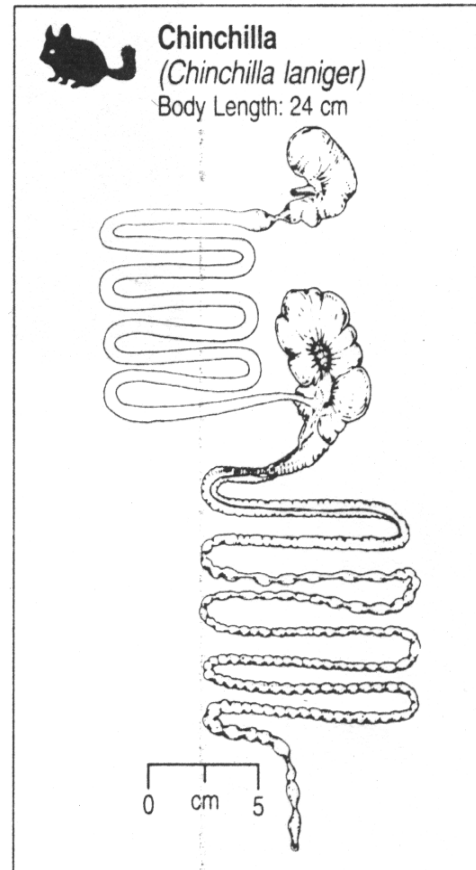
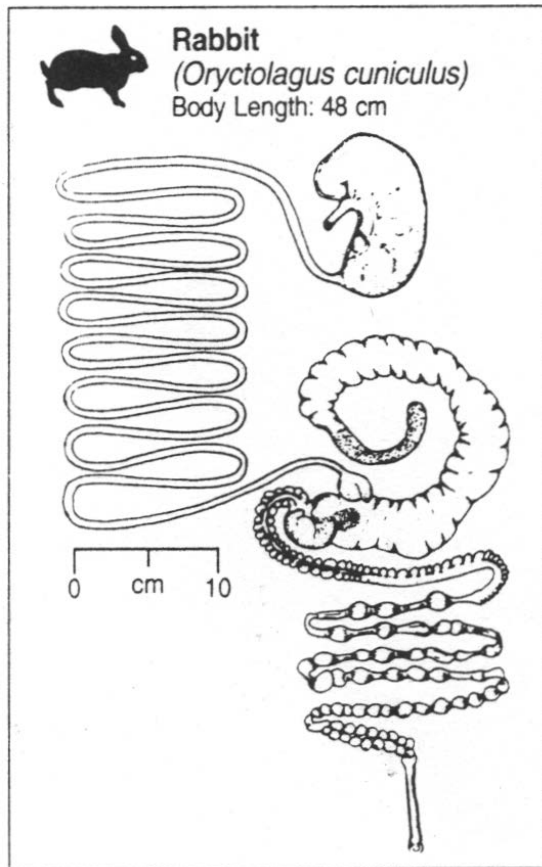


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- Enhancement of digestive efficiency
 - Rumination reduces particle size and hence allows faster digestion at constant intake
 - => Ruminants should have smaller digesta particle sizes (and higher intakes) than other herbivores



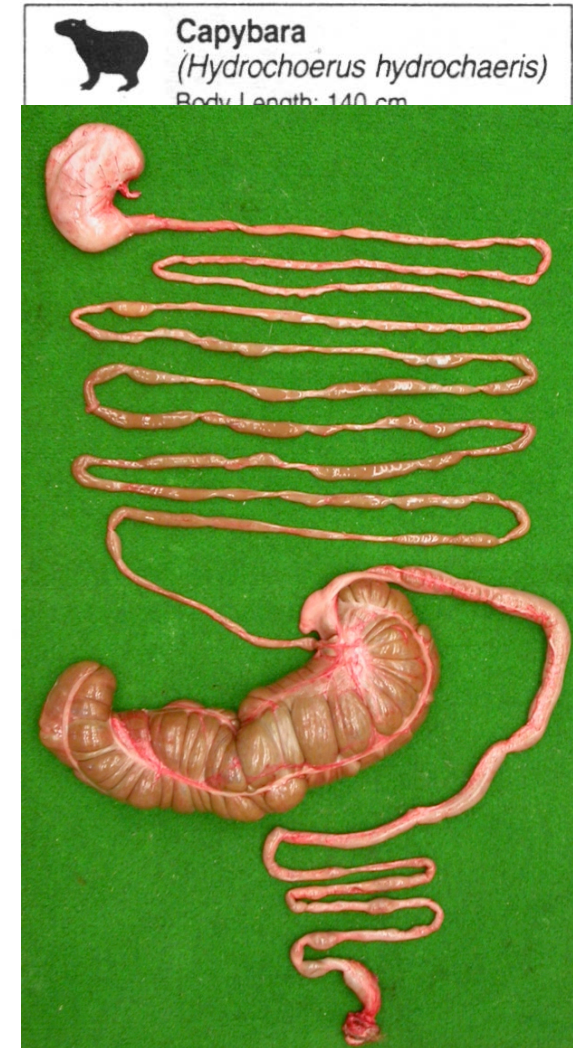
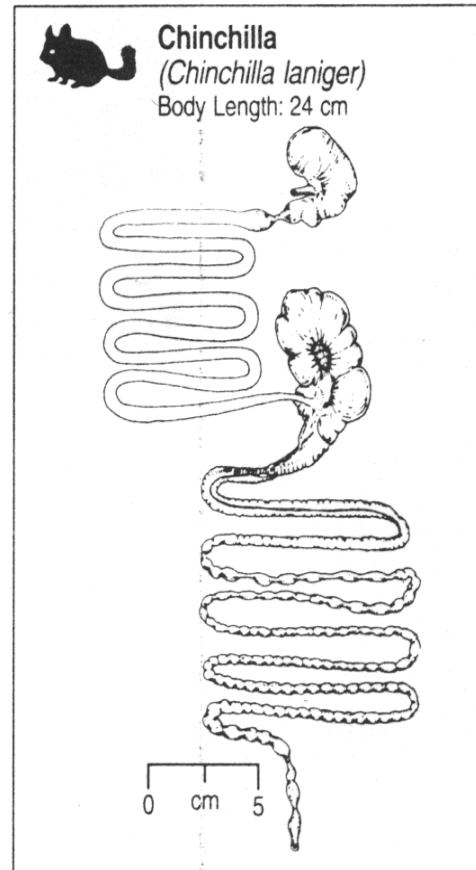
Hindgut Fermentation - Caecum



from Stevens und Hume (1995)



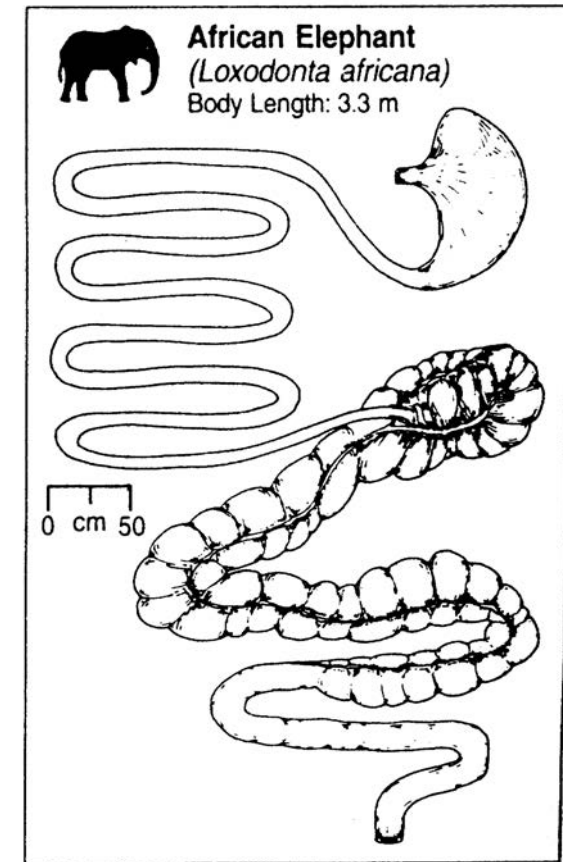
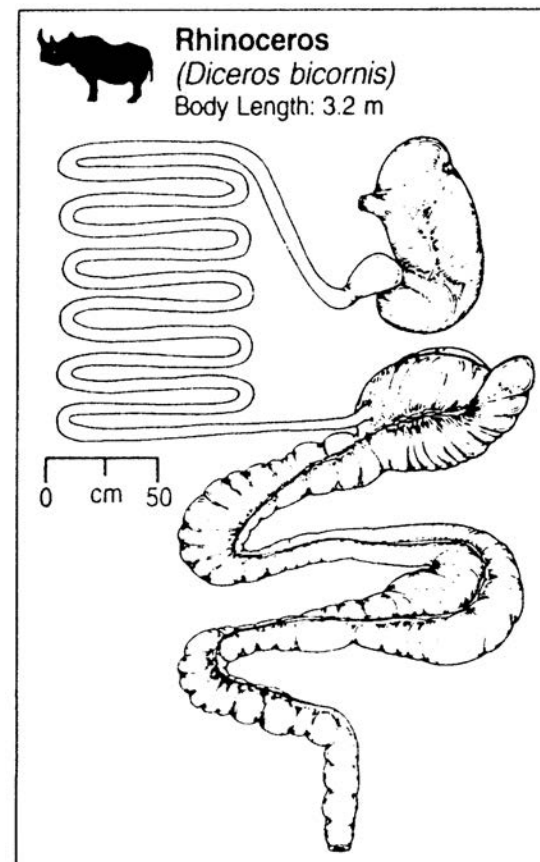
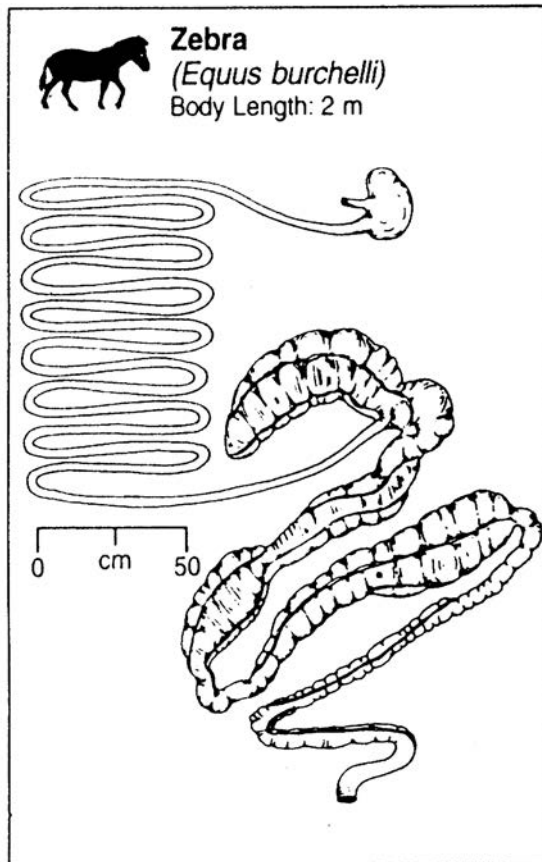
Hindgut Fermentation - Caecum



from Stevens und Hume (1995), Fotos J. Fritz/M. Clauss



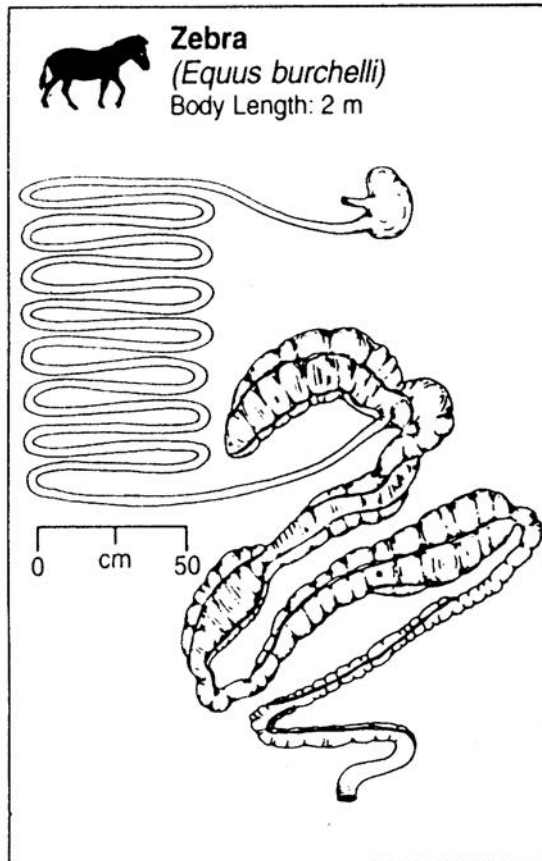
Hindgut Fermentation - Colon



from Stevens & Hume (1995)



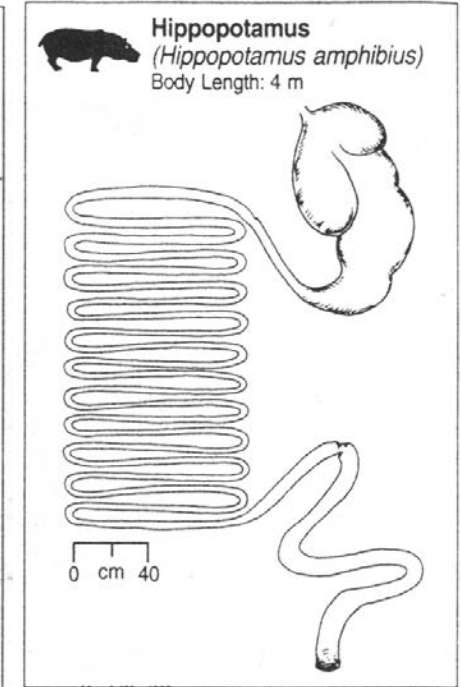
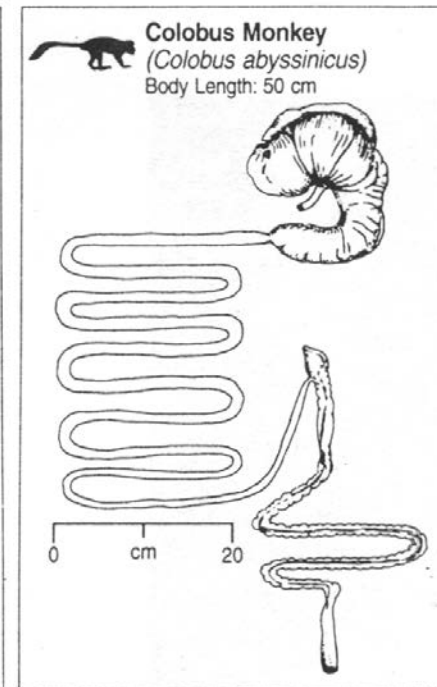
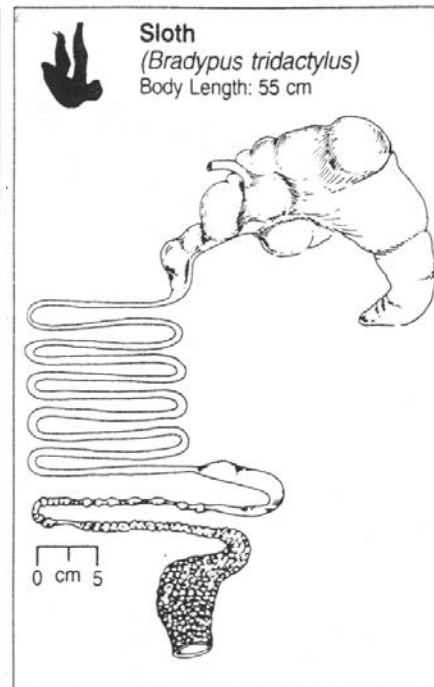
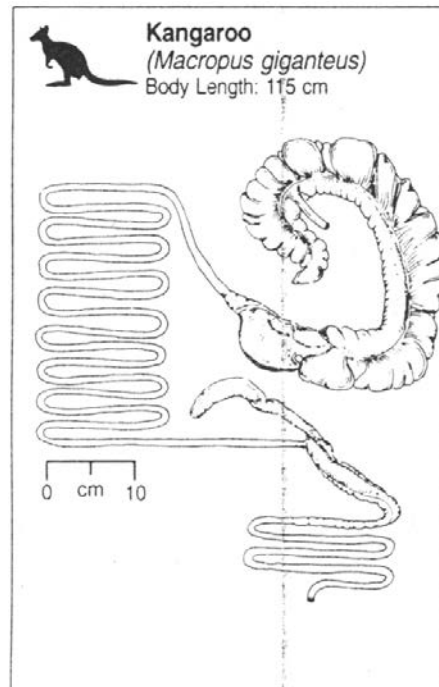
Hindgut Fermentation - Colon



from Stevens & Hume (1995)



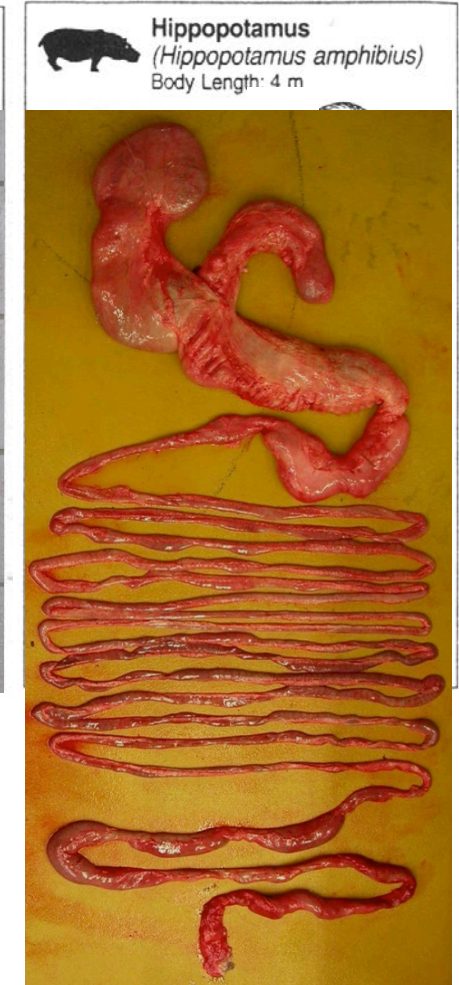
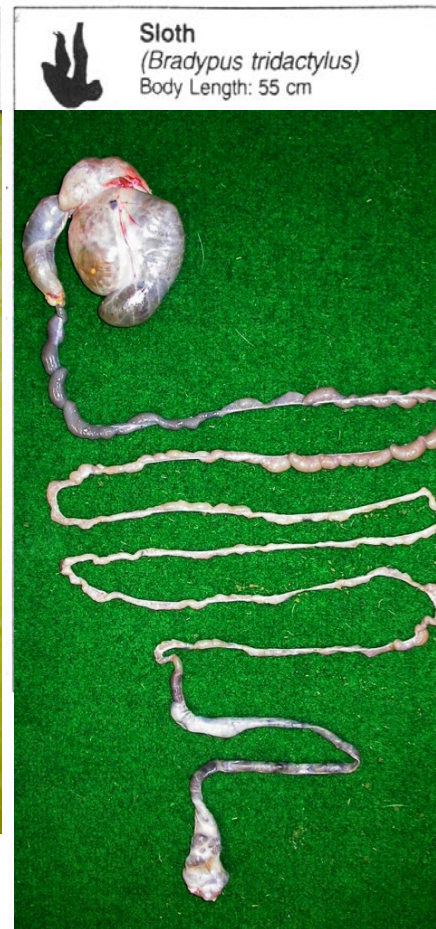
Foregut Fermentation



from Stevens & Hume (1995)



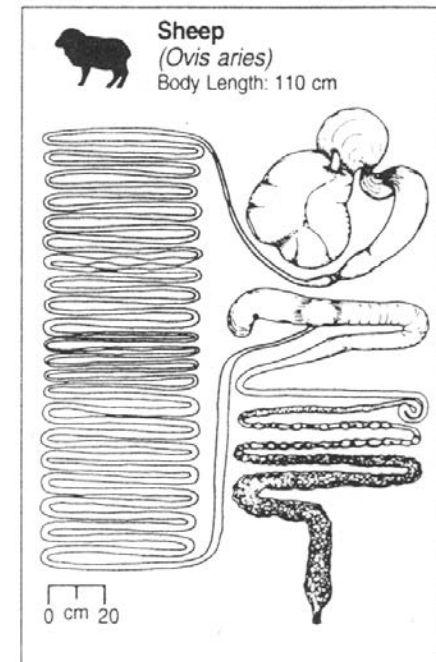
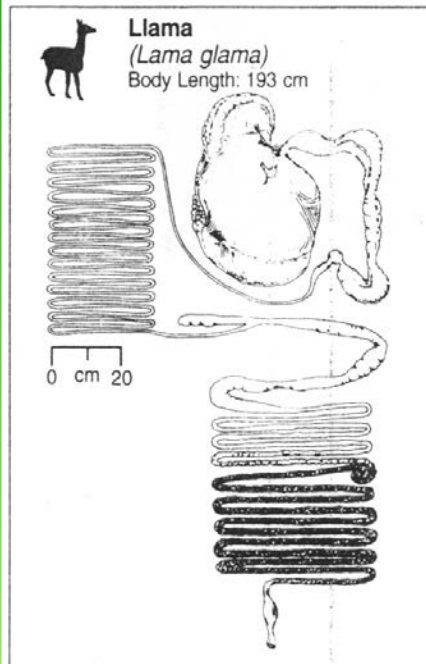
Foregut Fermentation



Photos A. Schwarm/
M. Clauss



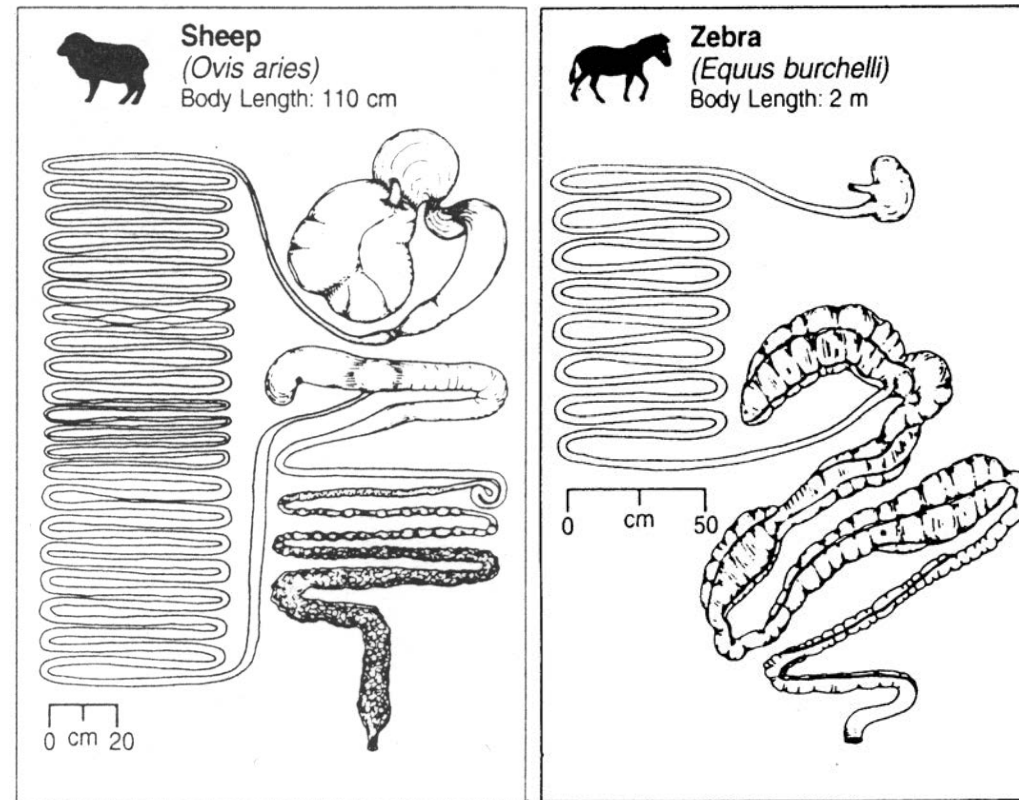
Foregut Fermentation - Ruminant



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



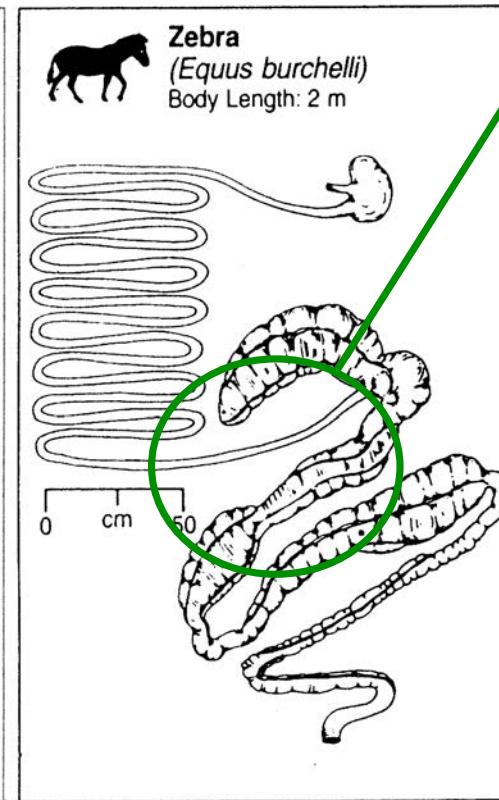
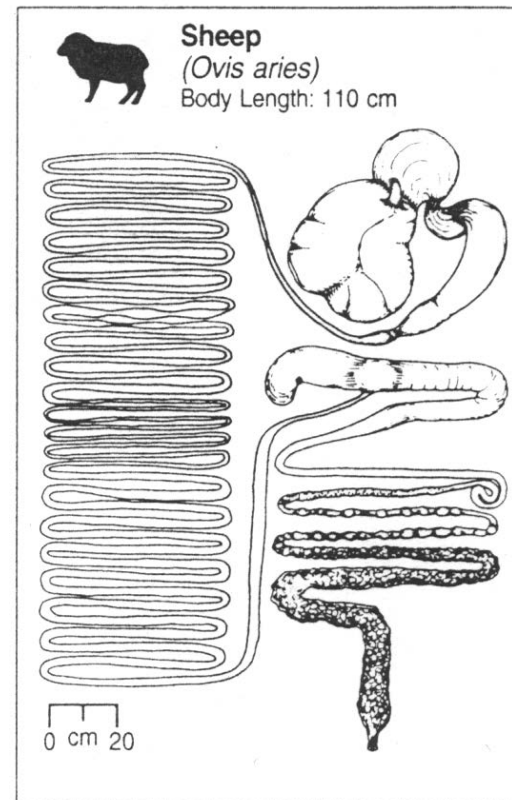
Foregut vs. Hindgut Fermentation



from Stevens & Hume (1995)



Foregut vs. Hindgut Fermentation

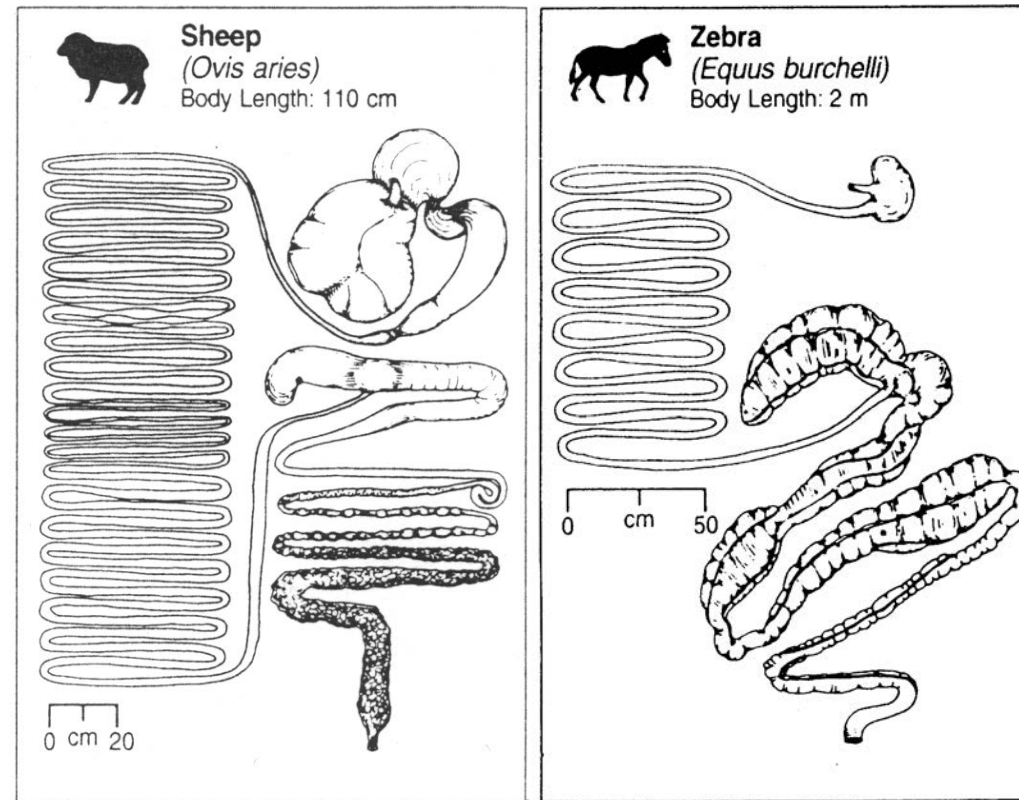


Fermentation
after
enzymatic
digestion and
absorption:

from Stevens & Hume (1995)



Foregut vs. Hindgut Fermentation



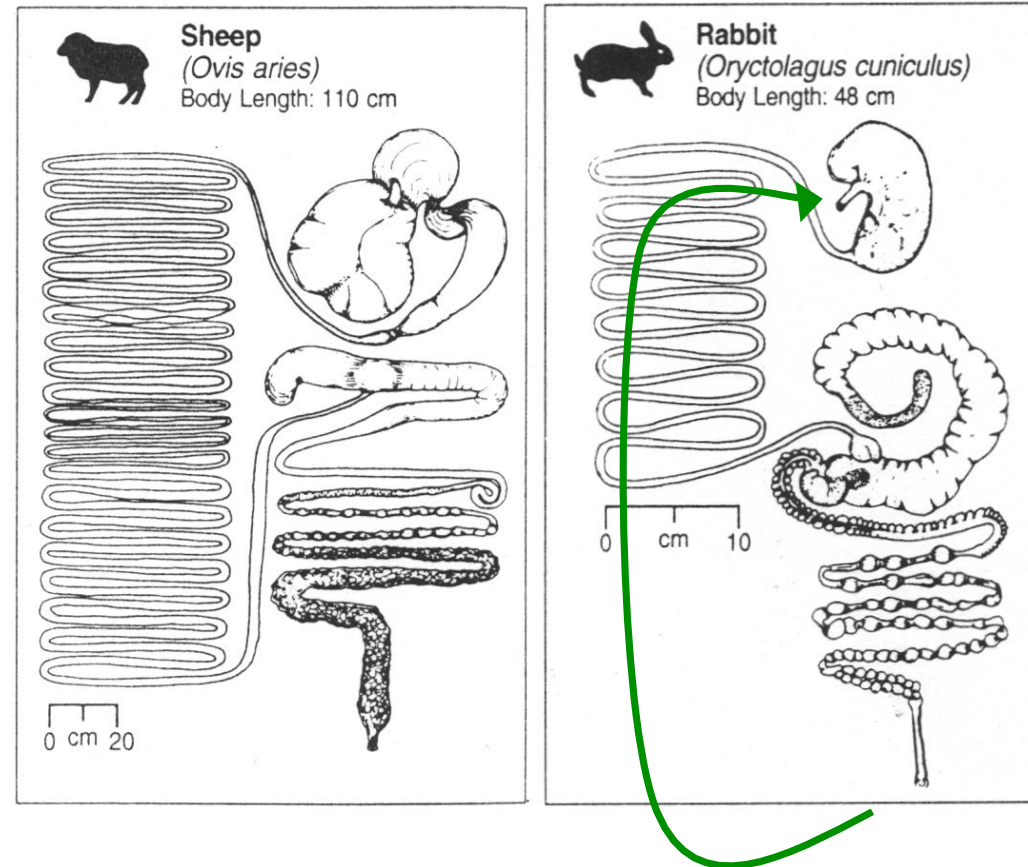
Fermentation after enzymatic digestion and absorption:

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

from Stevens & Hume (1995)



Foregut vs. Hindgut Fermentation



Fermentation
after
enzymatic
digestion and
absorption:

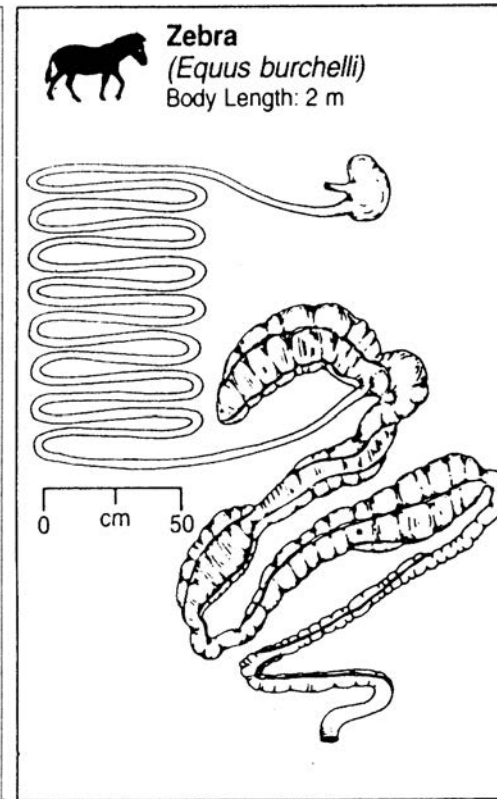
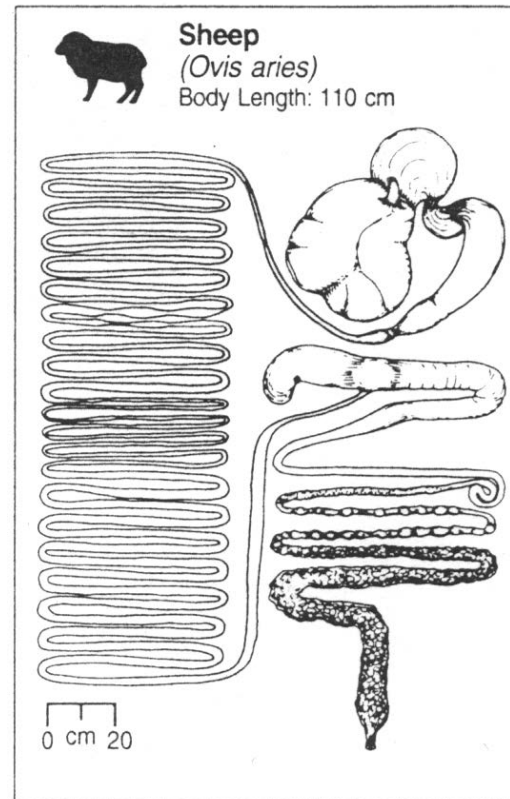
'Loss' of
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(coprophagy)

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Foregut vs. Hindgut Fermentation



