Digestive physiology of primates

Marcus Clauss

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Institute of Anthropology 2011

University of Zurich[UZH]

Clinic of Zoo Animals, Exotic Pets and Wildlife

based on a true story

Why are primates fascinating for digestive physiologists?

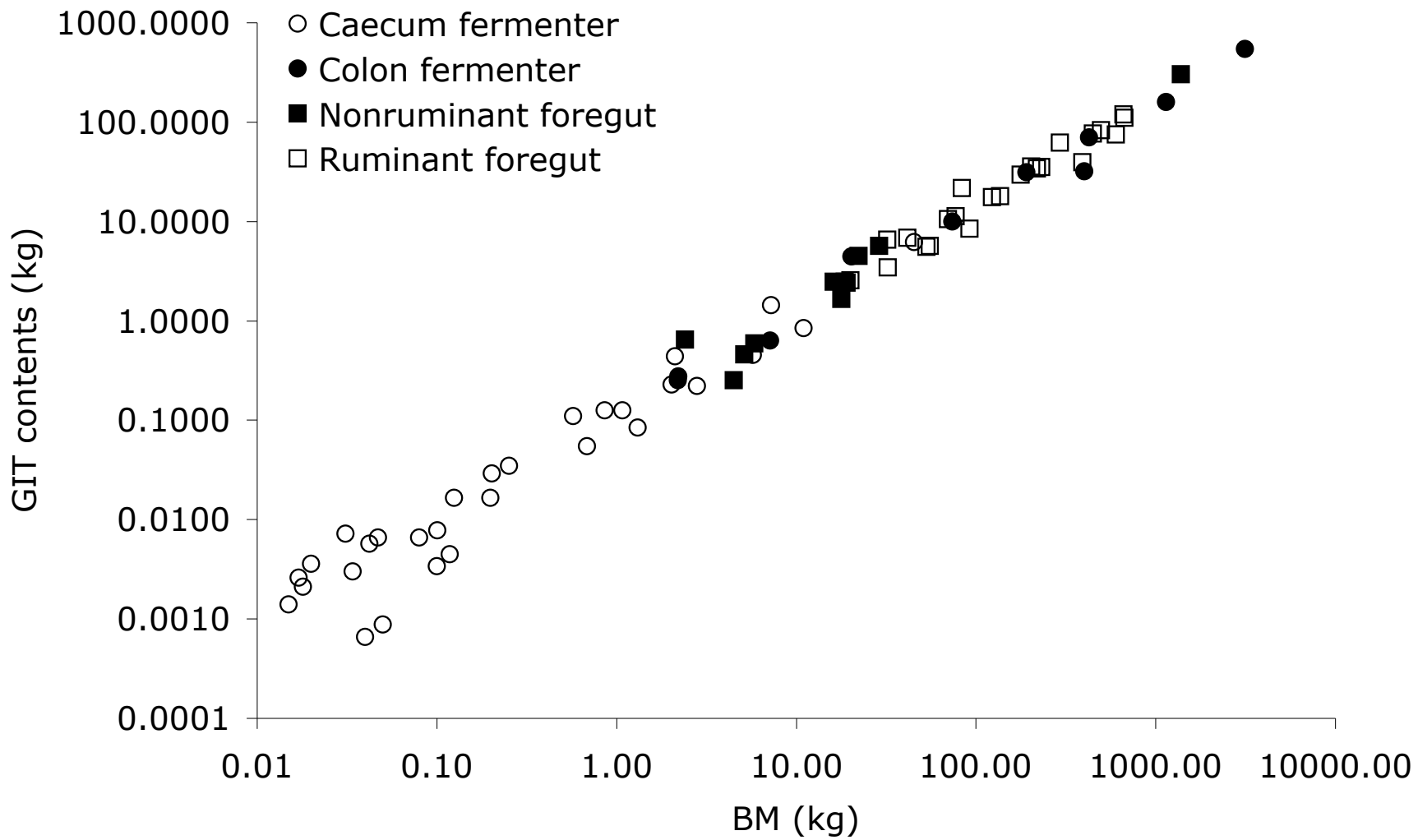
- A broad variety of anatomical and physiological digestive adaptations ***within one taxonomic group***
- Experimental work is particularly challenging

Anim. Behav., 1993, **46**, 741–746

Effects of experience with live insects on the development of fear of snakes in squirrel monkeys, *Saimiri sciureus*

NOBUO MASATAKA

Major ‘limitation’: ethical responsibility



from Clauss et al. (2007)

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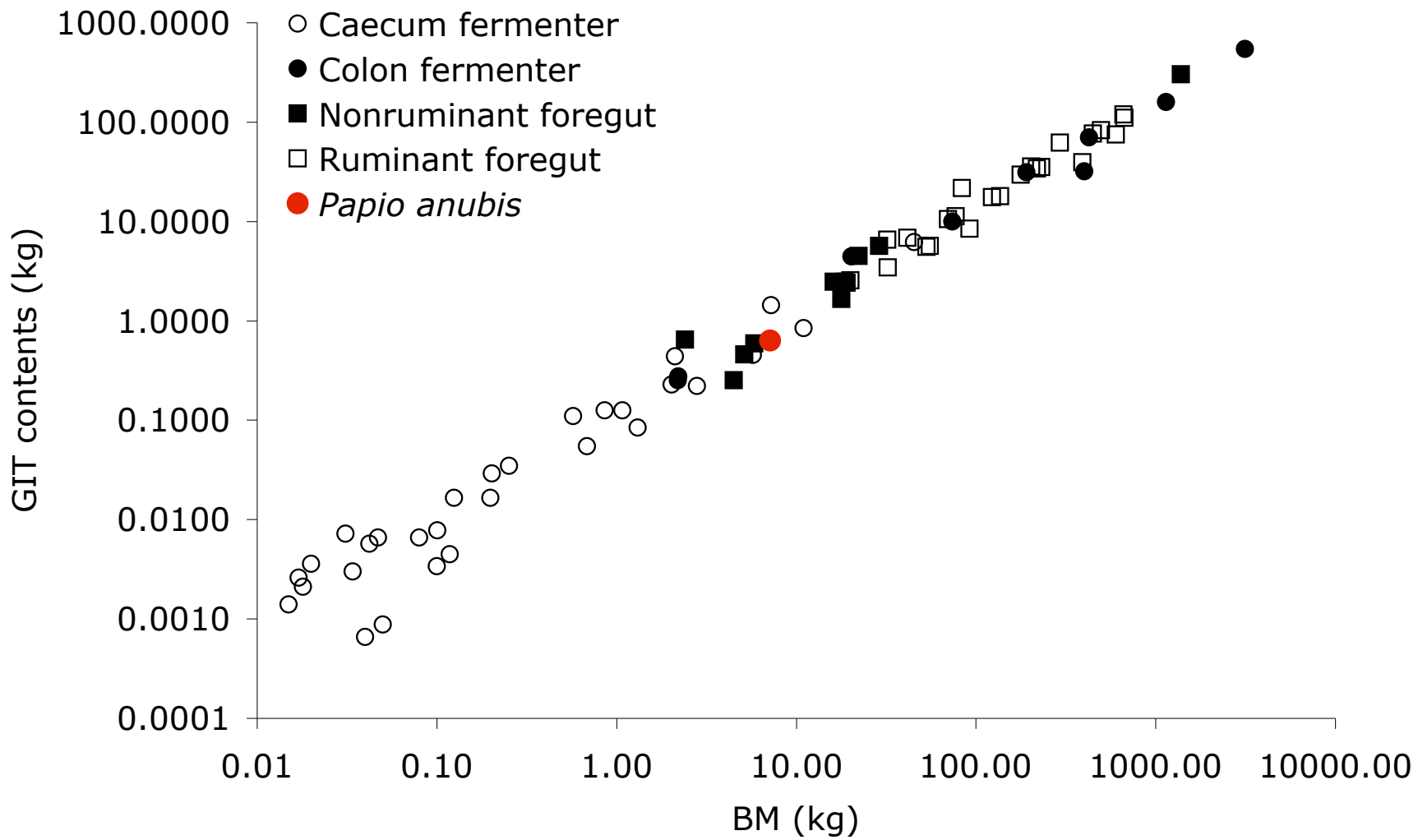

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Major limitation: diets used in digestion studies

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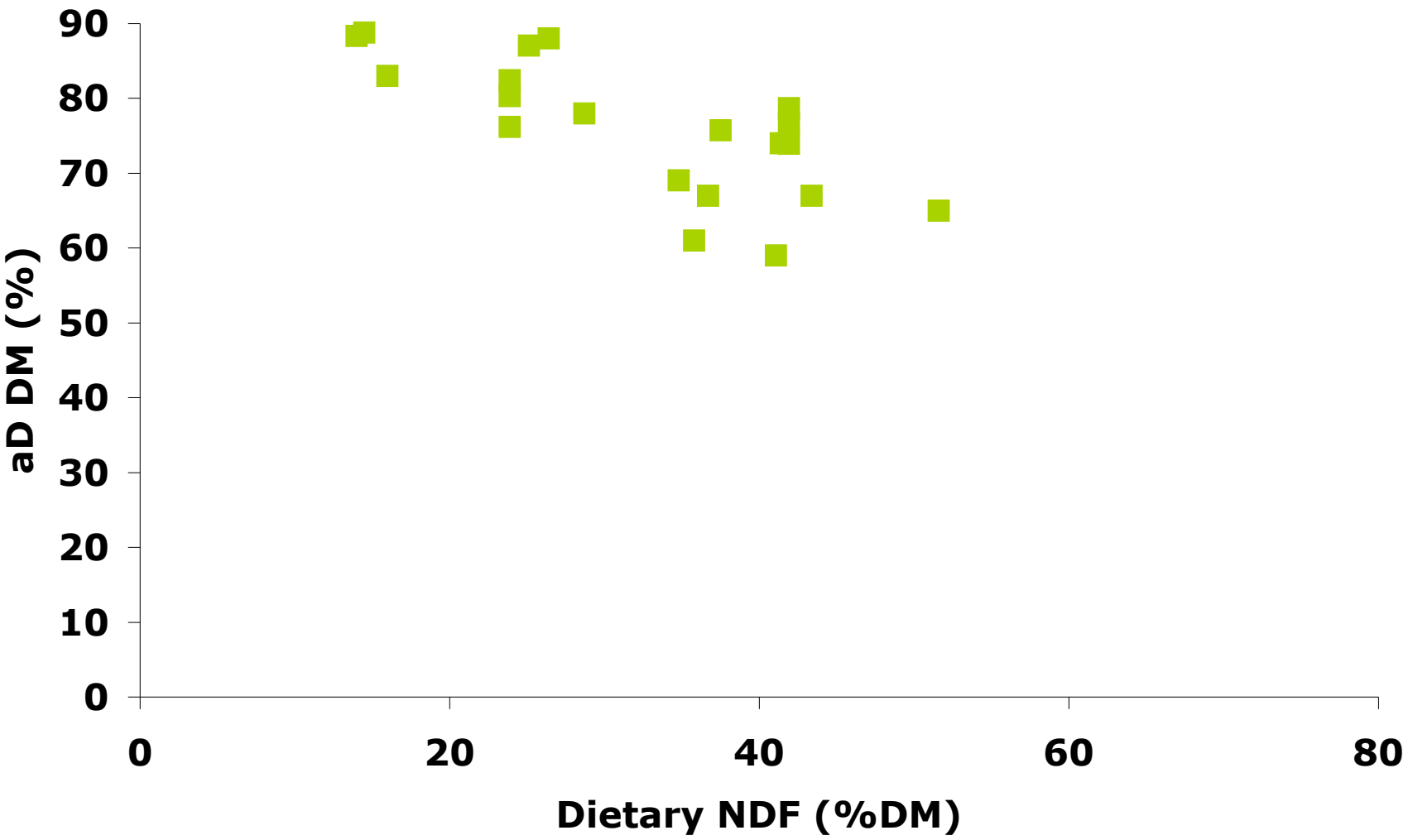

Data collection on langurs from Nijboer & Clauss (2006)

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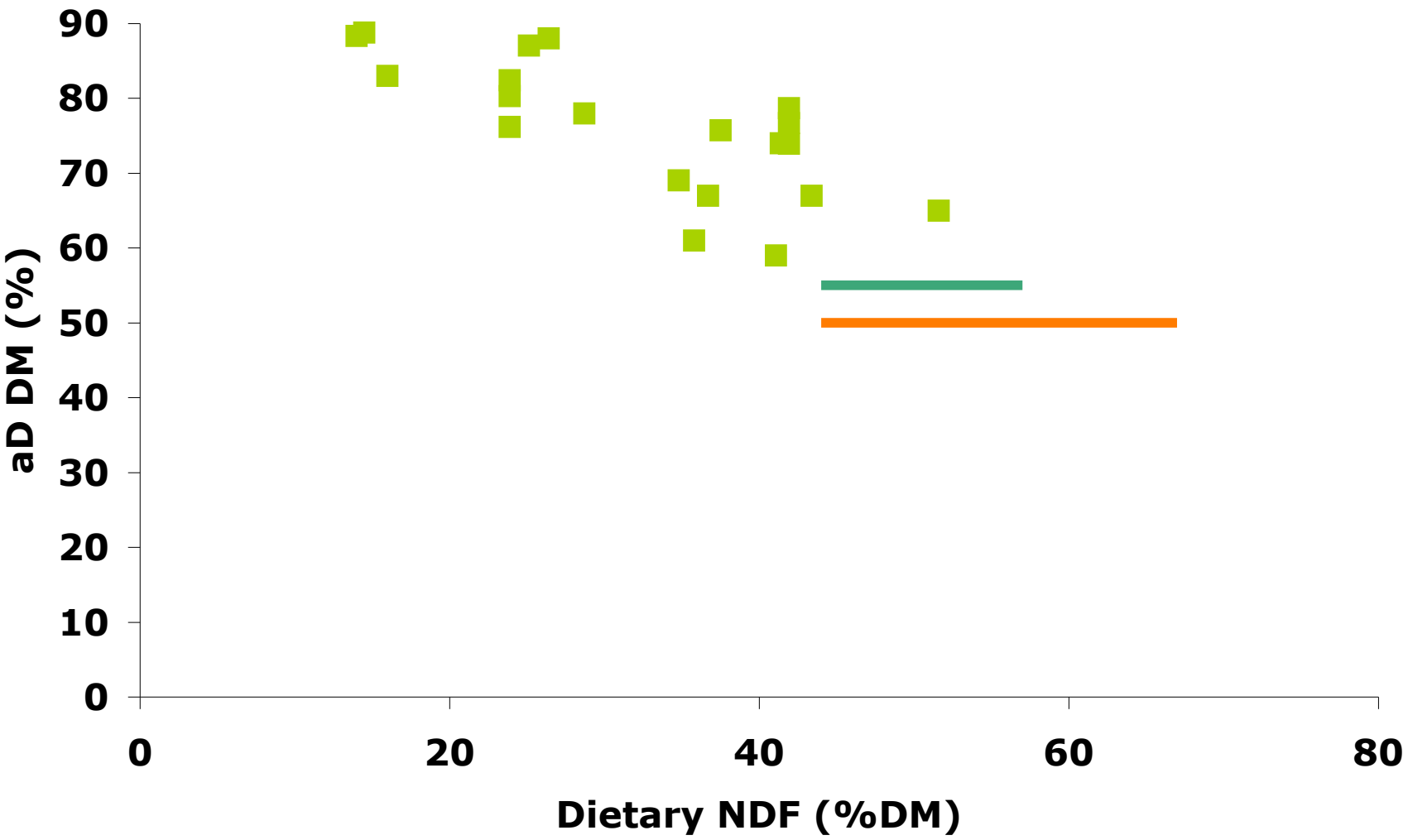

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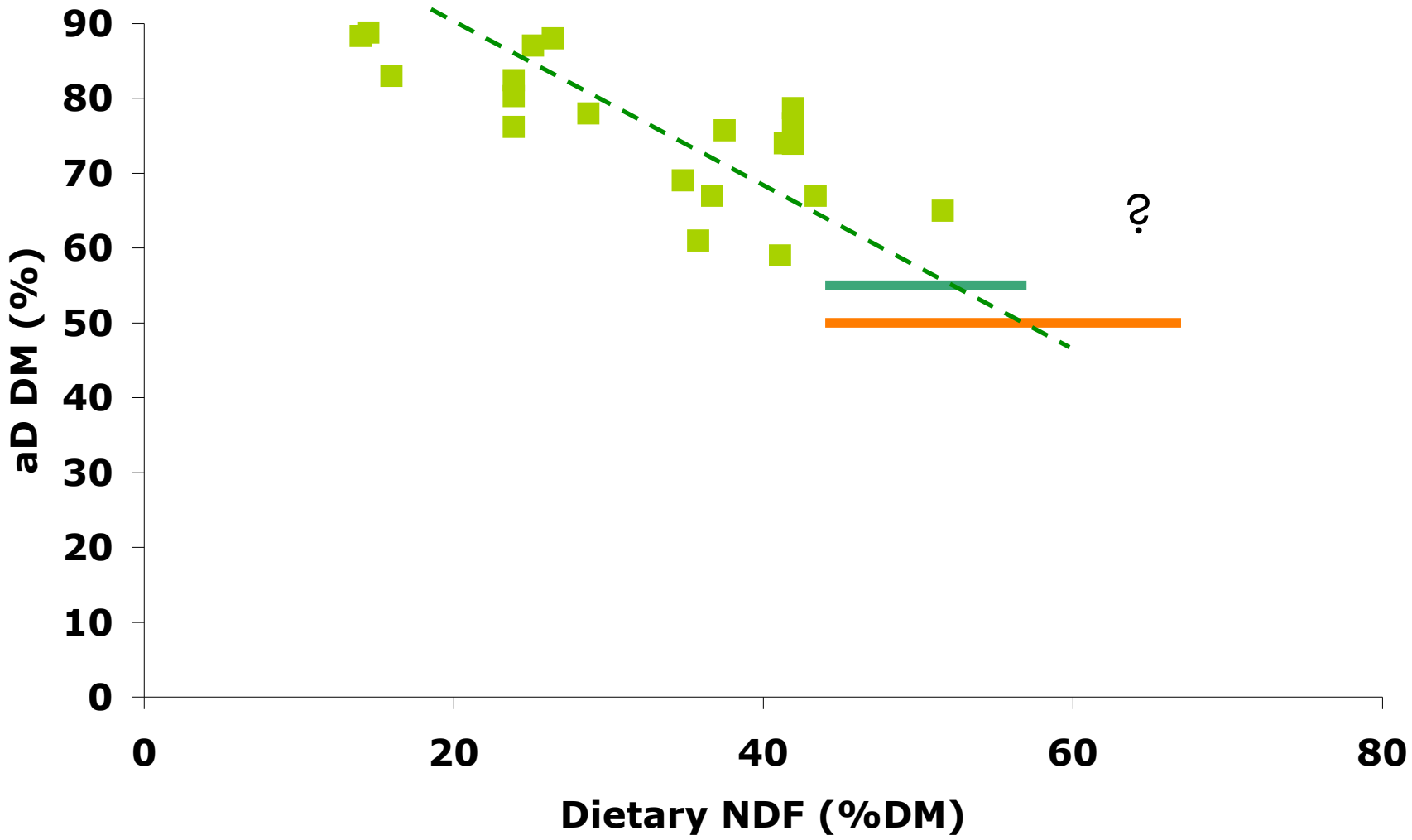

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Comparing fibre fractions: Foods in "increasing quality"-order from Gaulin (1979)

Table 1. Composition of the Foods of Feral Primates[a]

Food		% H_2O	% of dry weight								
			Protein	Carbohydrates	Reducing sugars	Lipids	Cellulose	Fiber	Total ash	Ca	P
Stems, pith	$\bar{X}$	91.3	12.1			4.8		20.6	11.6		
	SD	1.6	1.0			2.3		12.8	2.0		
	n	2	3			3		3	3		
Leaves	$\bar{X}$	78.6	14.0	61.7	11.6	3.7	18.6	15.3	11.4	1.86	.31
	SD	7.4	7.9	11.5	10.3	2.0	8.3	4.8	3.7	1.02	.34
	n	6	14	8	4	14	5	7	9	7	7
Flowers flower buds	$\bar{X}$	78.4	16.7	82.0	10.4	3.4	16.6	5.6	7.5	.20	.41
	SD	4.1	5.2		8.1	3.6	1.2	0.8	2.0		
	n	5	5	1	3	5	2	2	4	1	1
Fruits (monocots)	$\bar{X}$	70.4	6.6	77.7	29.0	15.6	25.2	14.3	4.0	.27	.28
	SD	12.9	4.9	17.0	21.2	21.9		12.1	2.0	.16	.34
	n	7	8	3	3	9	1	3	3	4	4
Fruits (dicots)	$\bar{X}$	77.2	6.4	84.0	34.0	4.3	10.0	9.3	5.5	.35	.20
	SD	10.3	3.4	11.2	15.2	9.7	3.1	6.1	8.1	.37	.11
	n	53	50	23	20	50	20	23	23	34	34
Seeds	$\bar{X}$	11.6	17.7	67.3		7.7	5.0	5.5	3.8	.19	.22
	SD	4.0	8.5	15.9		8.1	2.0	2.1	1.2	.06	.10
	n	6	6	6		6	4	2	6	2	2
Gums	$\bar{X}$	14.7		98.5	1.9				1.5		
	SD										
	n	1		1	1				1		
Insects	$\bar{X}$		54.4		2.0	24.2				.03	.64
	SD		4.6			8.1				.03	.59
	n		2		1	2				2	2

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Against many evidence, "fruits" are considered higher quality!

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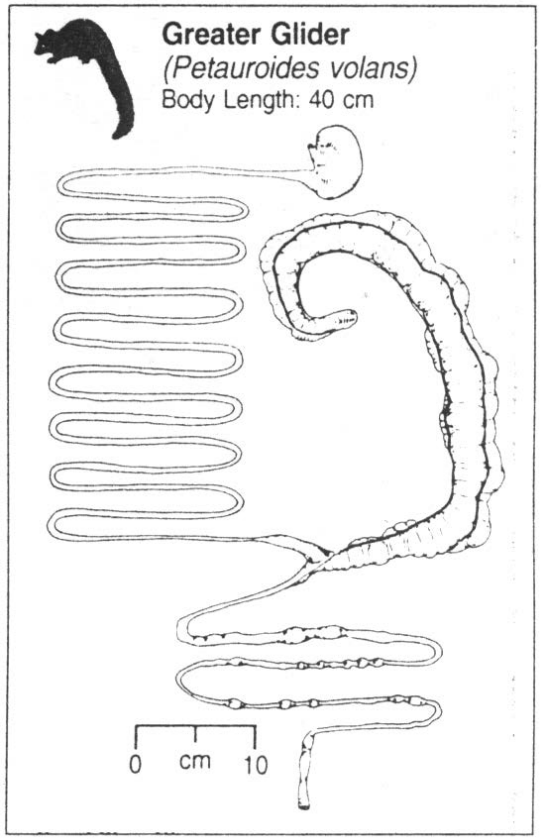
Evident discrepancies in the data given!

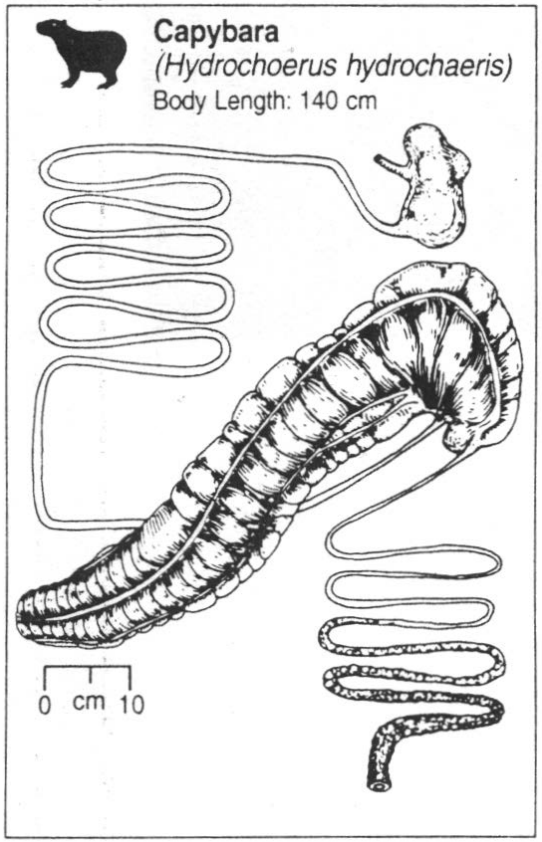
Outline

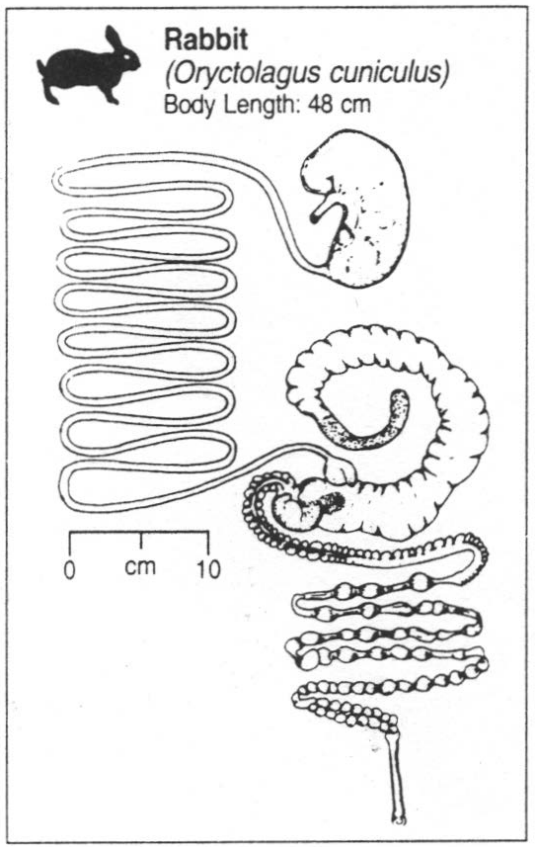
- Digestive anatomy
- Digestive physiology I
- The Jarman-Bell principle
- Digestive physiology II
- Feed your monkey

Digestive anatomy

Hindgut Fermentation - Caecum

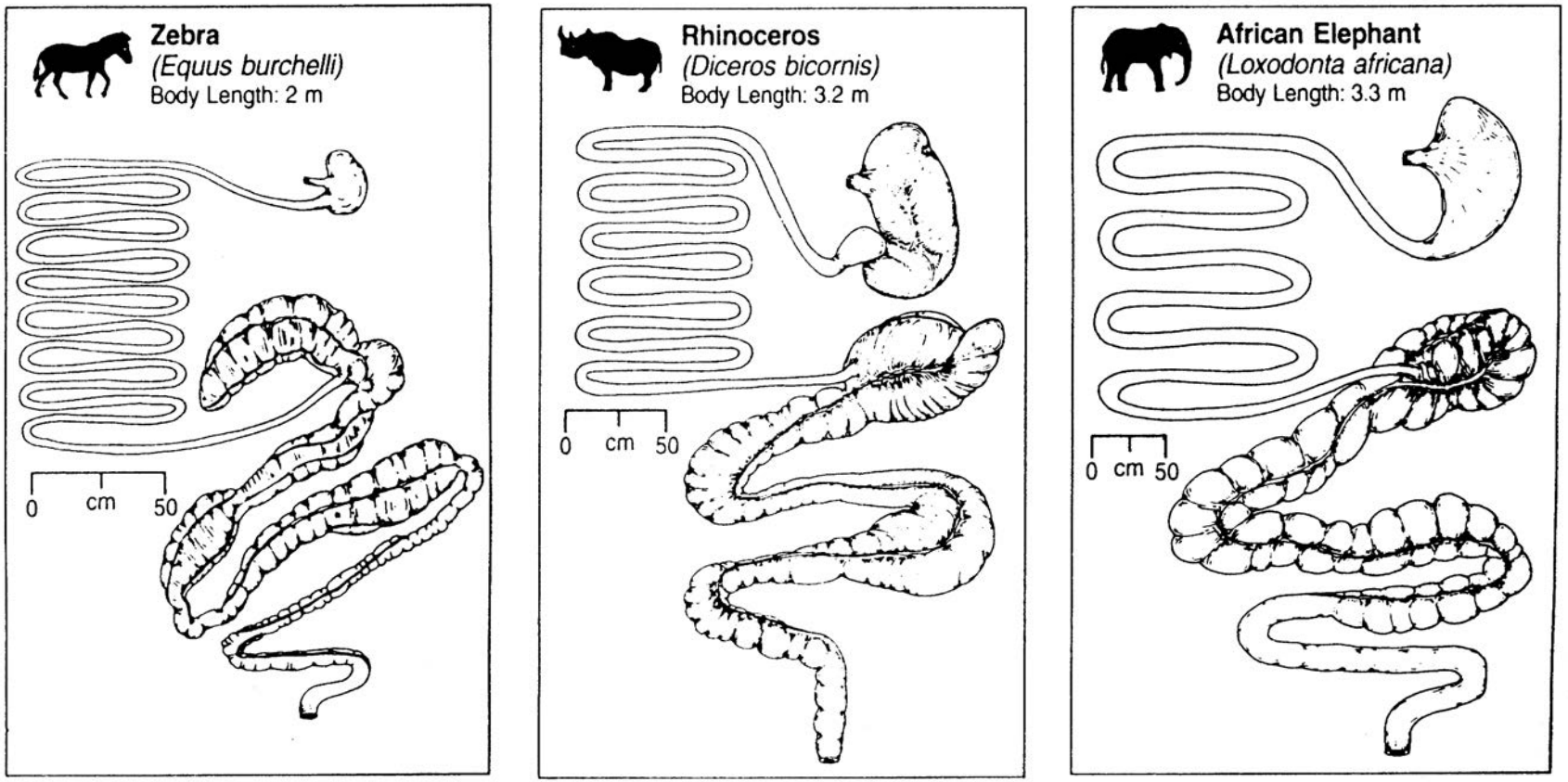






from Stevens & Hume (1995)

Hindgut Fermentation - Colon



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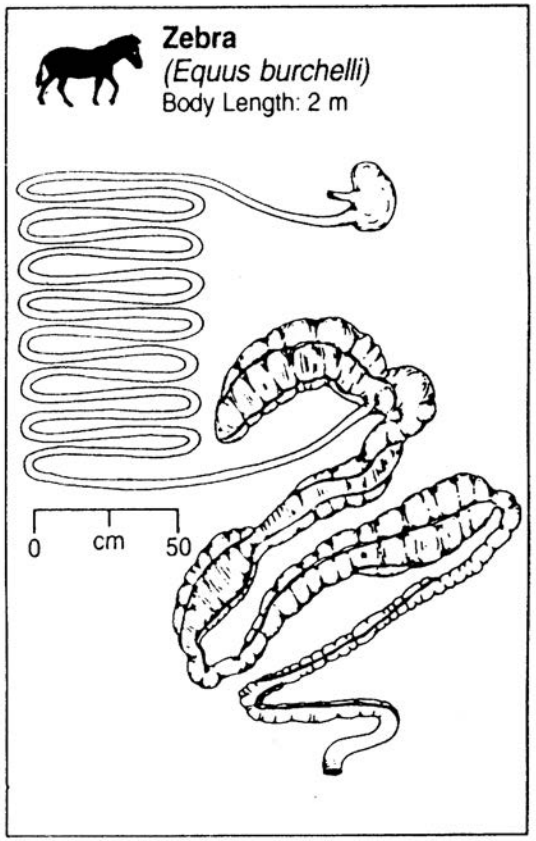

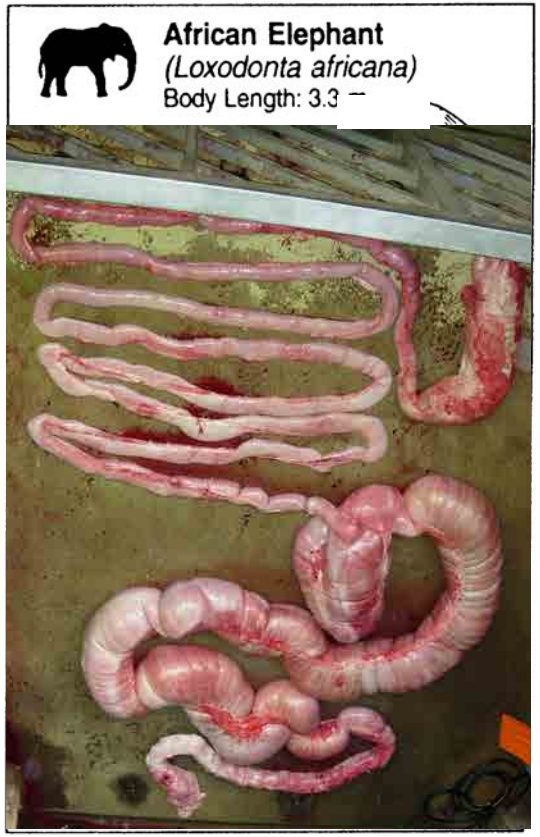

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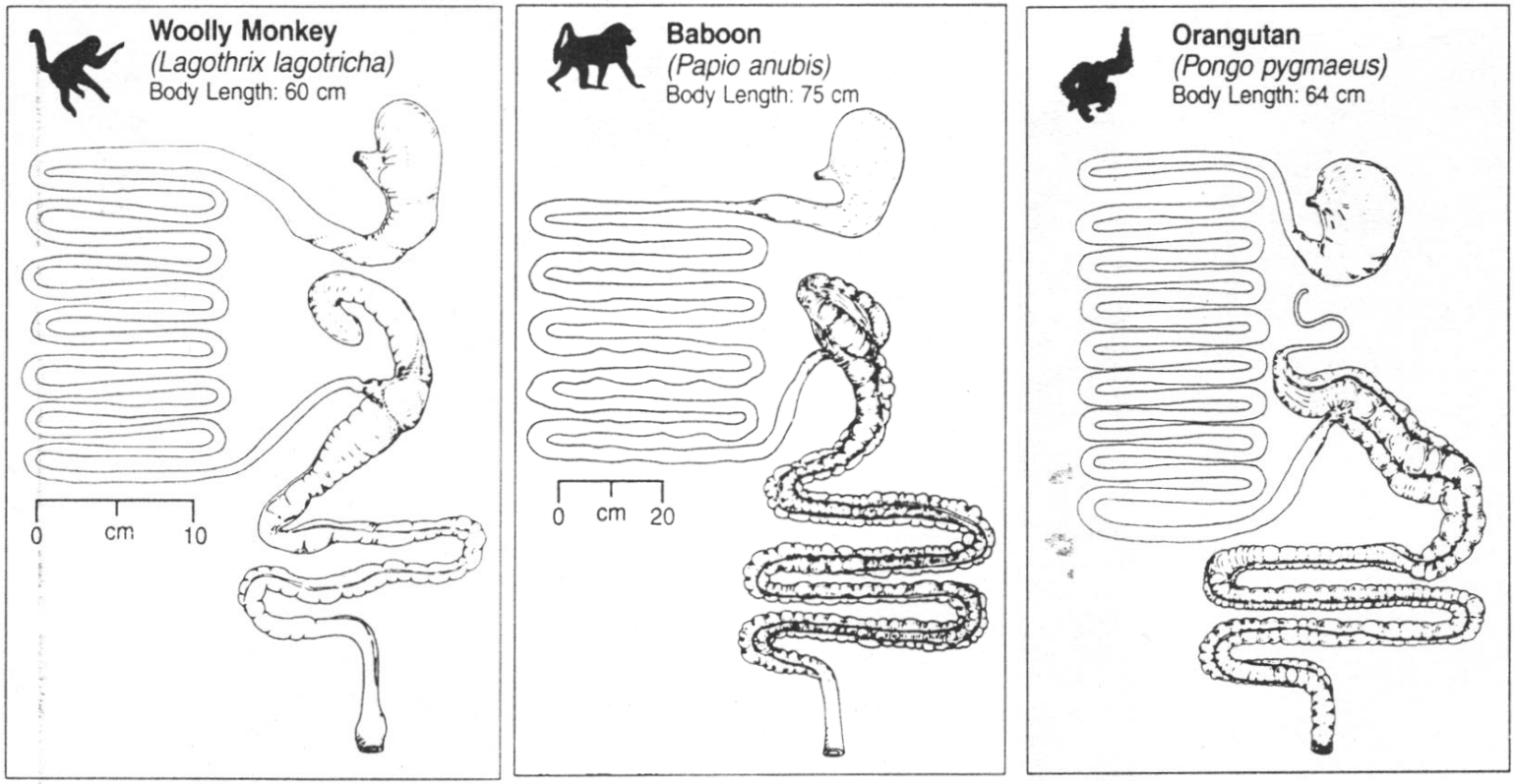
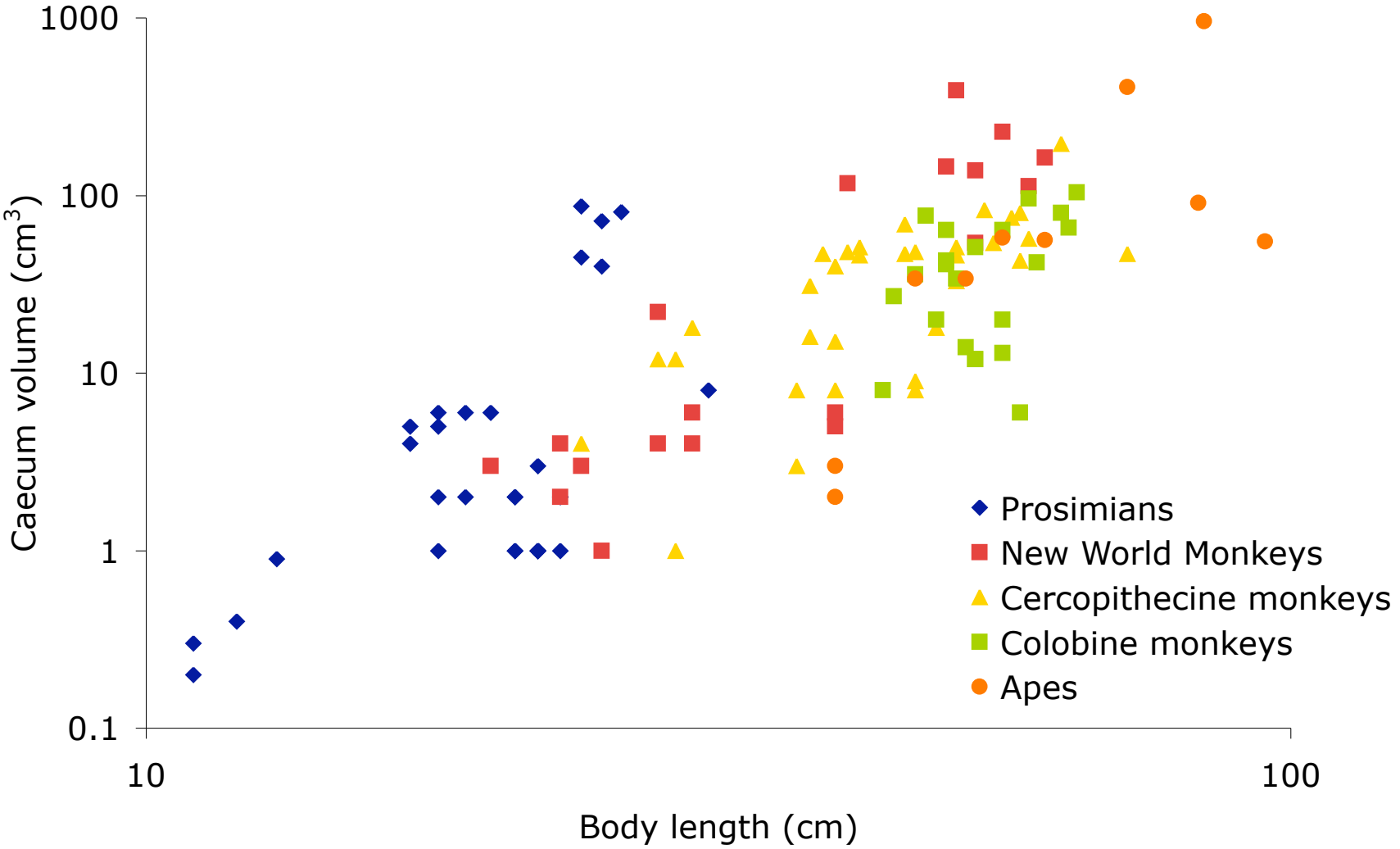
Primate caecum/colon fermenters