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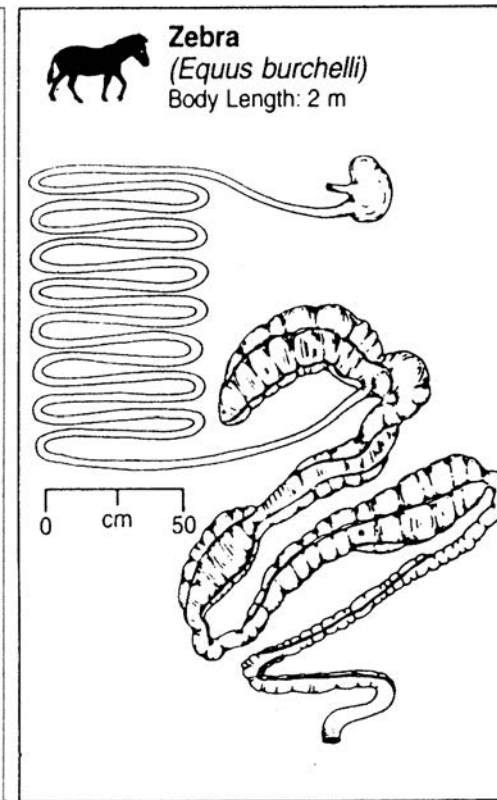
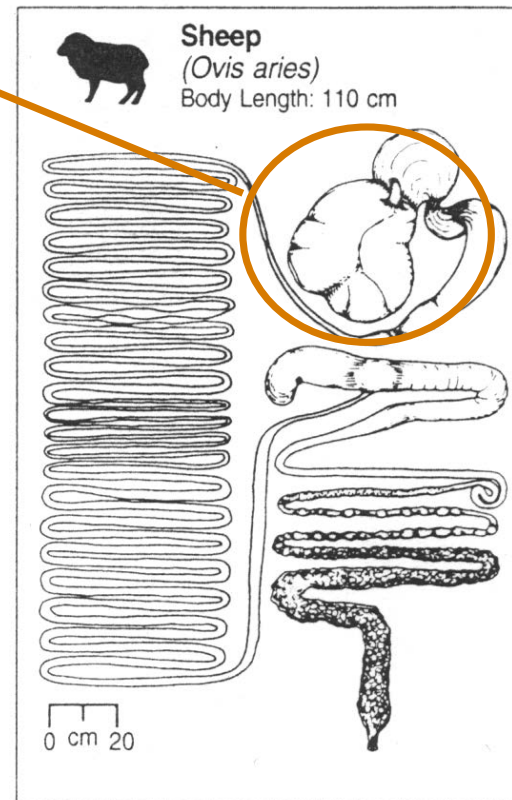
Use of easily digestible substrates

from Stevens & Hume (1995)



Foregut vs. Hindgut Fermentation

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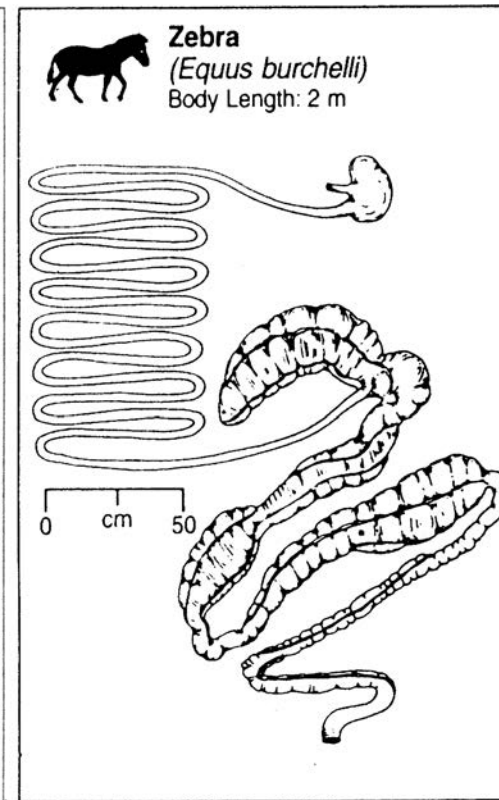
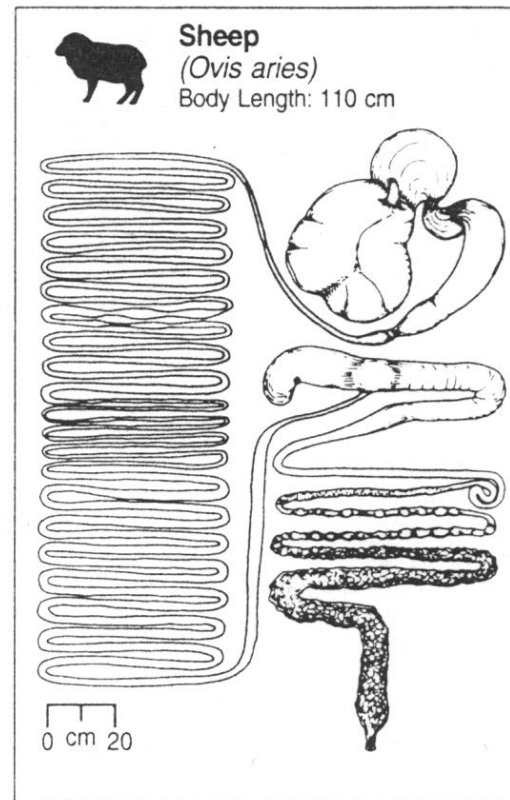
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Foregut vs. Hindgut Fermentation

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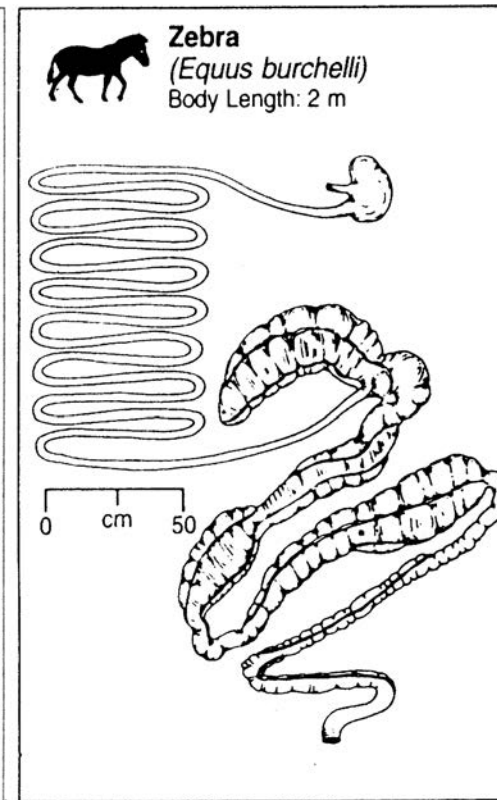
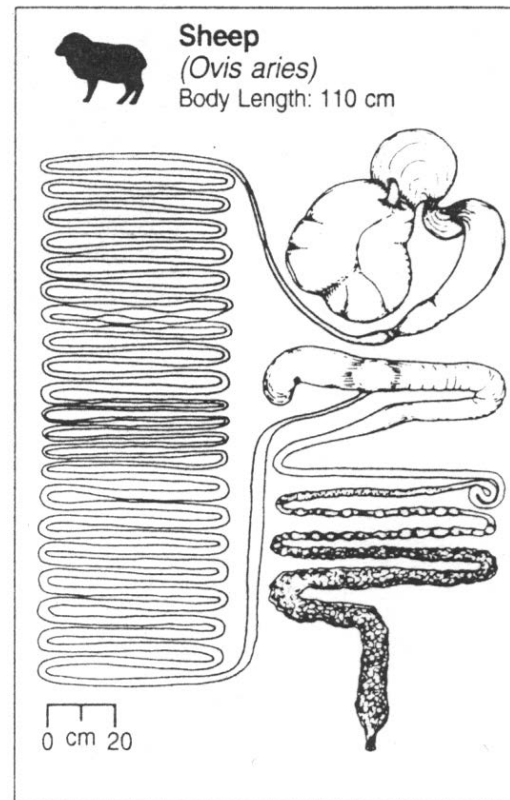


Foregut vs. Hindgut Fermentation

Fermentation prior to enzymatic digestion and absorption:

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

Bacterial detoxification?



Fermentation after enzymatic digestion and absorption:

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(coprophagy)

Use of easily digestible substrates

from Stevens & Hume (1995)



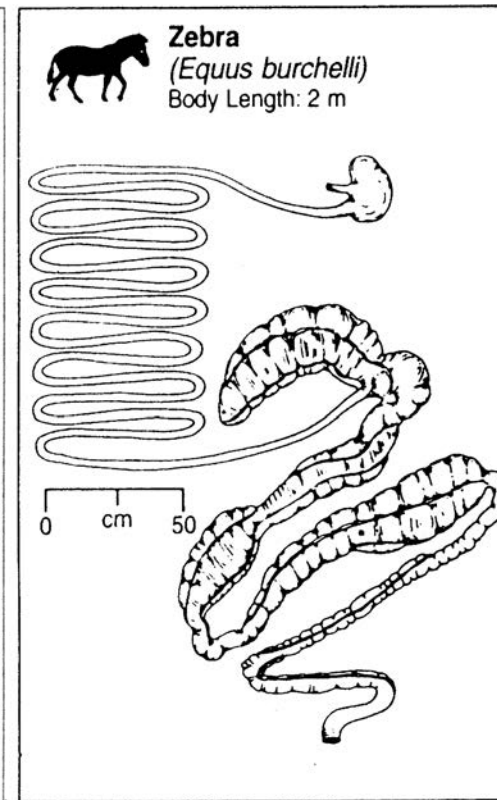
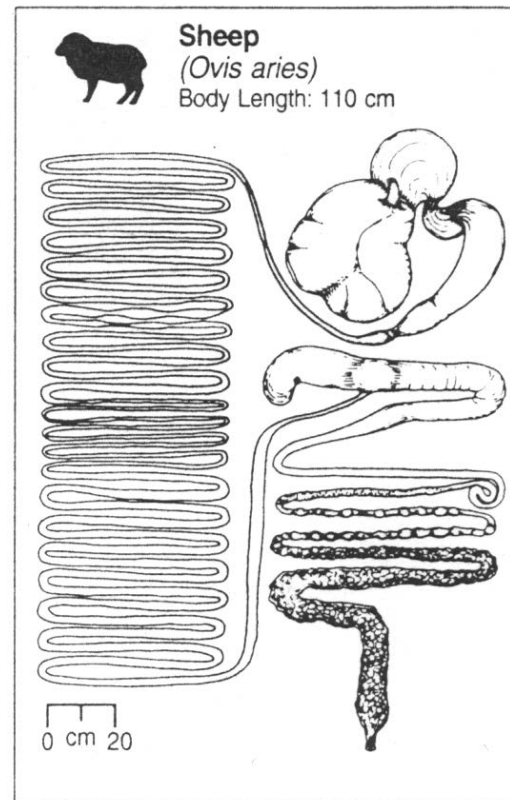
Foregut vs. Hindgut Fermentation

Fermentation prior to enzymatic digestion and absorption:

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'Loss' of easily digestible substrates and bacterial modification



Fermentation after enzymatic digestion and absorption:

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Use of easily digestible substrates

from Stevens & Hume (1995)



Foregut vs. Hindgut Fermentation

Fermentation prior to enzymatic digestion and absorption:

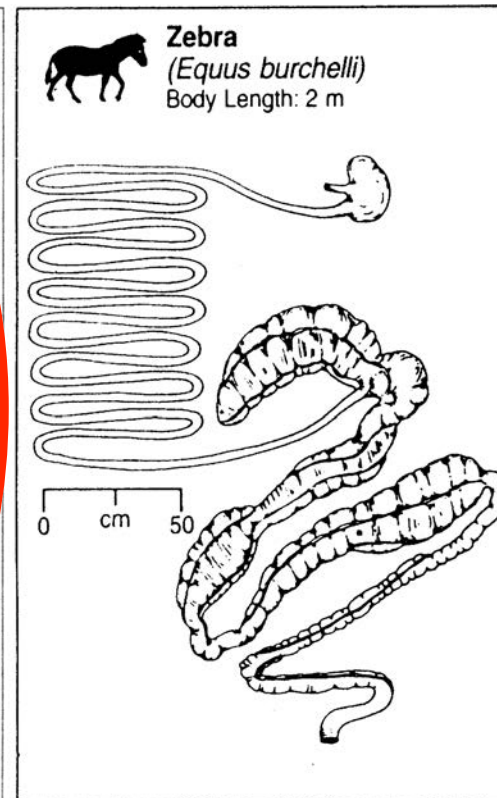
Use of bacterial protein, bacterial products (B-Vitamins)

Bacterial detoxification?

'Loss' of easily digestible substrates and bacterial modification



particularly suited for fibre fermentation



Fermentation after enzymatic digestion and absorption:

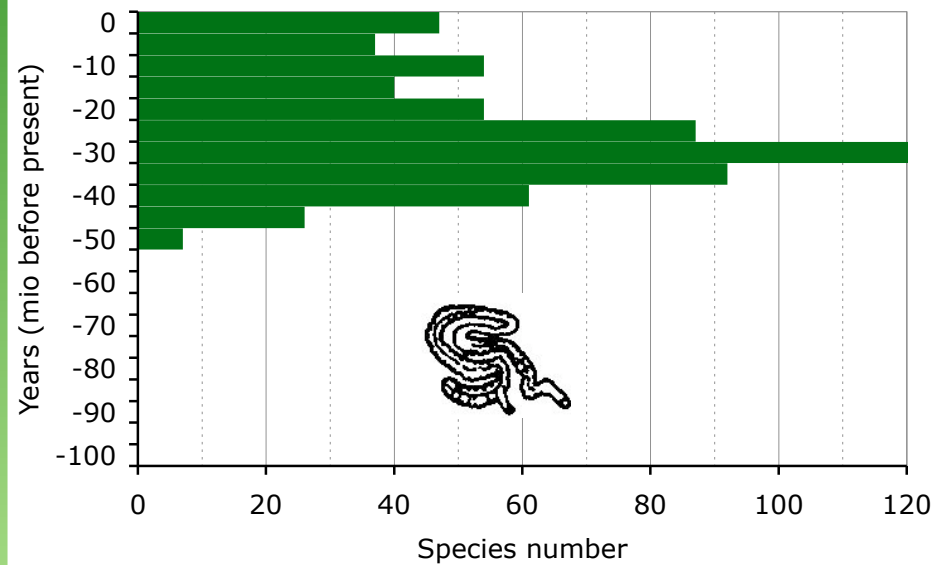
'Loss' of bacterial protein, bacterial products (B-Vitamins?)

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Use of easily digestible substrates



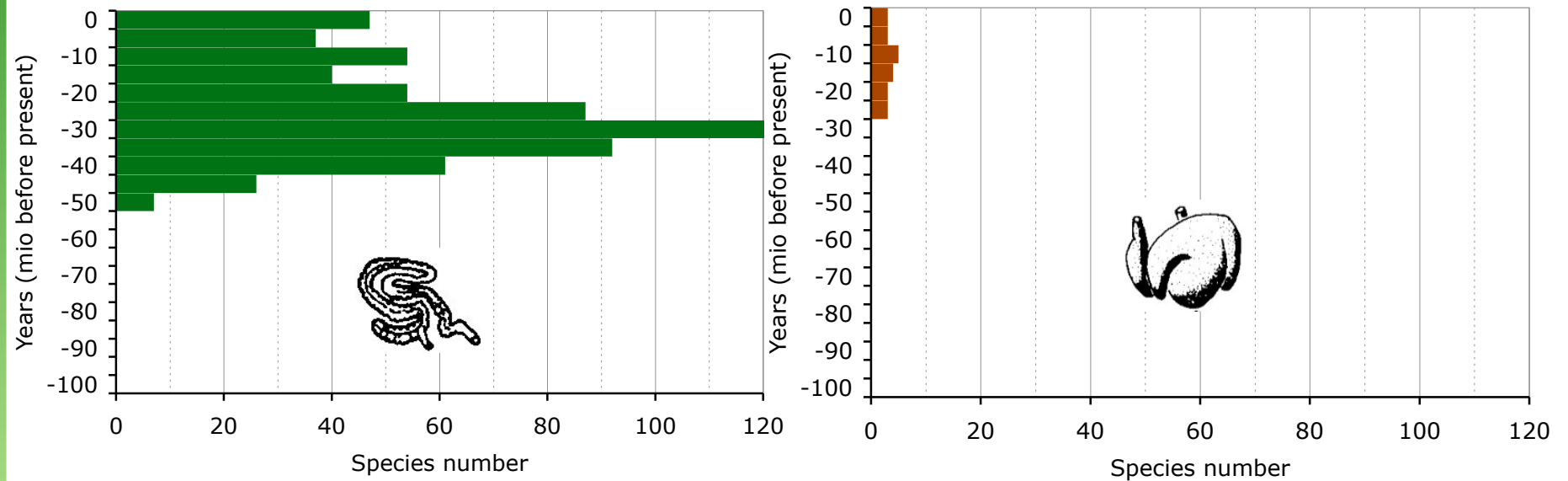
European Mammal Herbivores in Deep Time



from Langer (1991)



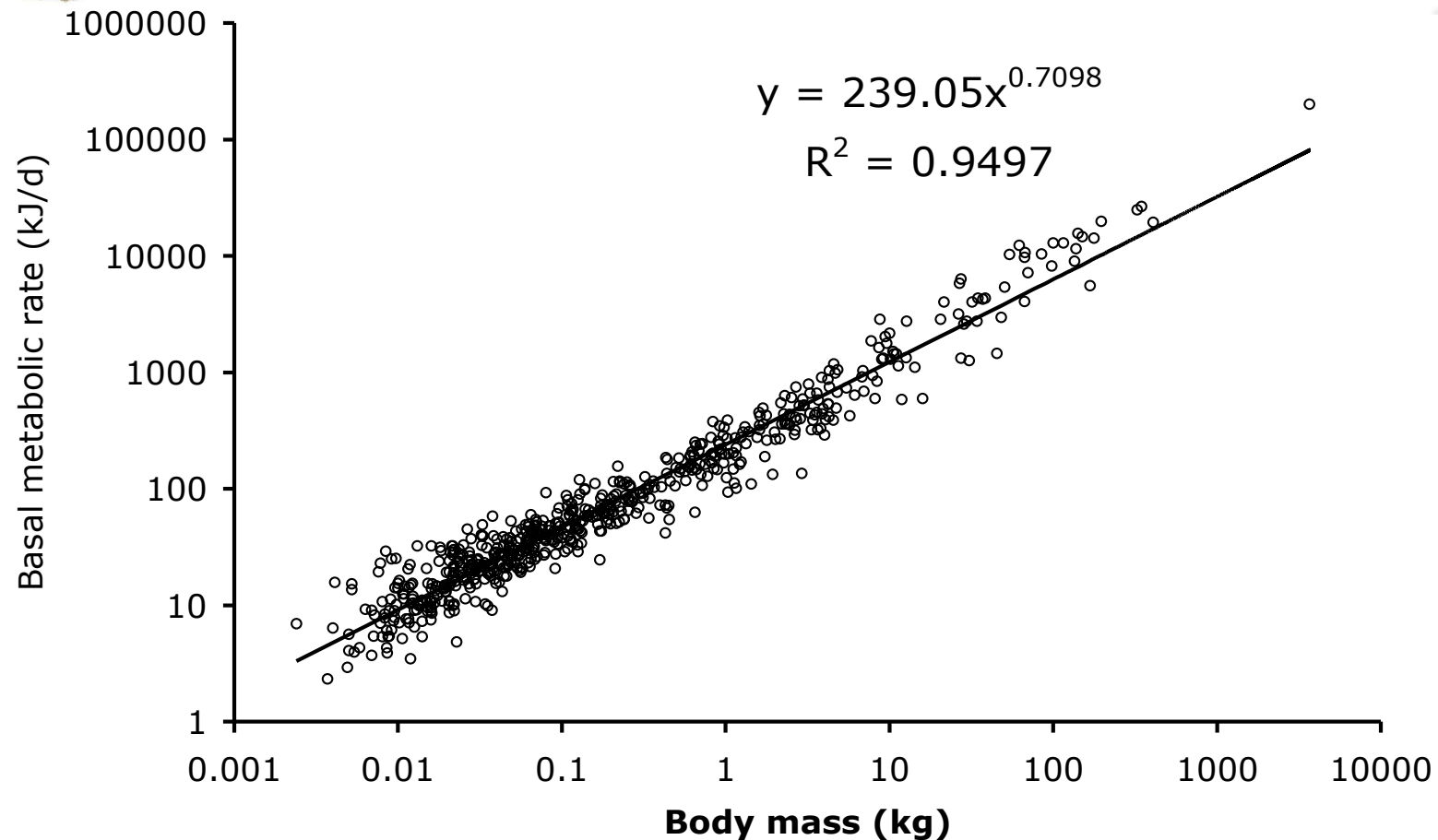
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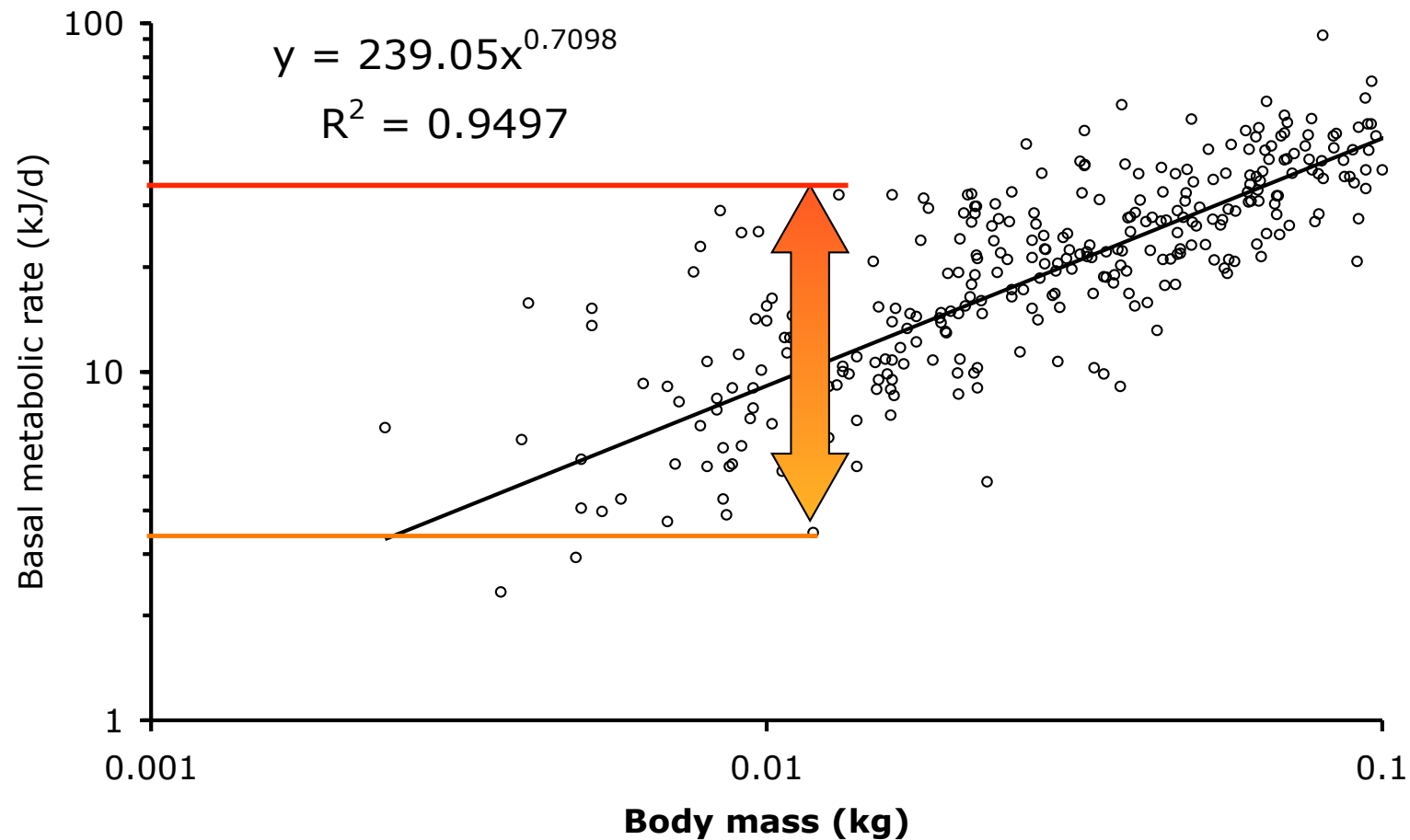


Conceptualizing herbivore diversity





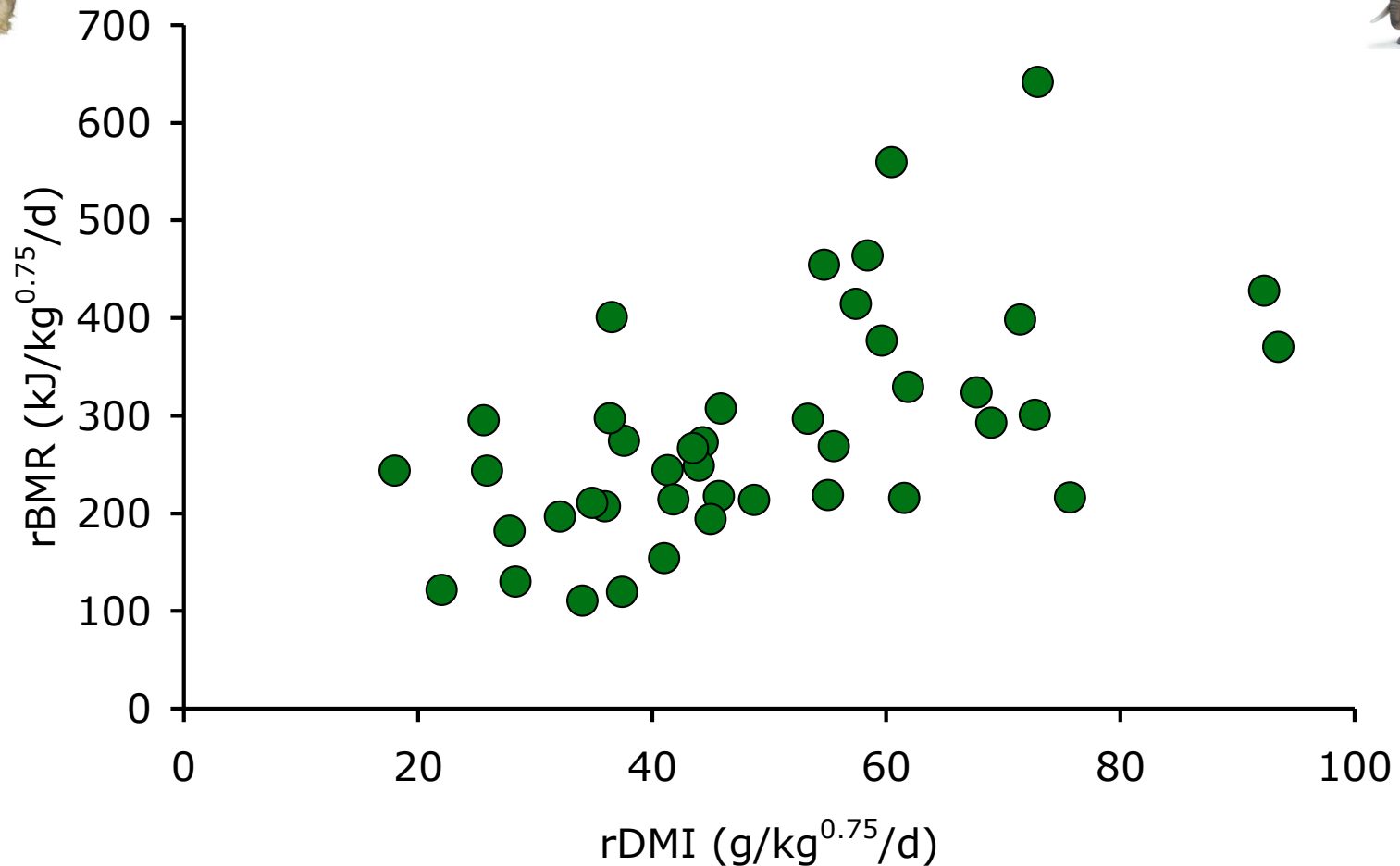
Conceptualizing herbivore diversity



Data from Savage et al. (2004)



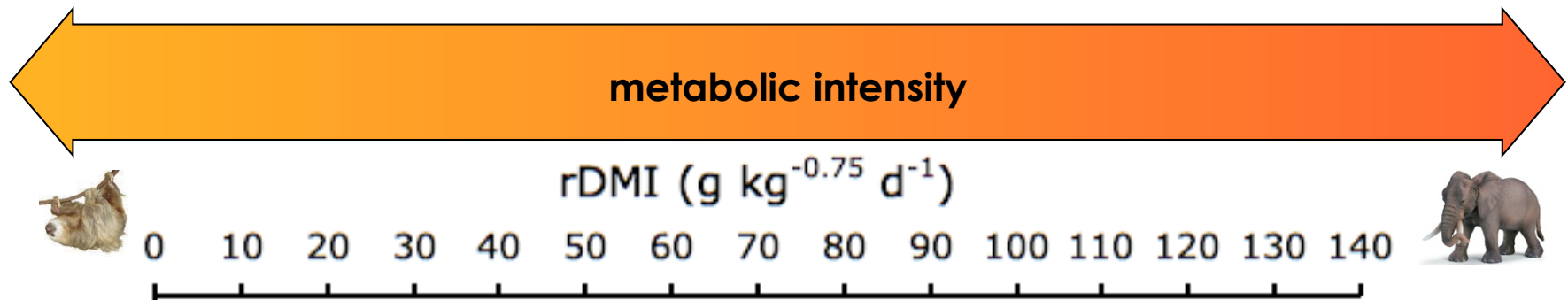
Conceptualizing herbivore diversity



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

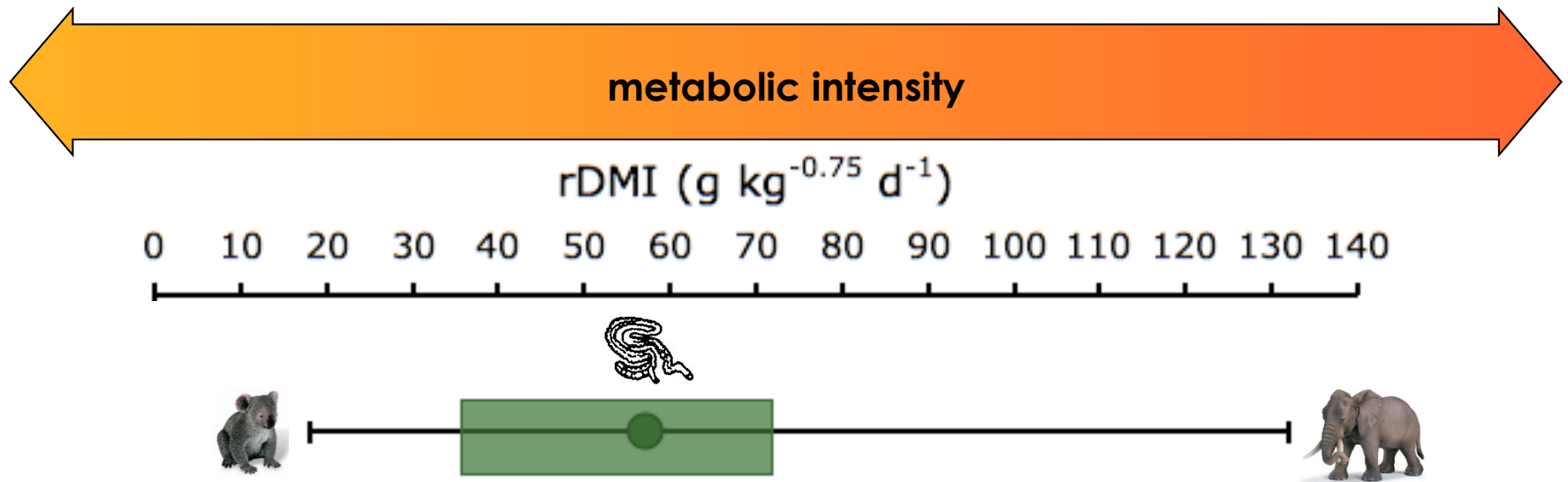


Conceptualizing herbivore diversity



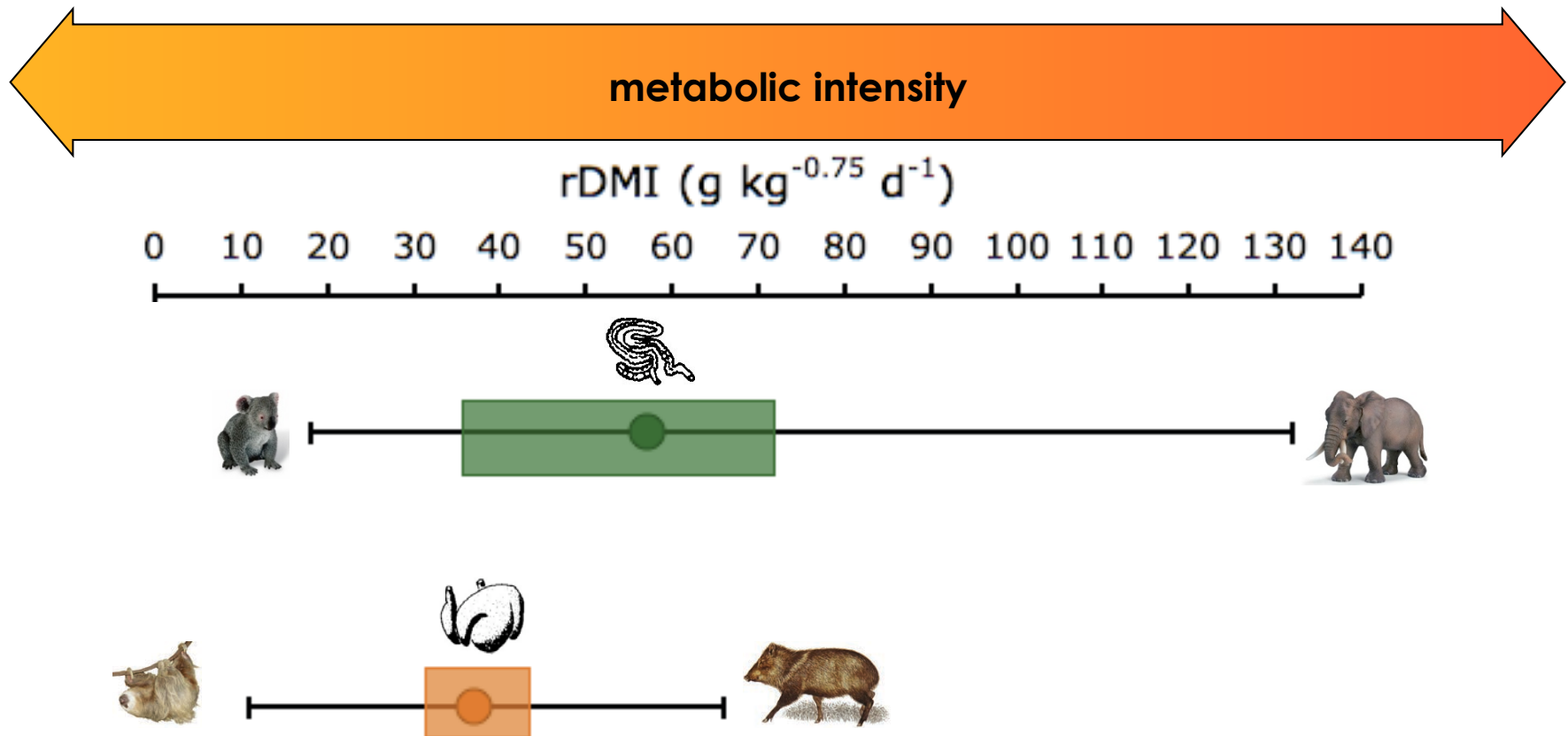


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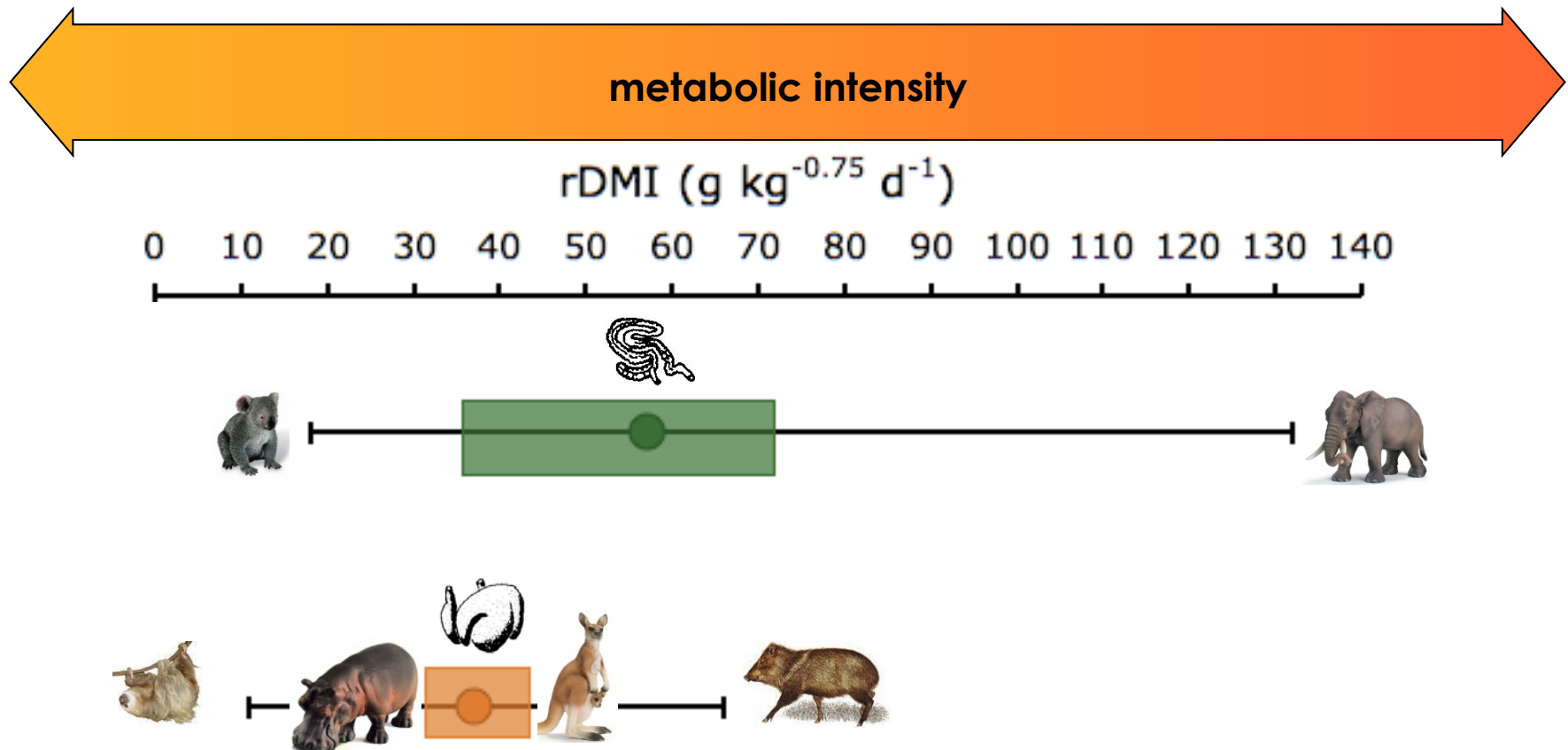