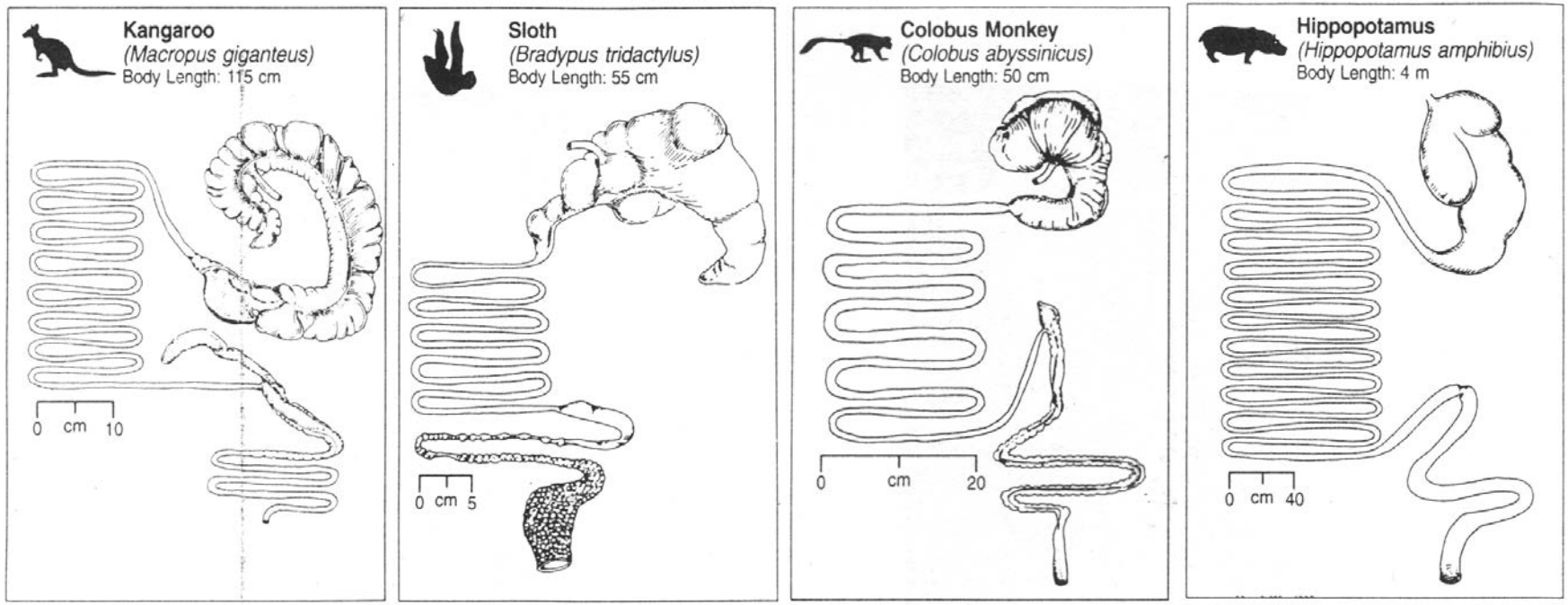
from Stevens & Hume (1995)

Caecum volume



Data from Chivers & Hladik (1980)

Foregut Fermentation



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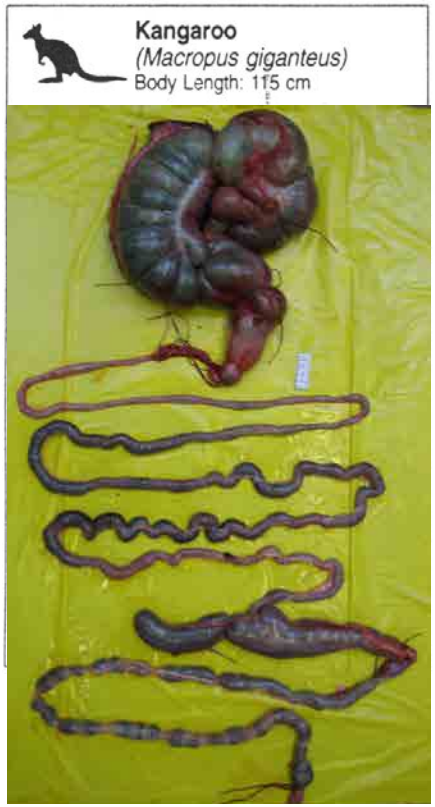
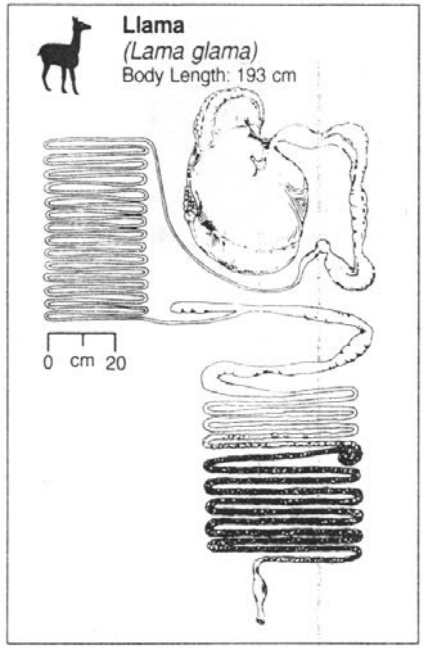
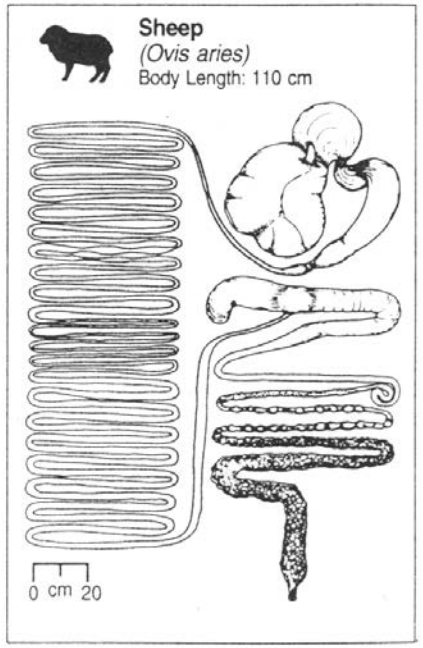
Foregut Fermentation



Photos A. Schwarm/
M. Clauss

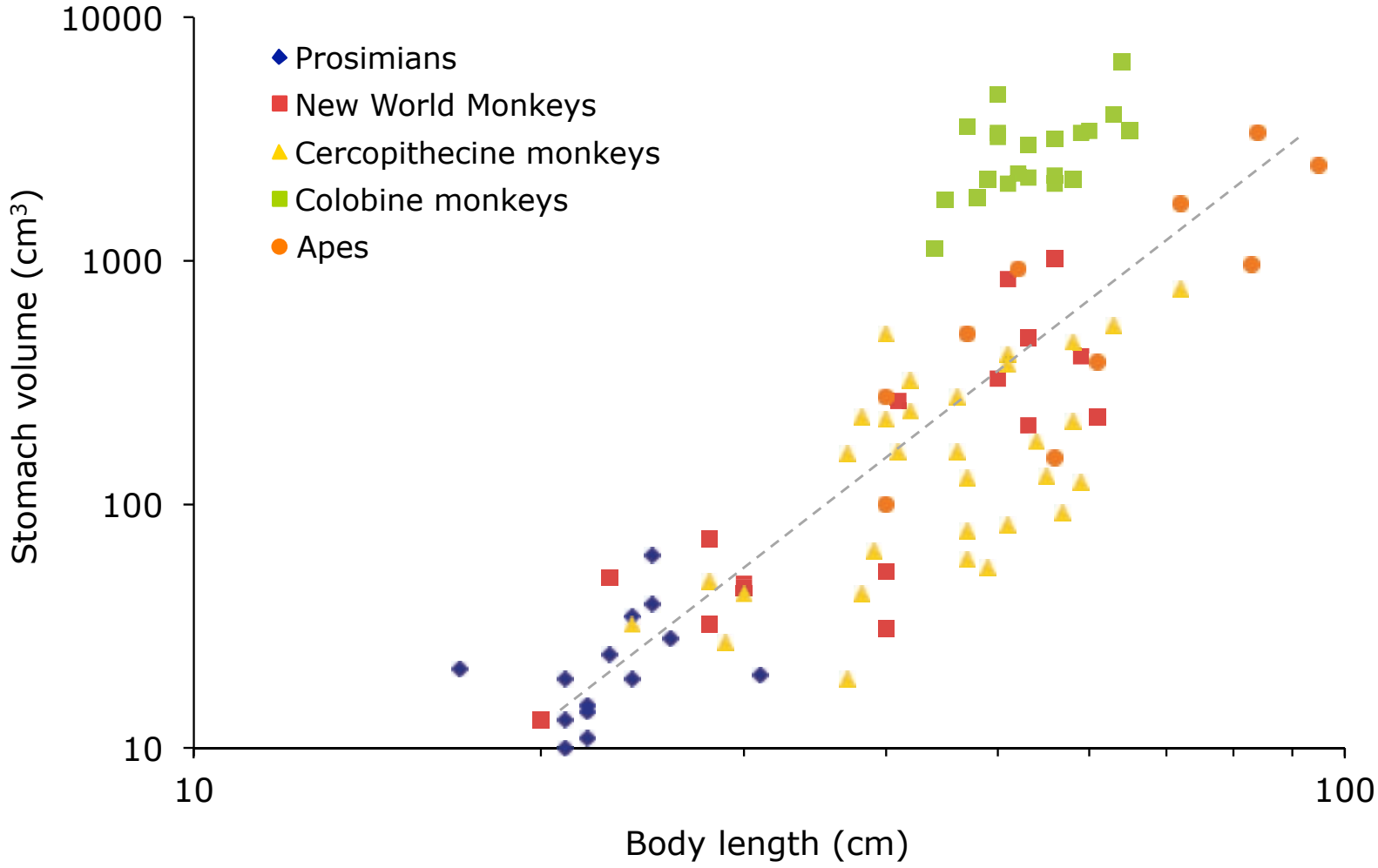
Foregut Fermentation - Ruminant





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

Stomach volume



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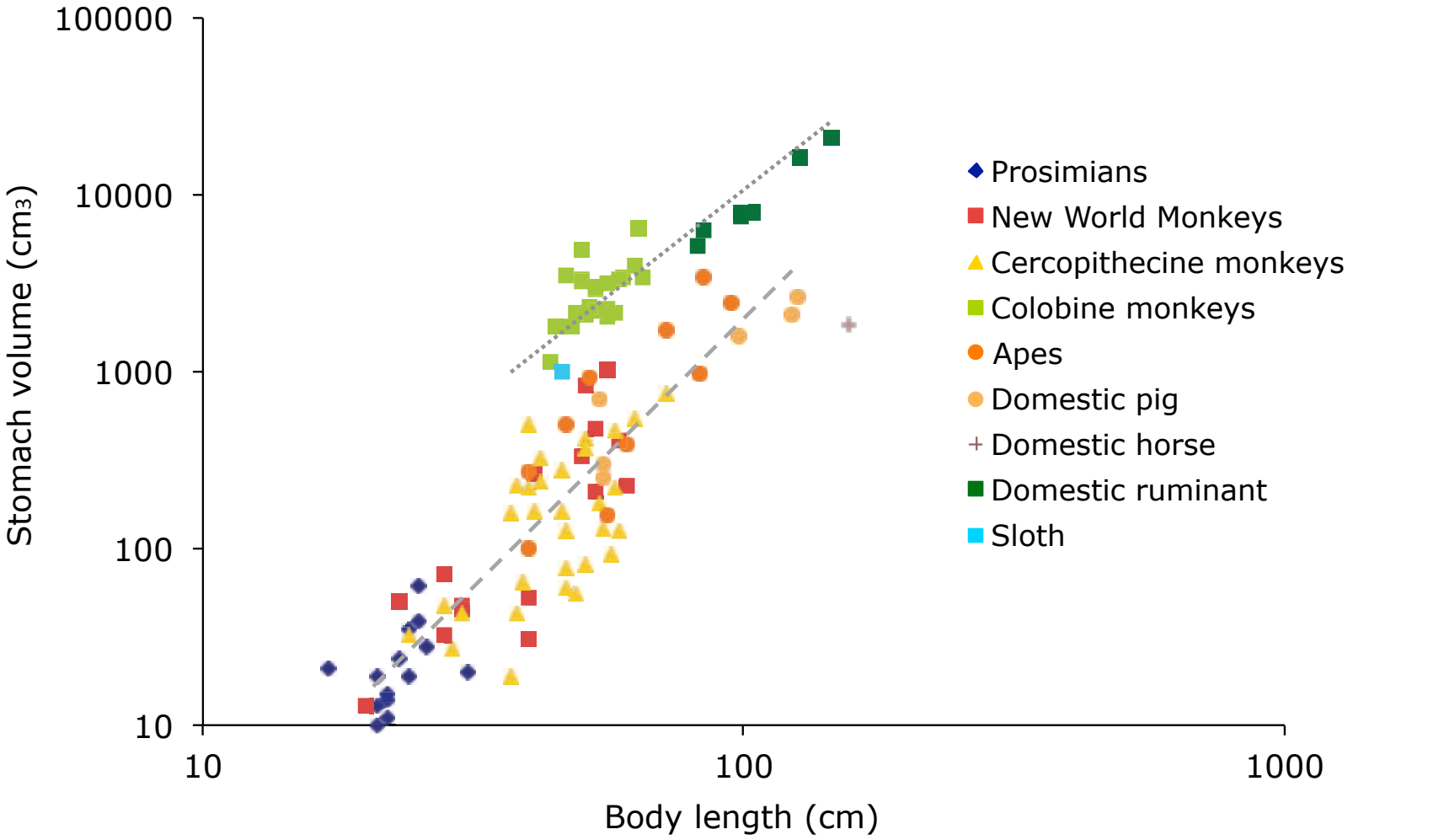
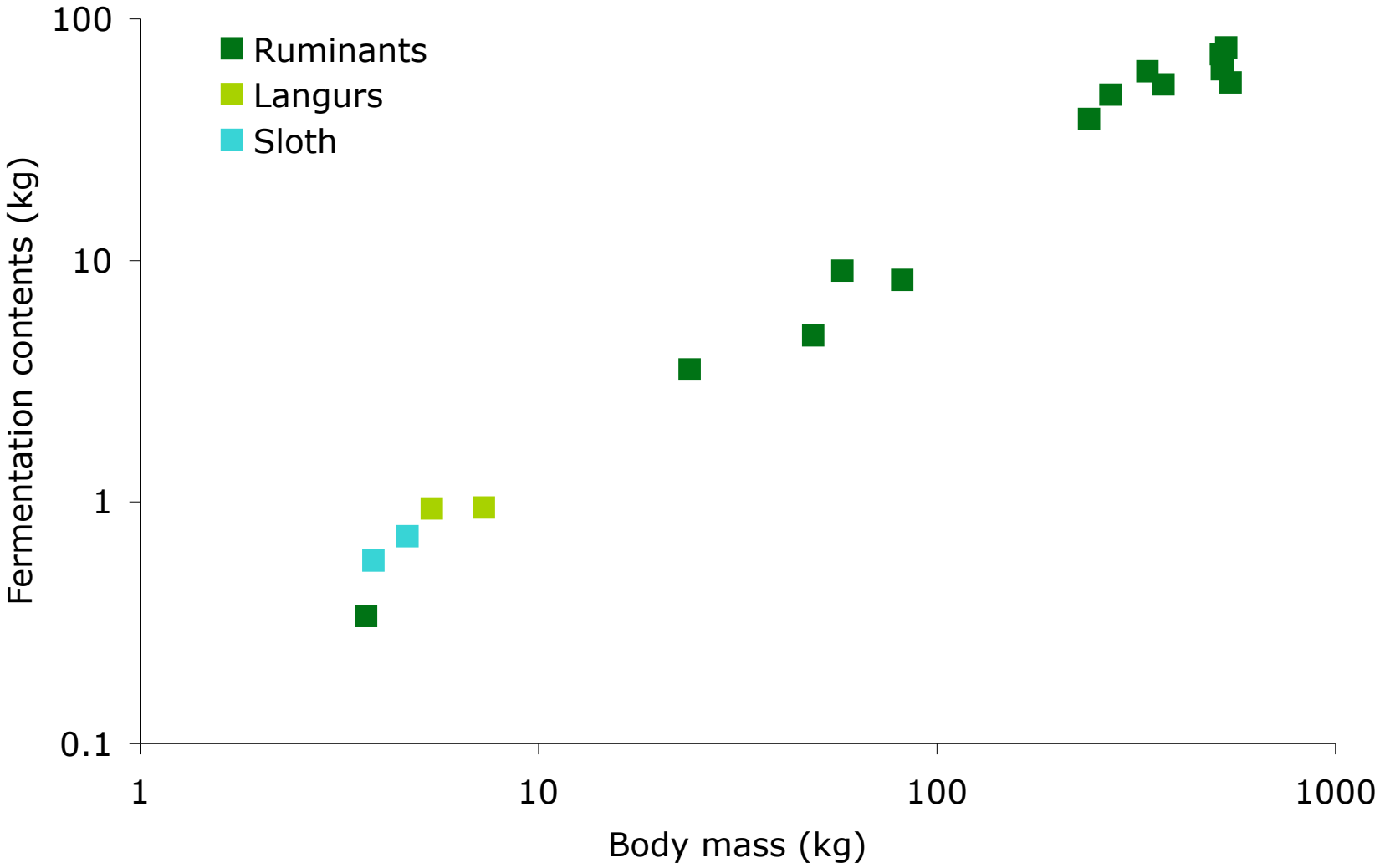


Data from Chivers & Hladik (1980)

Colobines: fermentation capacity



Data collection from Parra (1978)

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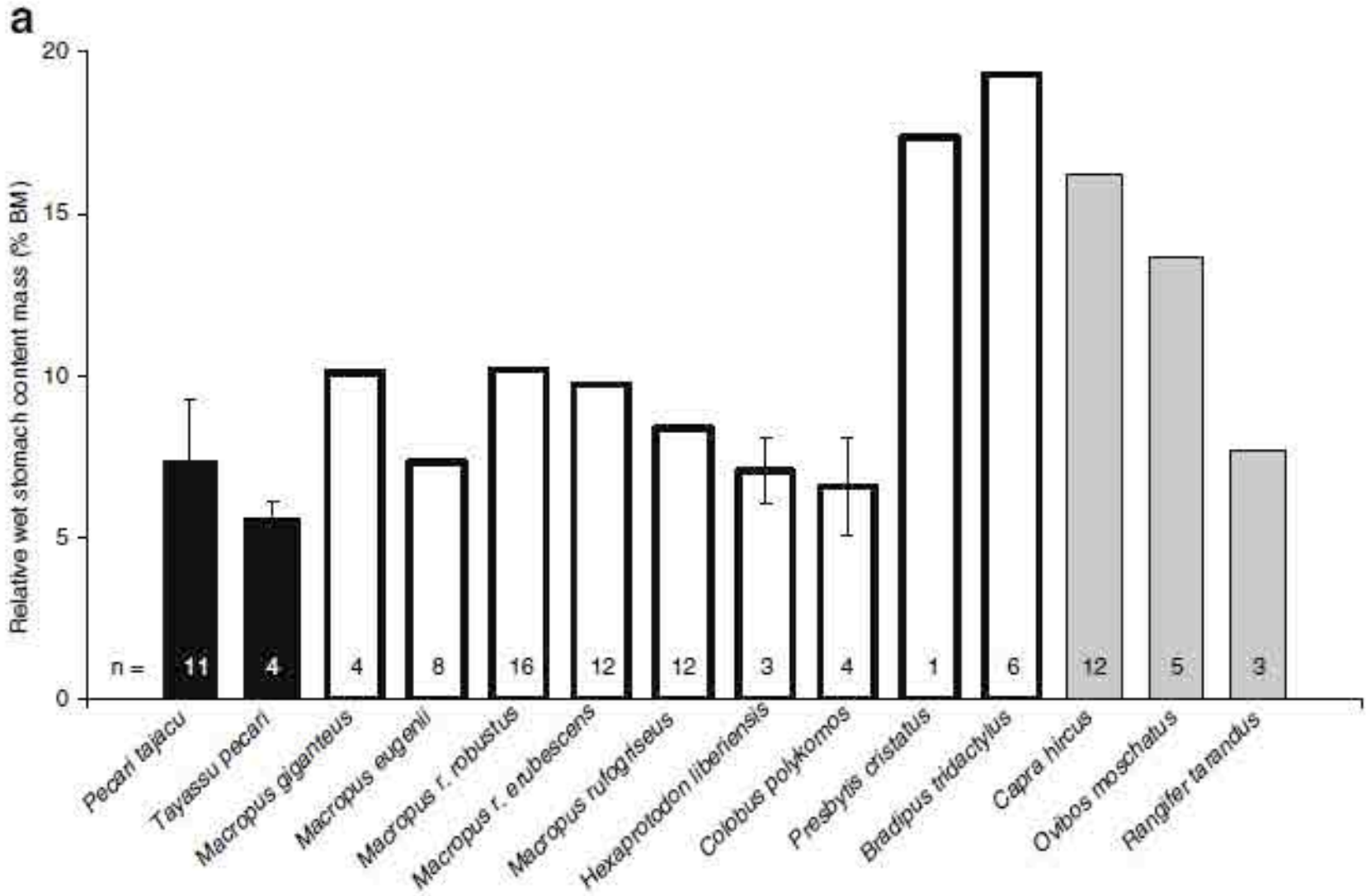
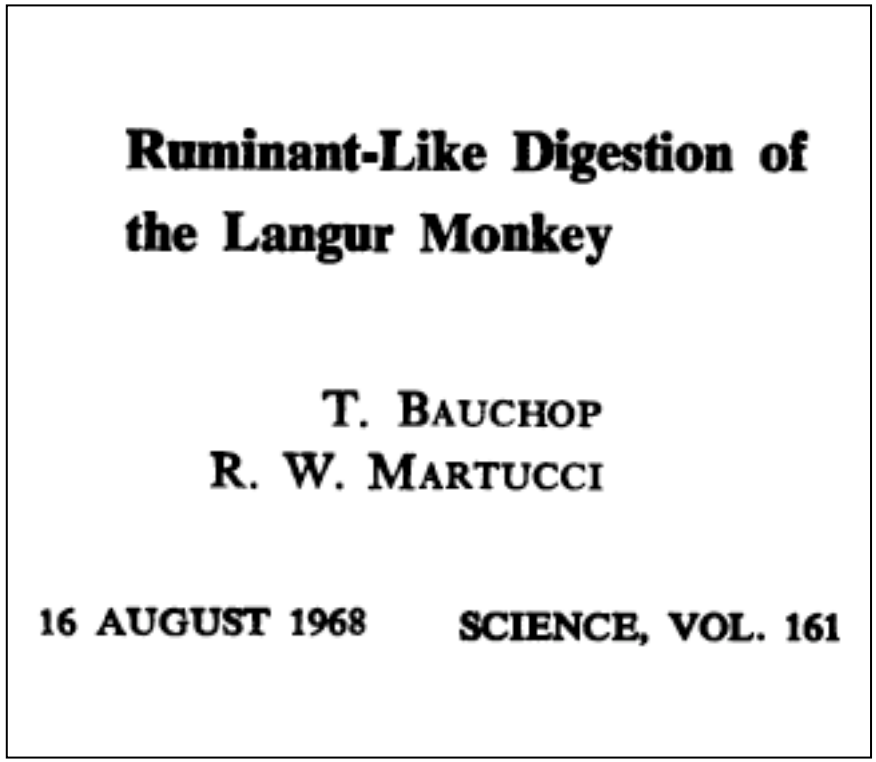


Data collection from Schwarm et al. (2010)

Digestive constraint I:

The ‘foregut fermentation trap‘

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?

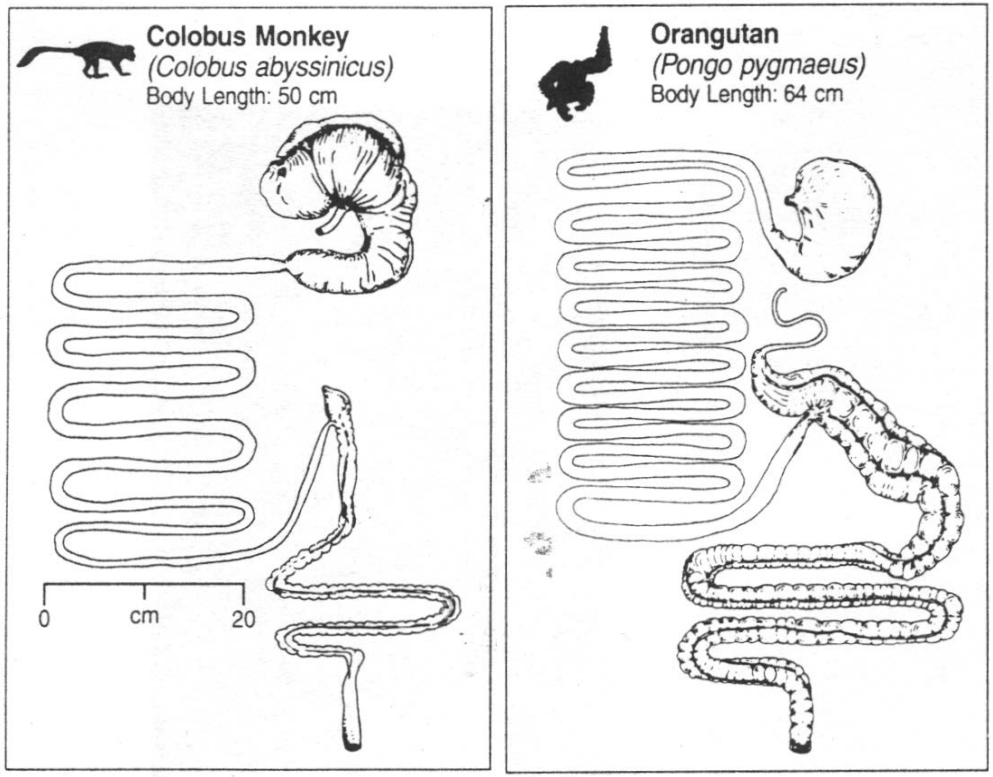
THE EVOLUTIONARY STRATEGY OF THE EQUIDAE AND THE ORIGINS OF RUMEN AND CECAL DIGESTION

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



from Stevens & Hume (1995)

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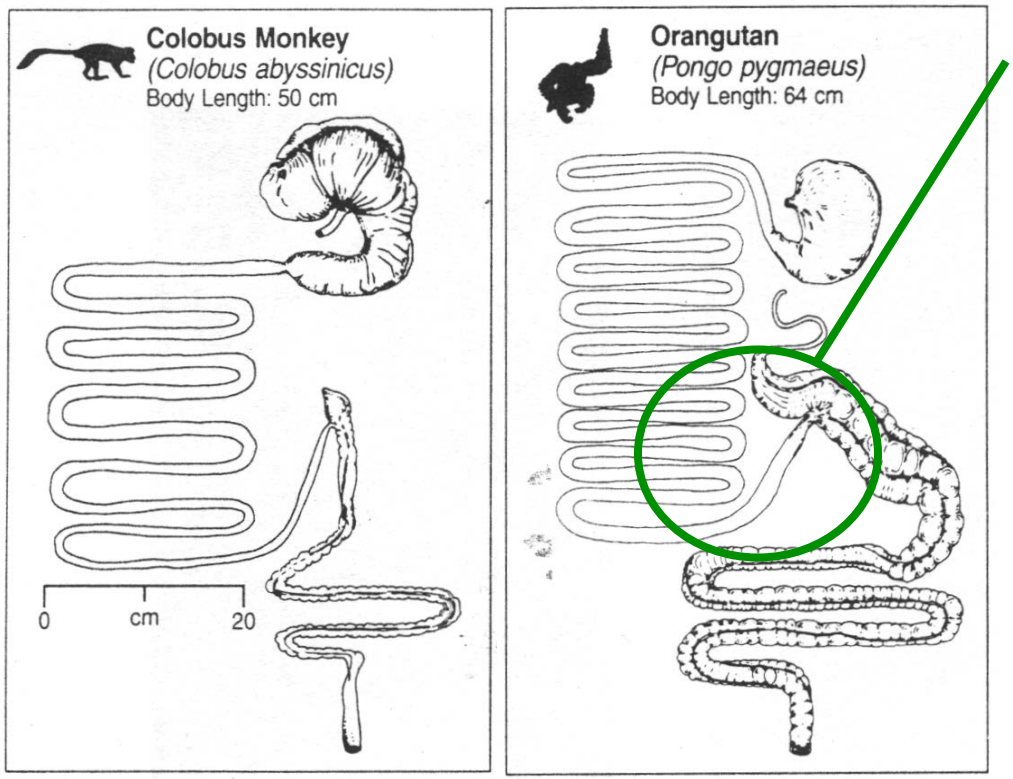
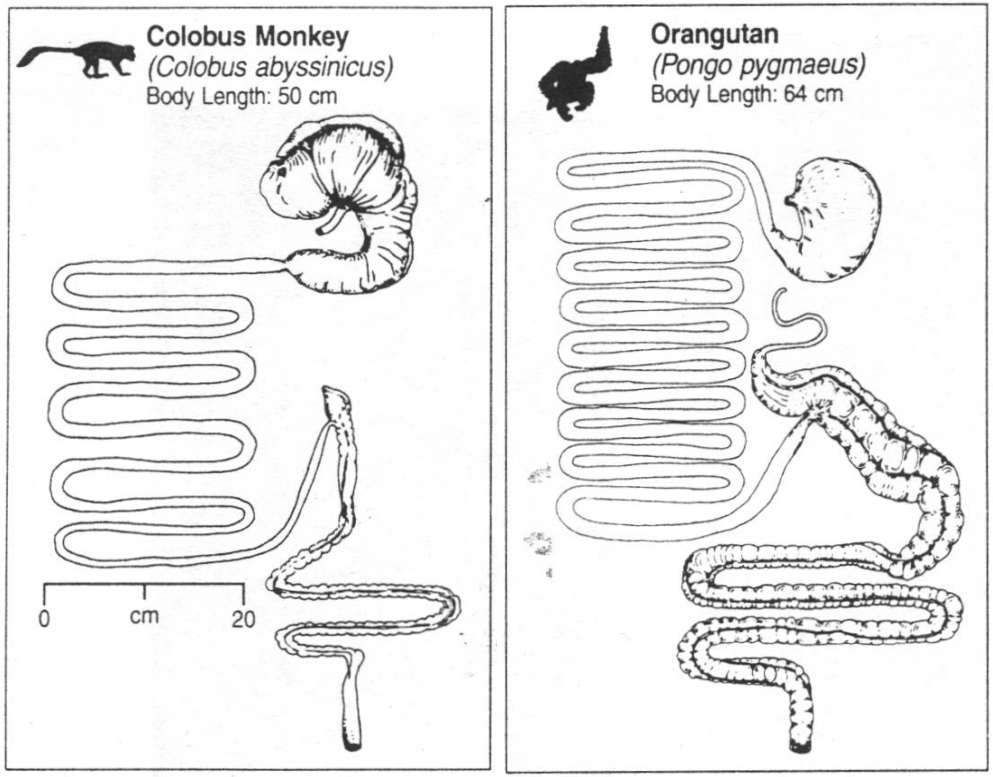


Fermentation <u>after</u> enzymatic digestion and absorption:

from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation

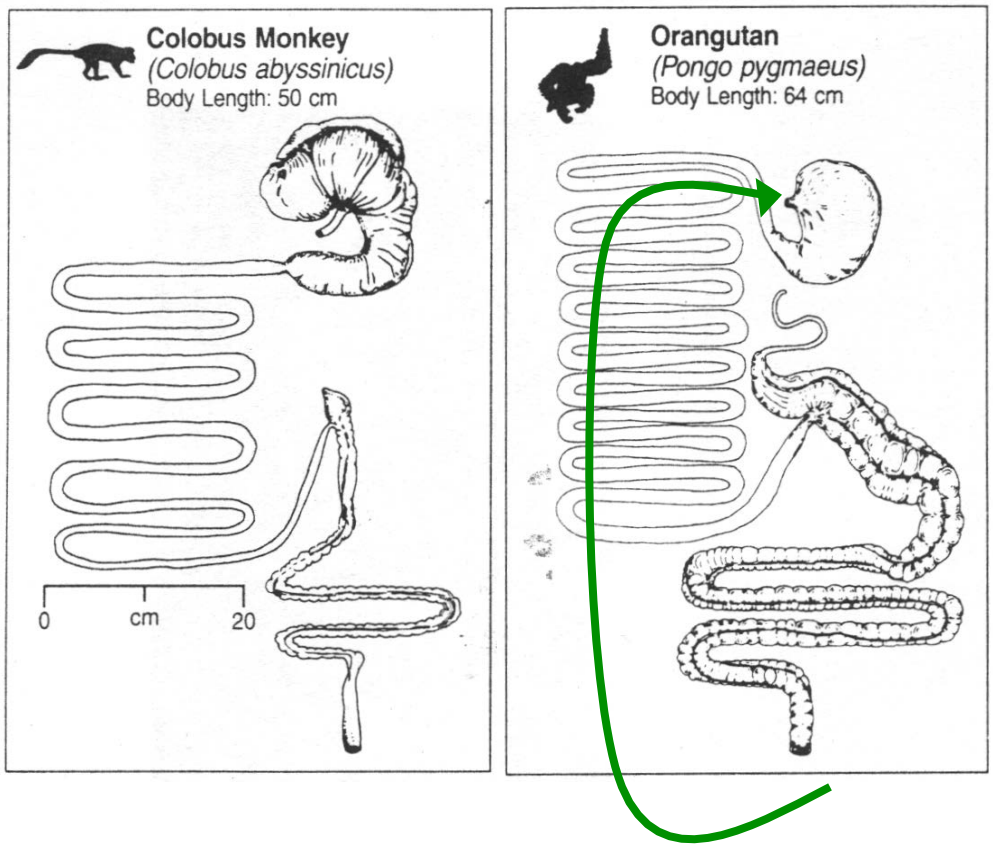


Fermentation after enzymatic digestion and absorption:

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

from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation



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(coprophagy)

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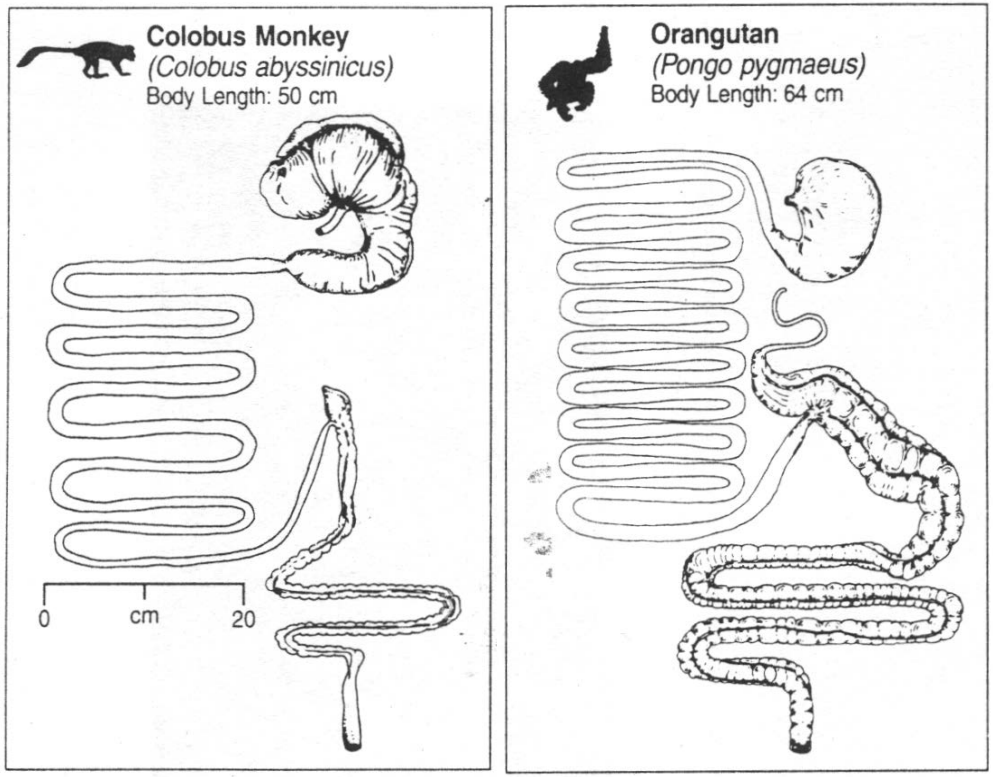

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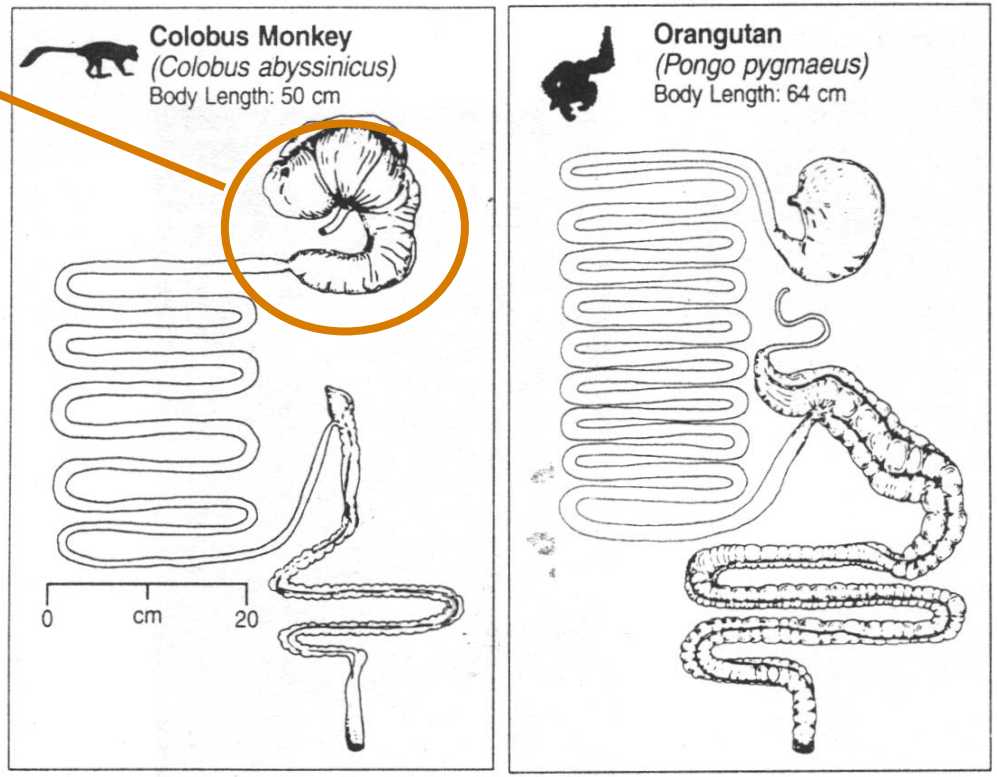
<u>Use</u> of easily digestible substrates

from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation

Fermentation prior to enzymatic digestion and absorption:



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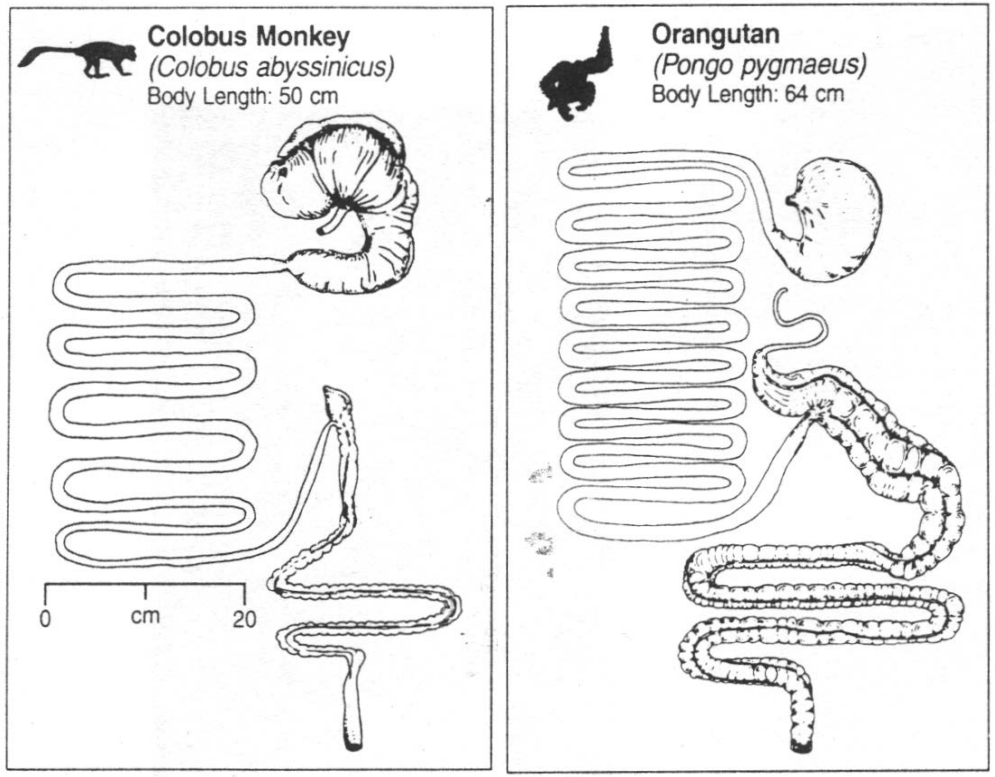

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Foregut vs. Hindgut Fermentation

Fermentation prior to enzymatic digestion and absorption:

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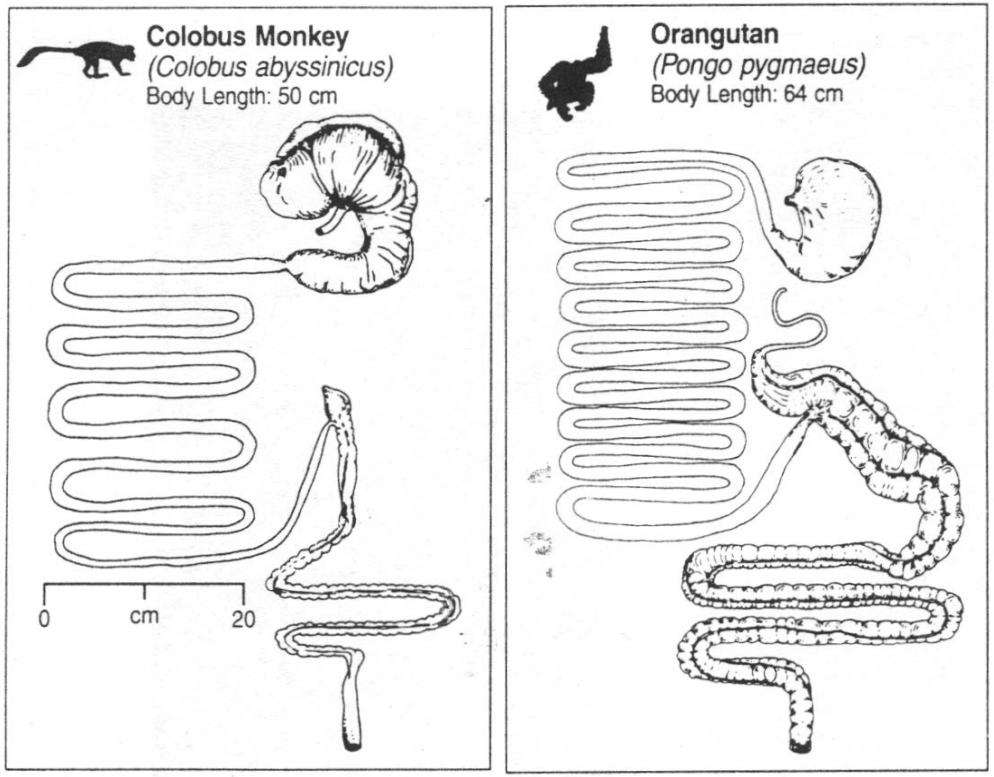
Bacterial detoxification?