Conceptualizing herbivore diversity



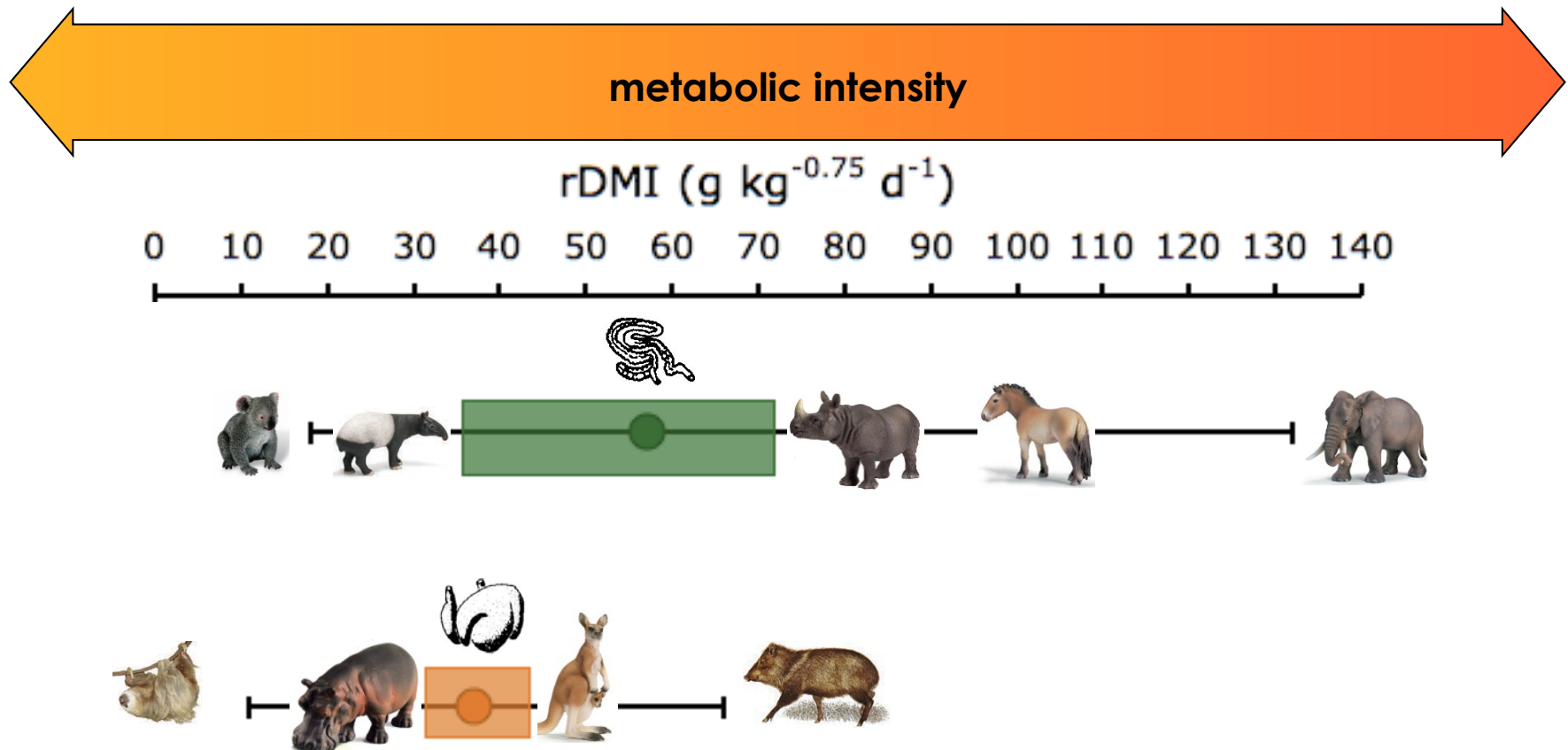


Conceptualizing herbivore diversity



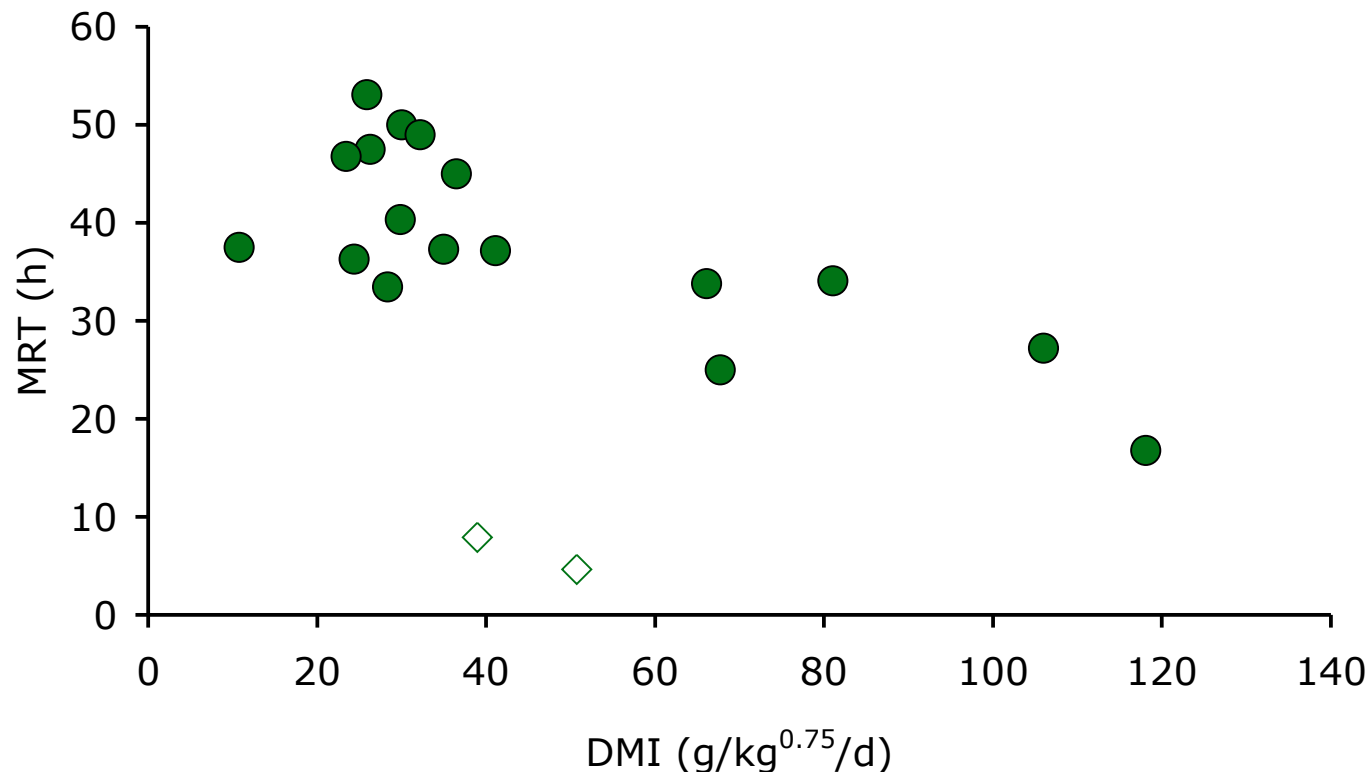


Conceptualizing herbivore diversity





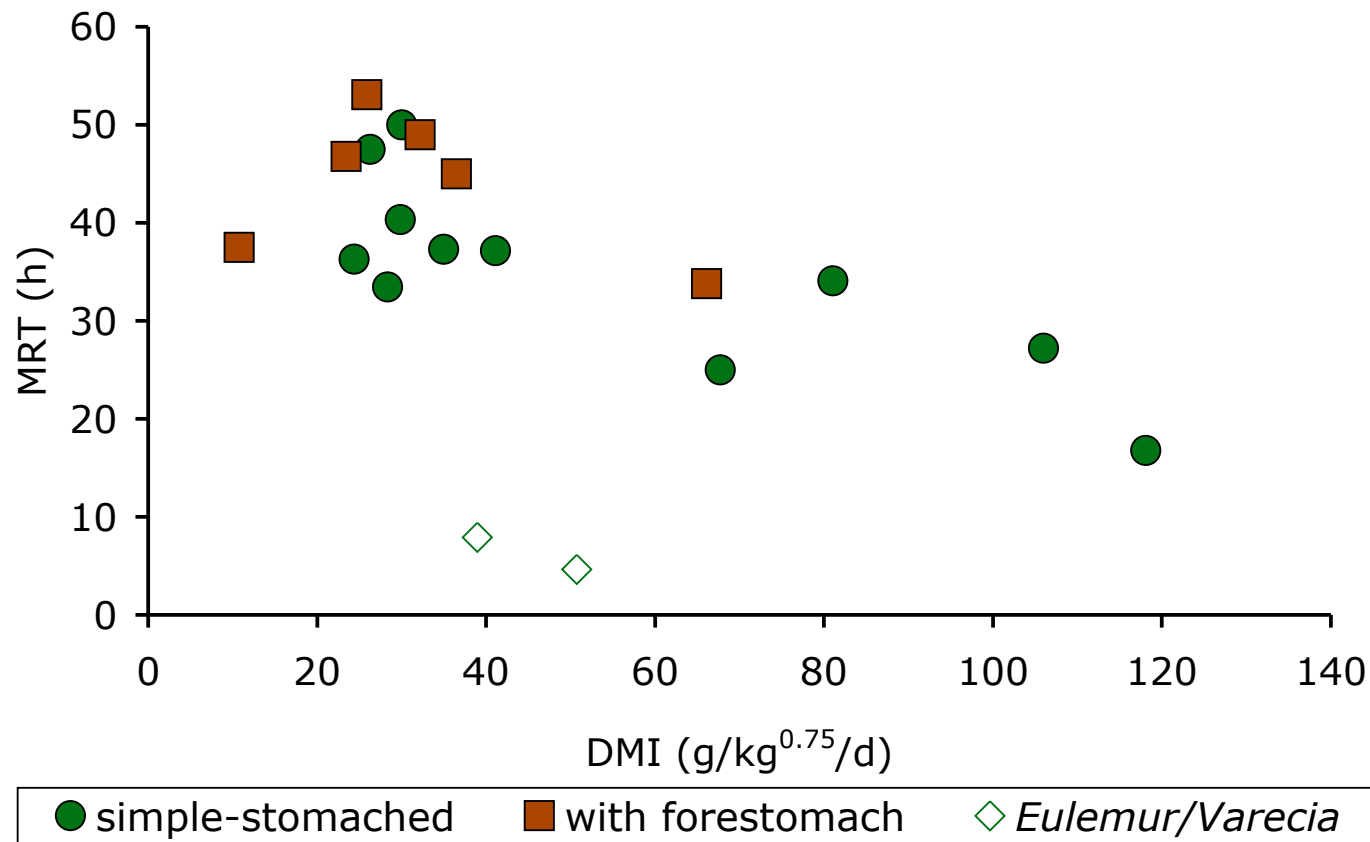
Intake and Passage in Primates



from Clauss et al. (2008)



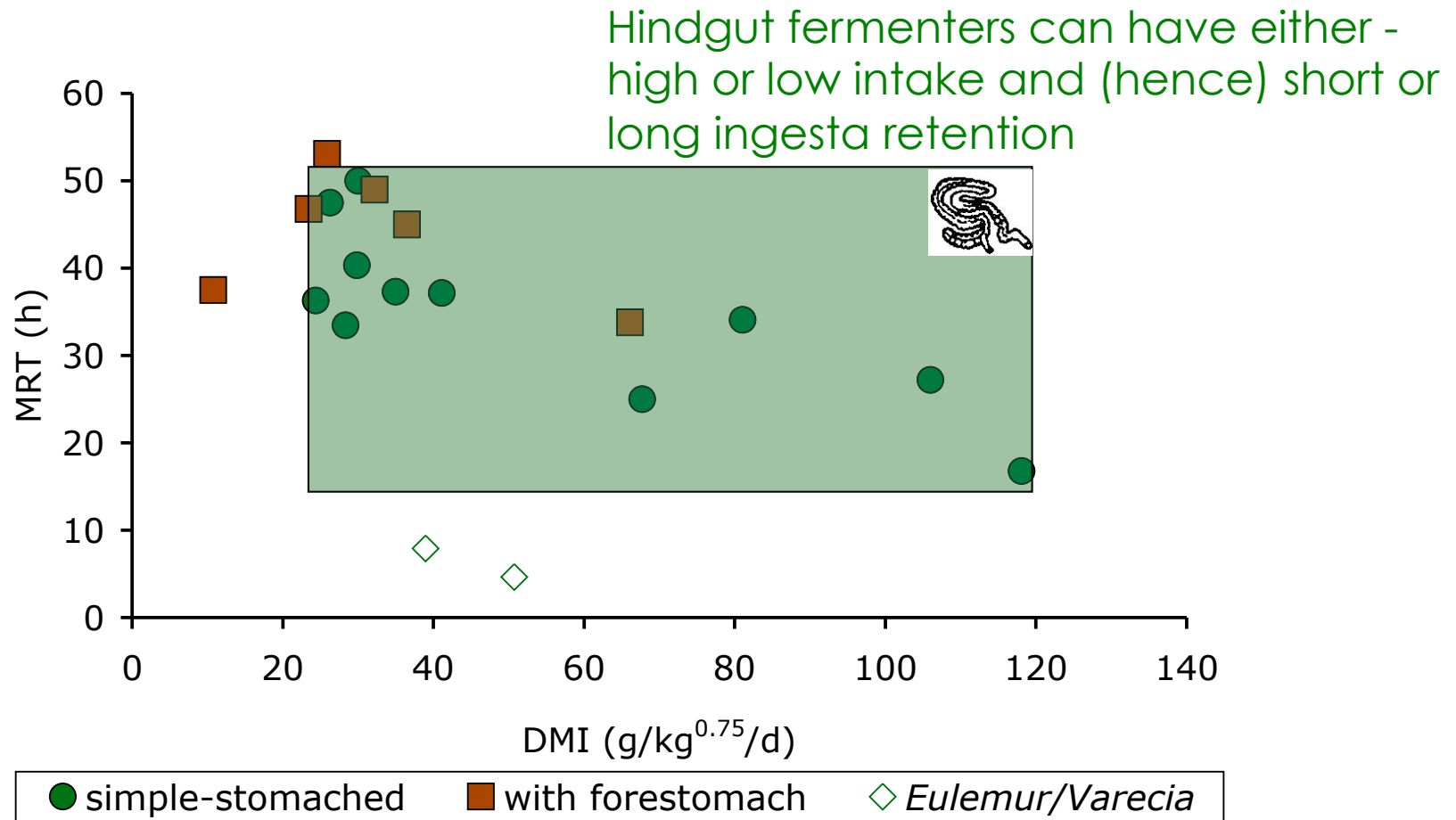
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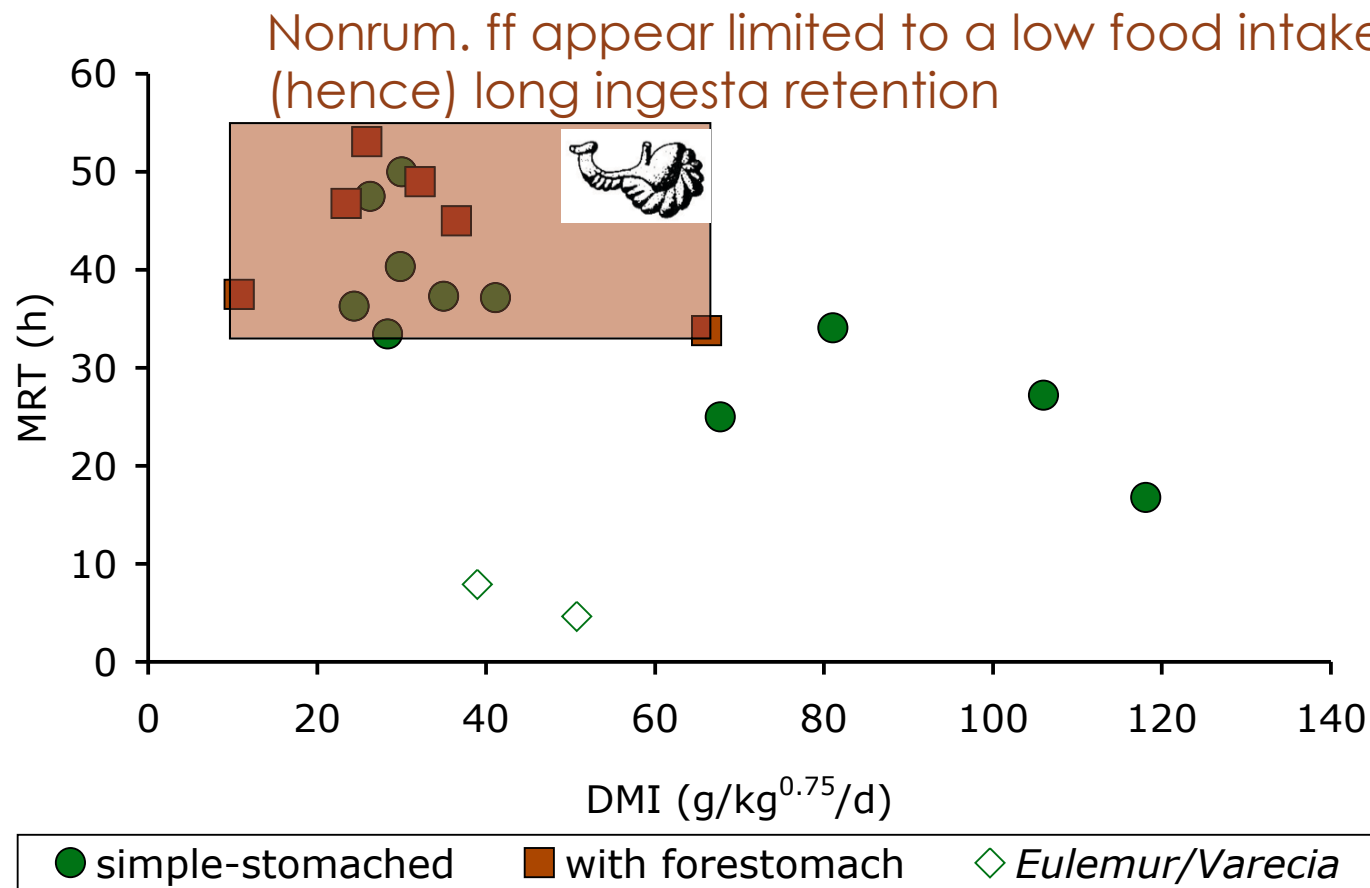


Intake and Passage in Primates





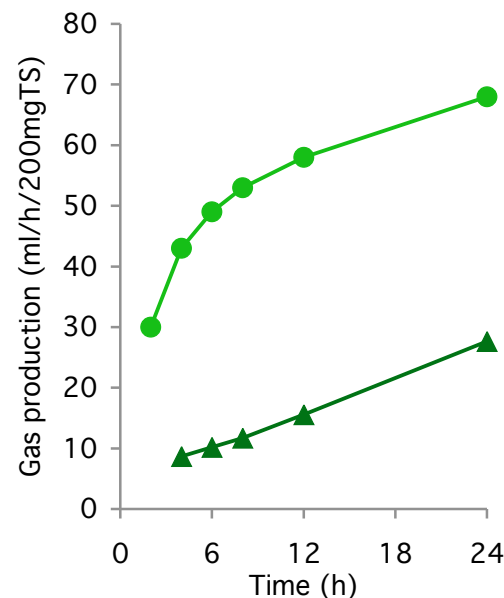
Intake and Passage in Primates





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



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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) ✓

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Digestive Strategies



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*Cursory fermentative
digestion mainly of
autoenzymatically
digestible components
followed by ineffective
autoenzymatic digestion
of undigested fiber?*



Digestive Strategies



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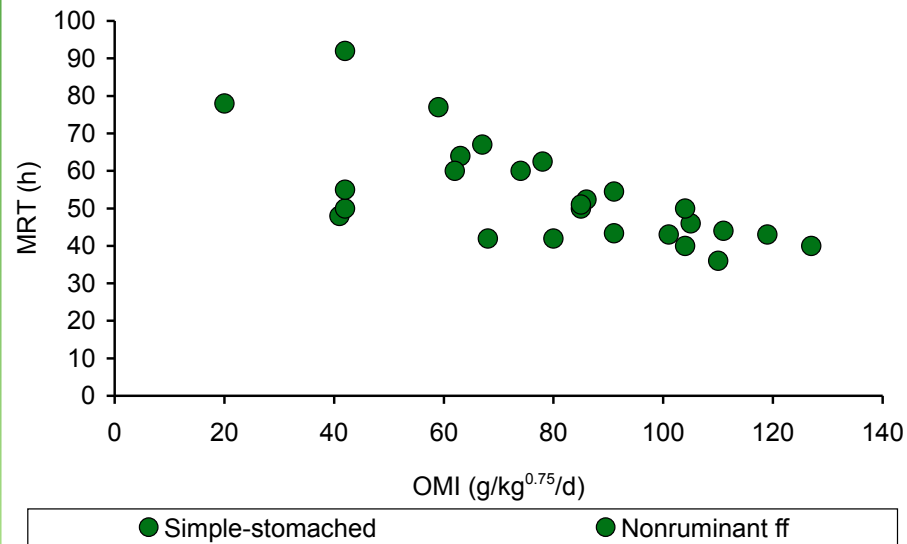
High intake
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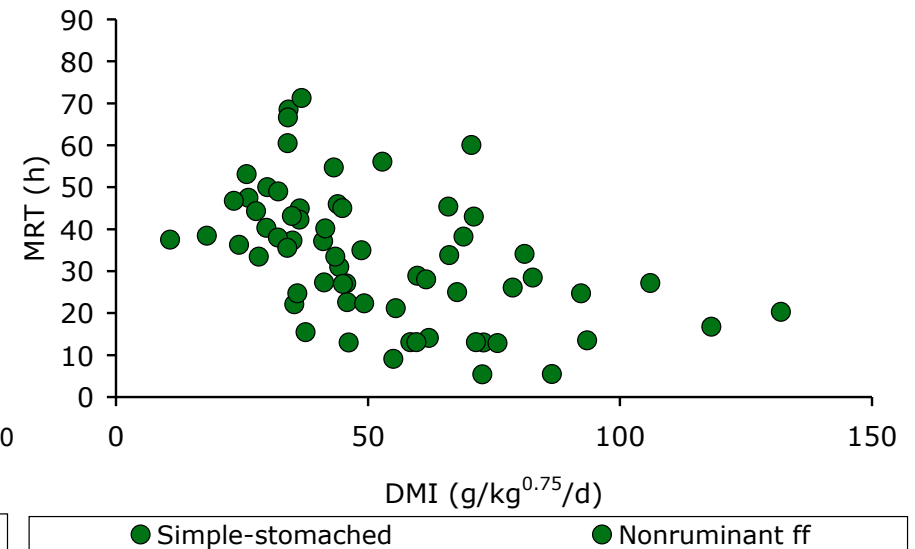
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Intake and Passage



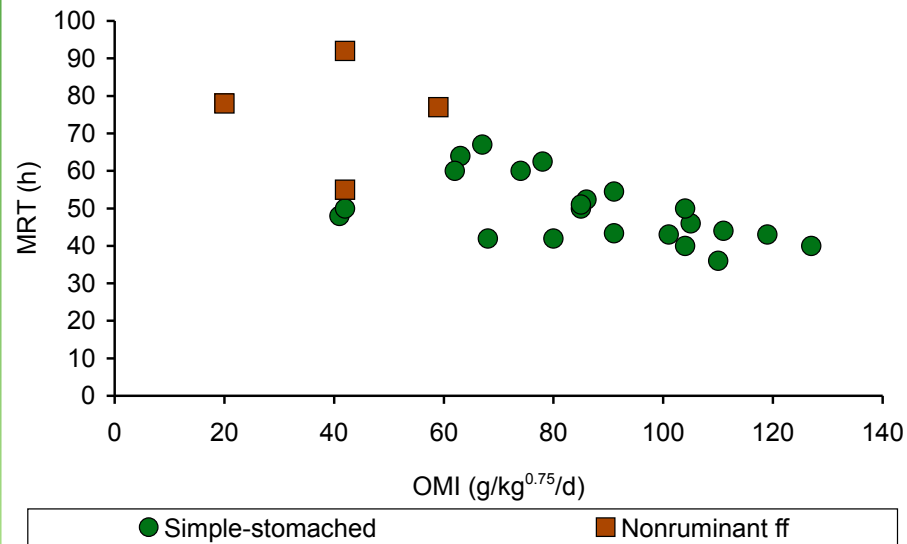
ungulates
from Foose (1982)



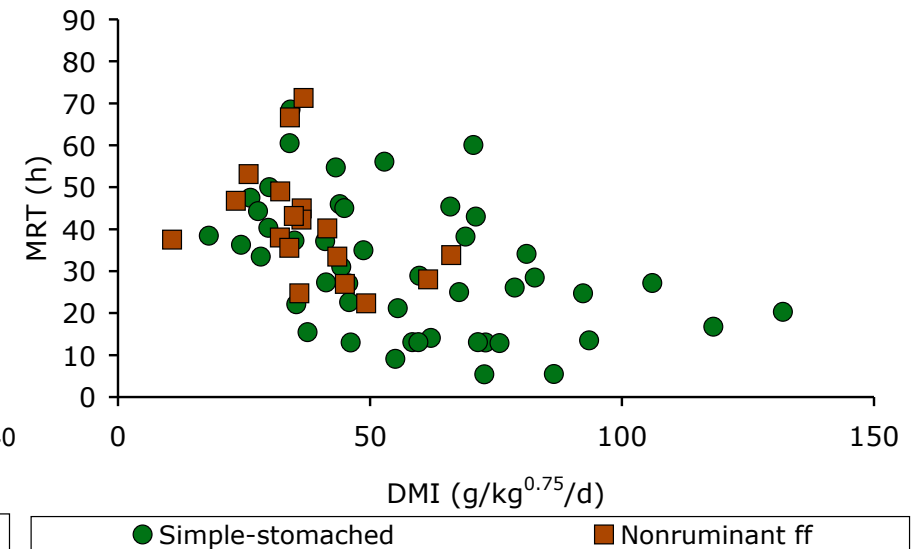
mammal herbivores
Clauss et al. (2007)



Intake and Passage



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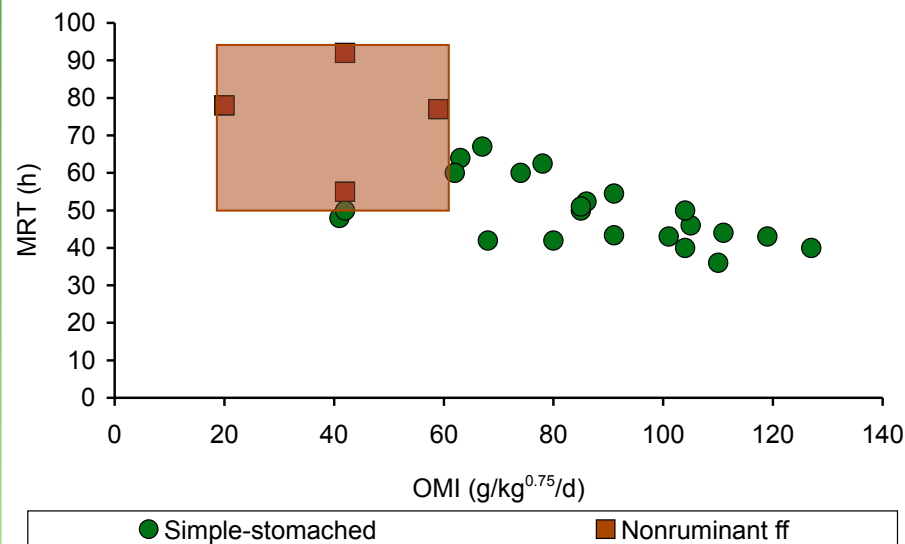


mammal herbivores
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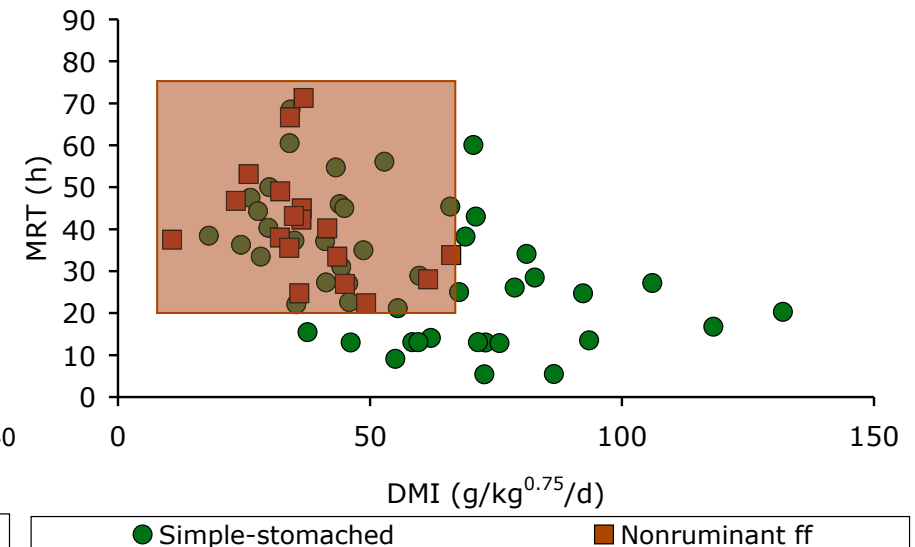


Intake and Passage

Nonrum. ff appear limited to a low food intake and (hence) long ingesta retention
while hindgut fermenters can cover the whole range



ungulates
from Foote (1982)



mammal herbivores
Clauss et al. (2007)



From Digestive to Metabolic Strategies



Low intake
⇒ long passage
⇒ **low BMR**

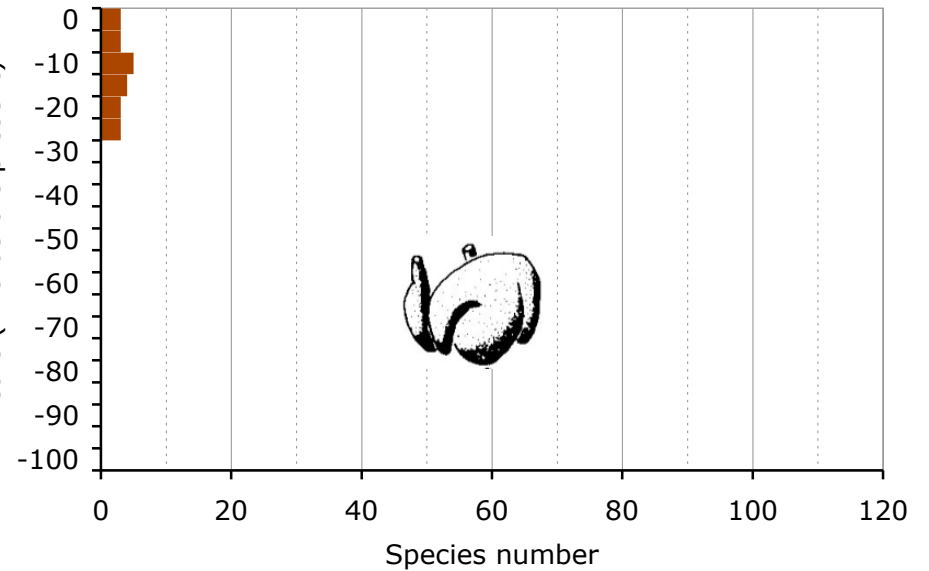
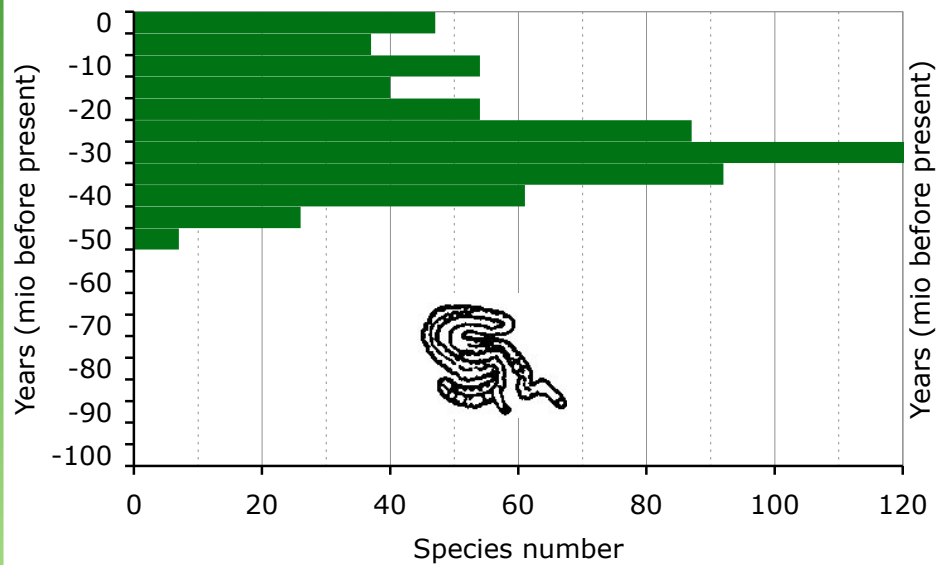


High intake
⇒ short passage
⇒ **high BMR**





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



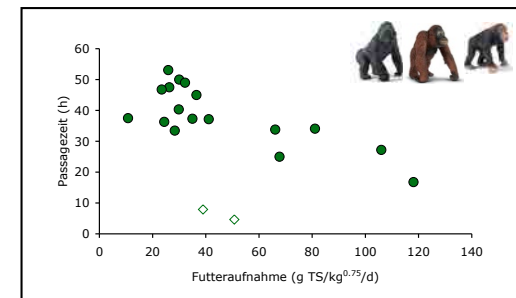
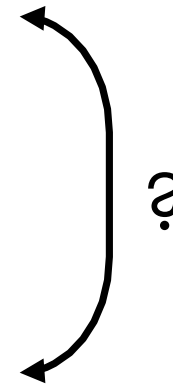
How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing



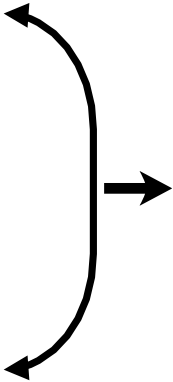
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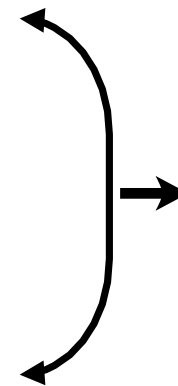
How can you increase energy intake?