Fermentation after enzymatic digestion and absorption:

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(coprophagy)

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from Stevens & Hume (1995)

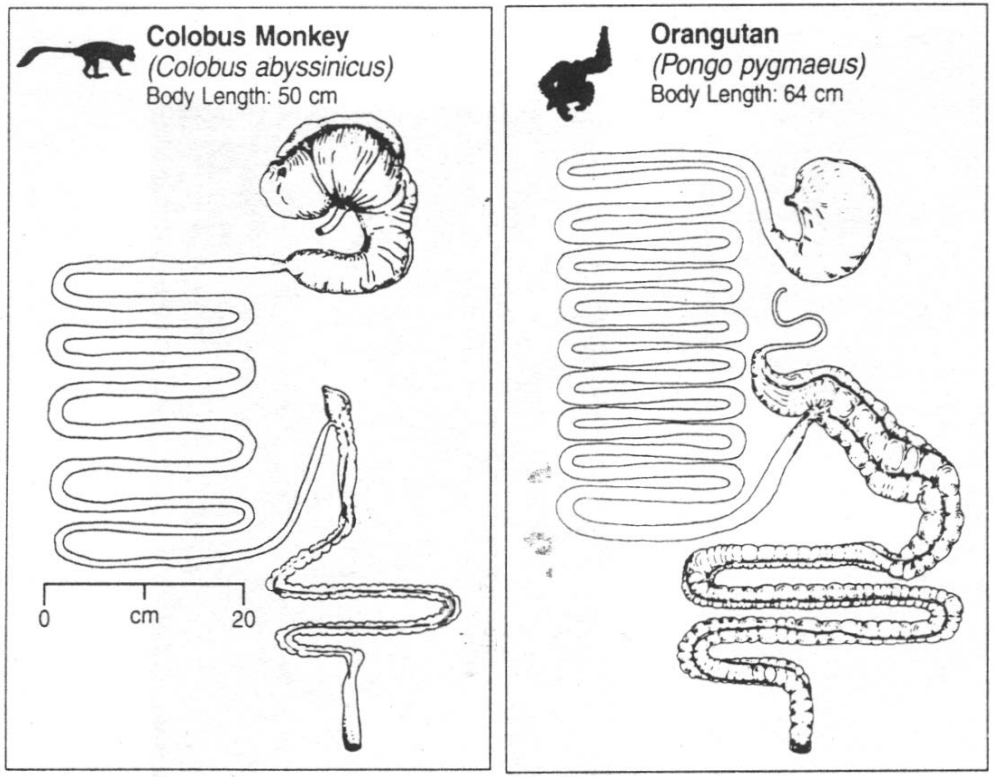
Foregut vs. Hindgut Fermentation

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



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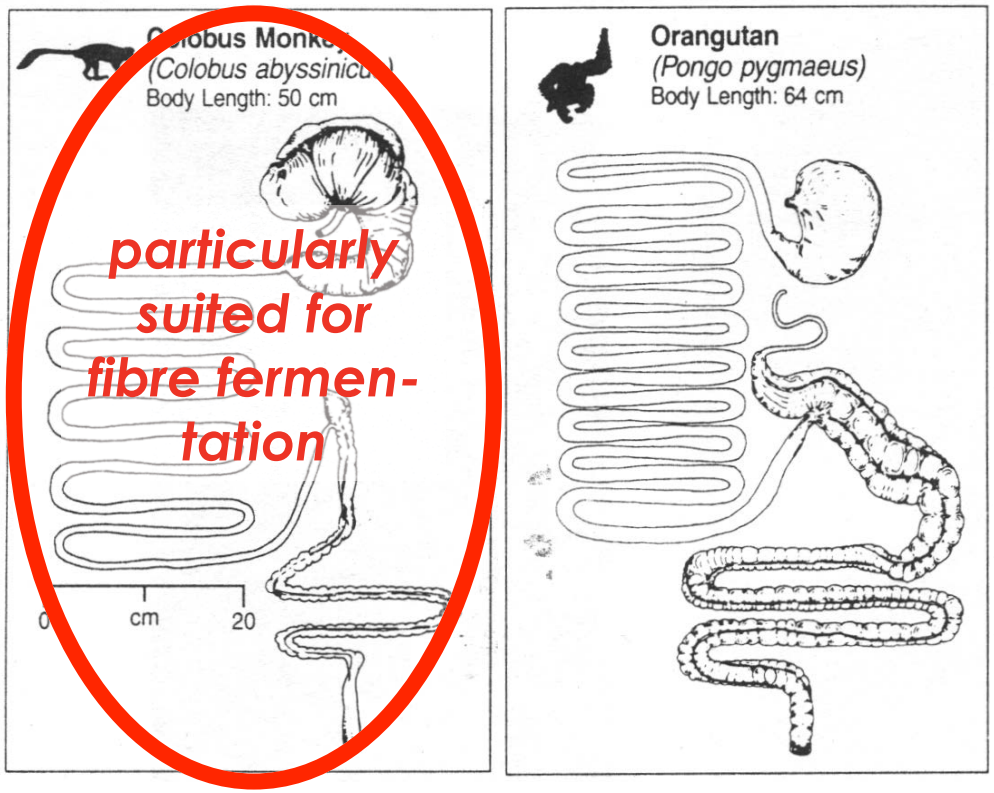
Foregut vs. Hindgut Fermentation

Fermentation <u>prior</u> to enzymatic digestion and absorption:

<u>Use</u> of bacterial protein, bacterial products (B-Vitamins)

Bacterial detoxification?

<u>'Loss'</u> of easily digestible substrates



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

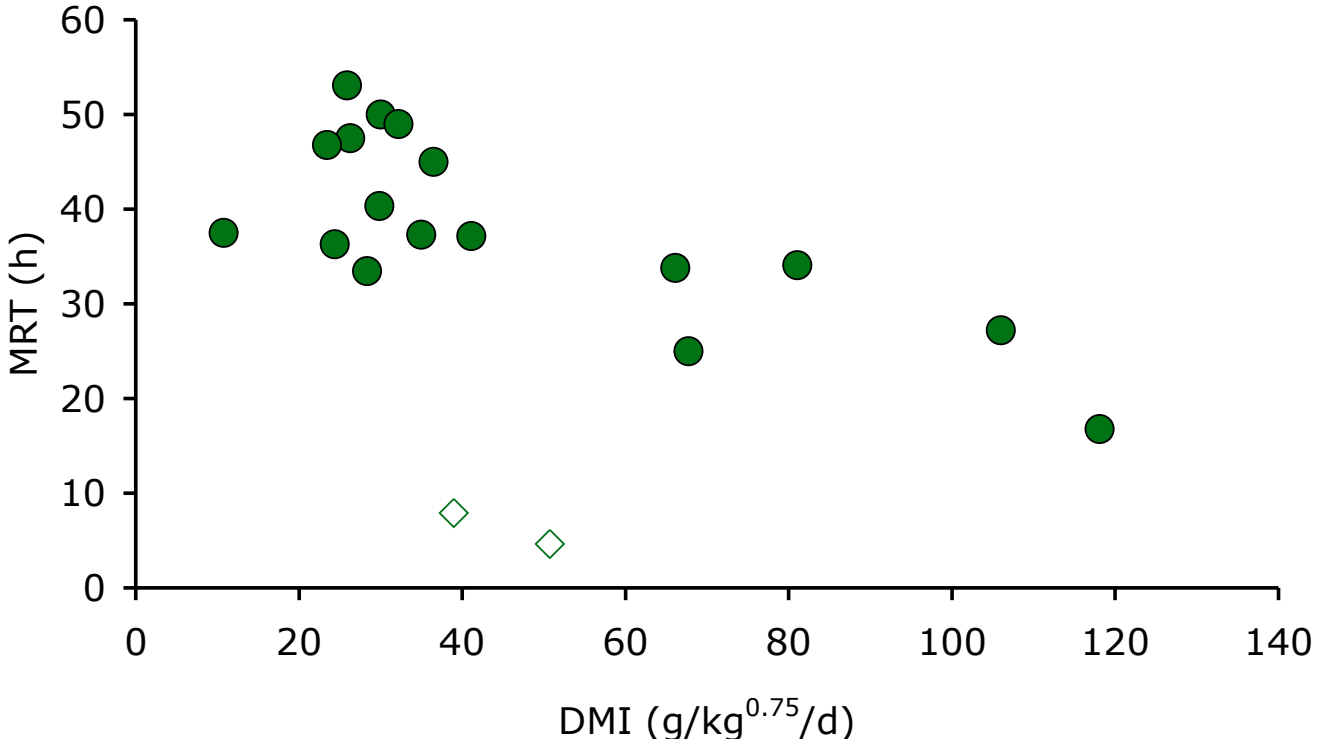
<u>'Loss'</u> of bacterial protein, bacterial products (B-Vitamins?)

(coprophagy)

<u>Use</u> of easily digestible substrates

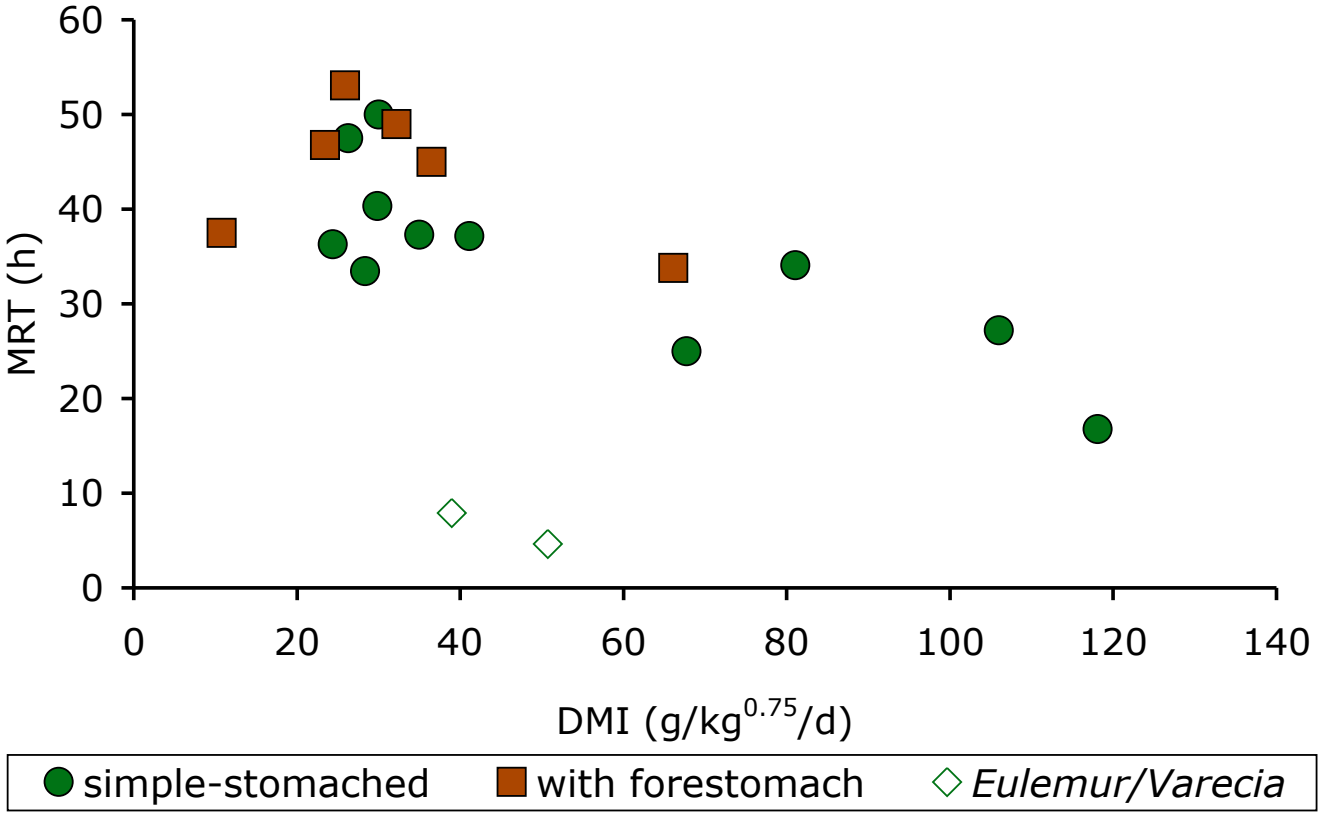
from Stevens und Hume (1995)

Intake and Passage in Primates



from Clauss et al. (2008)

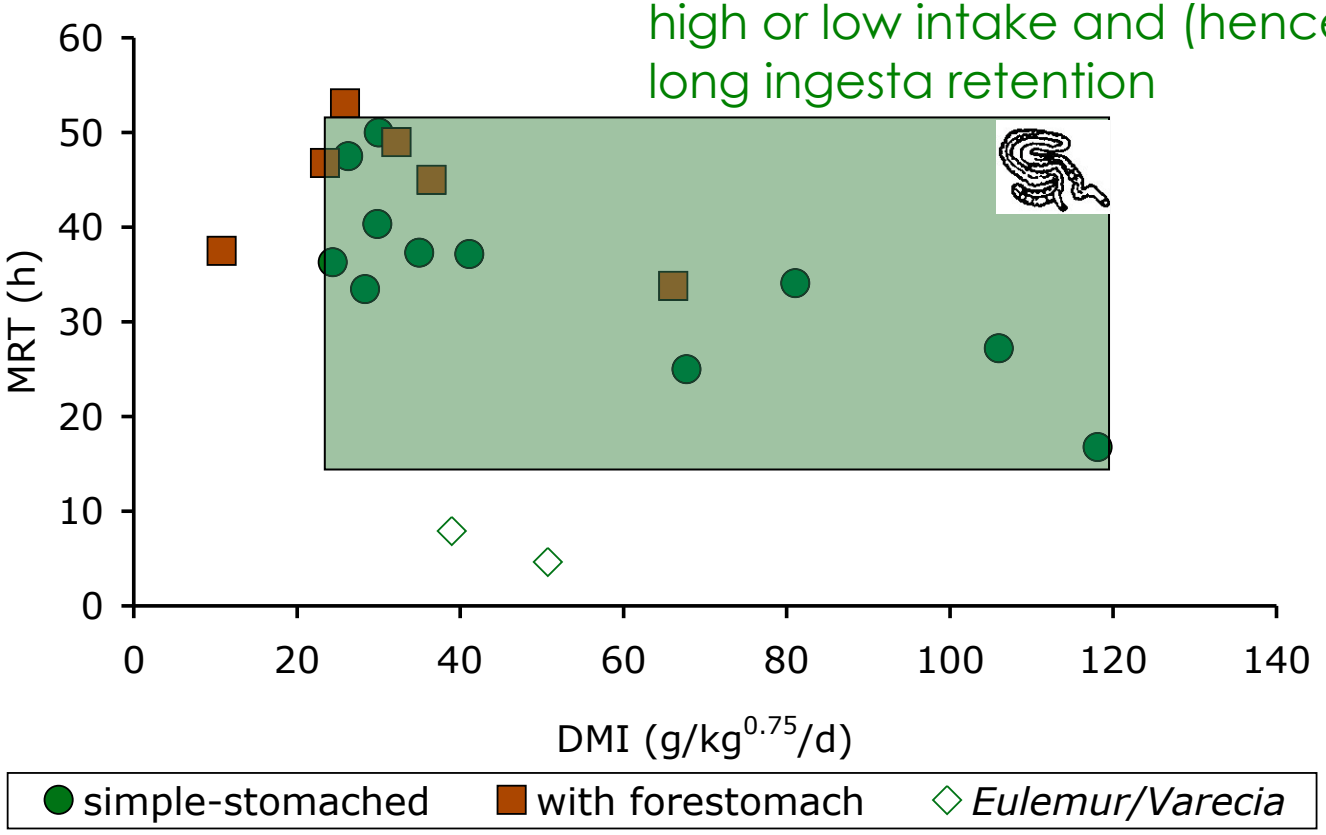
Intake and Passage in Primates



from Clauss et al. (2008)

Intake and Passage in Primates

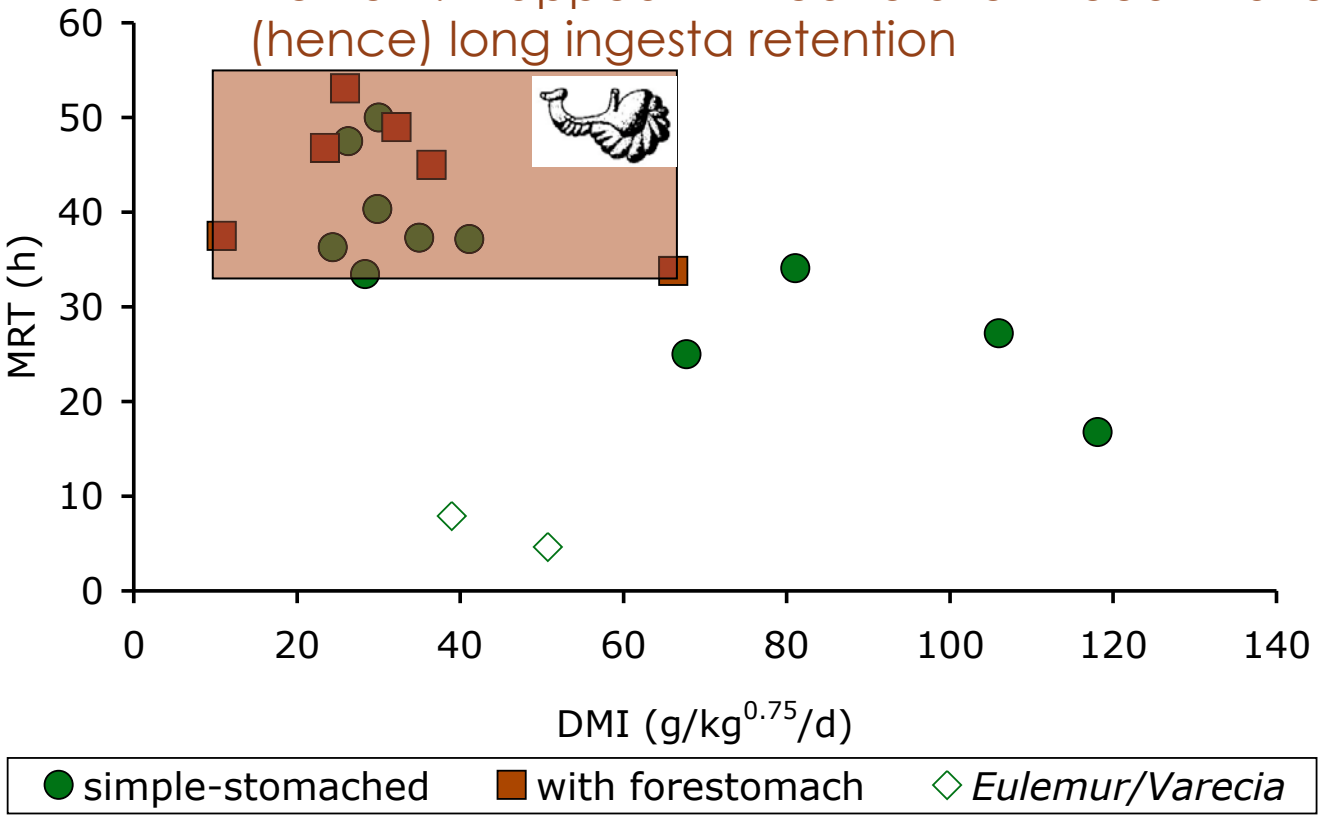
Hindgut fermenters can have either - high or low intake and (hence) short or long ingesta retention



from Clauss et al. (2008)

Intake and Passage in Primates

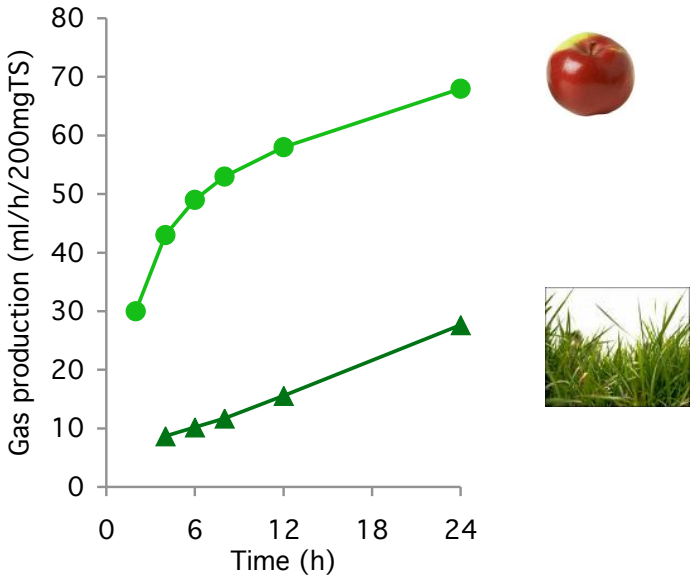
Nonrum. ff appear limited to a low food intake and (hence) long ingesta retention



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		

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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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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?*

From Digestive to Metabolic Strategies

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

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?

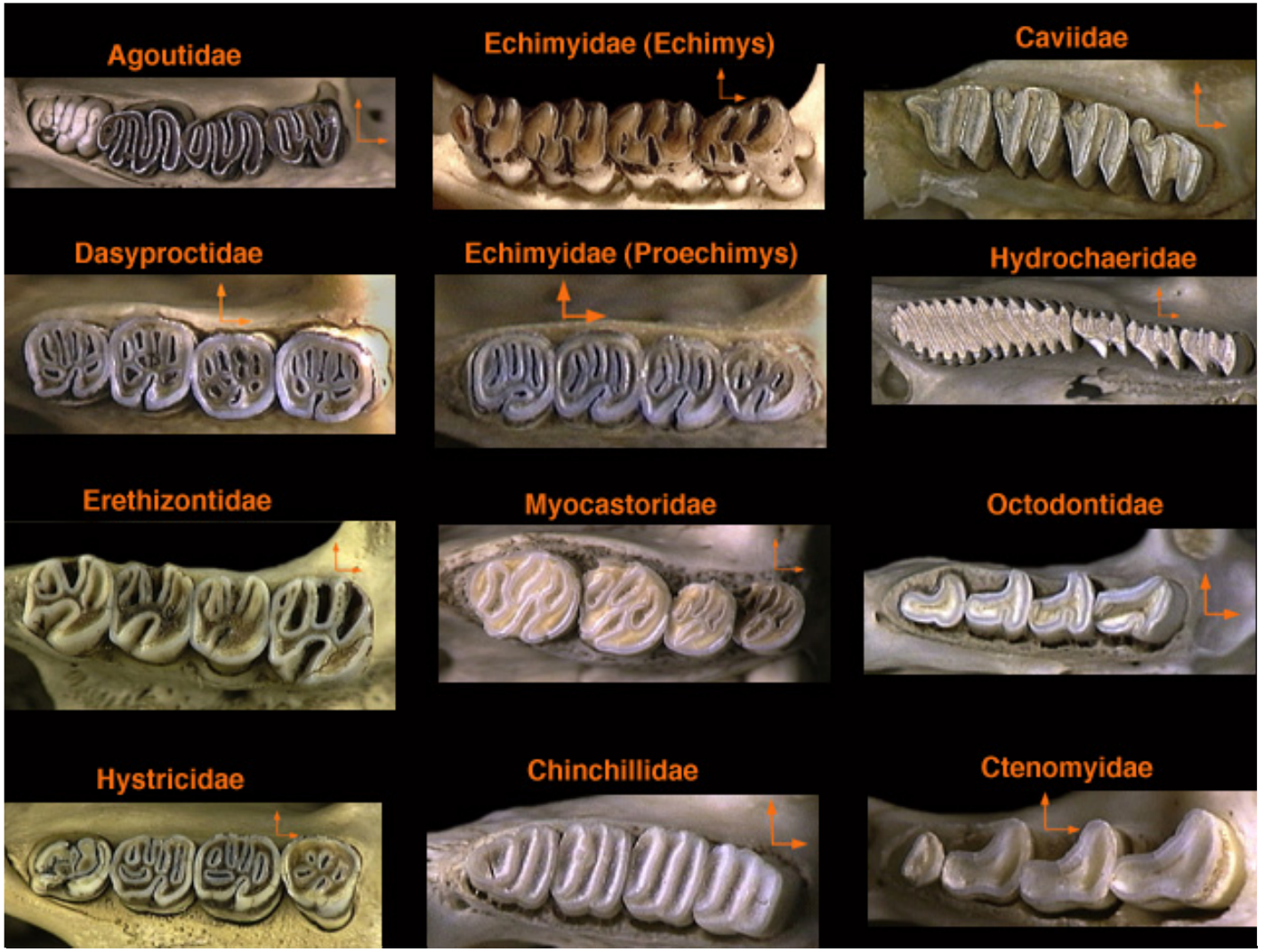
- higher food intake

- higher digestive efficiency

How can you increase energy intake?

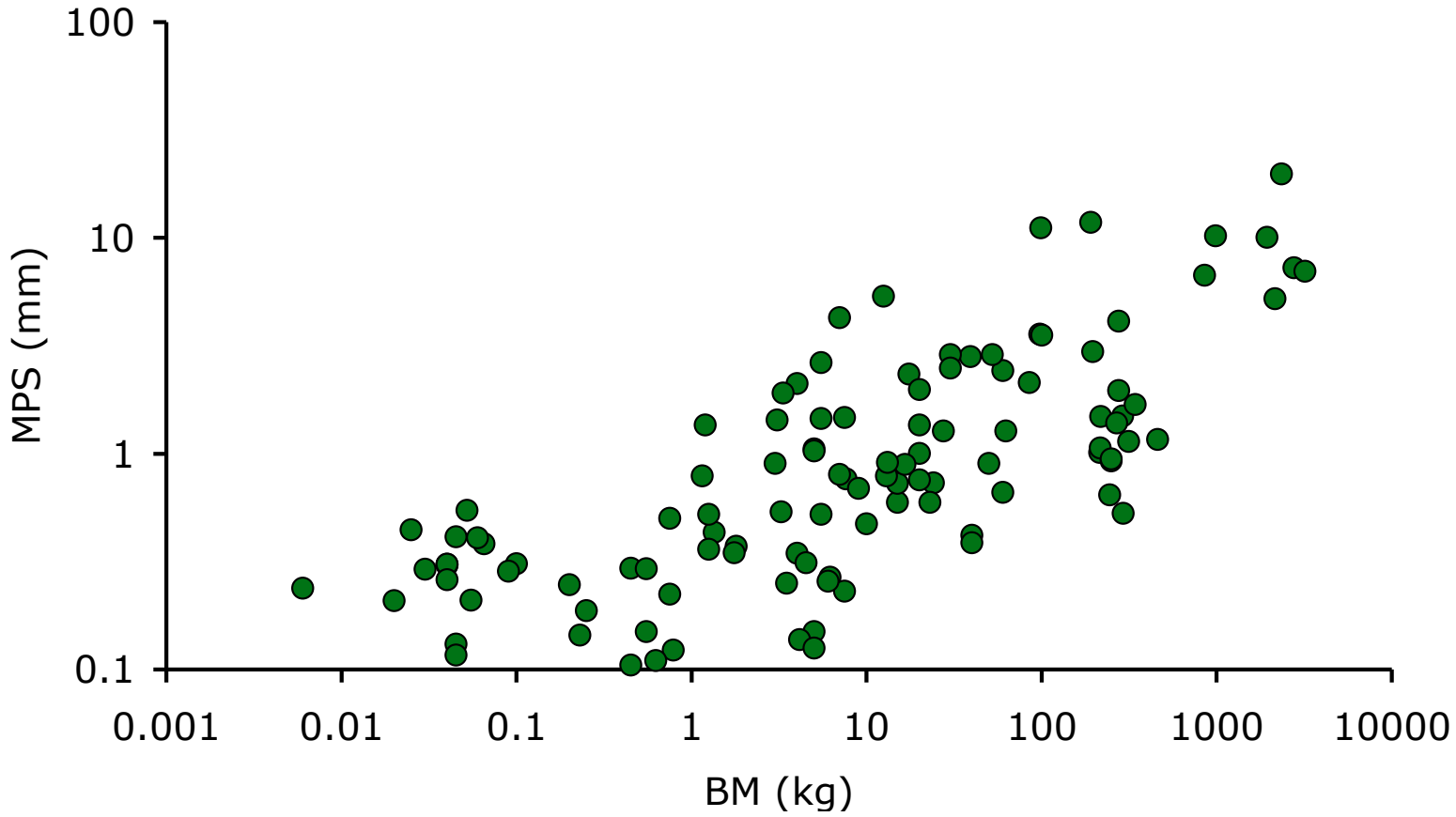
- higher food intake
- longer retention
- finer chewing

“Mammals are the definite chewers”



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

Ingesta particle size (chewing efficiency)



from Fritz (2007)

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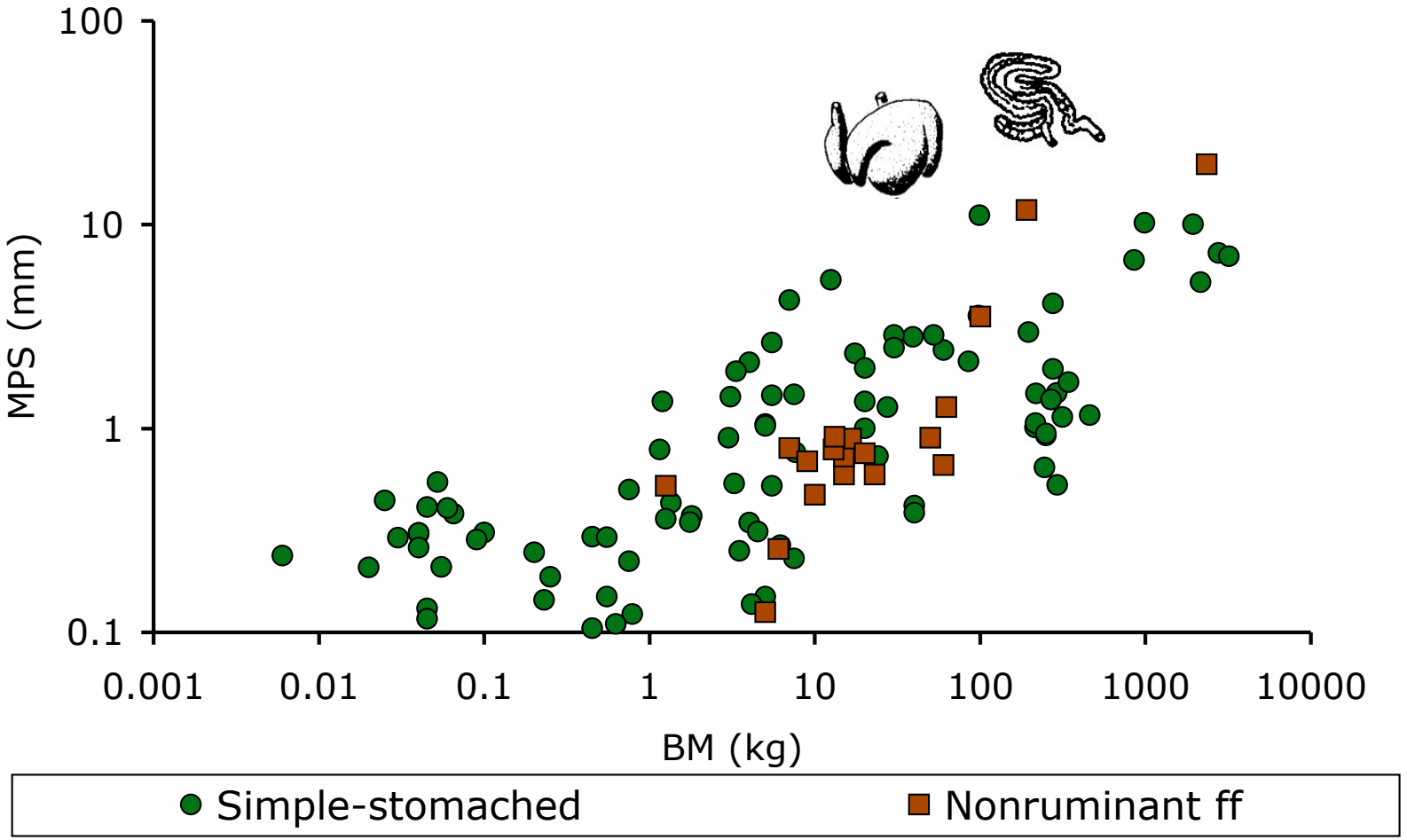

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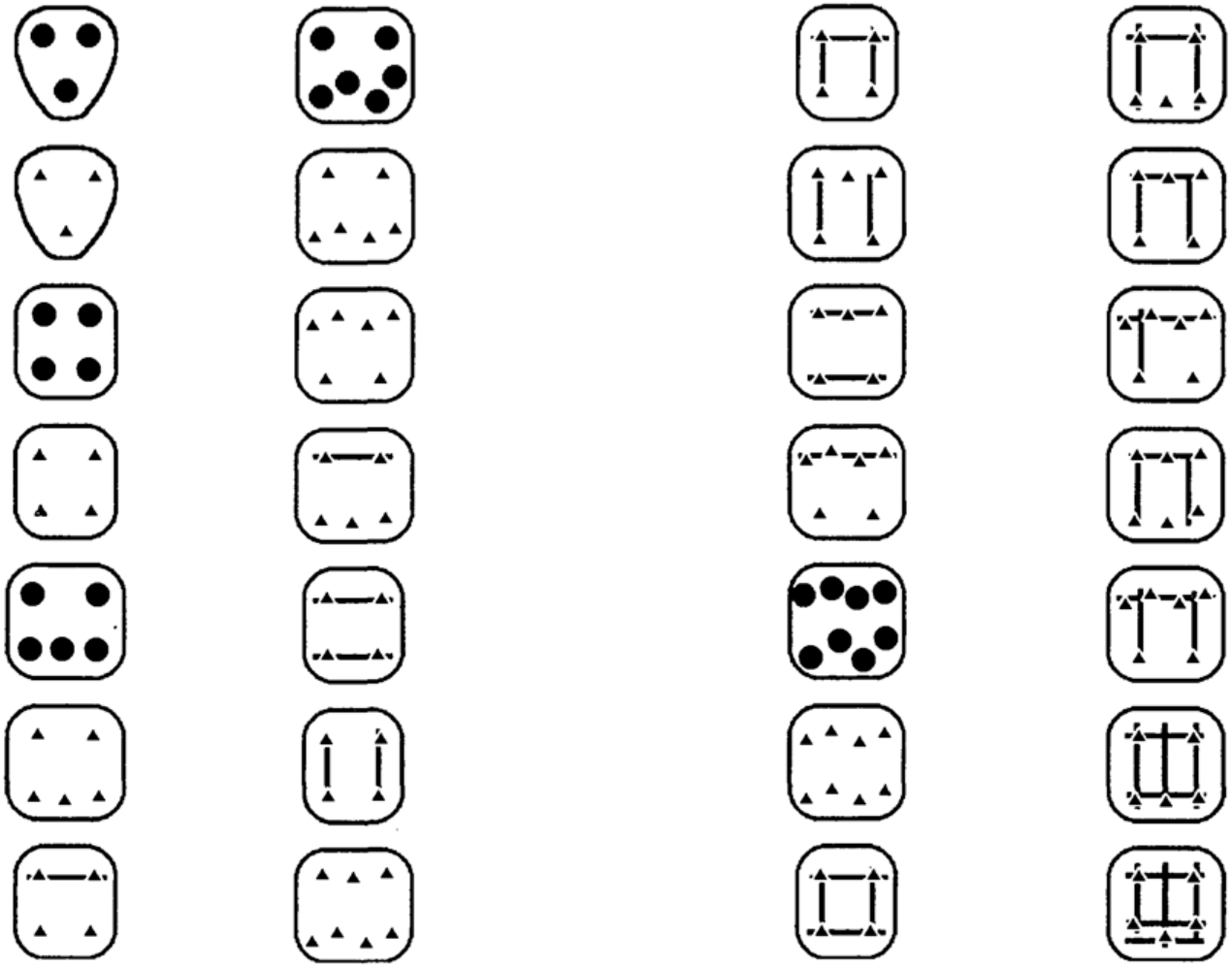

aus Jernvall et al. (1996)

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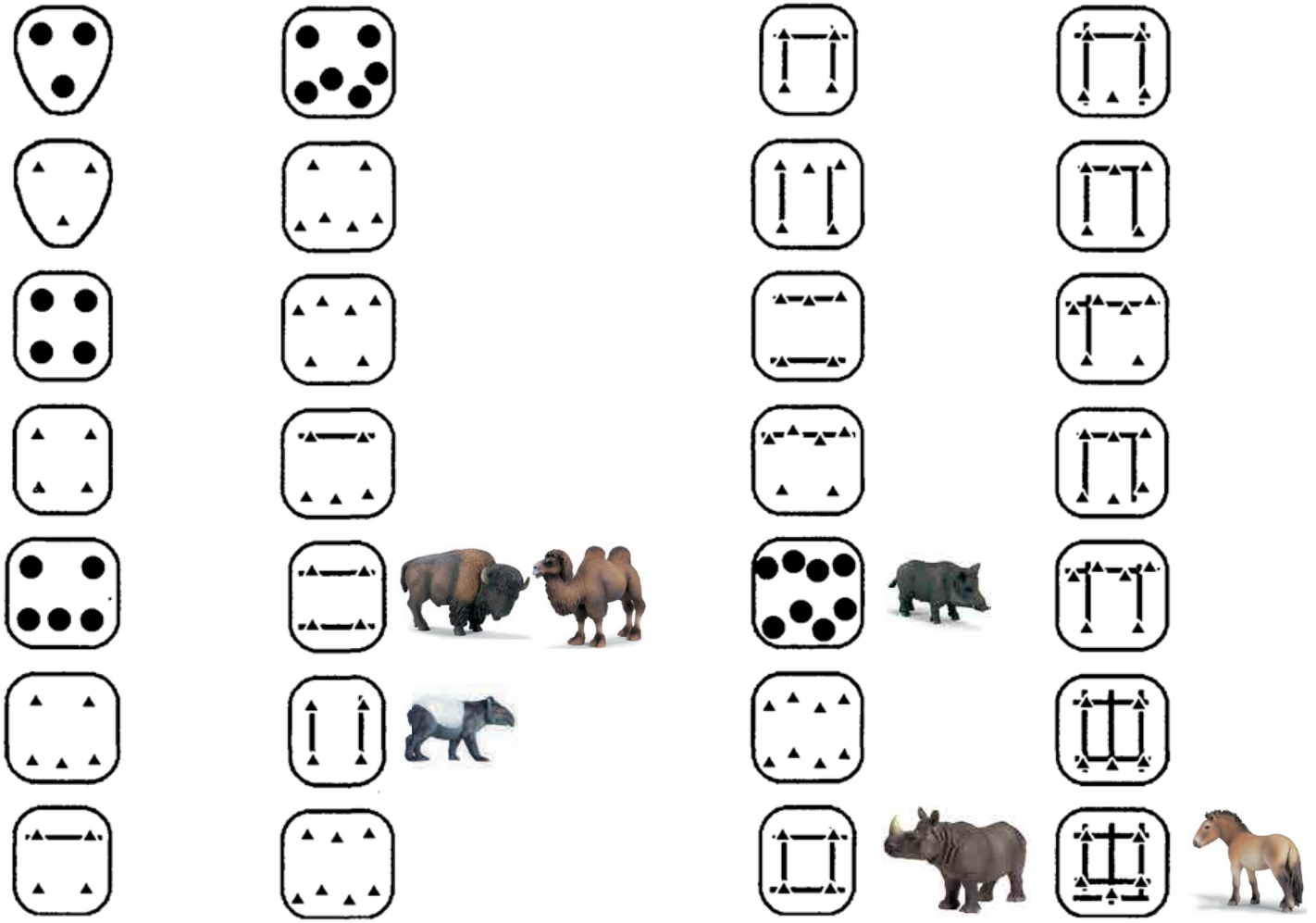