- higher food intake
 - longer retention
 - finer chewing
- higher gut volume
- 

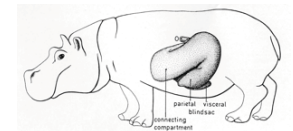


How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing



higher gut
volume





How can you increase energy intake?

- higher food intake
 - longer retention
 - finer chewing
- 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



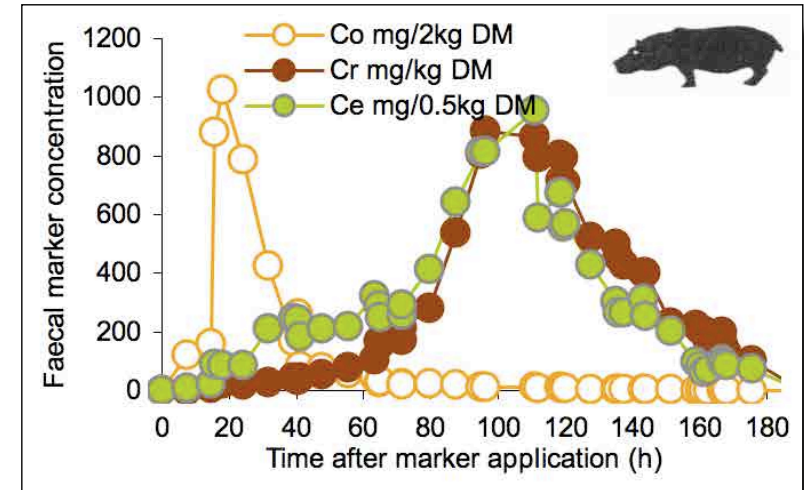


The power of sorting





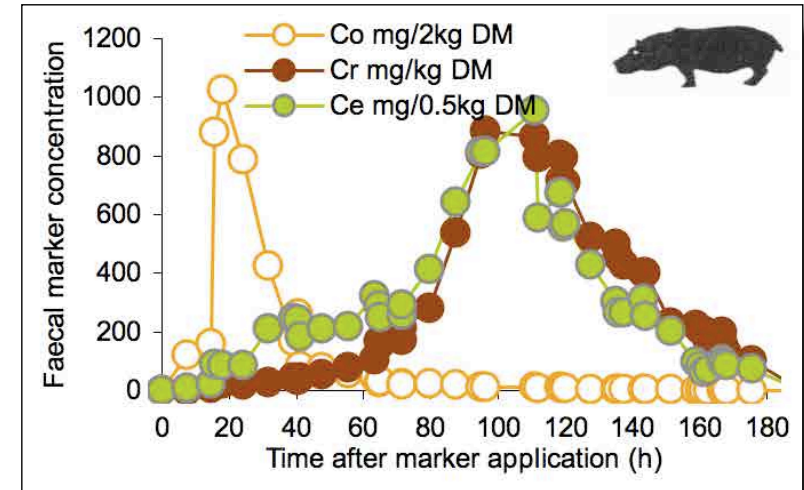
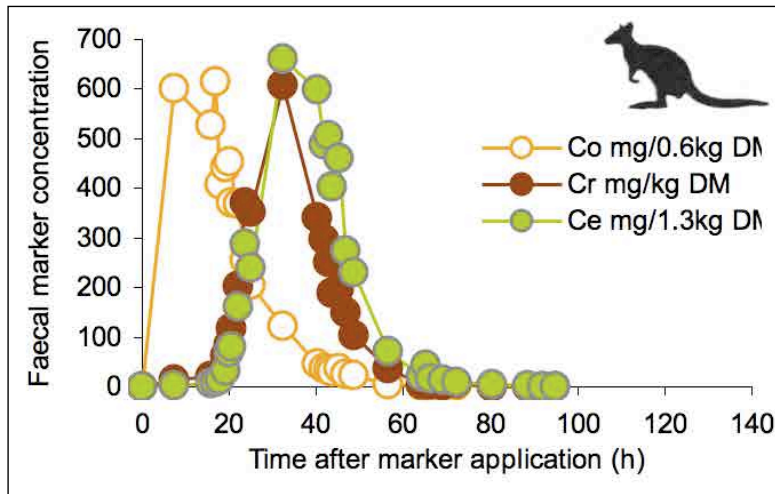
Ruminant vs. Nonruminant Foregut Fermentation



Schwarm et al. (2008)



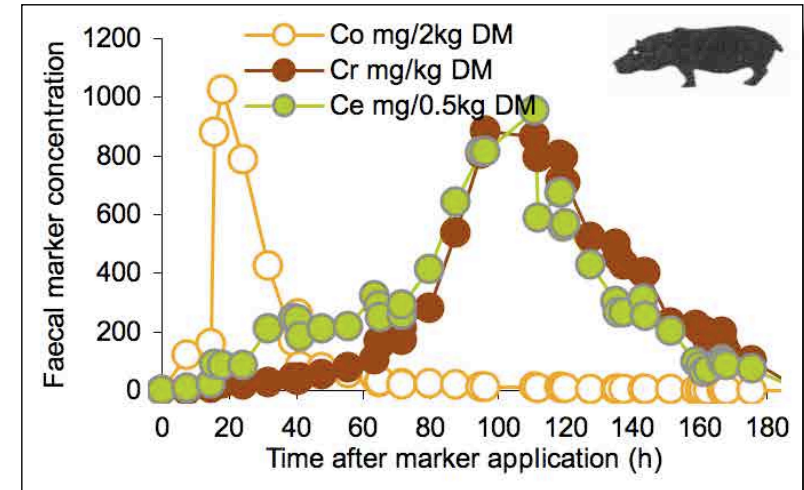
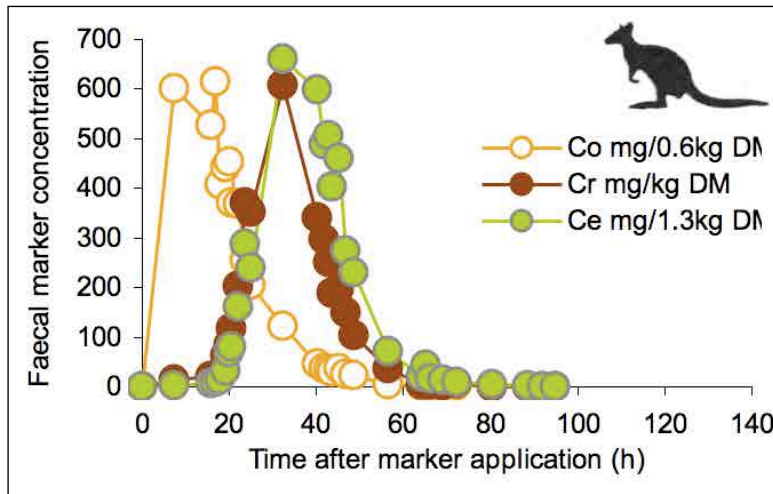
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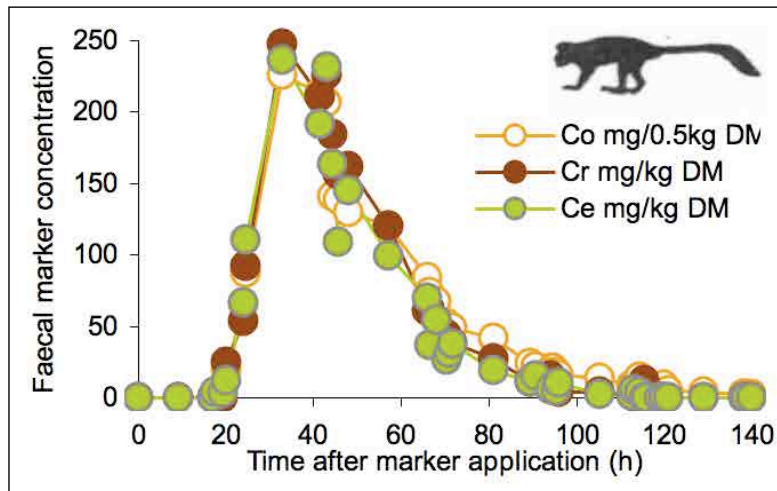
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Ruminant vs. Nonruminant Foregut Fermentation

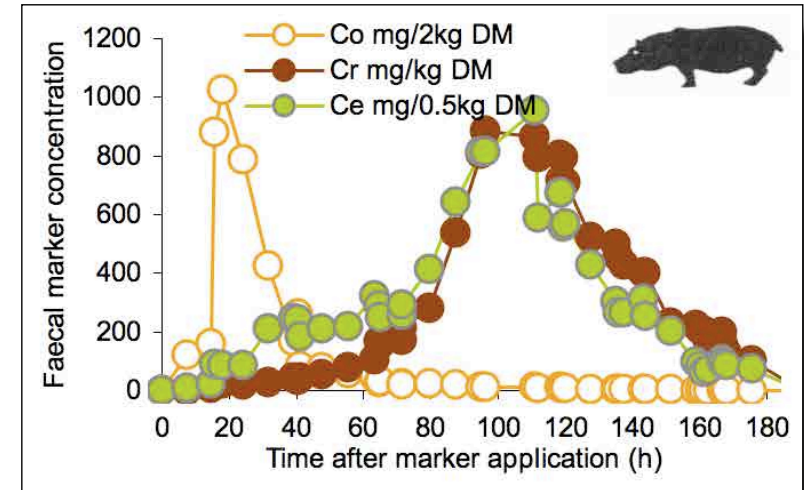
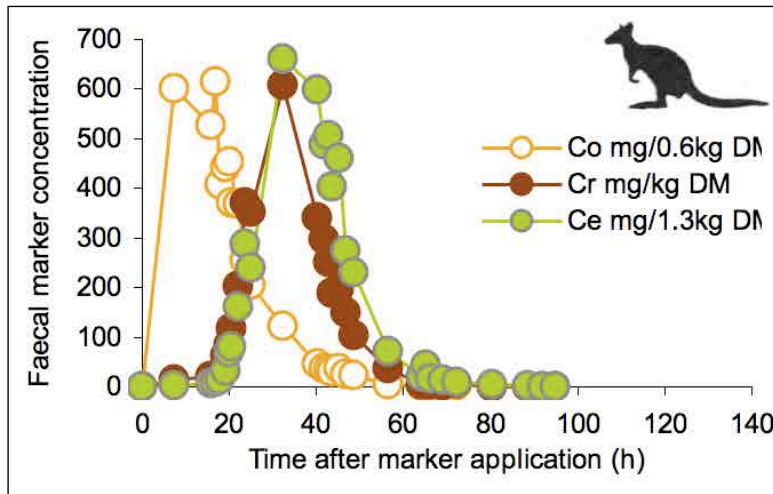


Schwarm et al. (2008,2009)

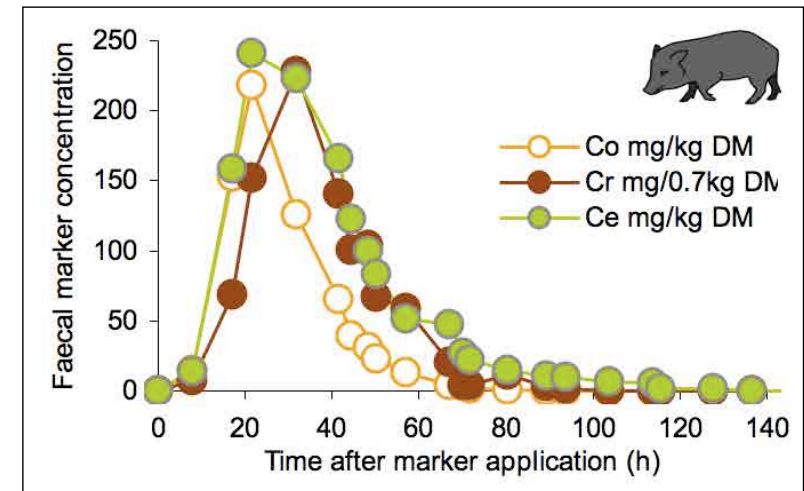
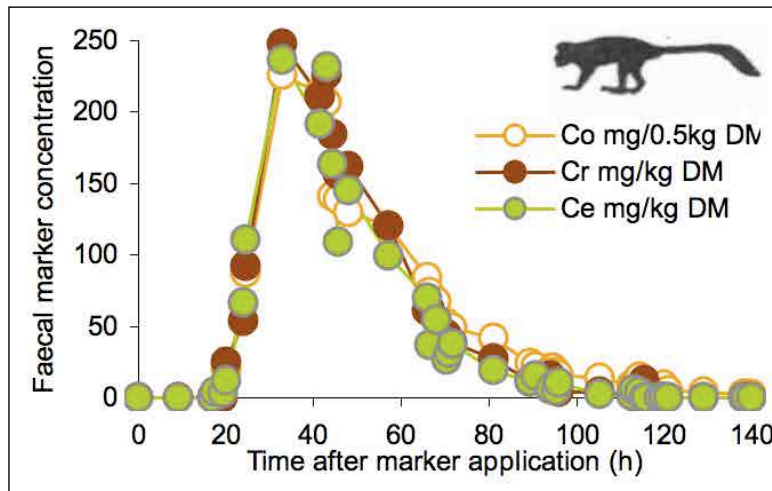




Ruminant vs. Nonruminant Foregut Fermentation

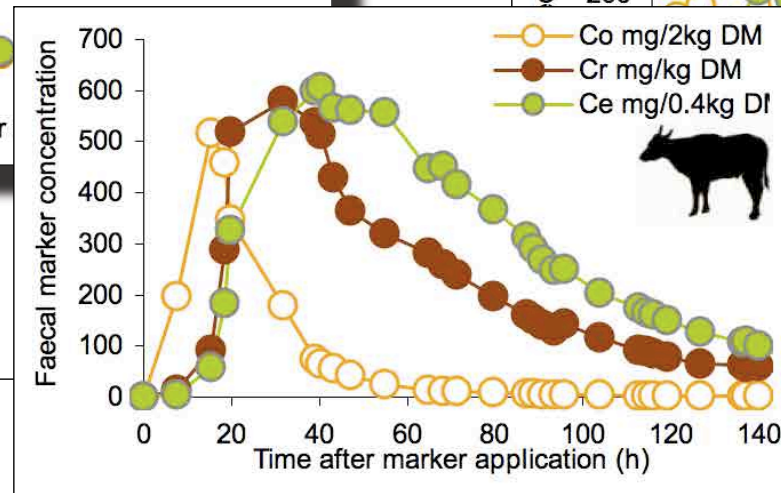
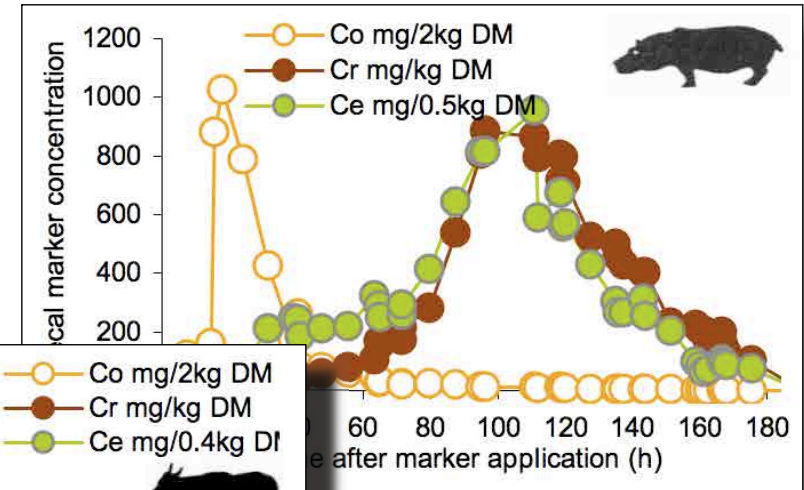
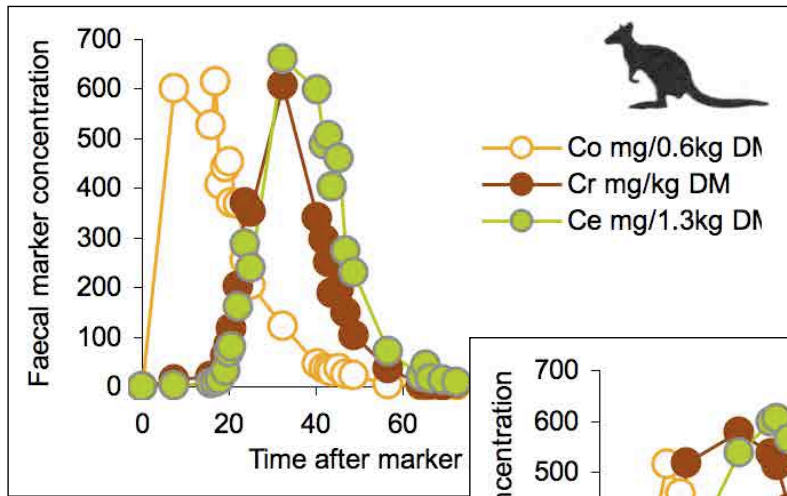


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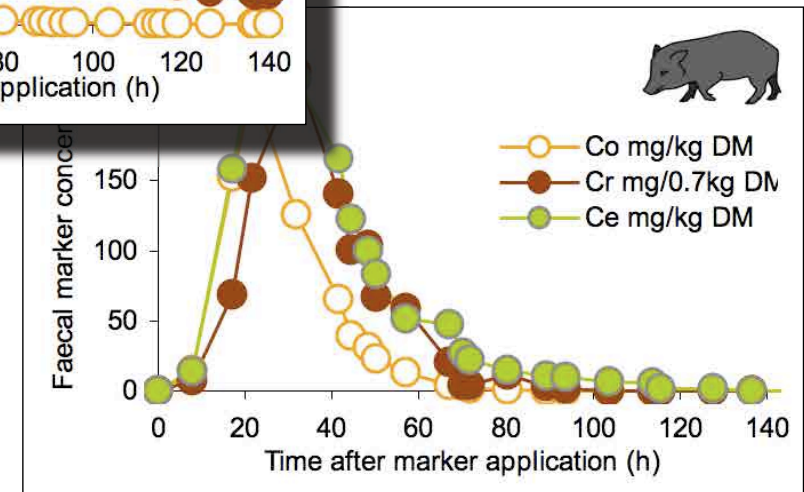
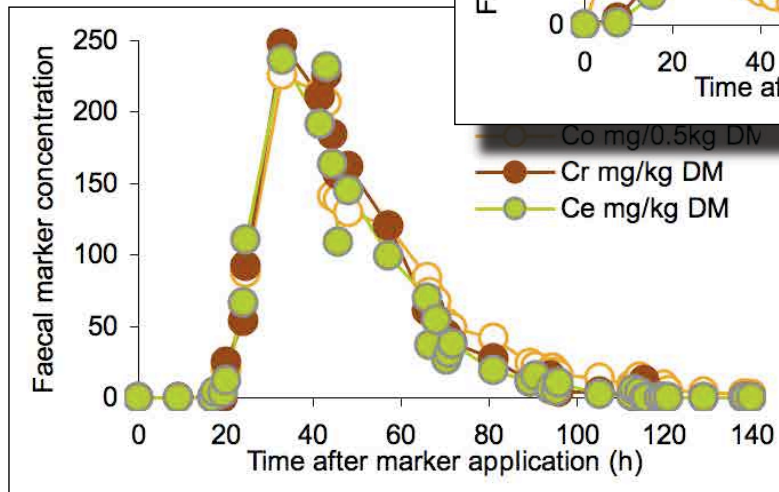




Ruminant vs. Nonruminant Foregut Fermentation



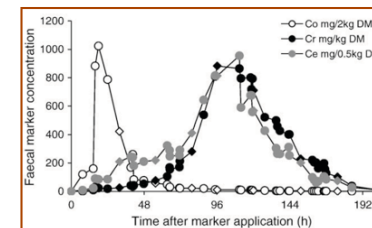
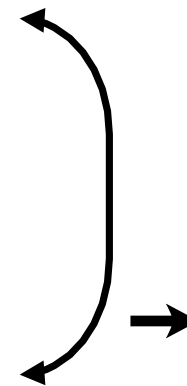
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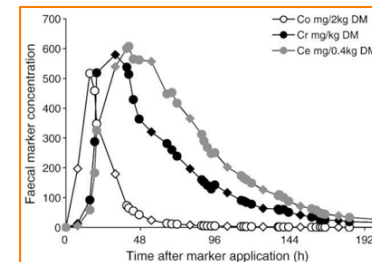


How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing

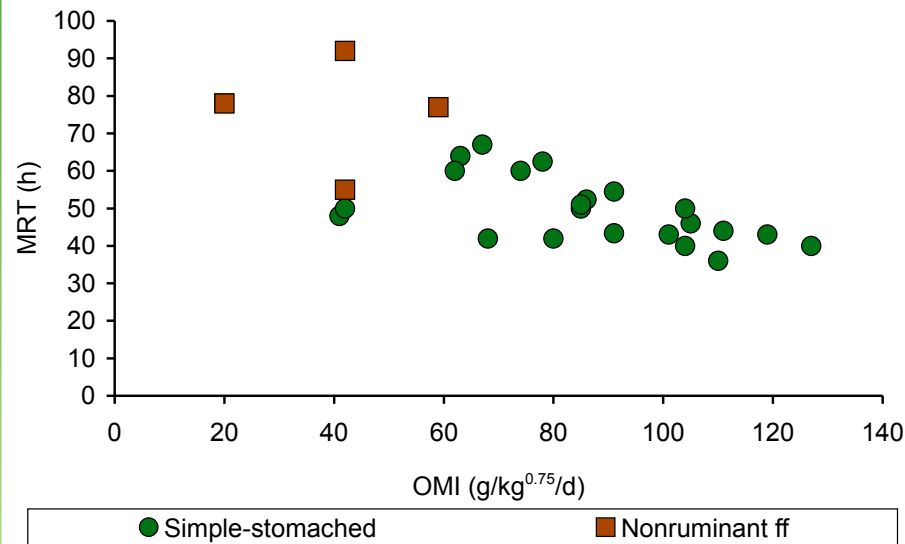


sorting !

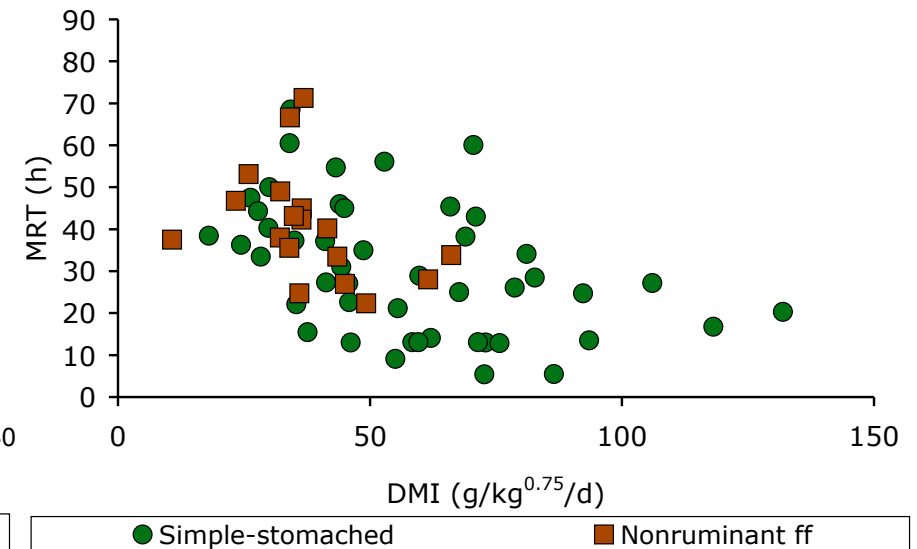




Intake and Passage

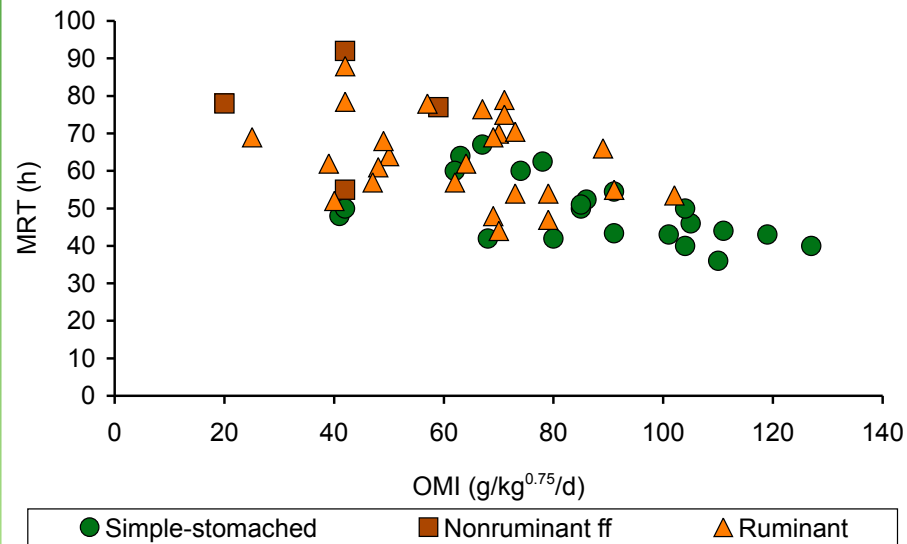


ungulates
from Foote (1982)

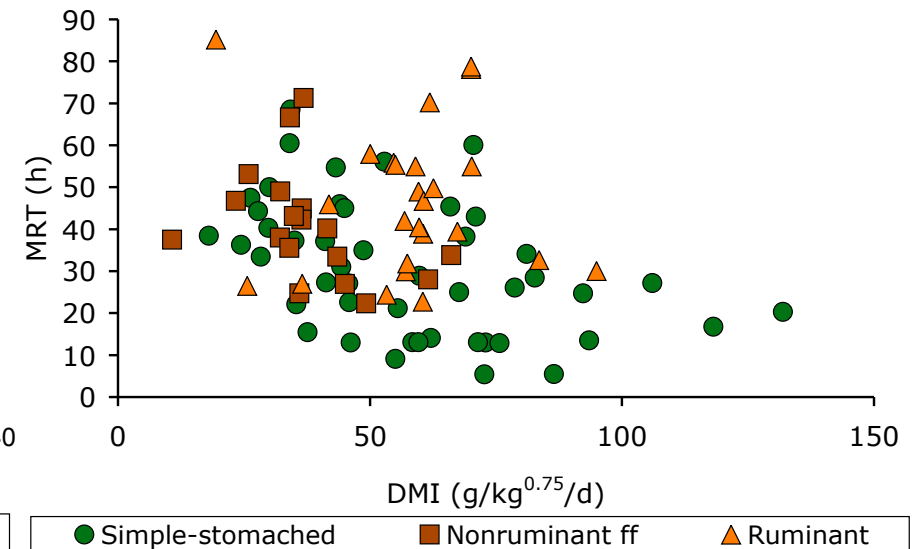




Intake and Passage



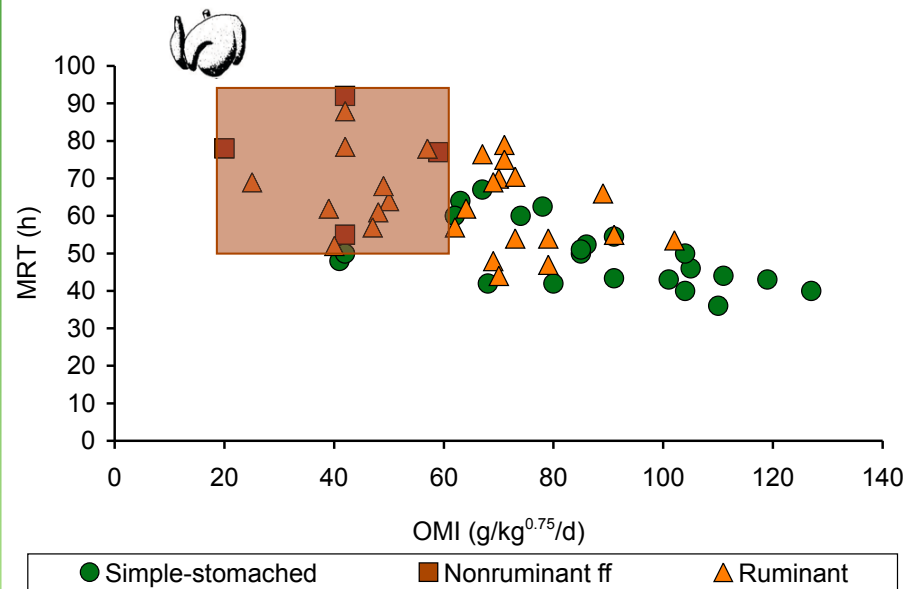
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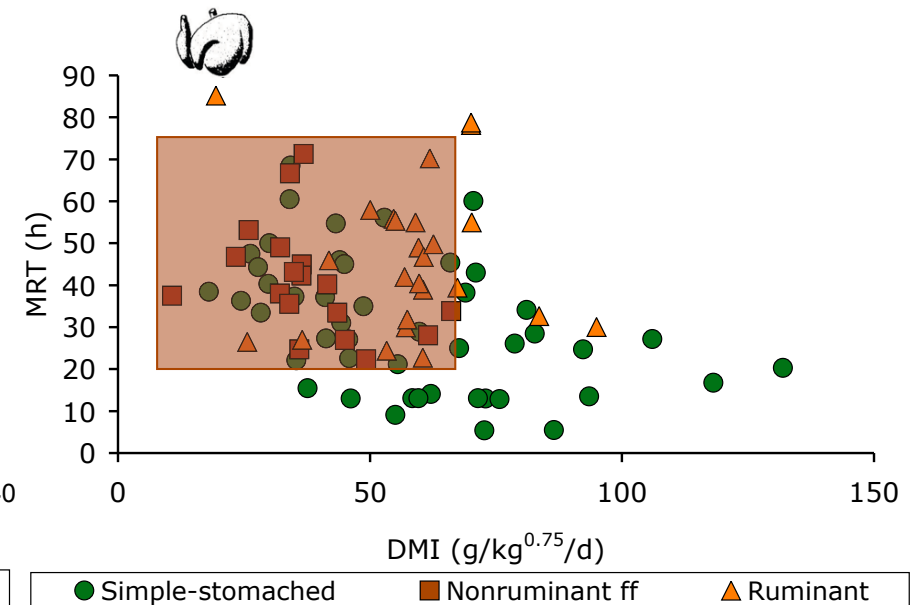
mammal herbivores
Clauss et al. (2007)



Intake and Passage



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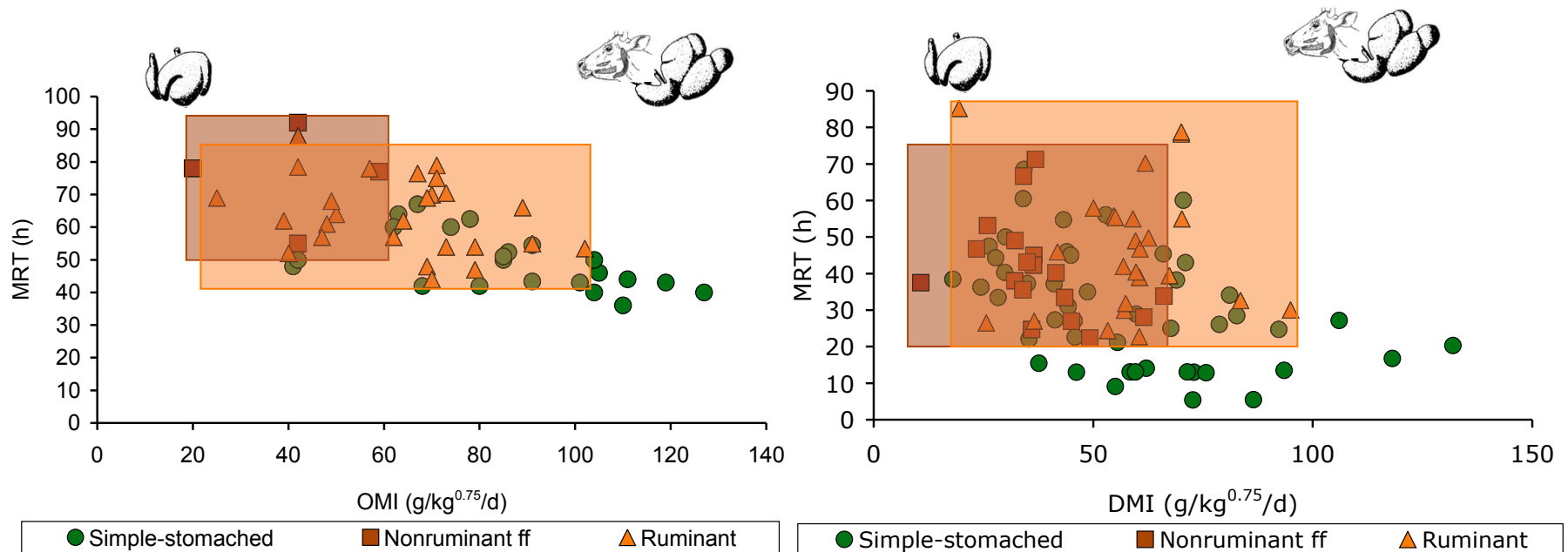


mammal herbivores
Clauss et al. (2007)