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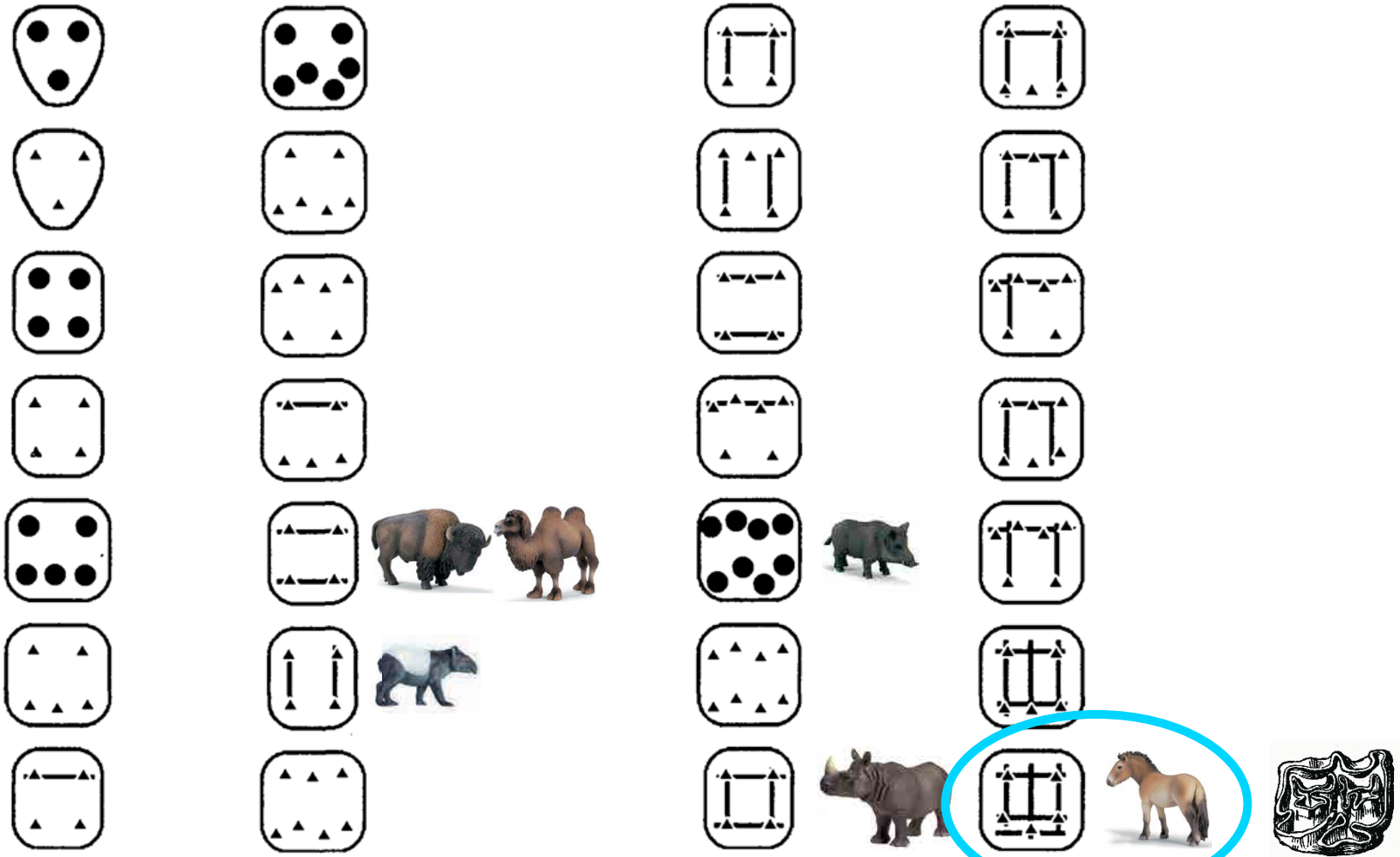

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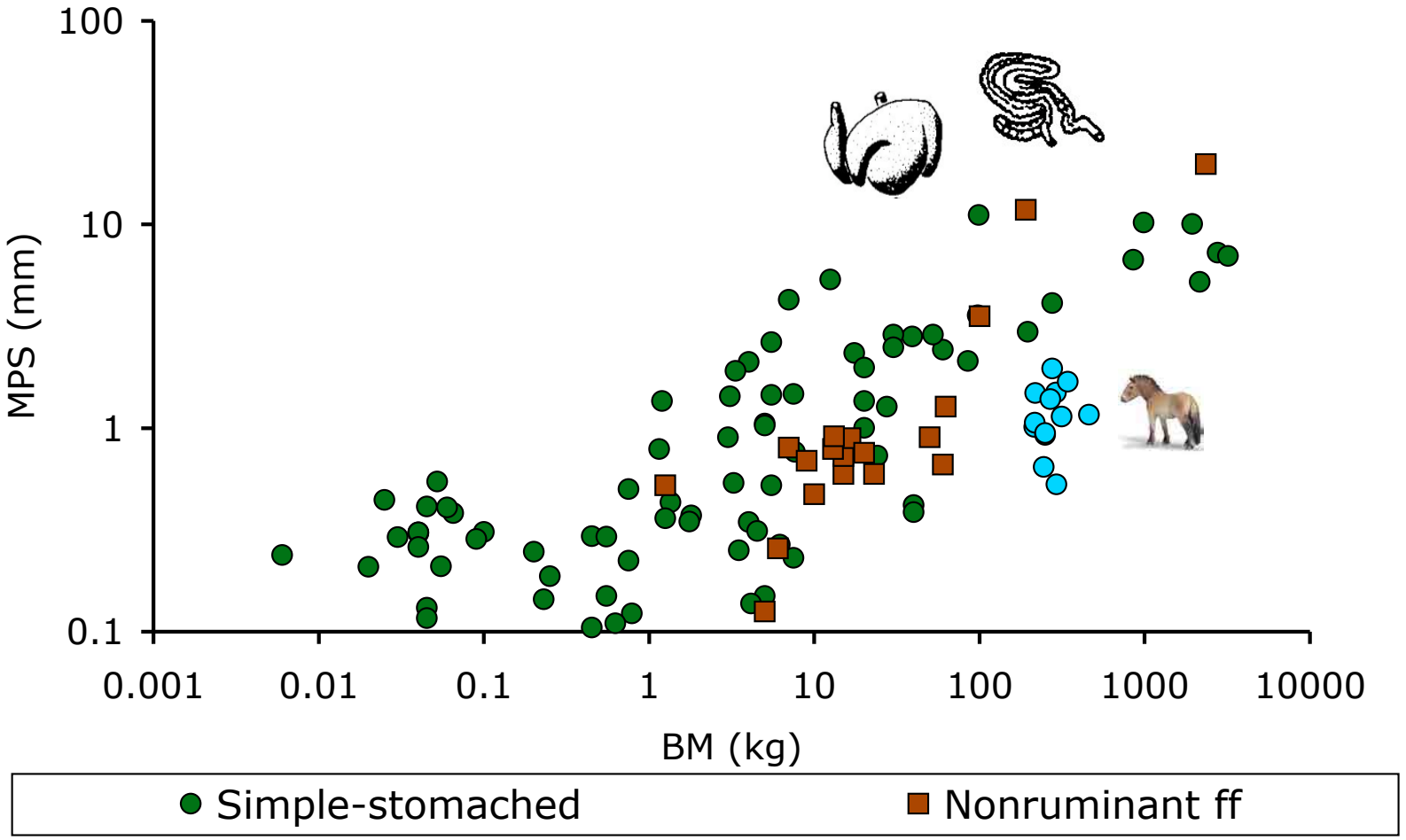

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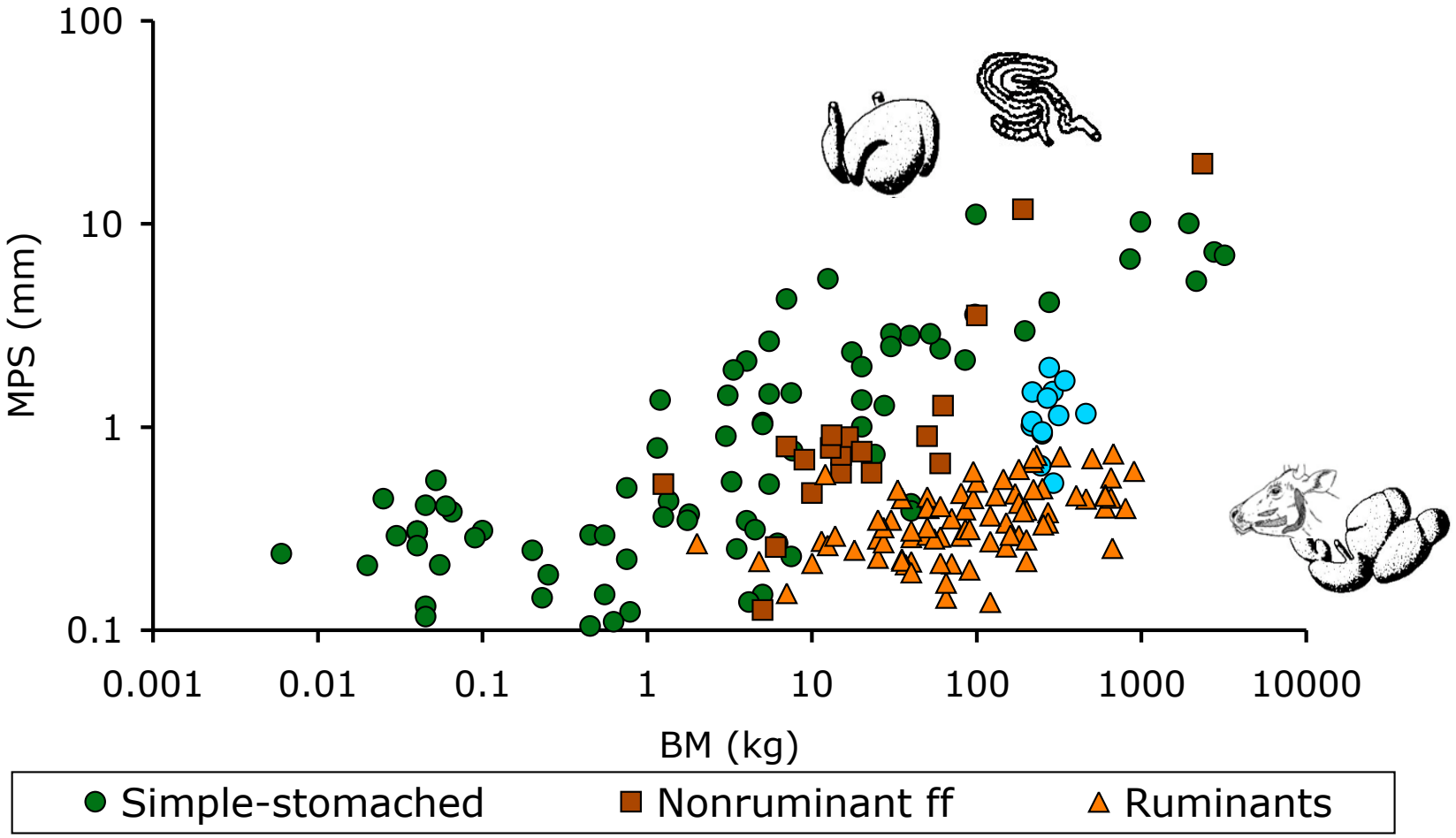

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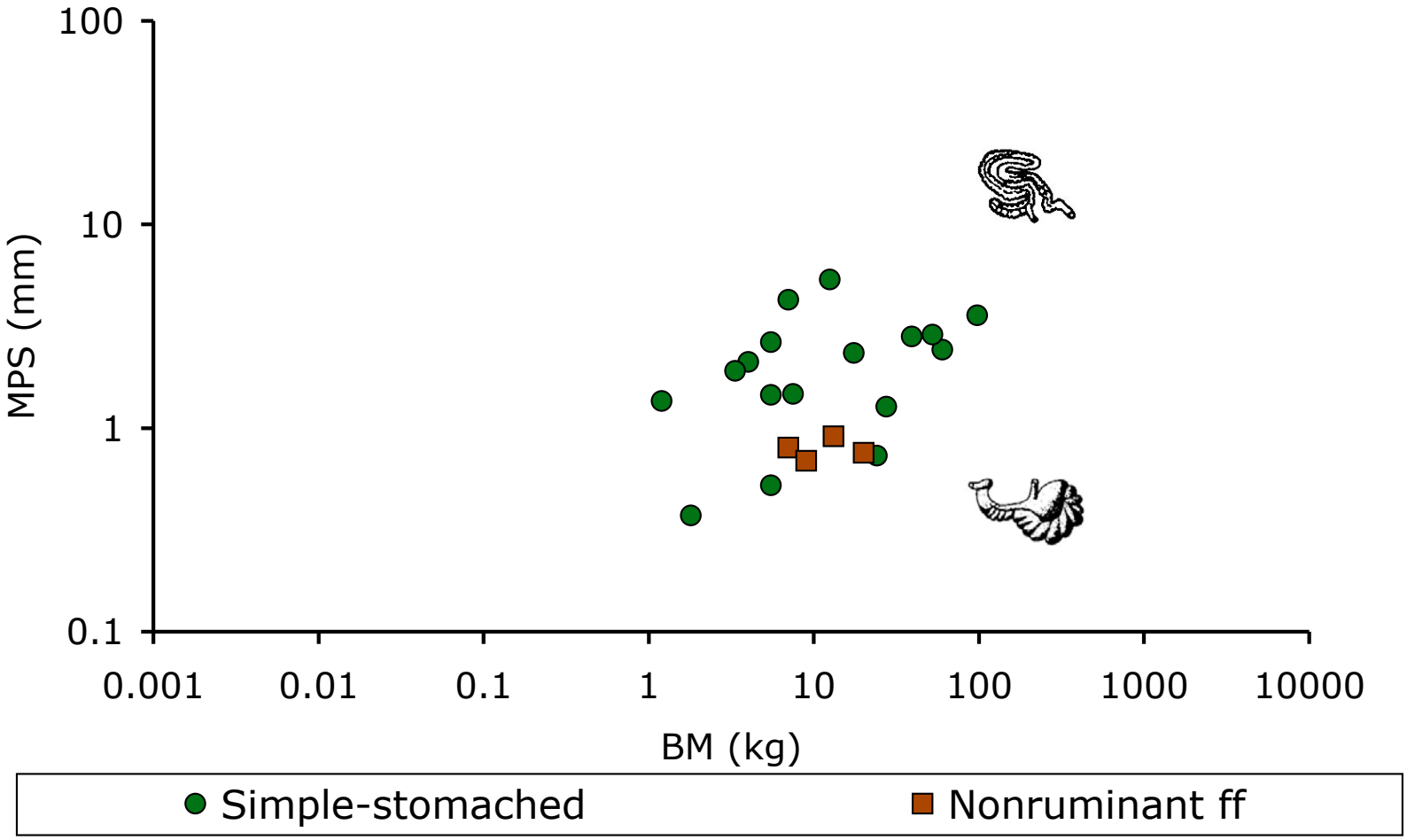


from Fritz (2007)

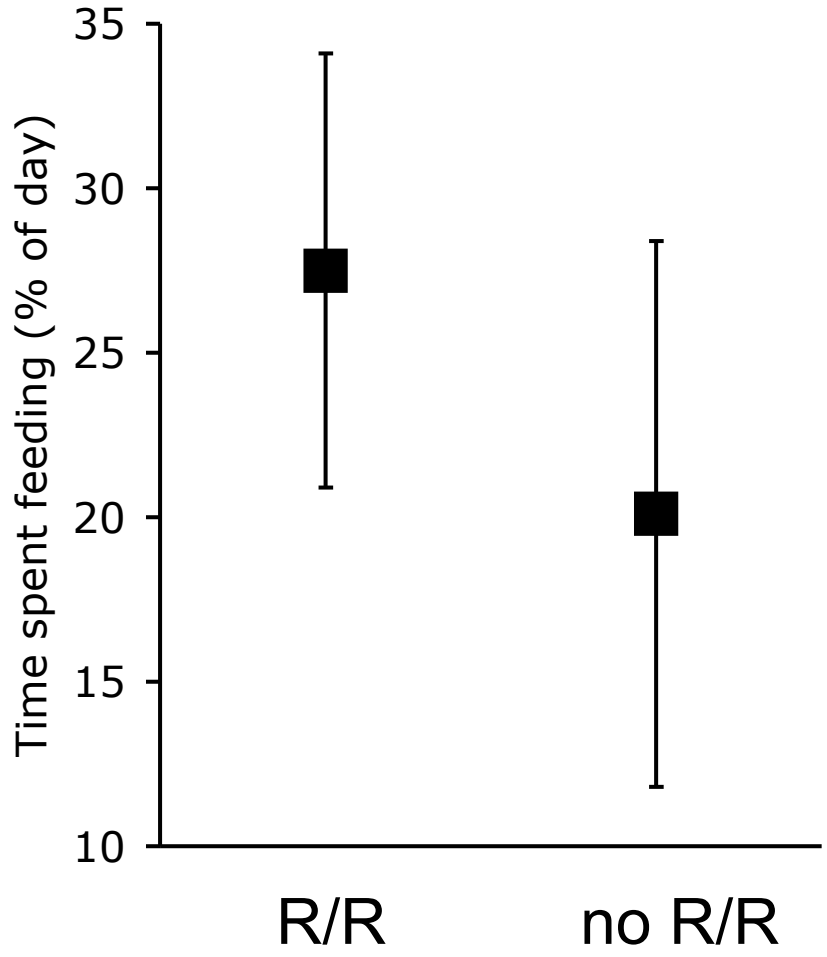
Matsuda et al. (2011)

Matsuda et al. (2011)

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)

The Jarman-Bell principle

The Jarman-Bell principle

A Jarman/Bell Model of Primate Feeding Niches

Steven J. C. Gaulin[1]

Human Ecology, Vol. 7, No. 1, 1979

	total nutrient requirement	$\frac{\text{nutrient requirement}}{\text{body weight}}$
large animal	large (abundant foods)	small (poor quality foods)
small animal	small (rare foods)	large (high quality foods)

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How do you quantify food abundance (for different-sized animals!)?

The Jarman-Bell principle

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How do you quantify food quality?