Intake and Passage

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



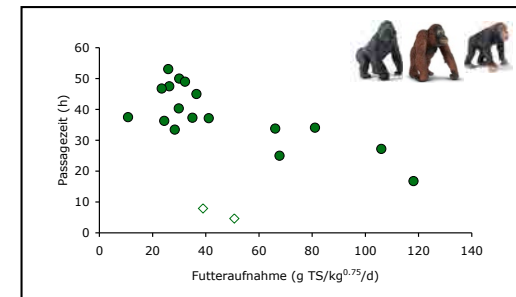
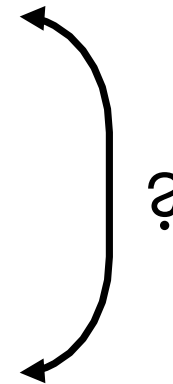
ungulates
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mammal herbivores
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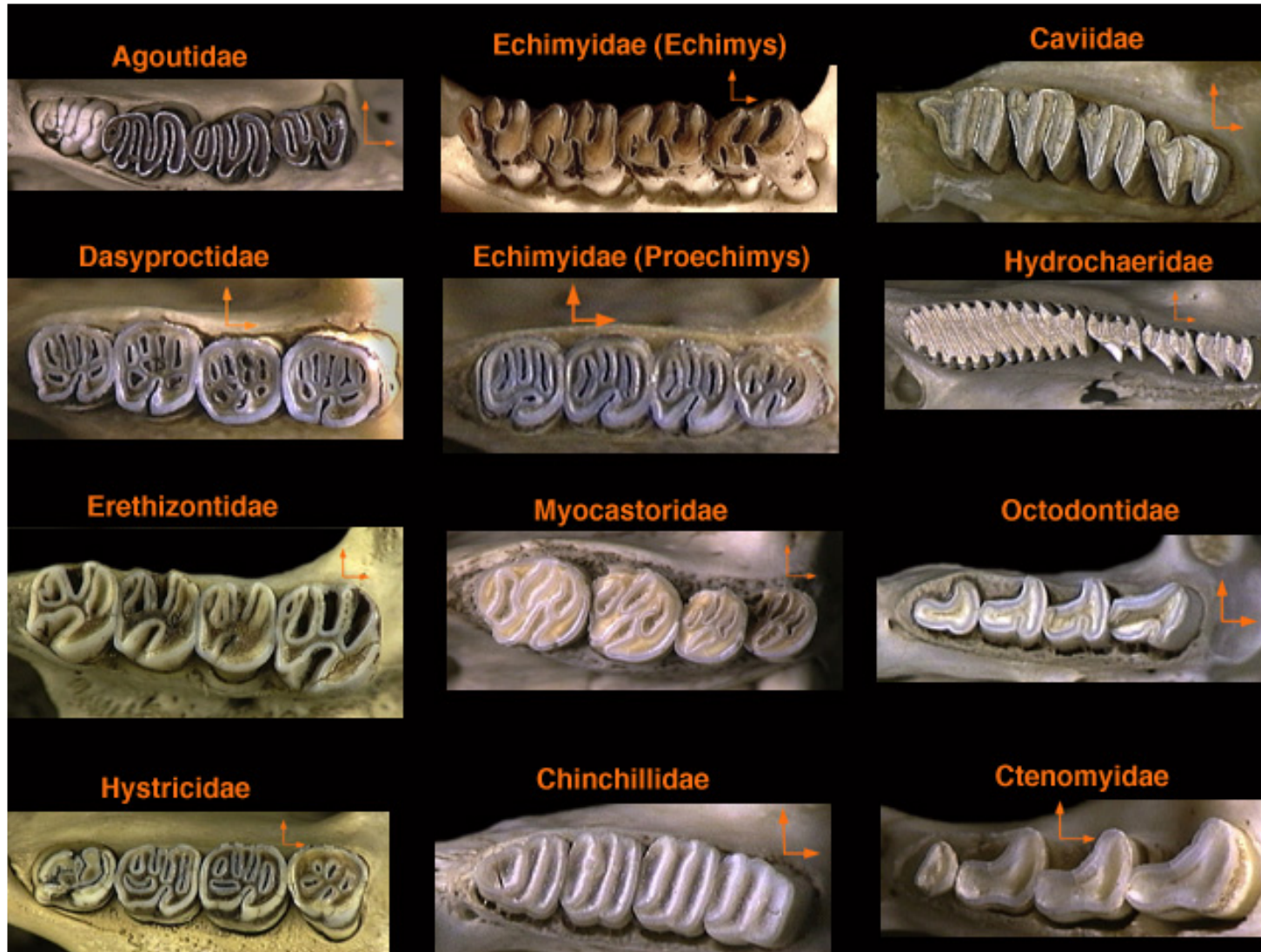
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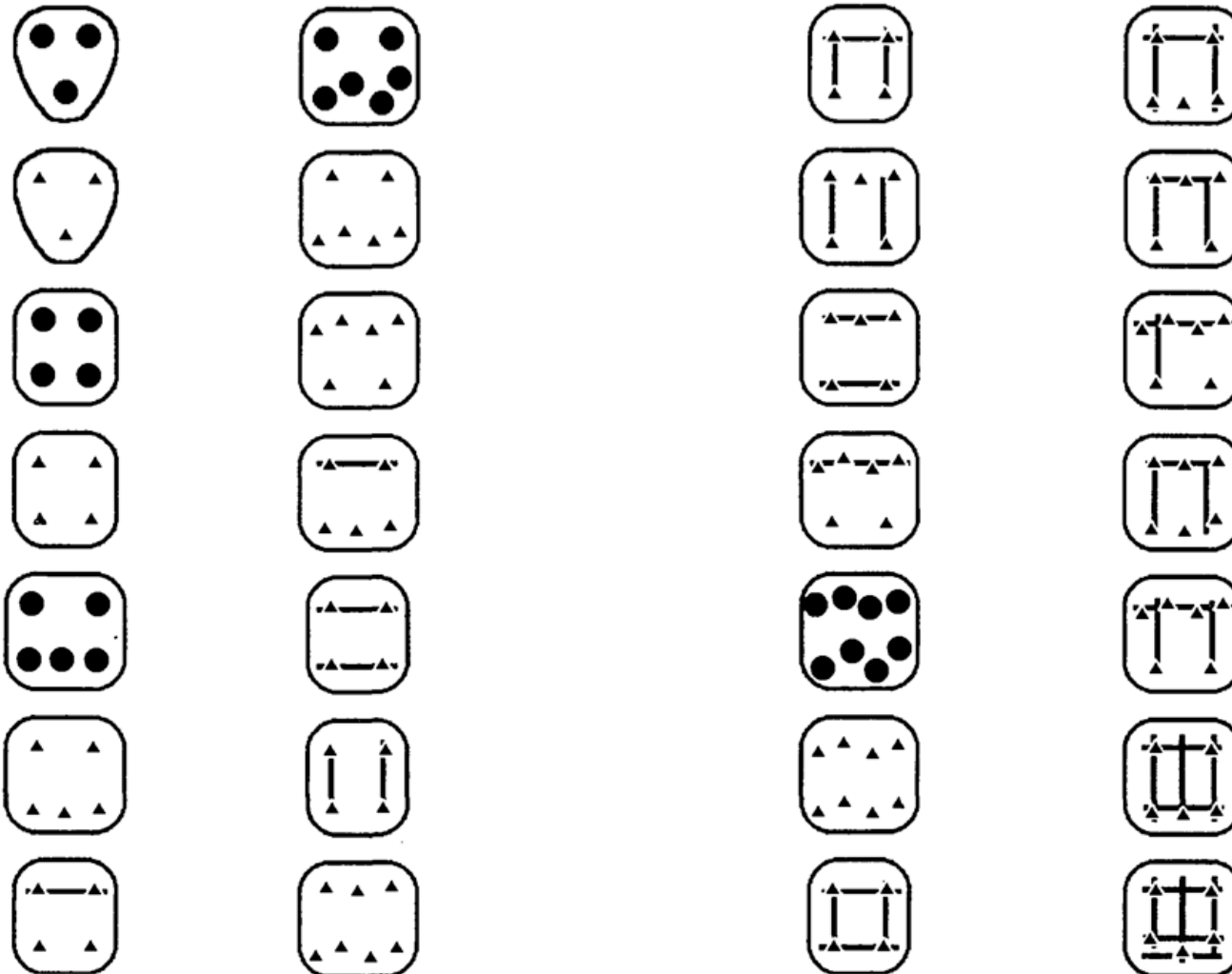


“Mammals are the definite chewers”





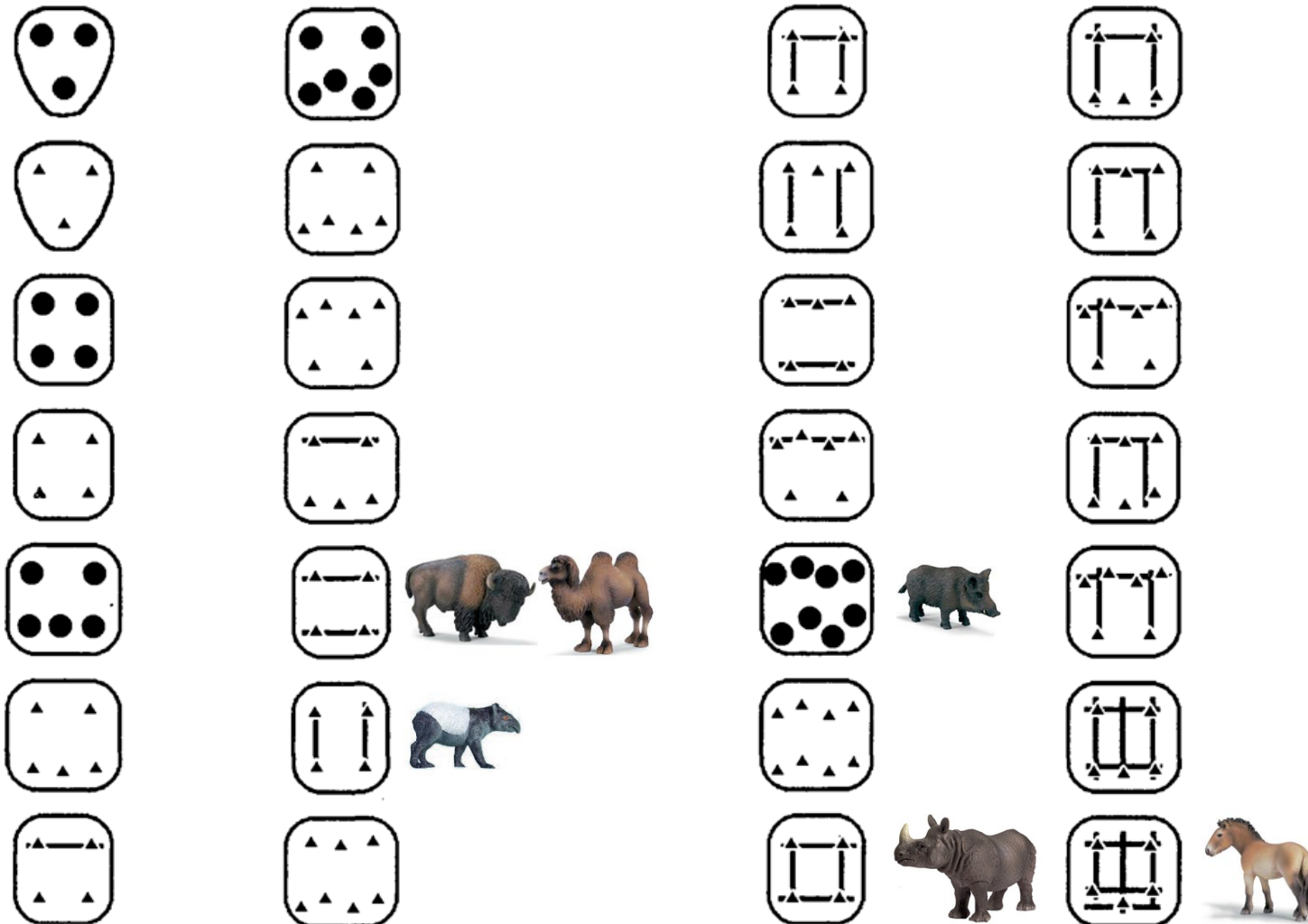
“Mammals are the definite chewers”



aus Jernvall et al. (1996)



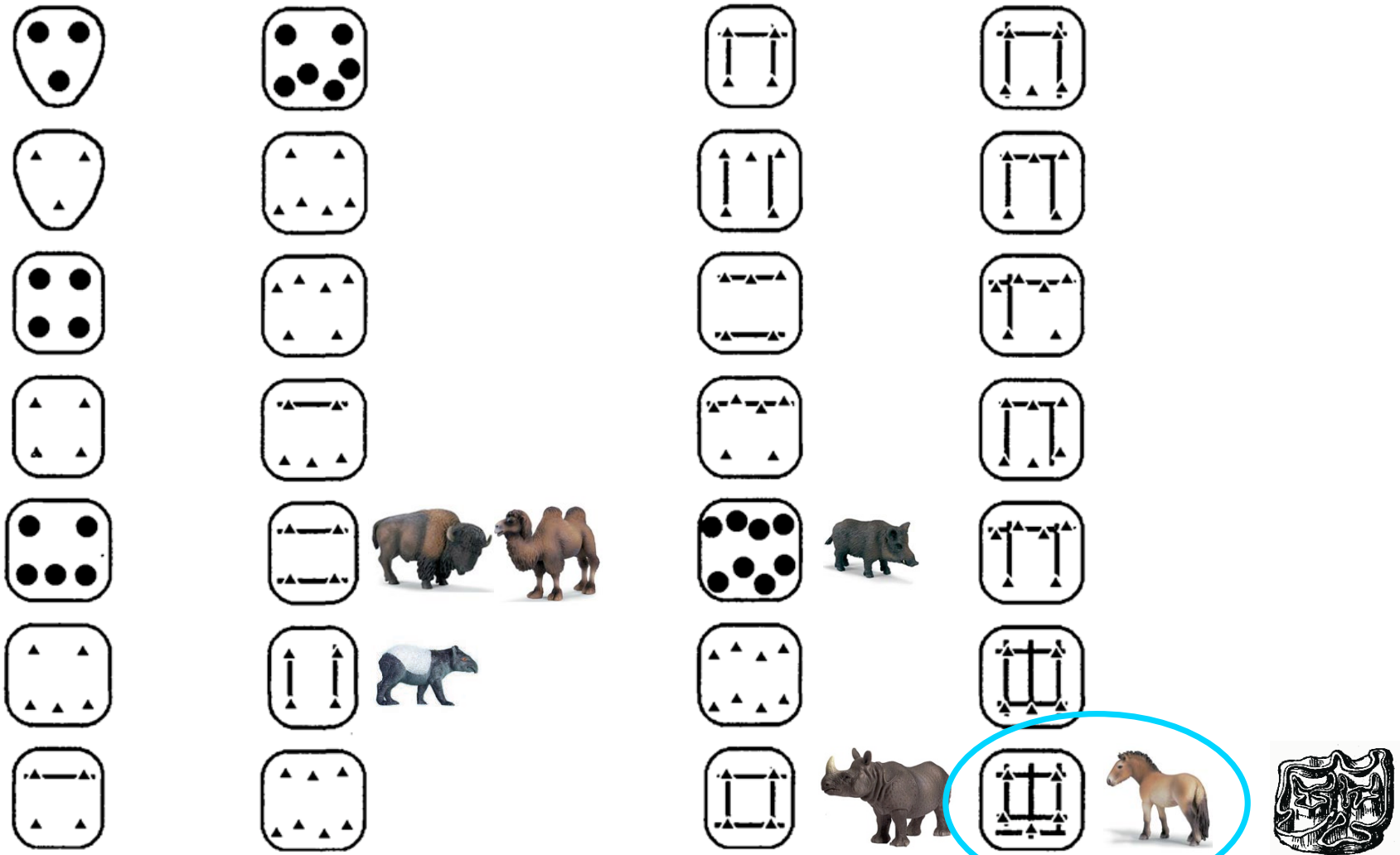
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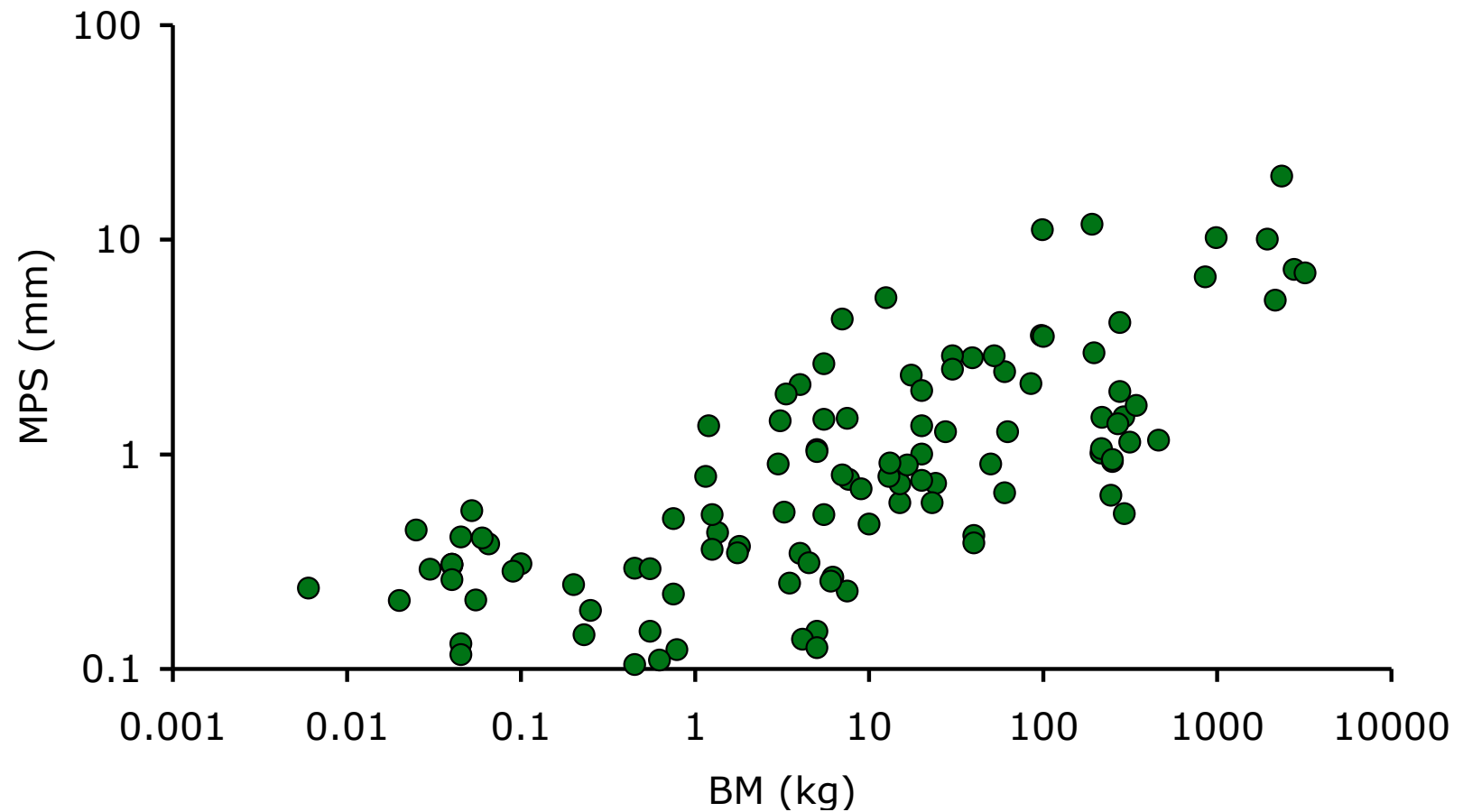
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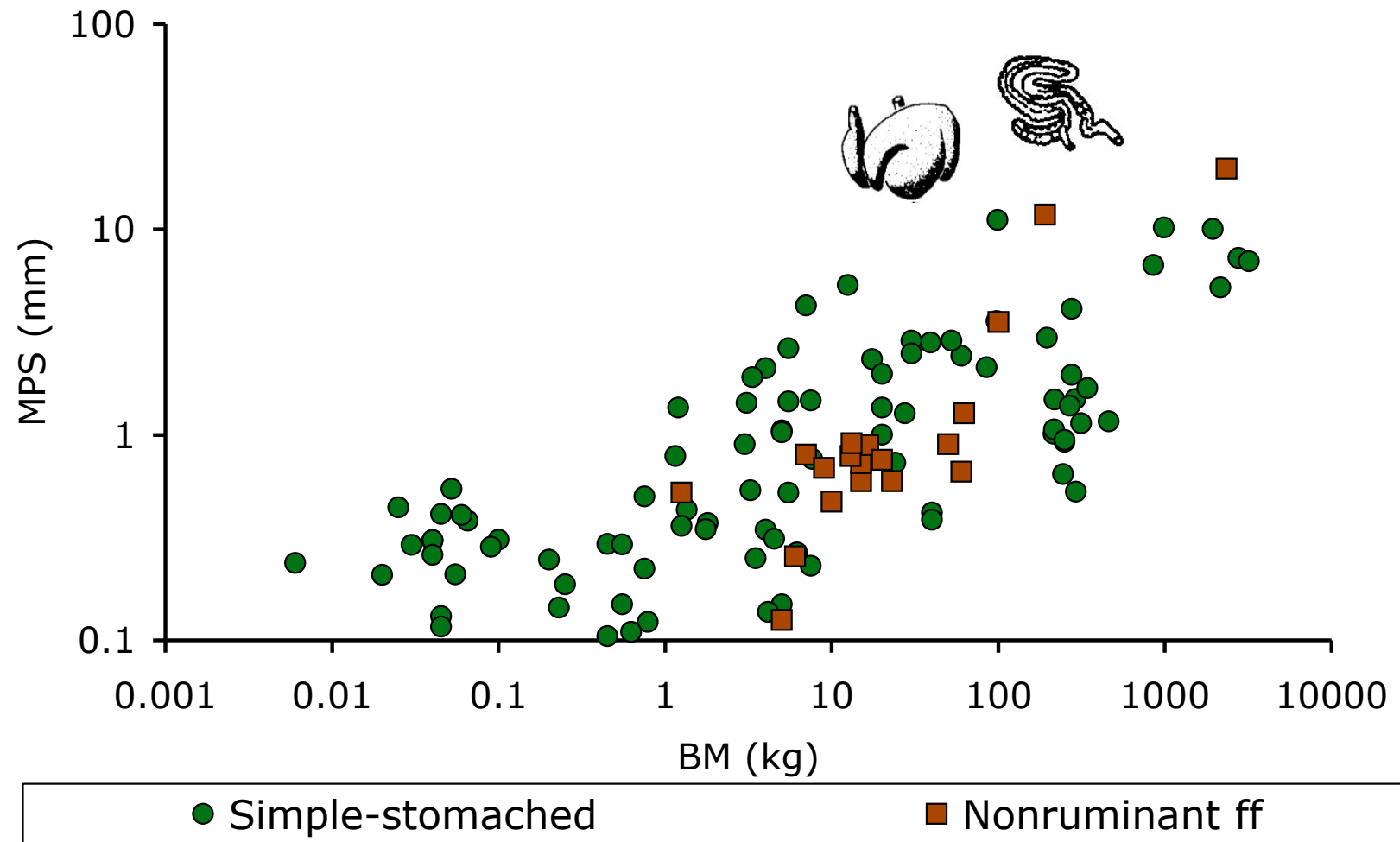
Ingesta particle size (chewing efficiency)



from Fritz (2007)



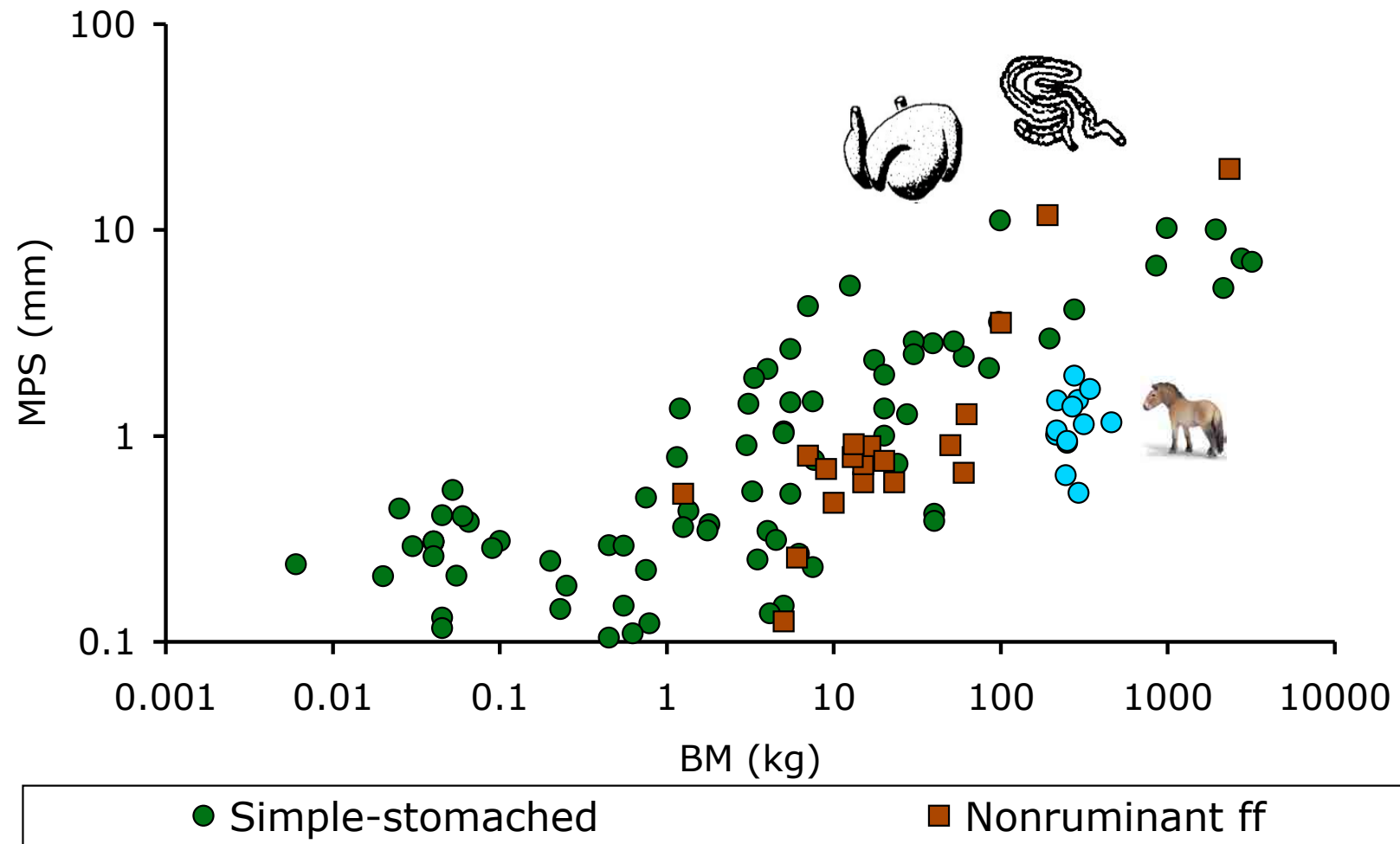
Ingesta particle size (chewing efficiency)



from Fritz (2007)



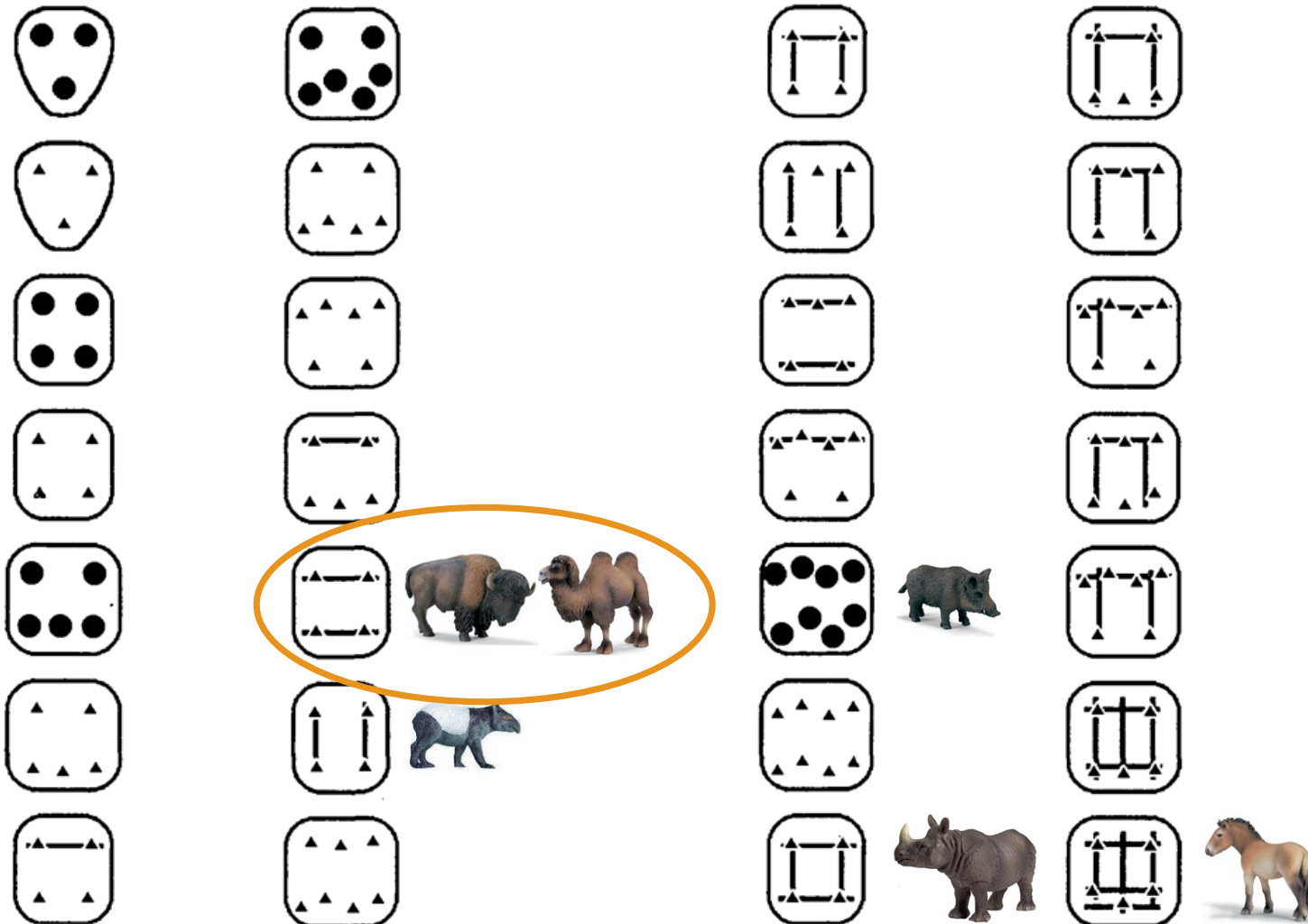
Ingesta particle size (chewing efficiency)



from Fritz (2007)



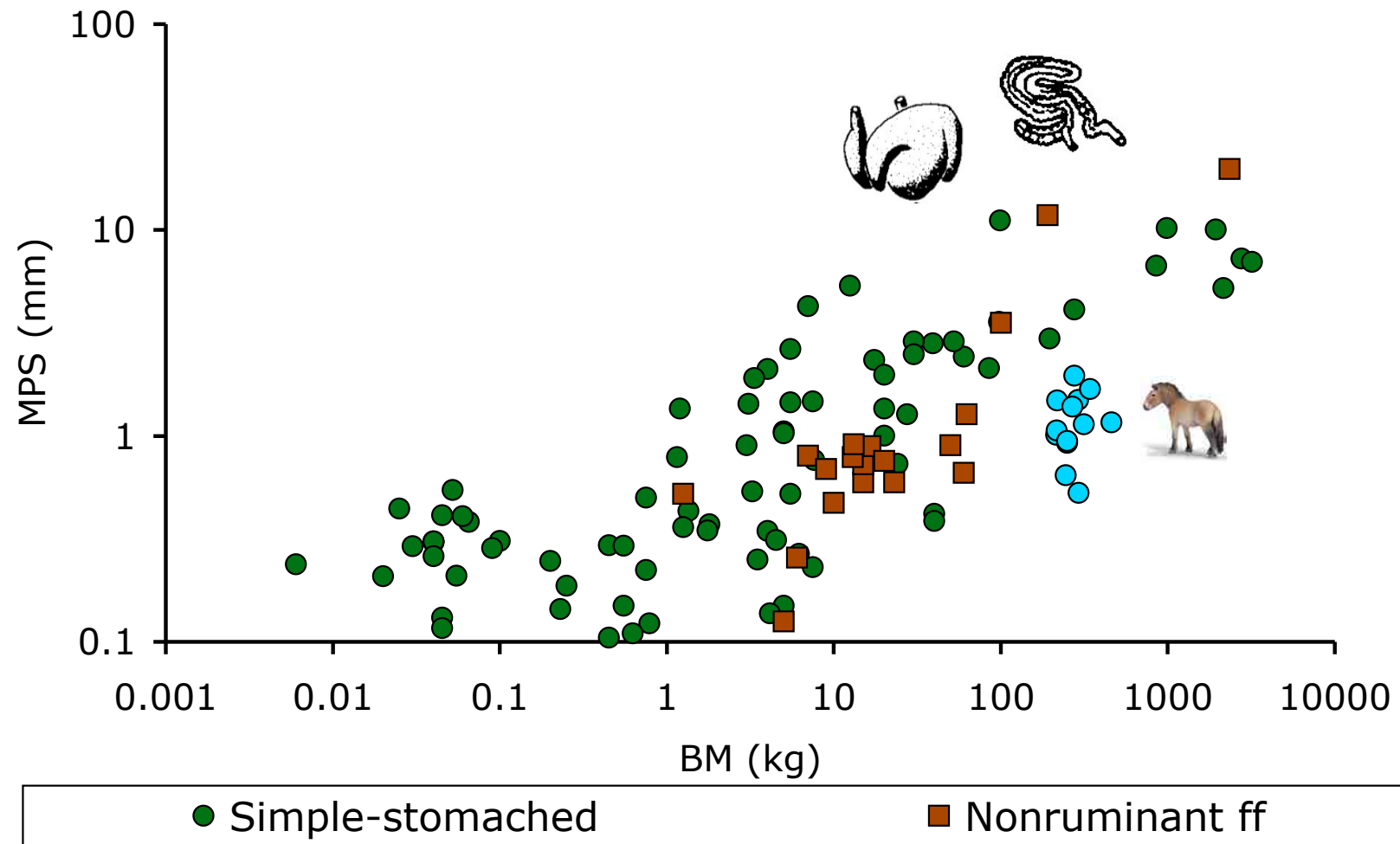
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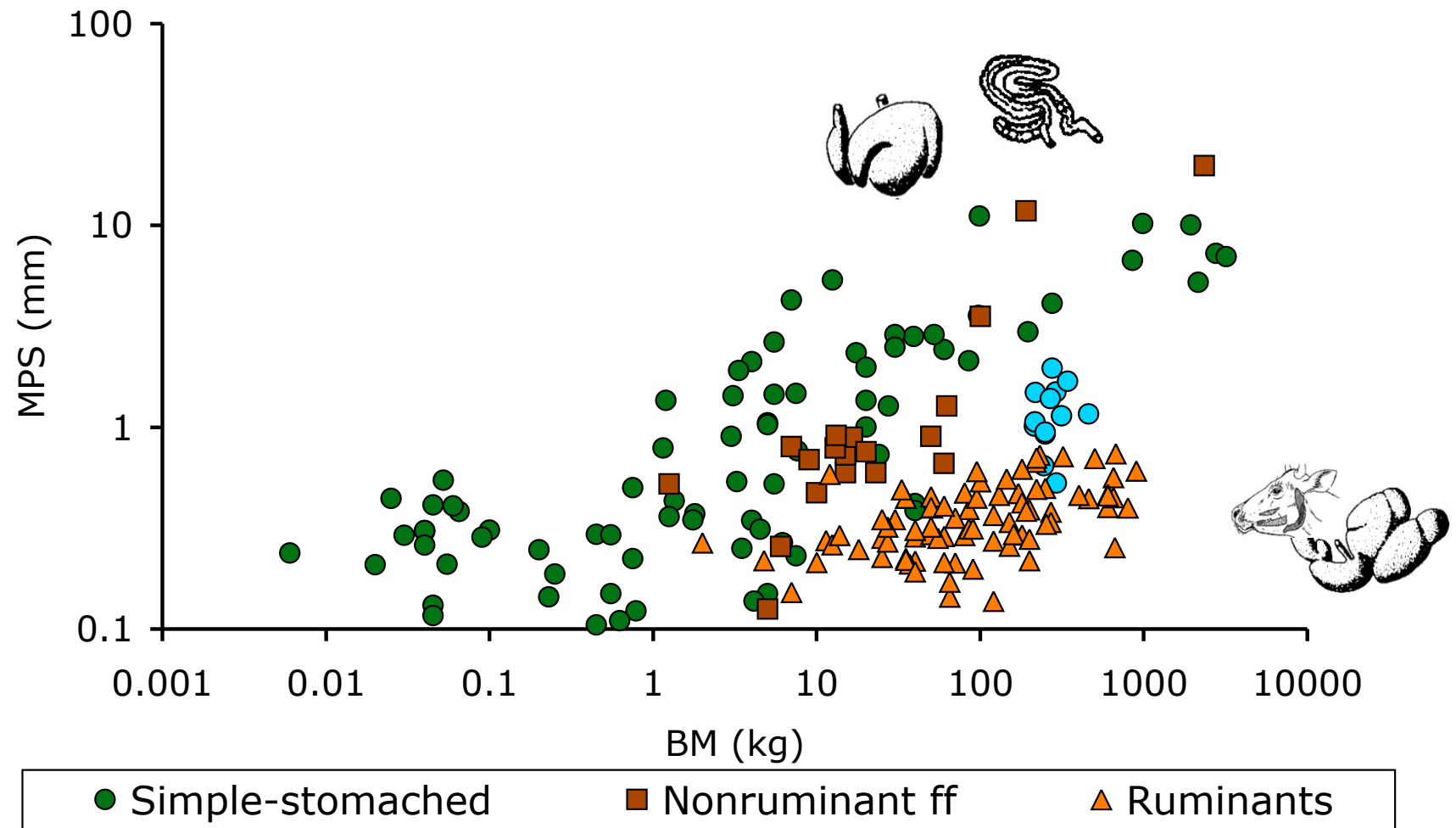
Ingesta particle size (chewing efficiency)



from Fritz (2007)



Ingesta particle size (chewing efficiency)



from Fritz (2007)



Why can 't everyone just chew more?





Chewing in ruminants and nonruminants

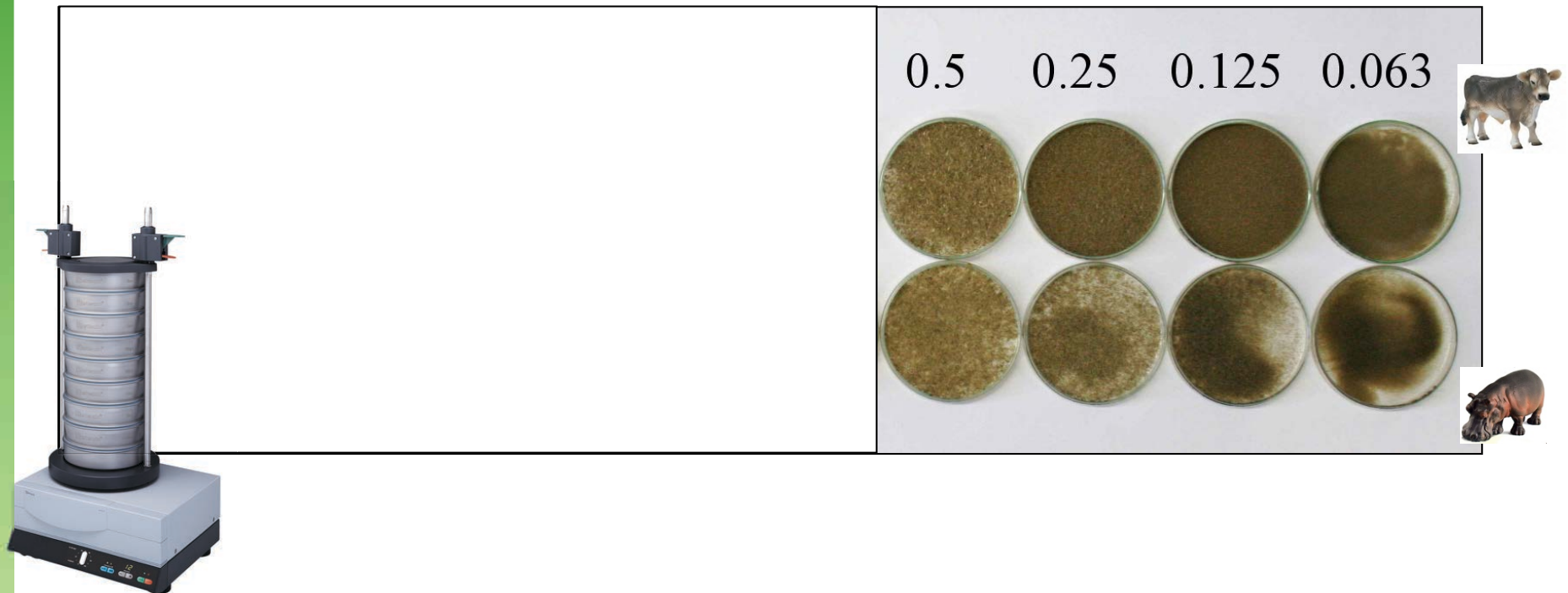


Photo A. Schwarm



Chewing in ruminants and nonruminants

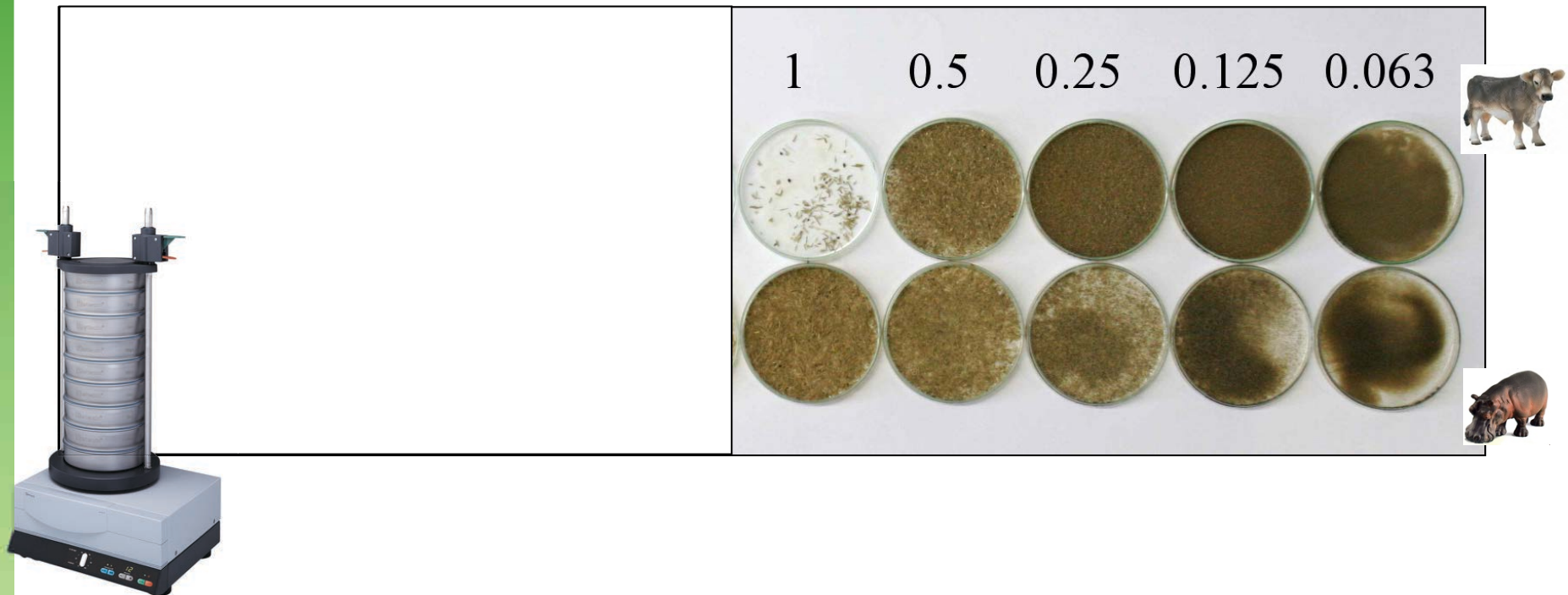


Photo A. Schwarm



Chewing in ruminants and nonruminants

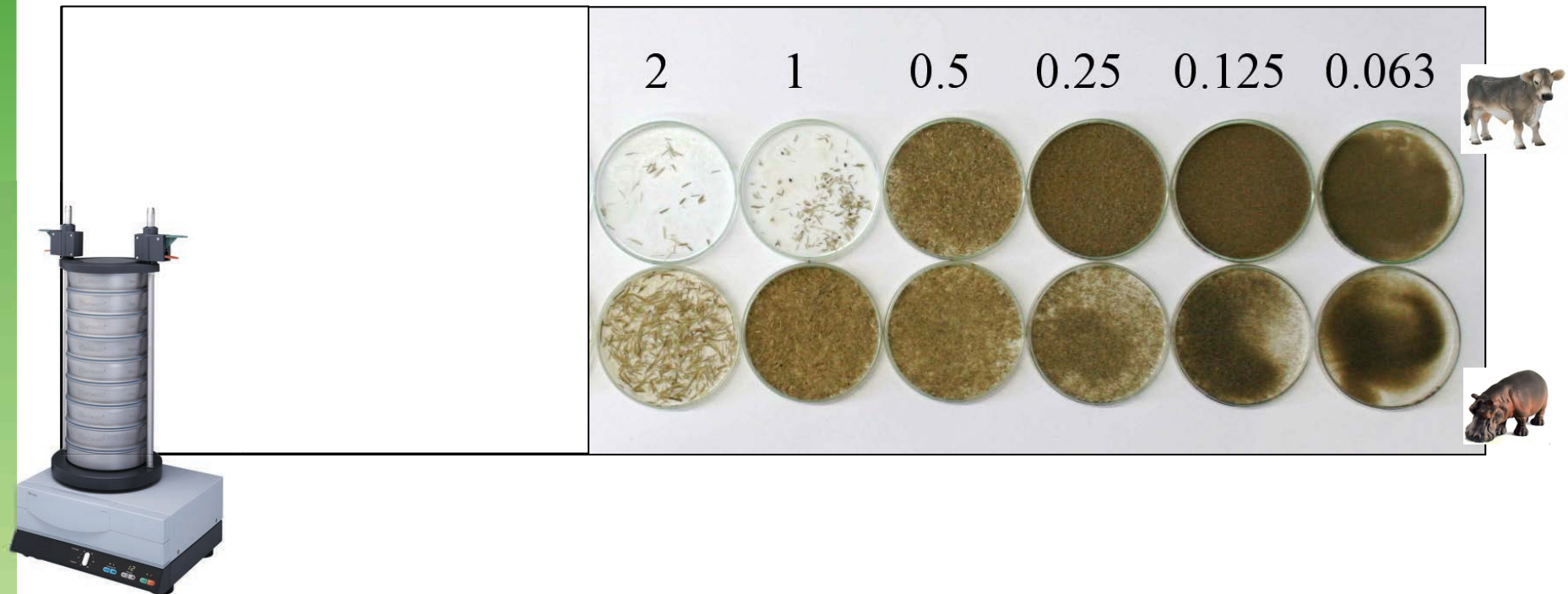


Photo A. Schwarm



Chewing in ruminants and nonruminants

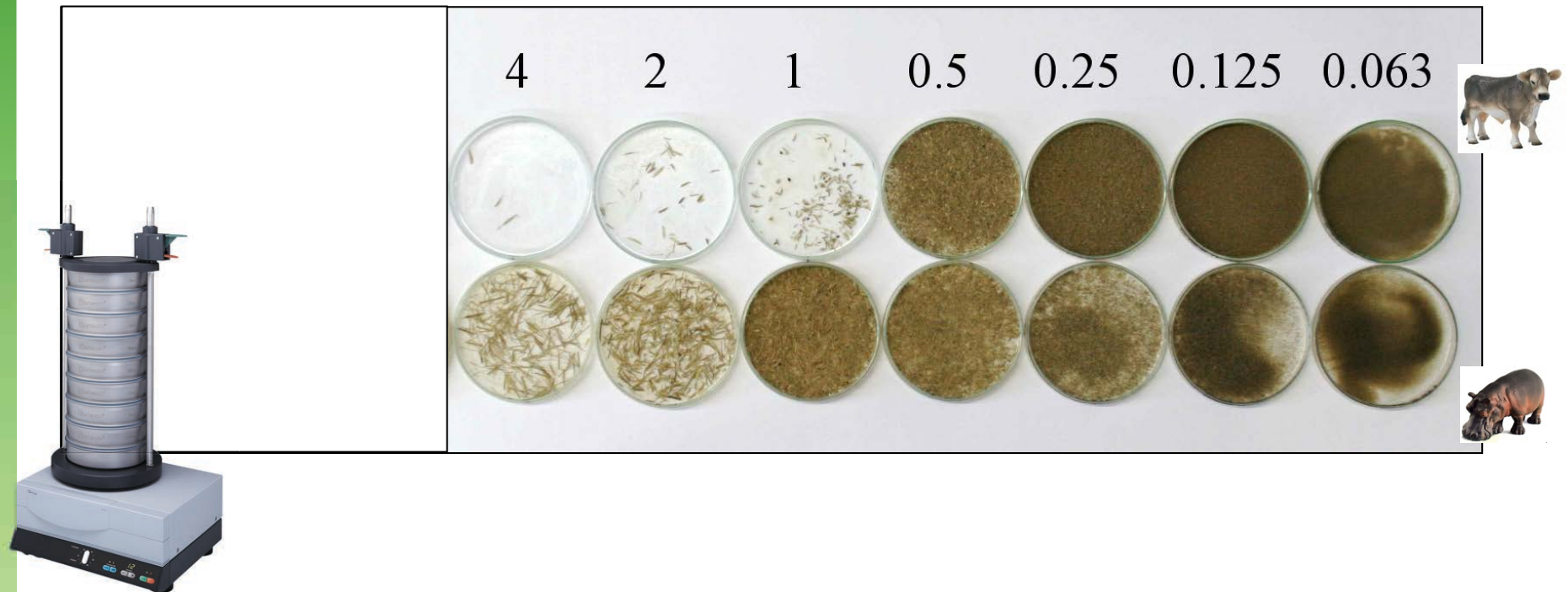


Photo A. Schwarm



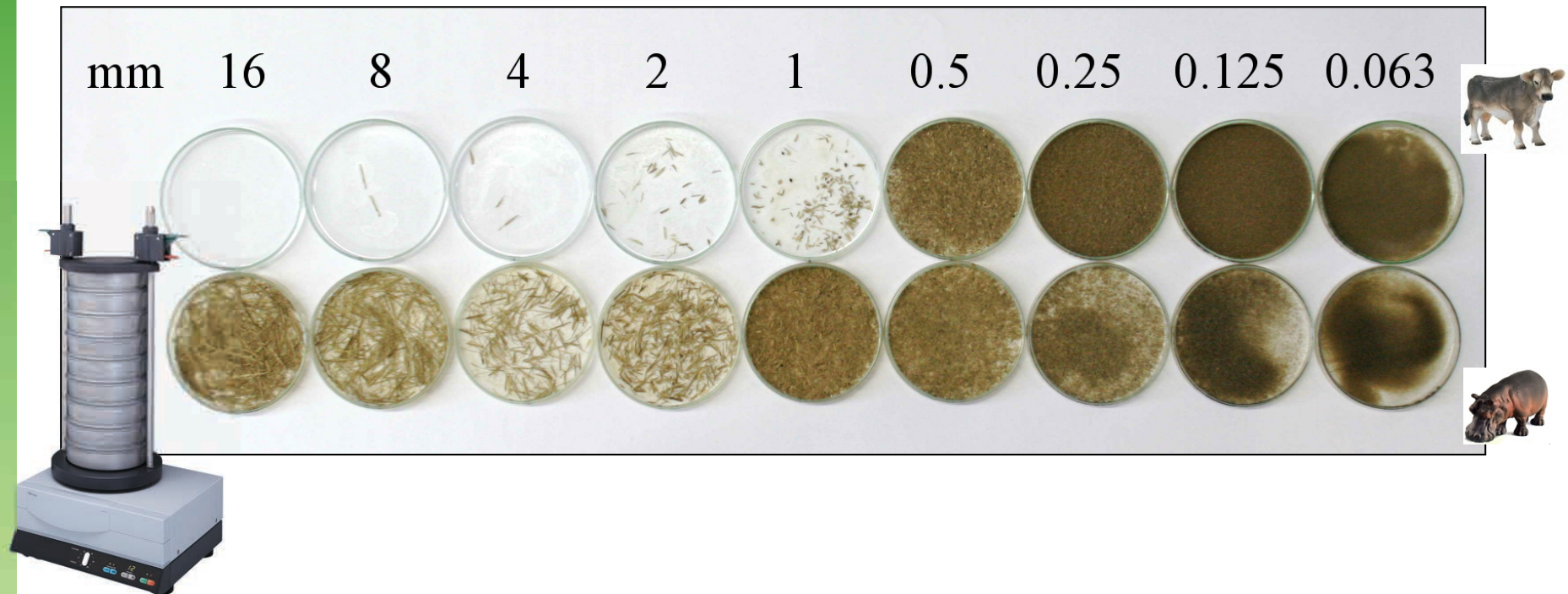
Chewing in ruminants and nonruminants



Photo A. Schwarm



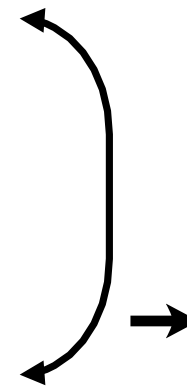
Chewing in ruminants and nonruminants



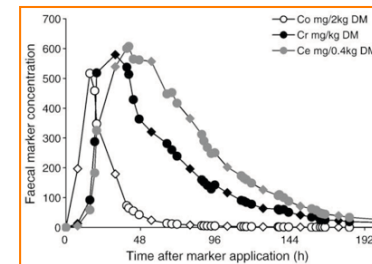


How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing



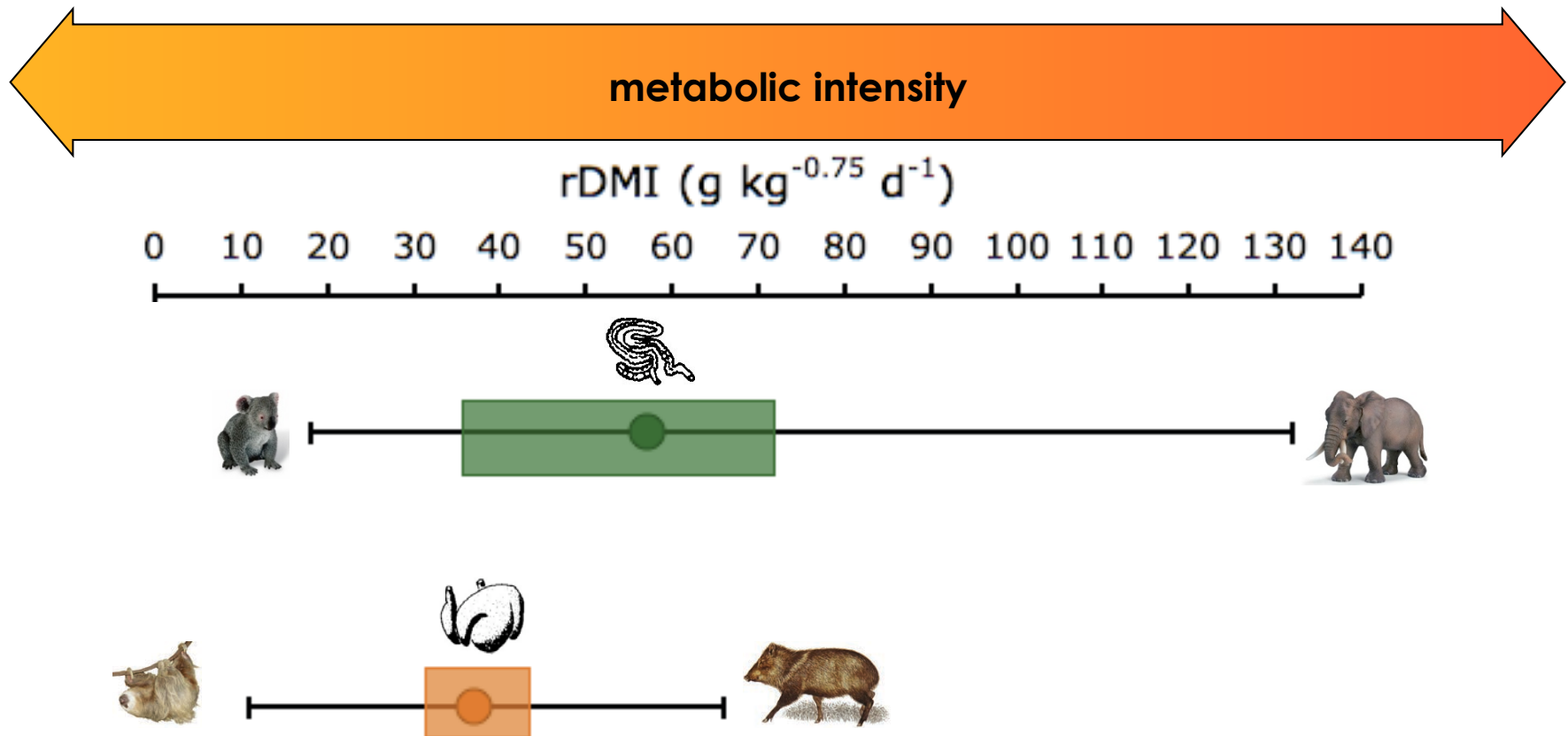
sorting !



sorting !

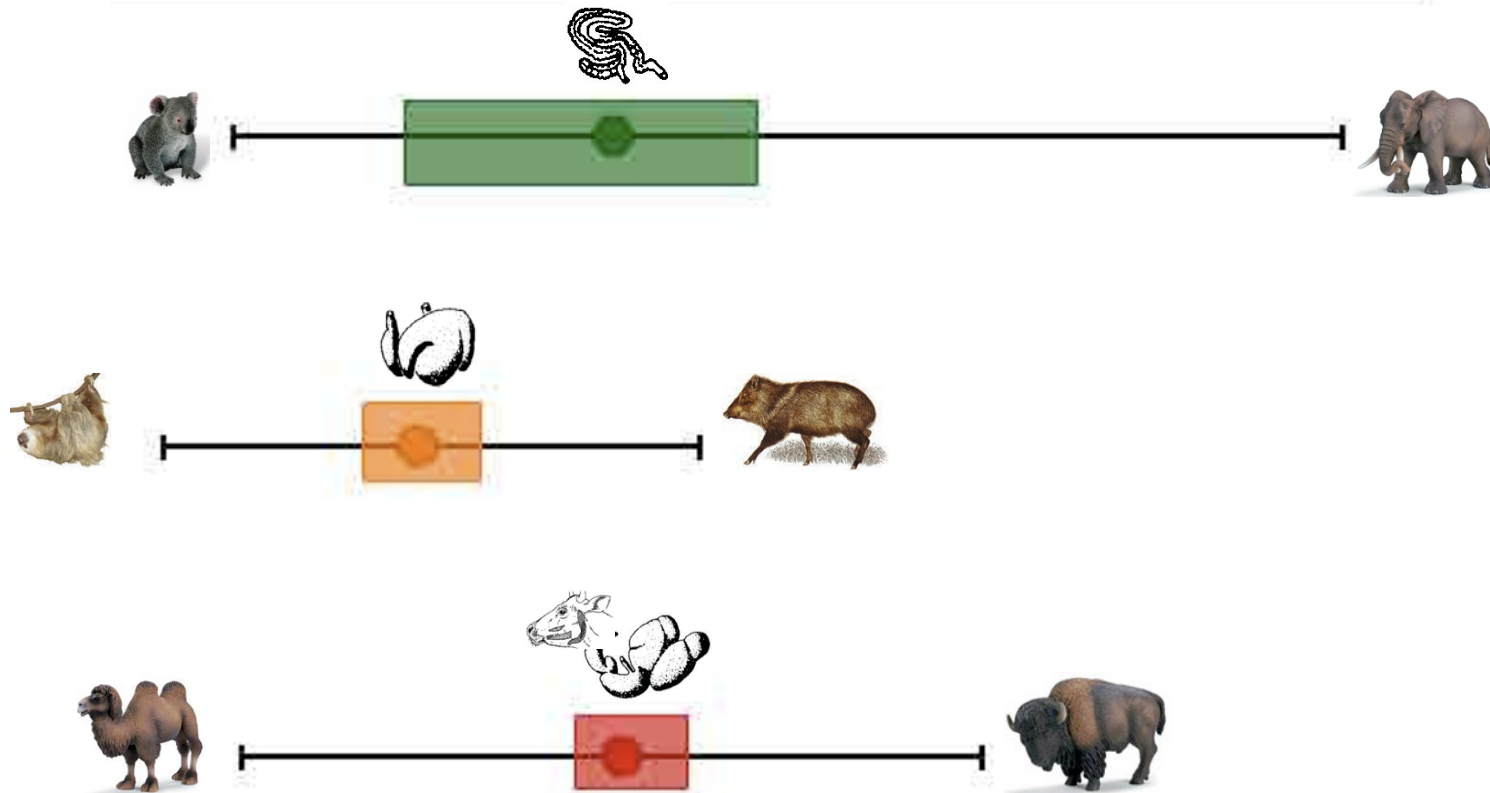
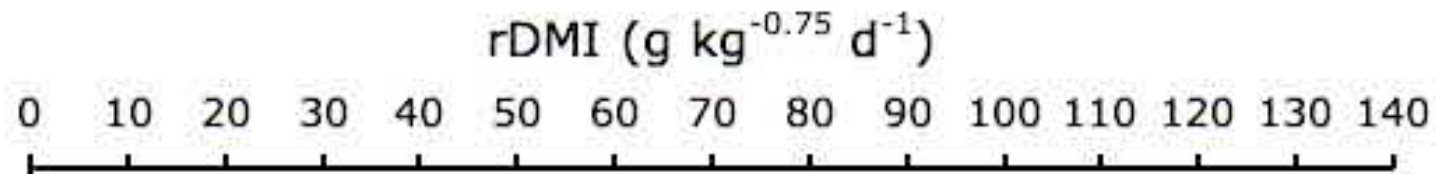


Conceptualizing herbivore diversity





Conceptualizing herbivore diversity





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**
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Digestive and Metabolic Strategies



Low intake
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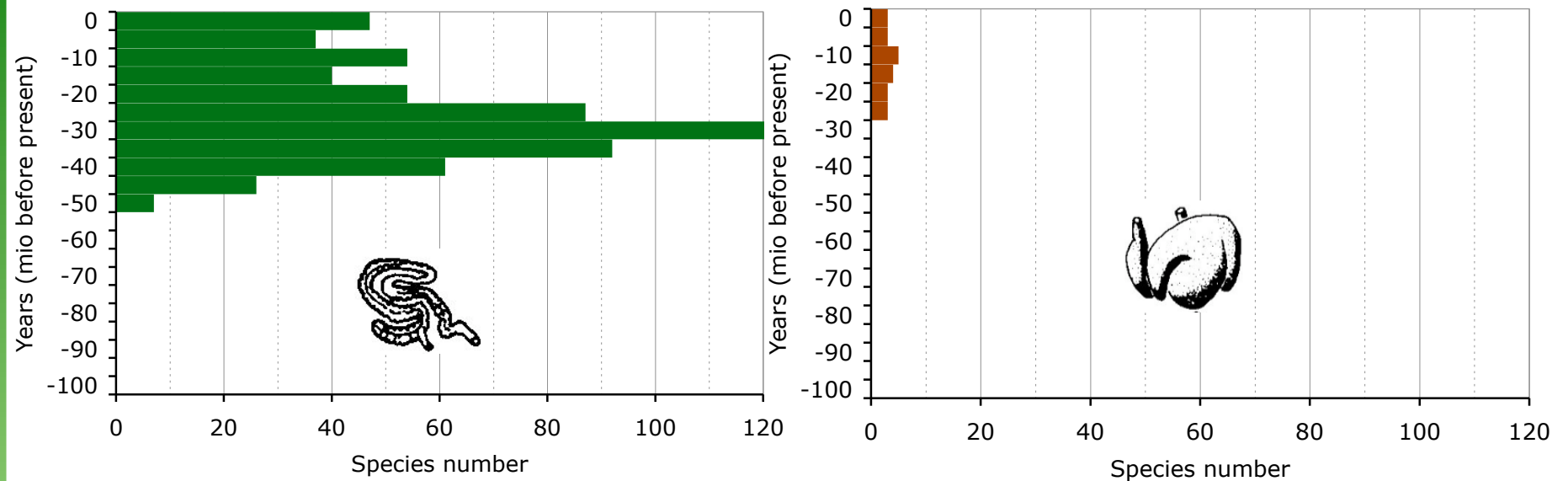


High intake
⇒ **differentiated**
passage
⇒ **high**
metabolism





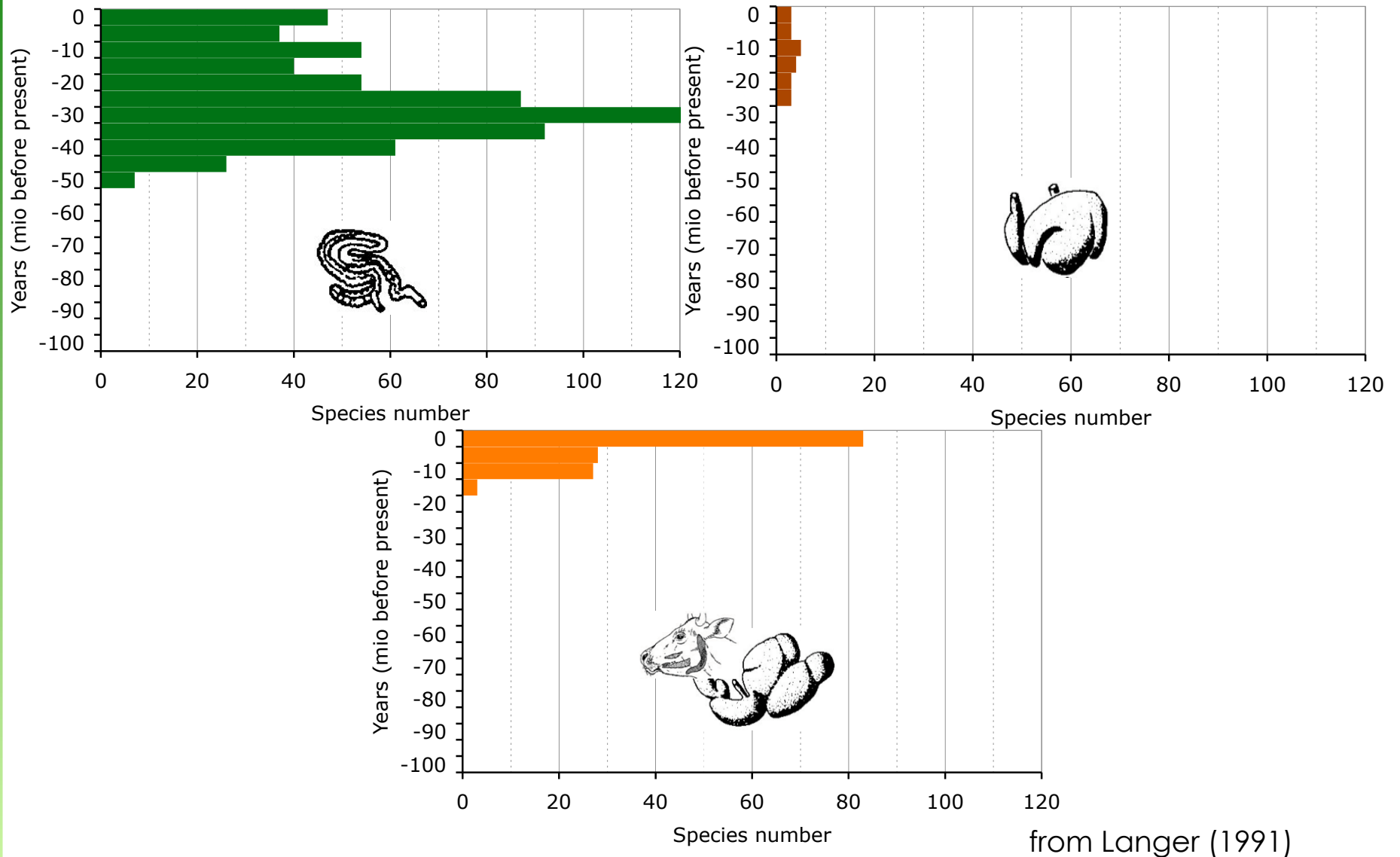
European Mammal Herbivores in Deep Time



from Langer (1991)



European Mammal Herbivores in Deep Time





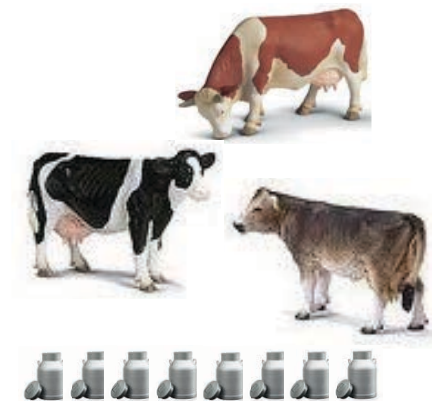
Digestive and Metabolic Strategies



Low intake
⇒ long passage
⇒ **low BMR**

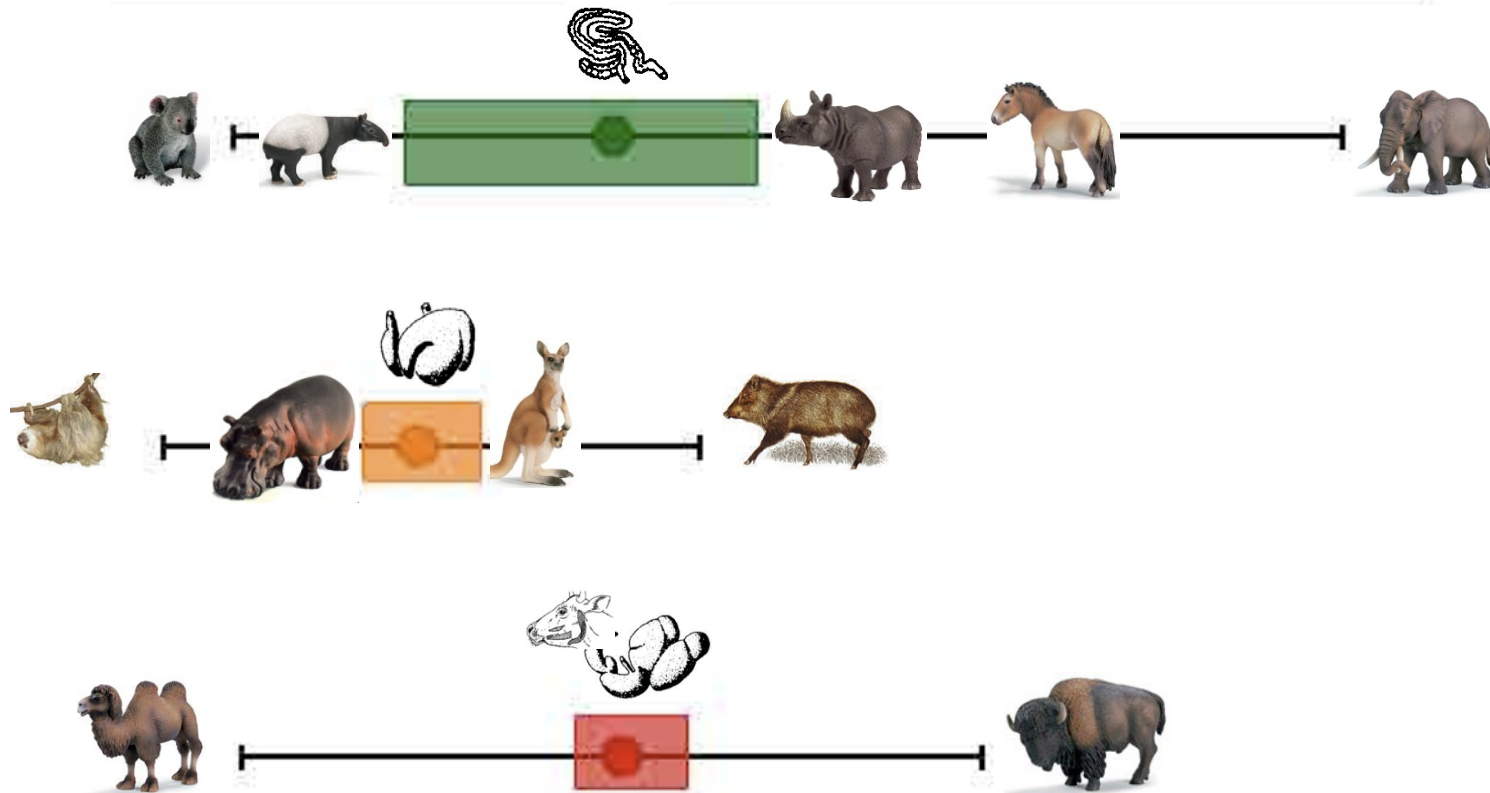
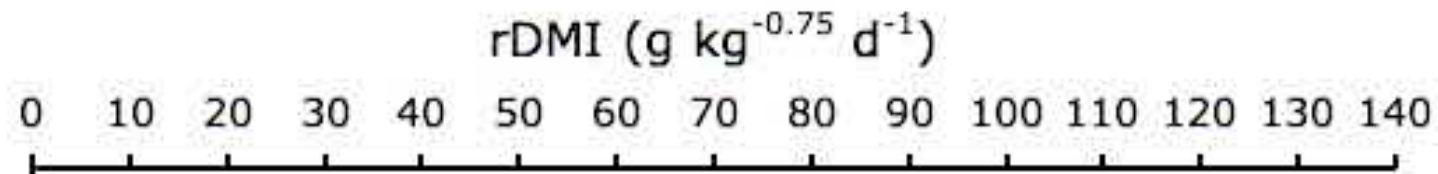


High intake
⇒ **differentiated**
passage
⇒ **high BMR**





Conceptualizing herbivore diversity



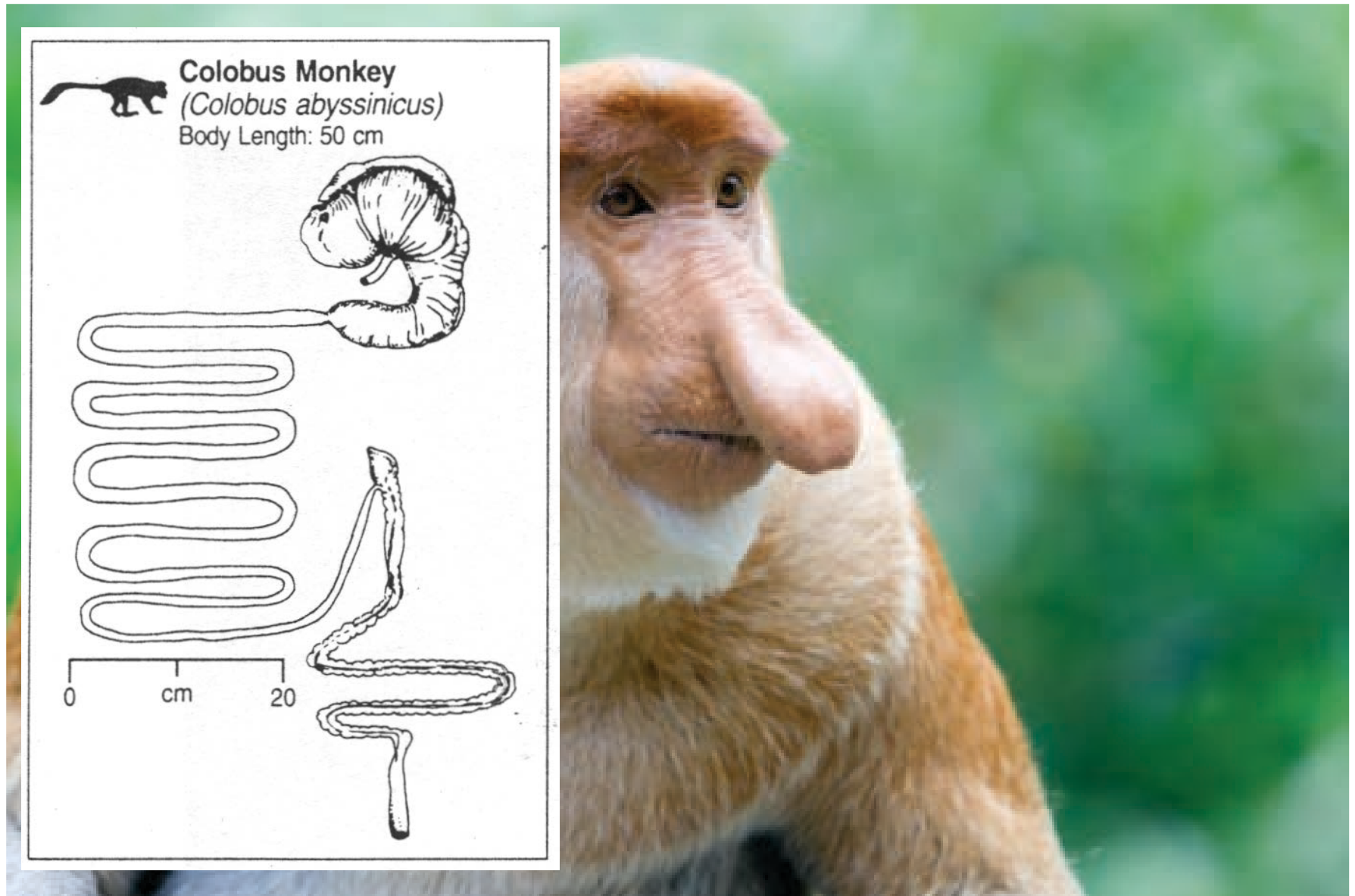


The case of the proboscis monkey





The case of the proboscis monkey



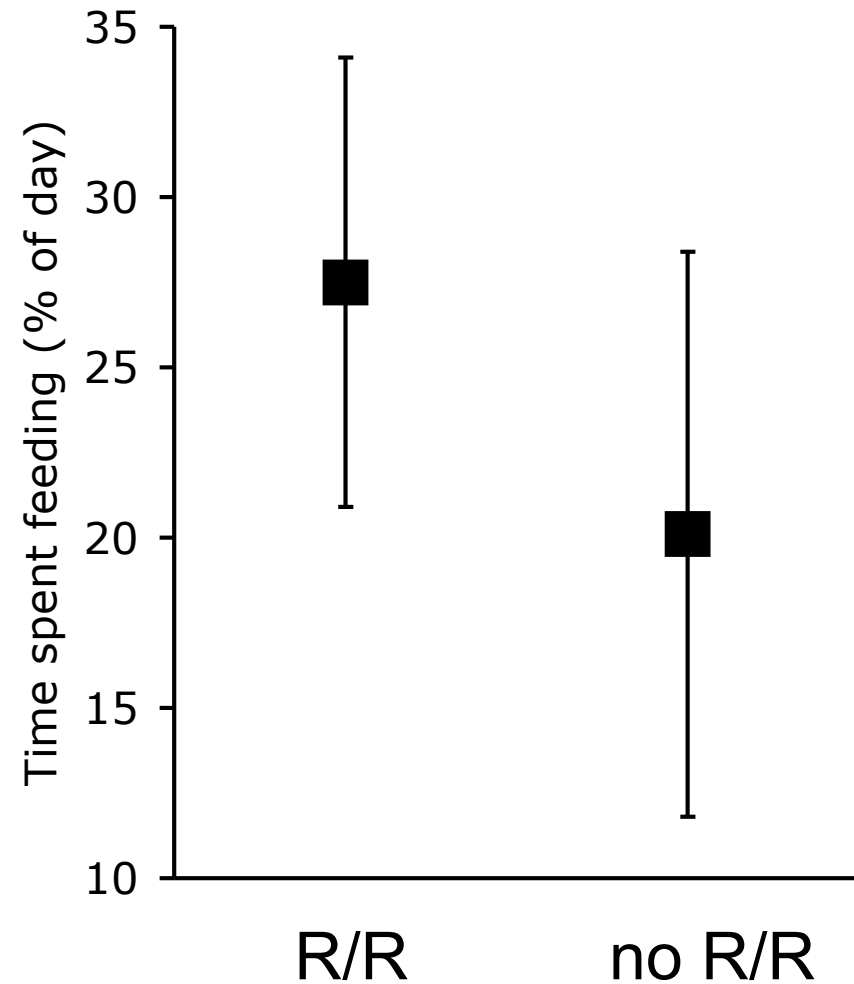
from Stevens und Hume (1995)





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

Ikki Matsuda^{1,*}, Tadahiro Murai¹,
Marcus Clauss², Tomomi Yamada³,
Augustine Tuuga⁴, Henry Bernard⁵
and Seigo Higashi⁶

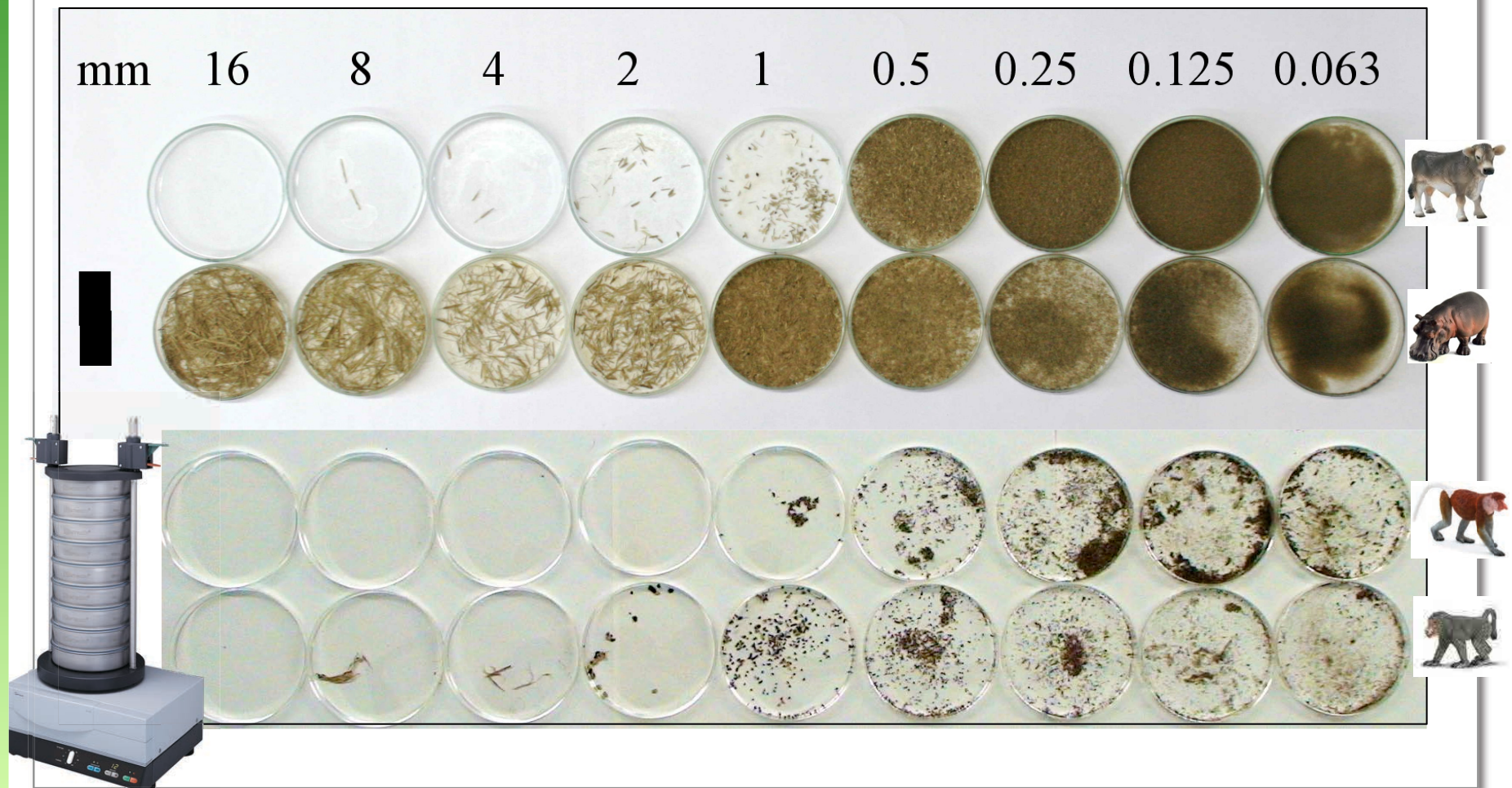




Faecal particle size in free-ranging primates supports a 'rumination' strategy in the proboscis monkey (*Nasalis larvatus*)

Ikki Matsuda · Augustine Tuuga · Chie Hashimoto · Henry Bernard ·
Juichi Yamagiwa · Julia Fritz · Keiko Tsubokawa · Masato Yayota ·
Tadahiro Murai · Yuji Iwata · Marcus Clauss

Oecologia
DOI 10.1007/s00442-013-2863-9

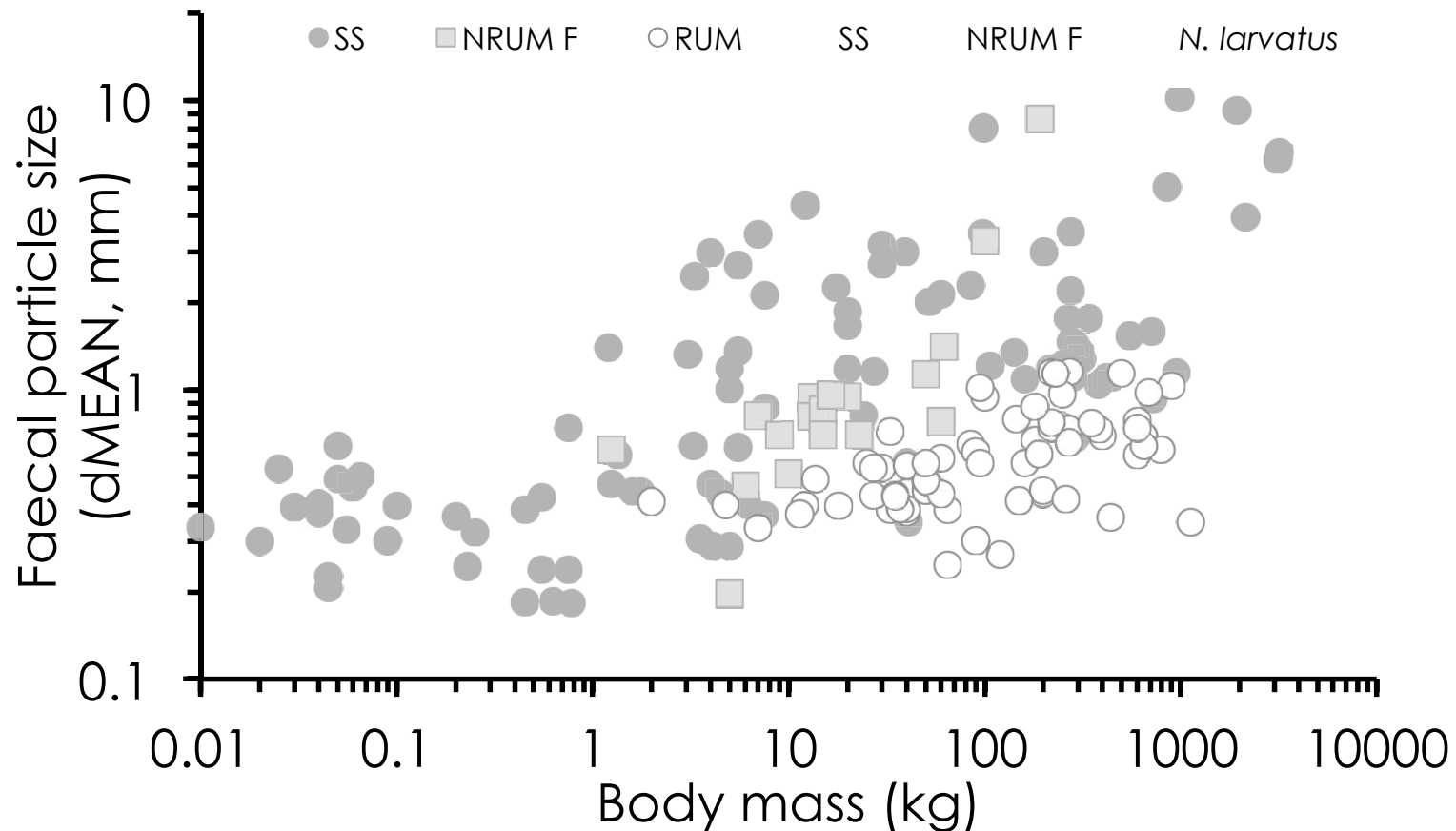




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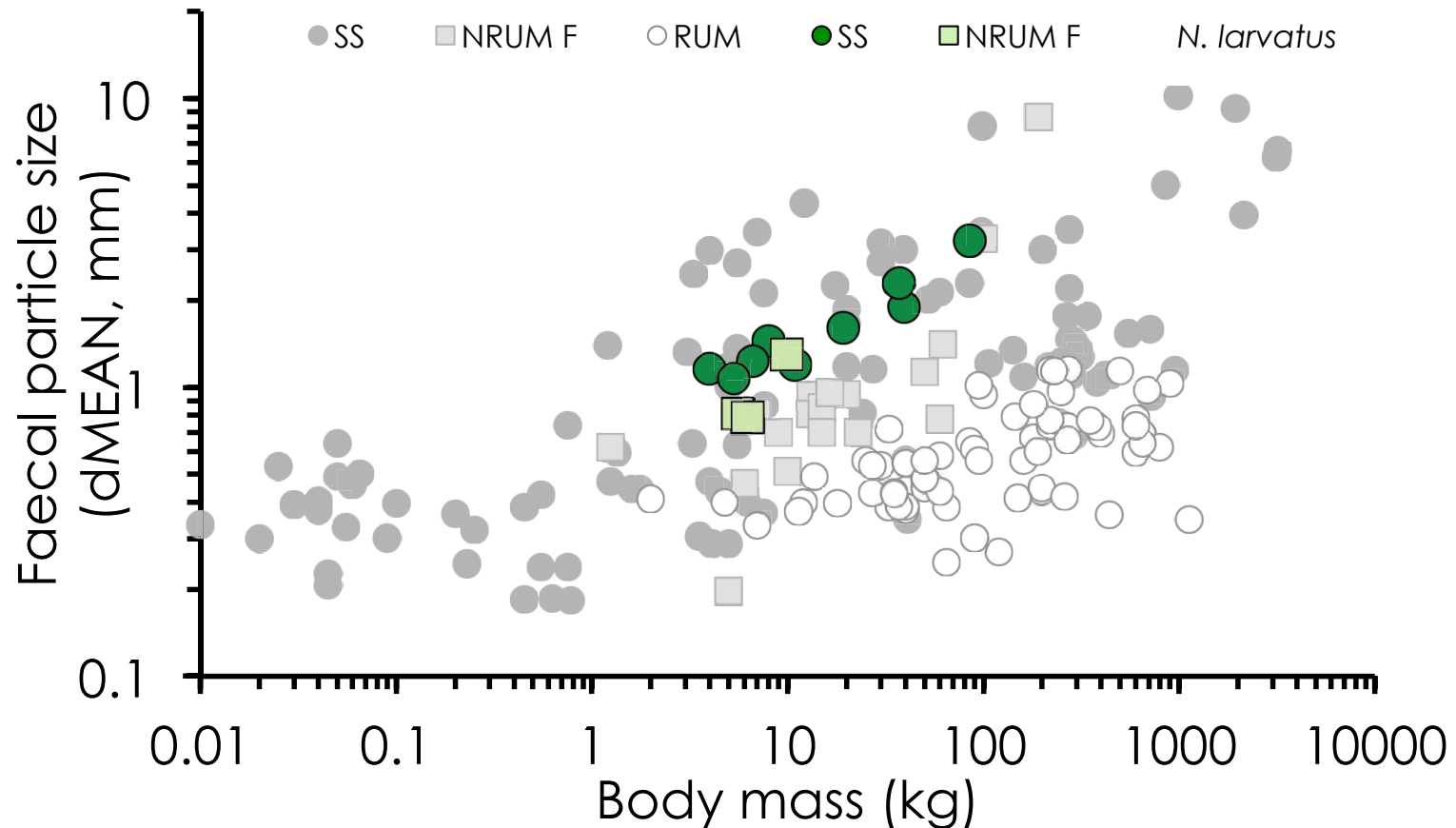




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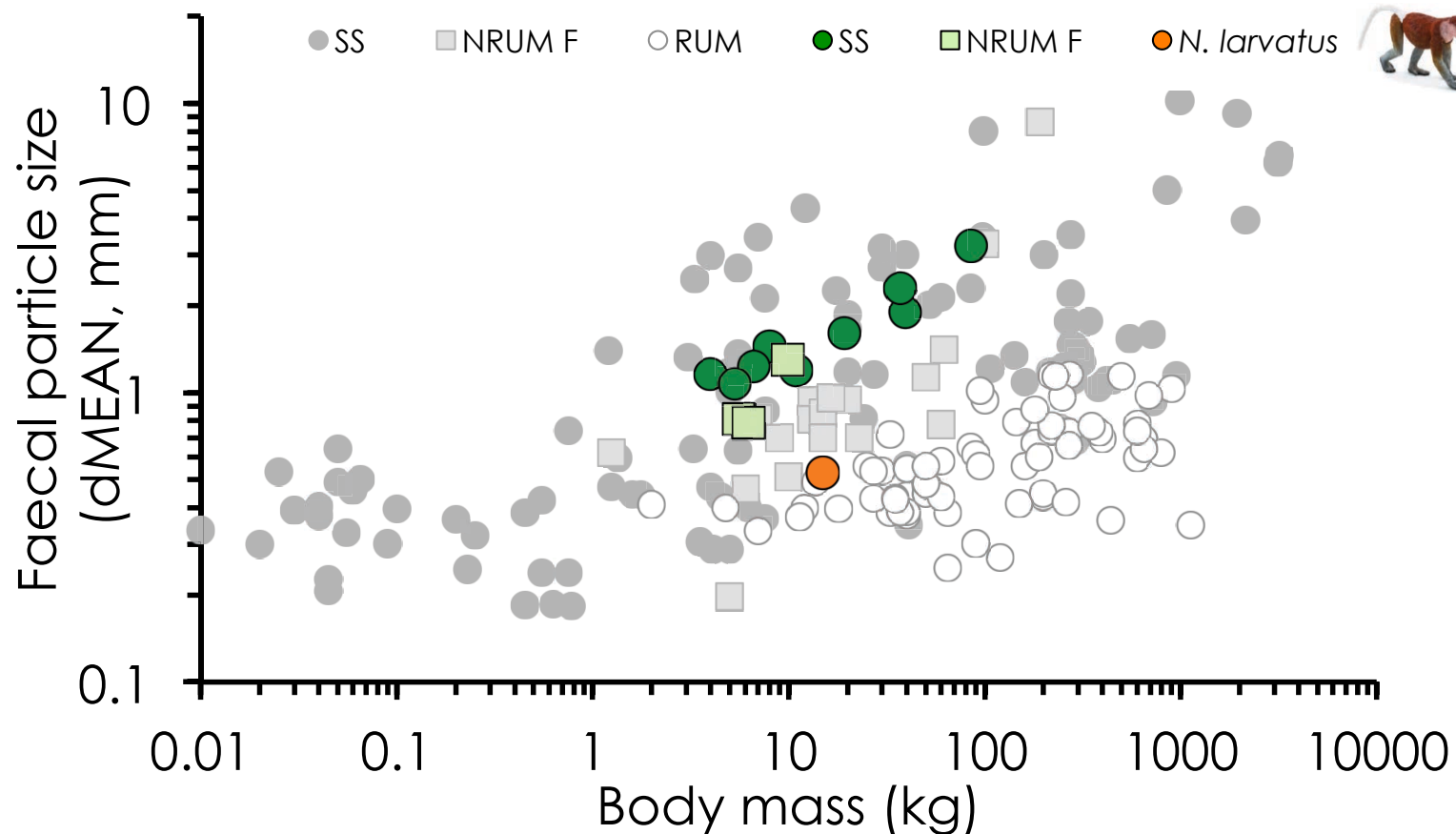




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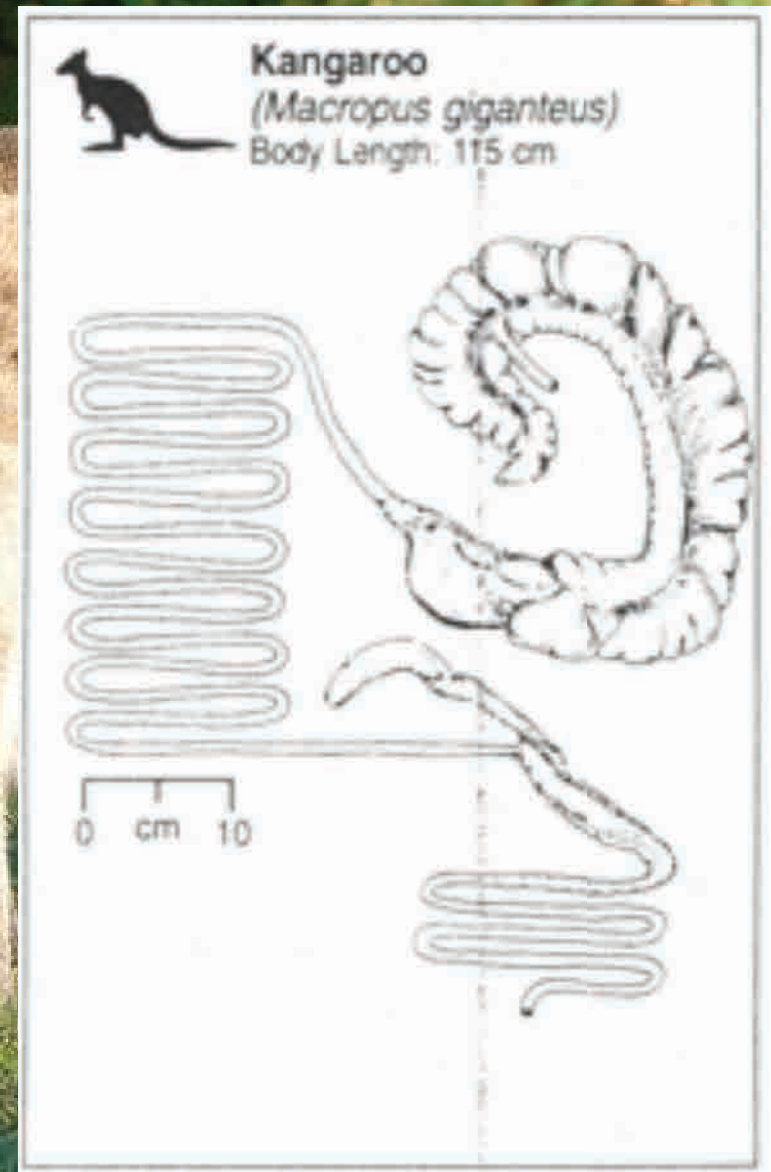


The case of the kangaroos





The case of the kangaroos



from Stevens und Hume (1995)



The case of the kangaroos

430

THE AUSTRALIAN JOURNAL OF SCIENCE

APRIL

Food Regurgitation in the Macropodidae

S. BARKER,* G. D. BROWN† and J. H. CALABY*

BIOLOGISCHES ZENTRALBLATT

Band 84

November–Dezember 1965

Heft 6

Vergleichende Untersuchung des Wiederkauverhaltens

VON HUBERT HENDRICH¹⁾

Dagegen sah ich folgende Marsupialier wiederkauen:

Thylogale eugenii (DESMAREST, 1817)
Setonix brachyurus (QOUY et GAIMARD, 1830)
Dendrolagus ursinus (TEMMINCK, 1836)
Dendrolagus ursinus inustus (MÜLLER, 1840)
Protemnodon agilis (GOULD, 1842)
Protemnodon rufogrisea (DESMAREST, 1817)
Macropus gigantea (ZIMMERMANN, 1777)
Macropus (Megaleia) rufus (DESMAREST, 1822)
Macropus (Osphranter) robustus (GOULD, 1841).



The case of the kangaroos



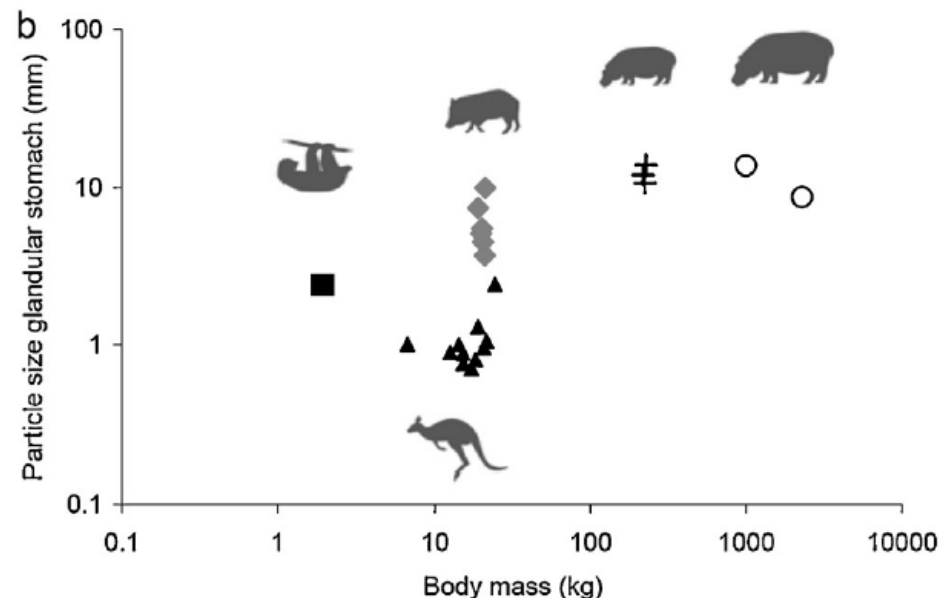


The case of the kangaroos

No distinct stratification of ingesta particles and no distinct moisture gradient in the fore-stomach of non-ruminants: The wallaby, peccary, hippopotamus, and sloth

Angela Schwarm^{a,b,*}, Sylvia Ortmann^a, Julia Fritz^c, Edmund Flach^d,
Wolfram Rietschel^e, Marcus Clauss^f

Mammalian Biology 78 (2013) 412–421



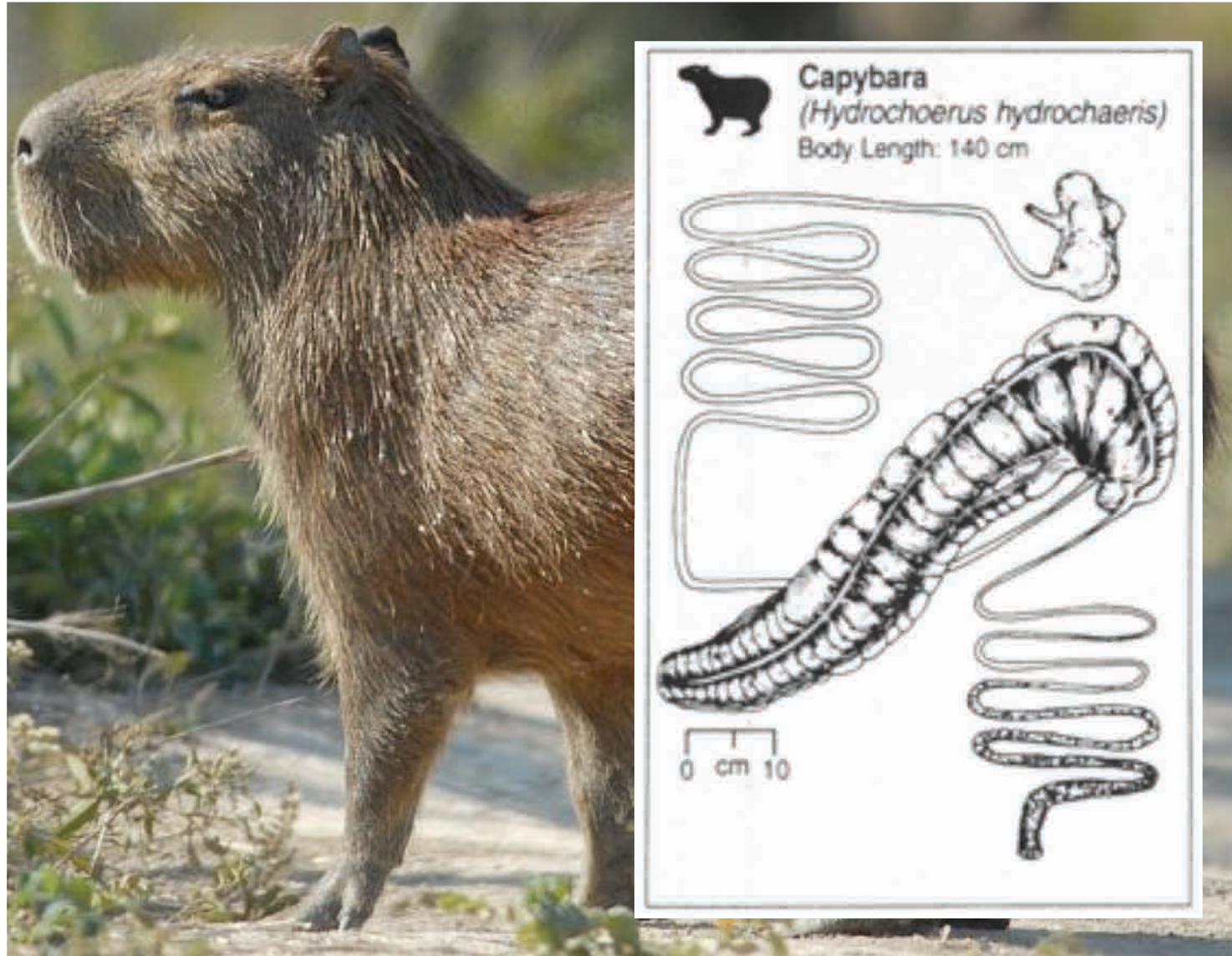


The case of the capybara





The case of the capybara



from Stevens und Hume (1995)



The case of the capybara

Studies on Neotropical Fauna and Environment
Vol. 29 (1994), No. 1, pp. 11-22

A Descriptive Account of Capybara Behaviour

Rexford D. LORD



Regurgitation and Coprophagy. – A significant new finding of this study was observations of capybaras regurgitating and masticating their food while resting, a parallel of rumination among the ruminants such as cattle.

Regurgitation and mastication of food by capybaras was seen only while resting on land, throughout the day, unlike coprophagy which is practised primarily in the morning (Lord 1991, Herrera 1985). Regurgitation is frequently preceded by a gaping yawn, followed by stretching of the neck, then about a minute of mastication. Sometimes the food material could be seen in the mouth and on occasion spilled out. A young capybara was videotaped eating some spilled regurgitation material from an adult female. The gape yawn may be preceded by a half roll on one side, and/or sitting up. Videotape analysis of this practice has shown the pattern to be somewhat ritualized. It is practised much more frequently than coprophagy, but was probably overlooked because it appears to be a simple yawn.

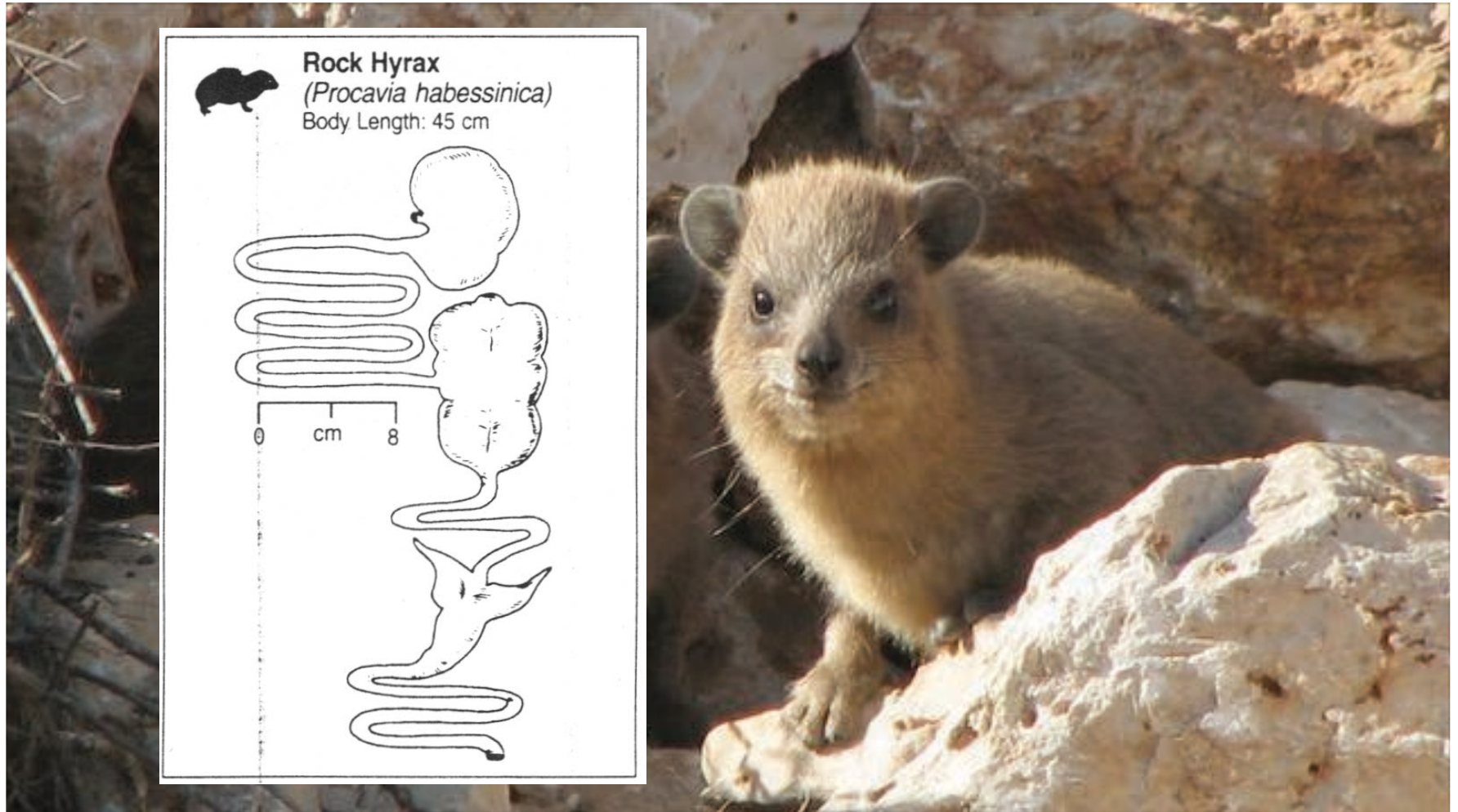


The case of the hyrax





The case of the hyrax



from Stevens und Hume (1995)



The case of the hyrax





The case of the hyrax



Leviticus 11 (New International Version NIV) Clean and Unclean Food

11 The Lord said to Moses and Aaron, ²“Say to the Israelites: ‘Of all the animals that live on land, these are the ones you may eat: ³You may eat any animal that has a divided hoof and that chews the cud. ⁴“There are some that only chew the cud or only have a divided hoof, but you must not eat them. The camel, though it chews the cud, does not have a divided hoof; it is ceremonially unclean for you. ⁵**The hyrax**, though it **chews the cud**, does not have a divided hoof; it is unclean for you.



The case of the hyrax

BIOLOGISCHES ZENTRALBLATT

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Vergleichende Untersuchung des Wiederkauverhaltens

VON HUBERT HENDRICH¹⁾

VI. Entdeckung von Wiederkauen bei einer Säugetierordnung

bereiste, schreibt vom „Aschkoko“, dem Klippschliefer: „Ich hörte nie einen Laut von ihm, aber er käuete zuverlässig wieder: um dies zu untersuchen unterhielt ich ihn hauptsächlich eine Zeitlang lebendig“.





The case of the hyrax



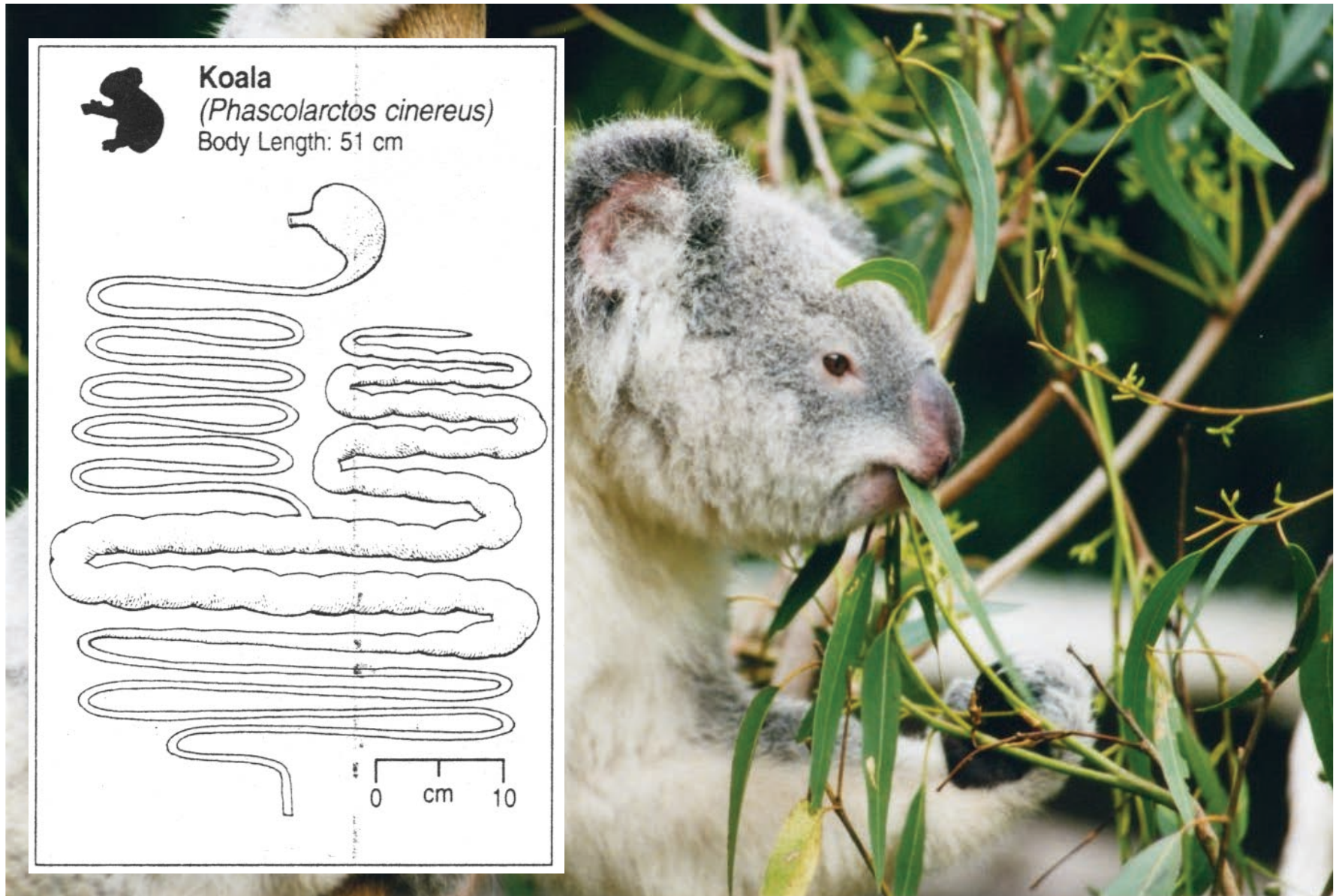


The case of the koala





The case of the koala



from Stevens und Hume (1995)



The case of the koala

J. Zool., Lond. (2001) **255**, 83–87 © 2001 The Zoological Society of London Printed in the United Kingdom

Evidence for the occurrence of rumination-like behaviour, or merycism, in the koala (*Phascolarctos cinereus*, Goldfuss)

M. Logan



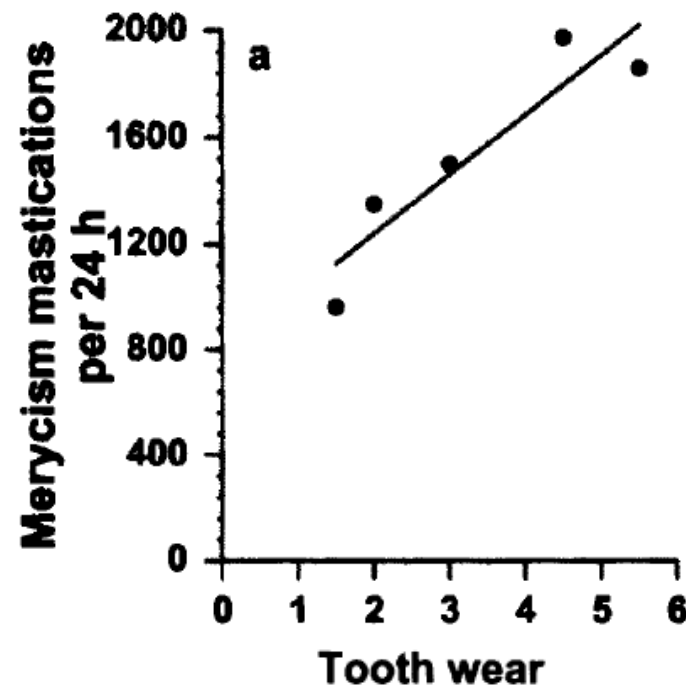


The case of the koala

EFFECT OF TOOTH WEAR ON THE RUMINATION-LIKE BEHAVIOR, OR MERYCISM, OF FREE-RANGING KOALAS (*PHASCOLARCTOS CINEREUS*)

M. LOGAN*

Journal of Mammalogy, 84(3):897–902, 2003



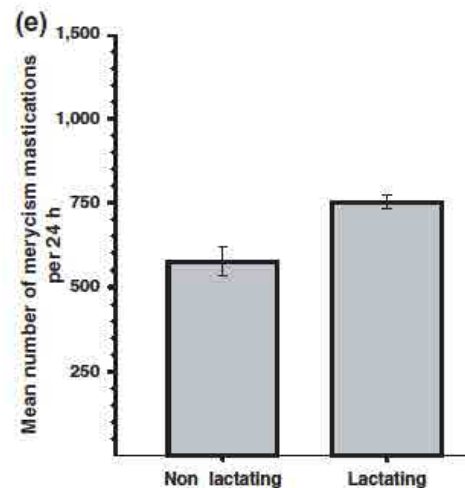


The case of the koala

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



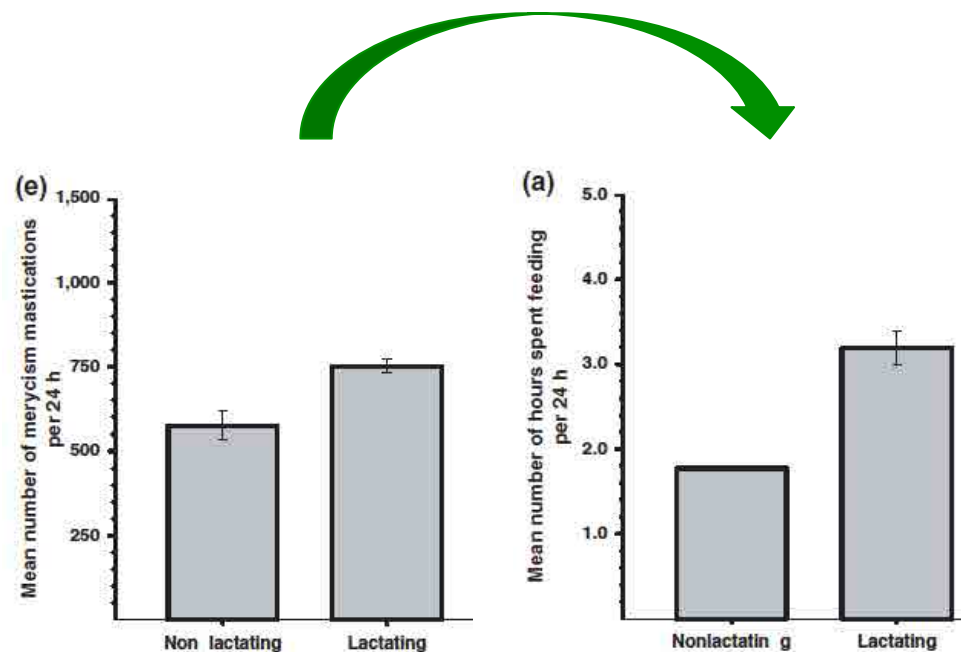


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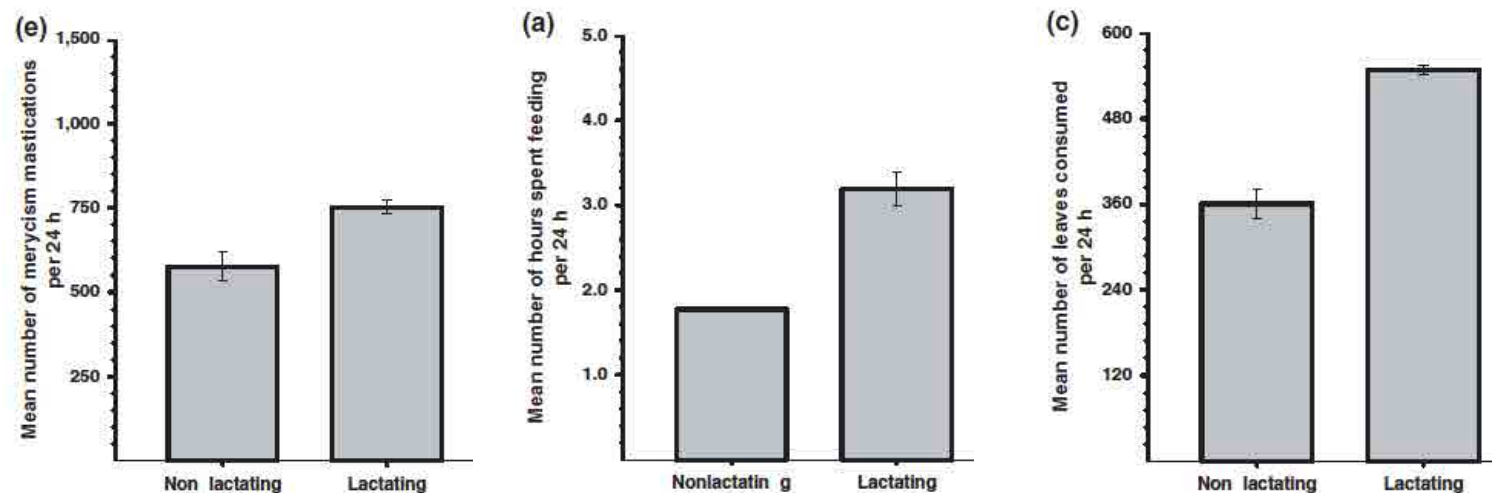


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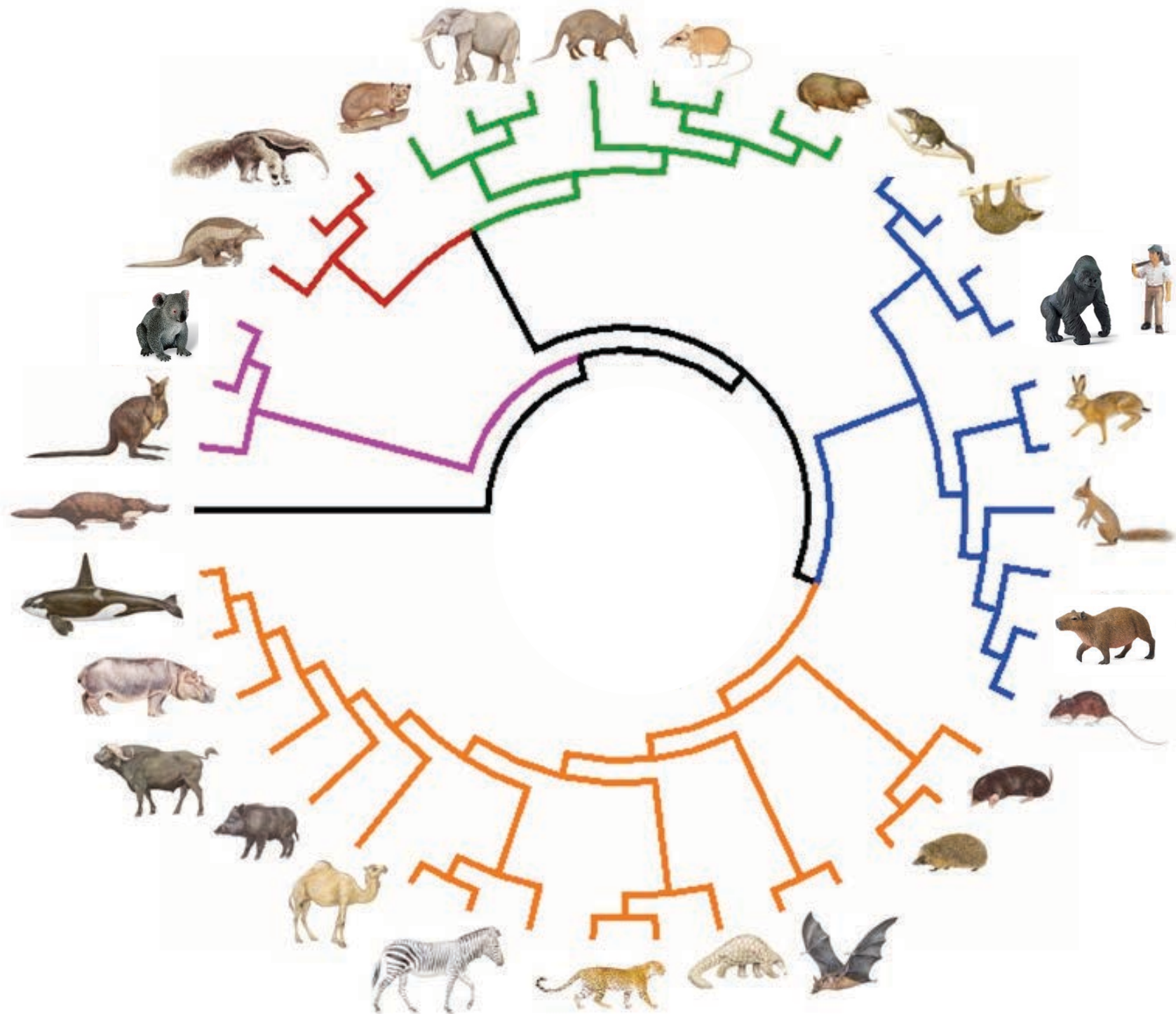
M. Logan and G. D. Sanson

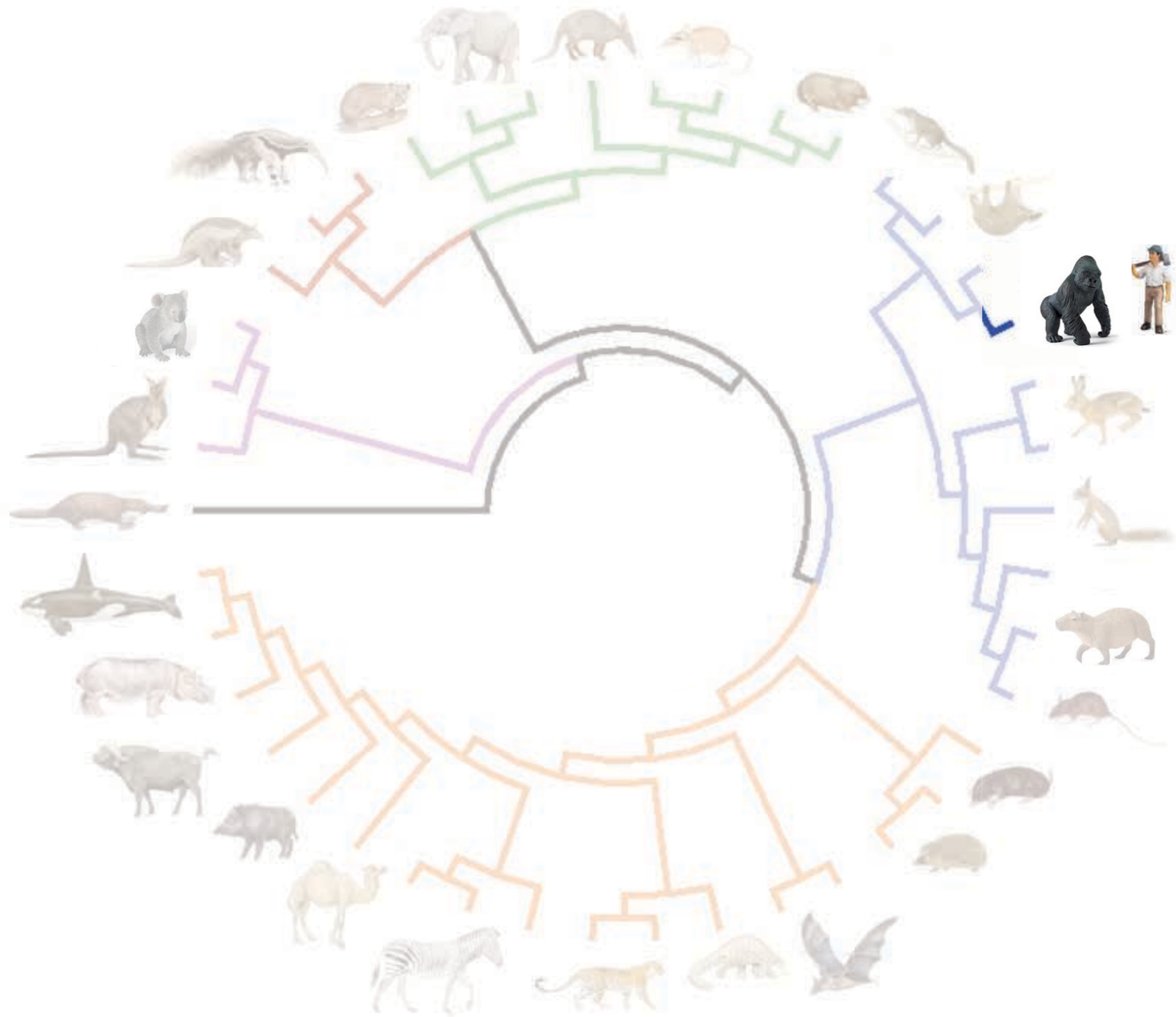


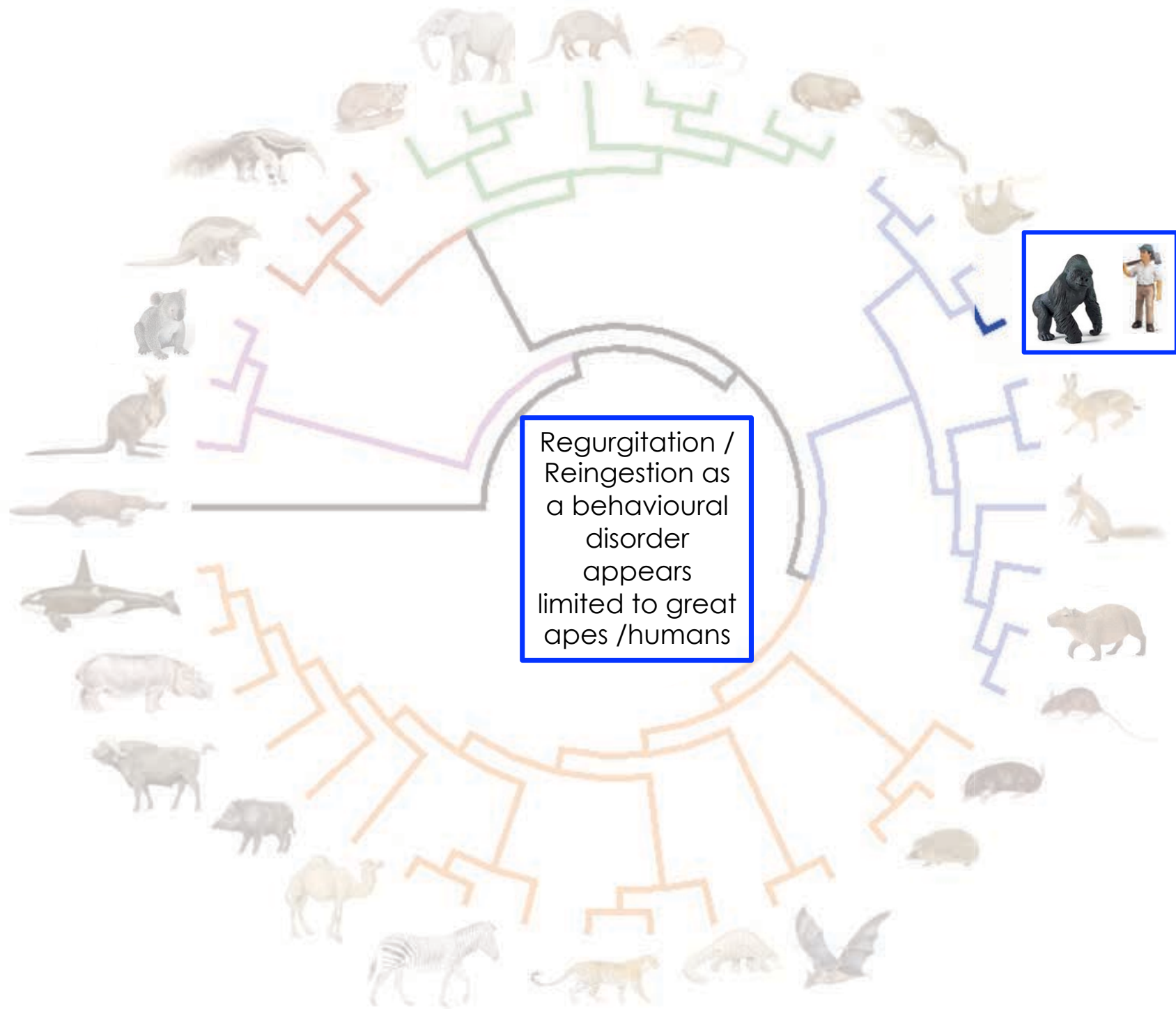


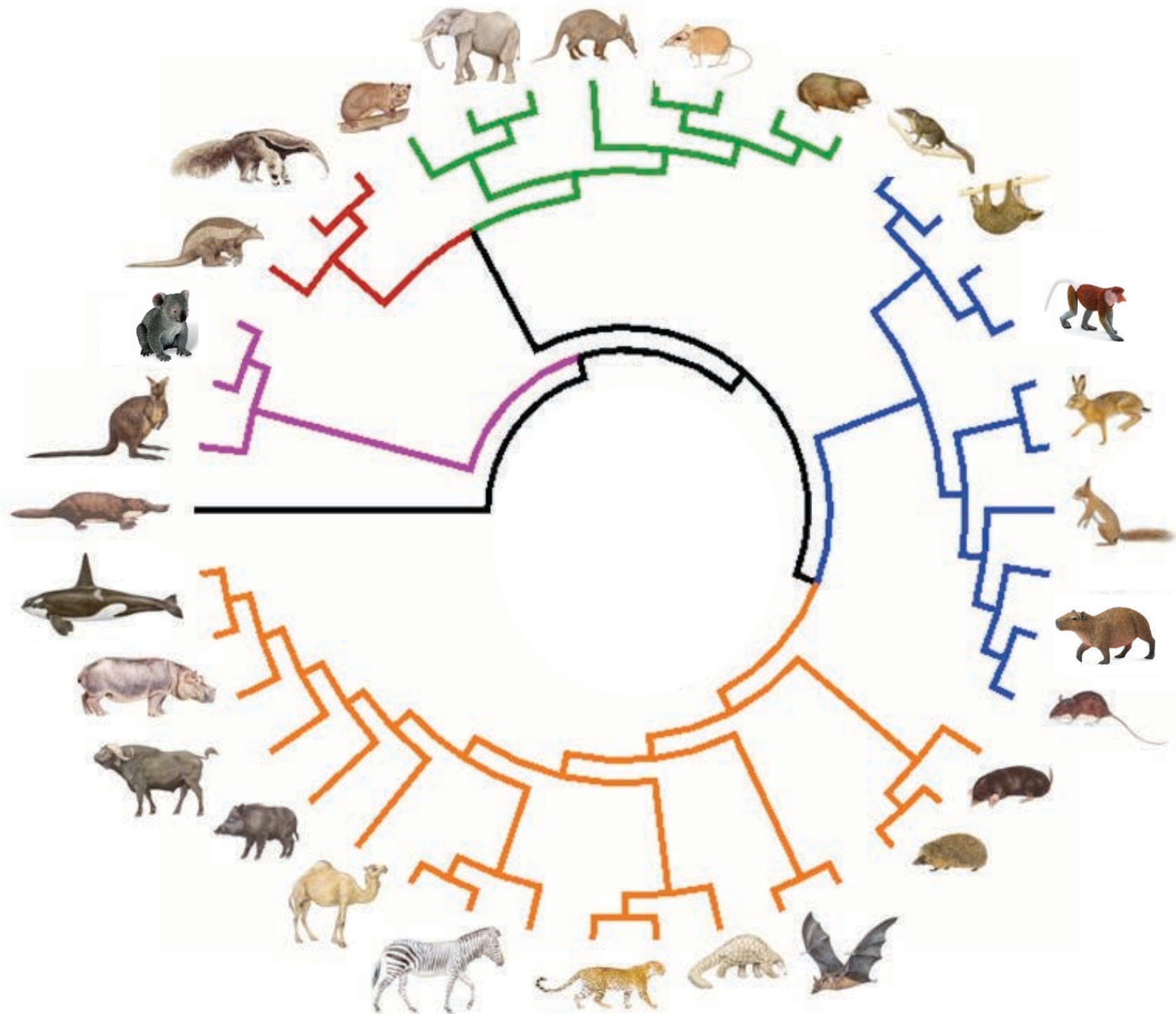
Why rumination?

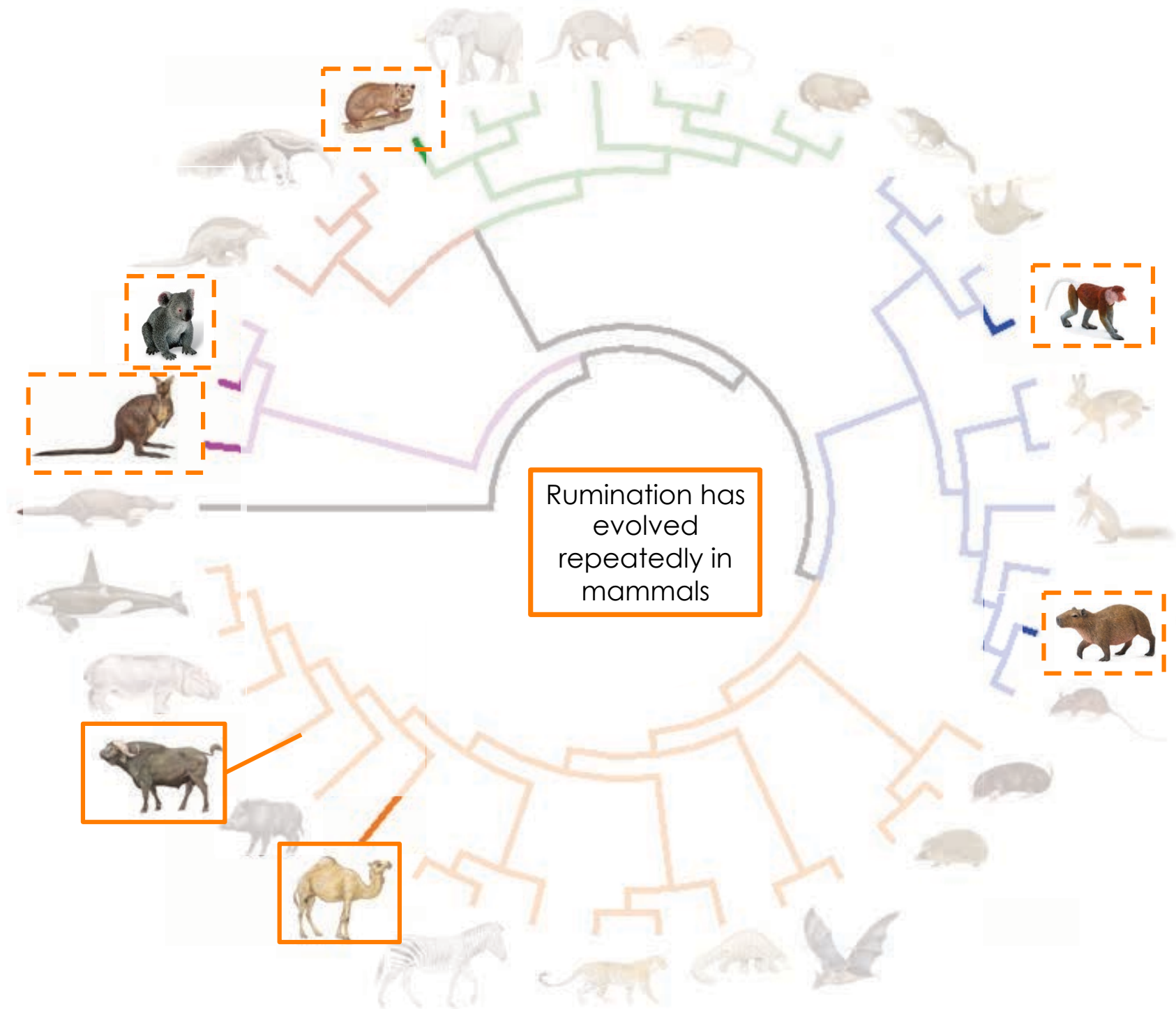
- Anti-predation strategy
 - “*Rumination seems to allow herbivores to ingest in haste and masticate at leisure*” (Karasov & Del Rio 2007)
 - => Ruminants should ingest similar amounts of food as other herbivores and just ‘chew later’ - or become time-constrained in intake
- Energy-saving mechanism
 - 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
 - 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

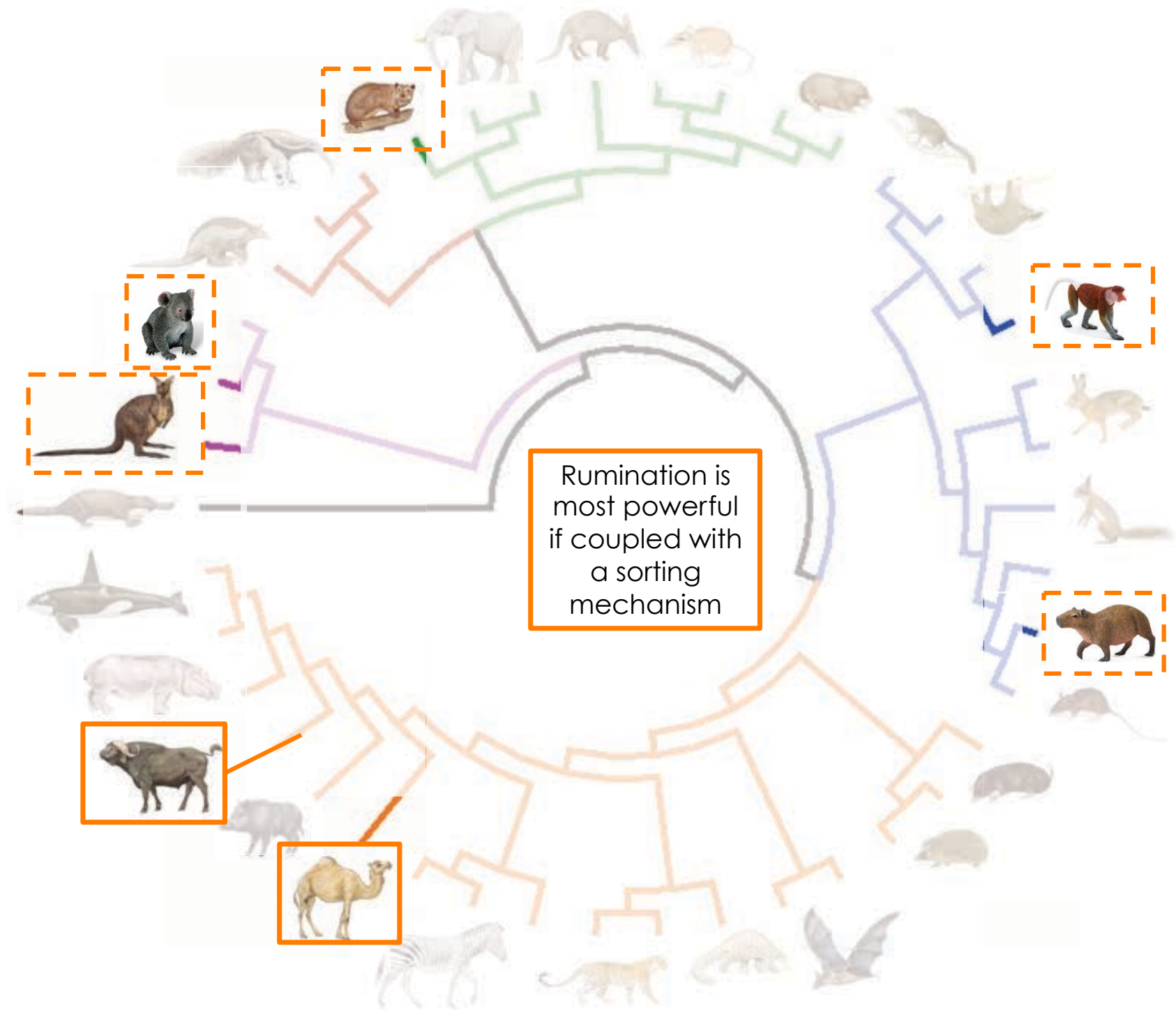














*thank you
for your attention*

outlook: cheek pouches // coprophagy