Body size and prey abundance

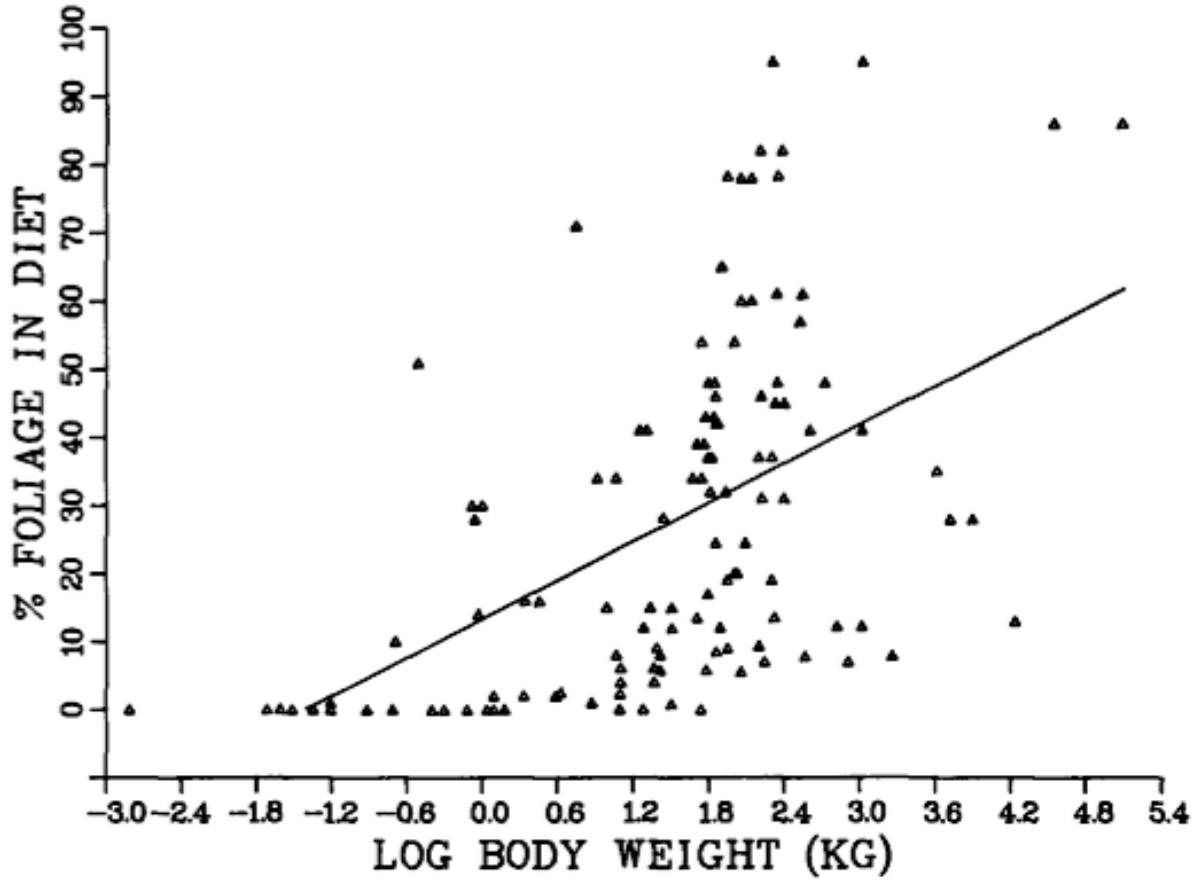
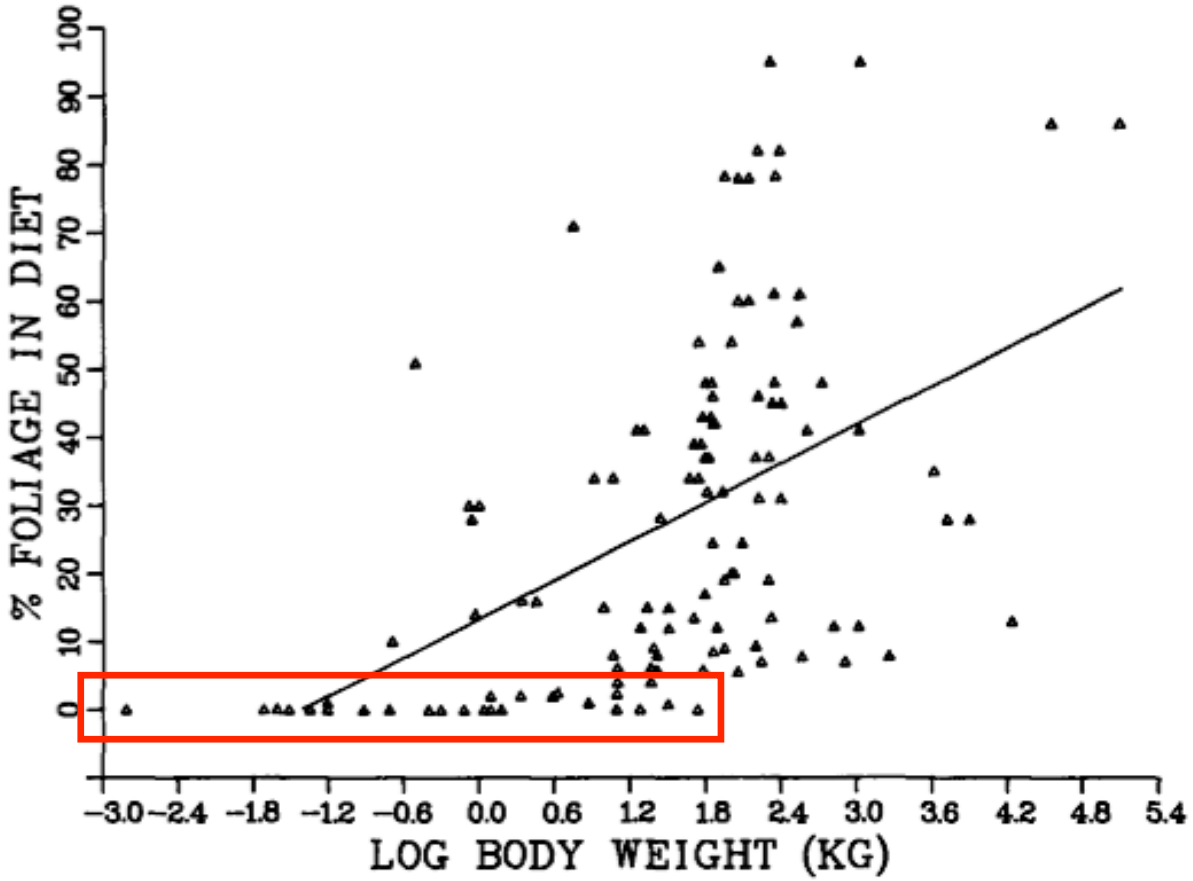


Fig. 1. Results of a least-squares regression of % foliage in the diet on log(body weight) for males and females of 72 primate species. The regression is significant ($p < .001$), but only 27.7% of the variance is explained.

from Sailer et al. (1985)

Body size and prey abundance



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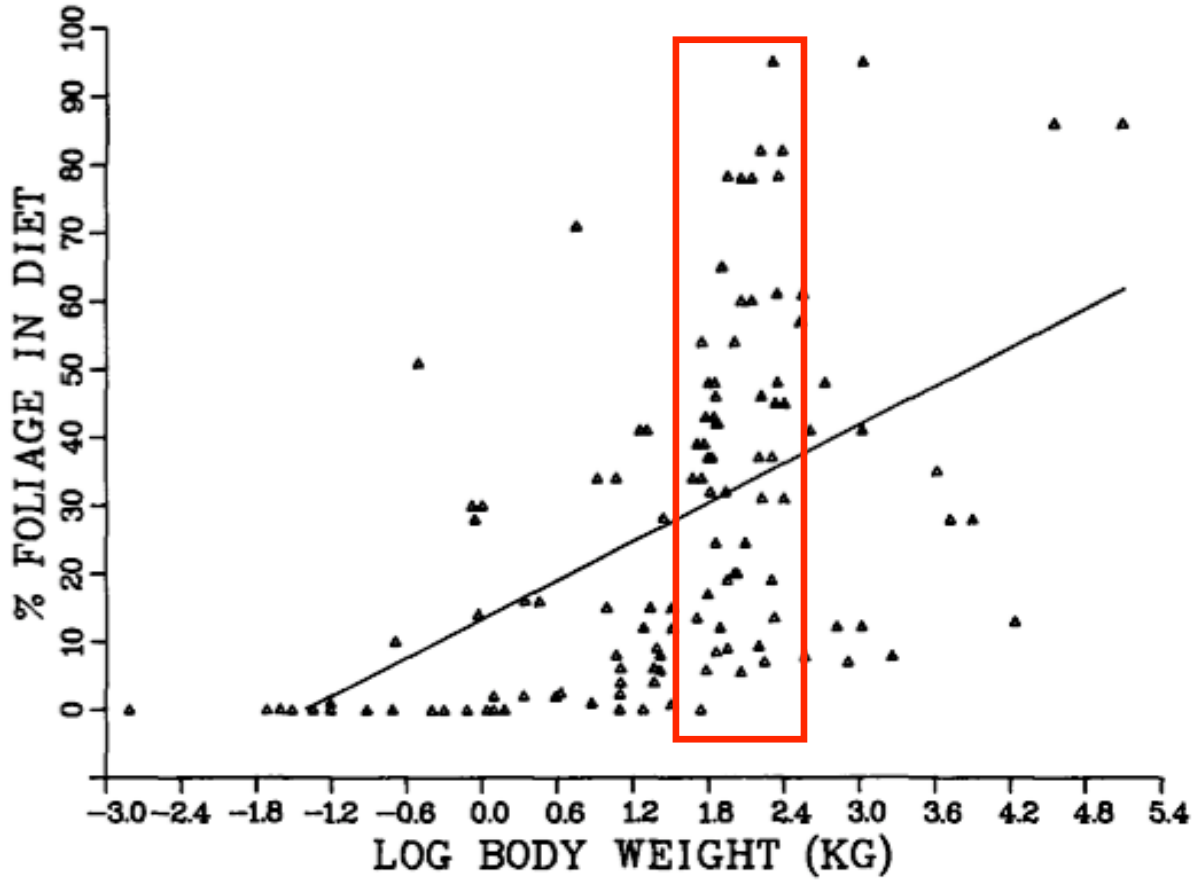

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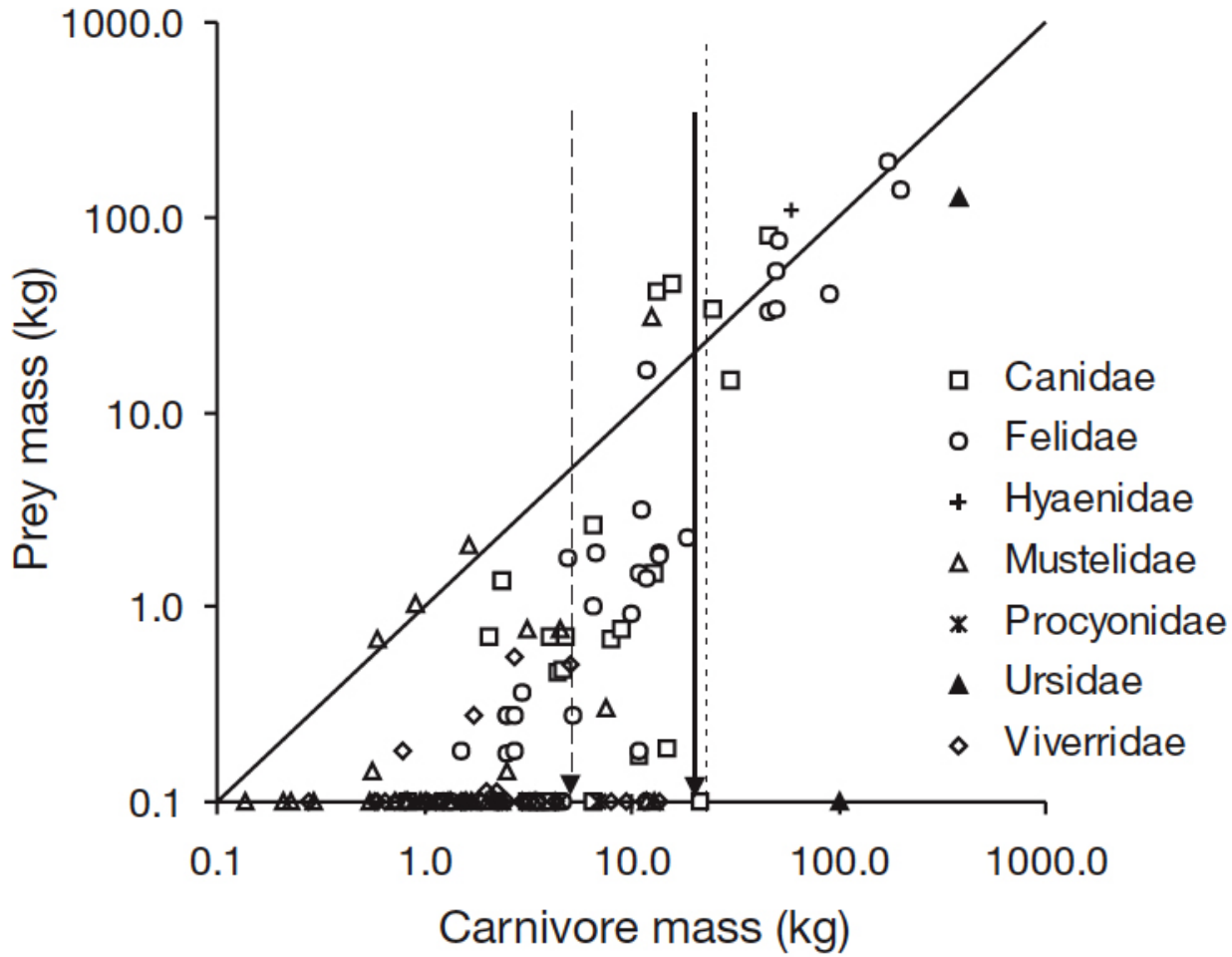
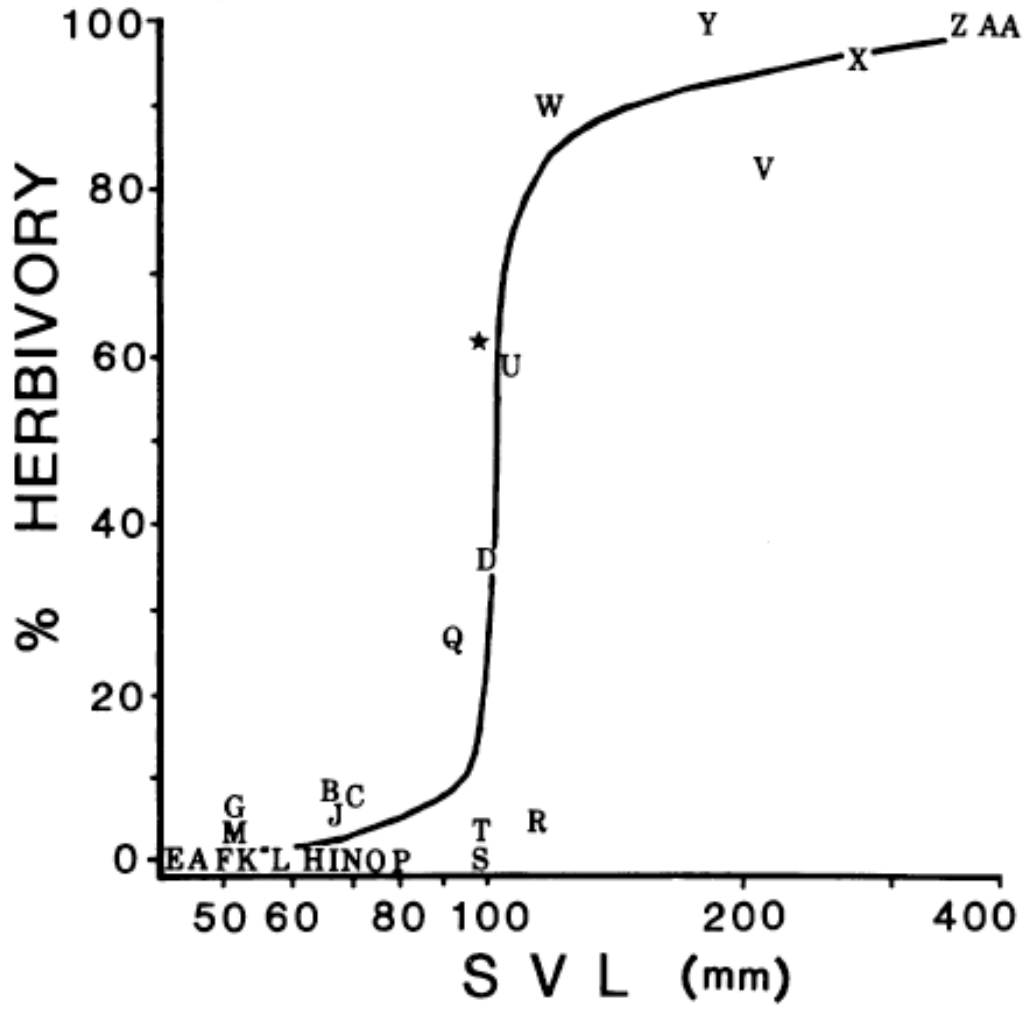


from Carbone et al. (1999)

Body size and prey abundance



from Schluter (1984)

Body size and diet quality

PRIMATES, 26(1): 14–27, January 1985

Measuring the Relationship Between Dietary Quality and Body Size in Primates

LEE DOUGLAS SAILER, STEVEN J. C. GAULIN, *University of Pittsburgh*
JAMES S. BOSTER, *Rensselaer Polytechnic Institute*
and JEFFREY A. KURLAND, *Pennsylvania State University*

ABSTRACT. The feeding niche and the body size of any species are fundamental parameters that constrain the evolution of many other phenotypic characters. Moreover, previous work has shown that body size and diet are correlated, as a consequence of the negative allometry of metabolic rate. Unfortunately, the precise form of the association between body size and diet has never been specified, principally because no suitable cross-species measure of diet has been advanced. Here we develop a measure of diet that is sensitive over the whole spectrum of primate feeding niches, and use this measure to define the relationship between body size and diet for a sample of 72 primate species. Subsequently, we present several examples of how behavioral and ecological hypotheses can be tested by examining the extent to which particular species deviate from the general diet-body size pattern.

Key Words: Primates; Jarman-Bell principle; Methods; Cross-species comparison; Feeding strategy.

Body size and diet quality

$$dq = 1s+2r+3.5a.$$

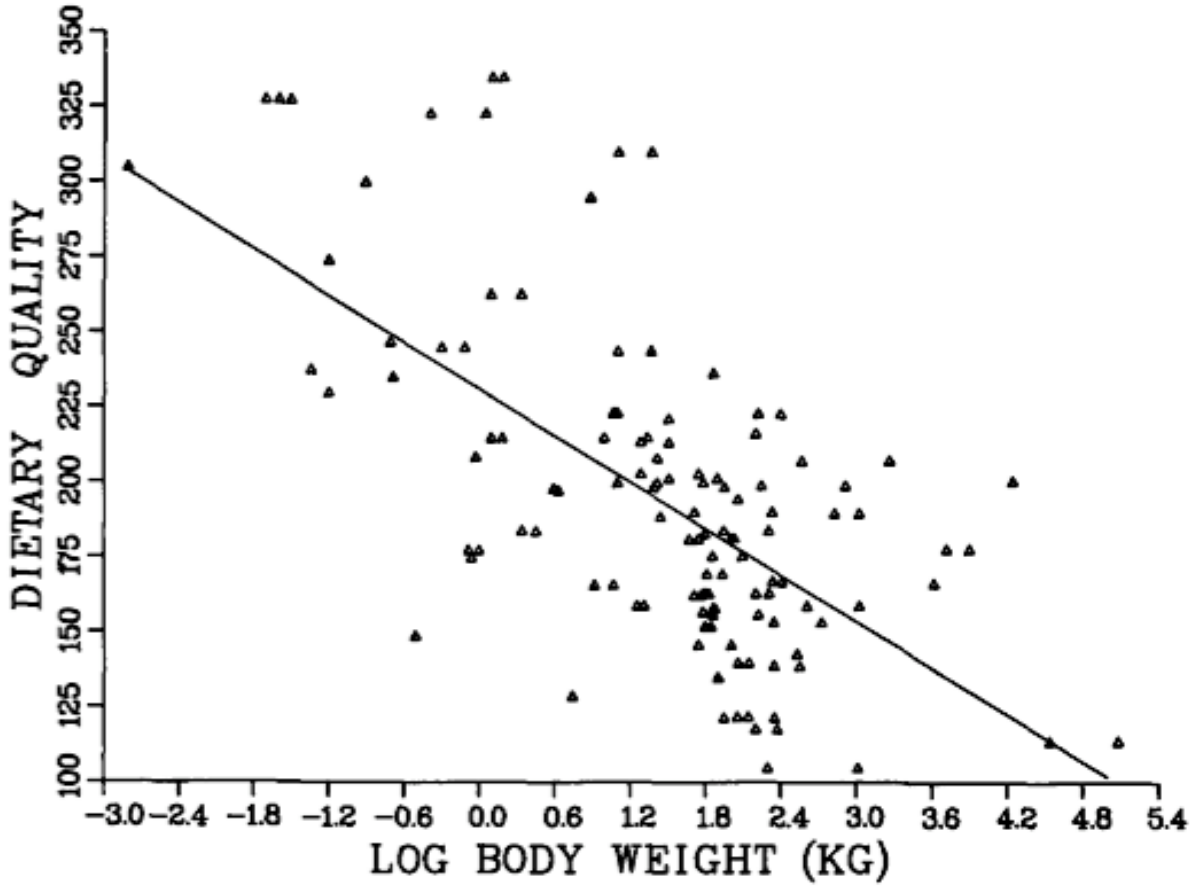
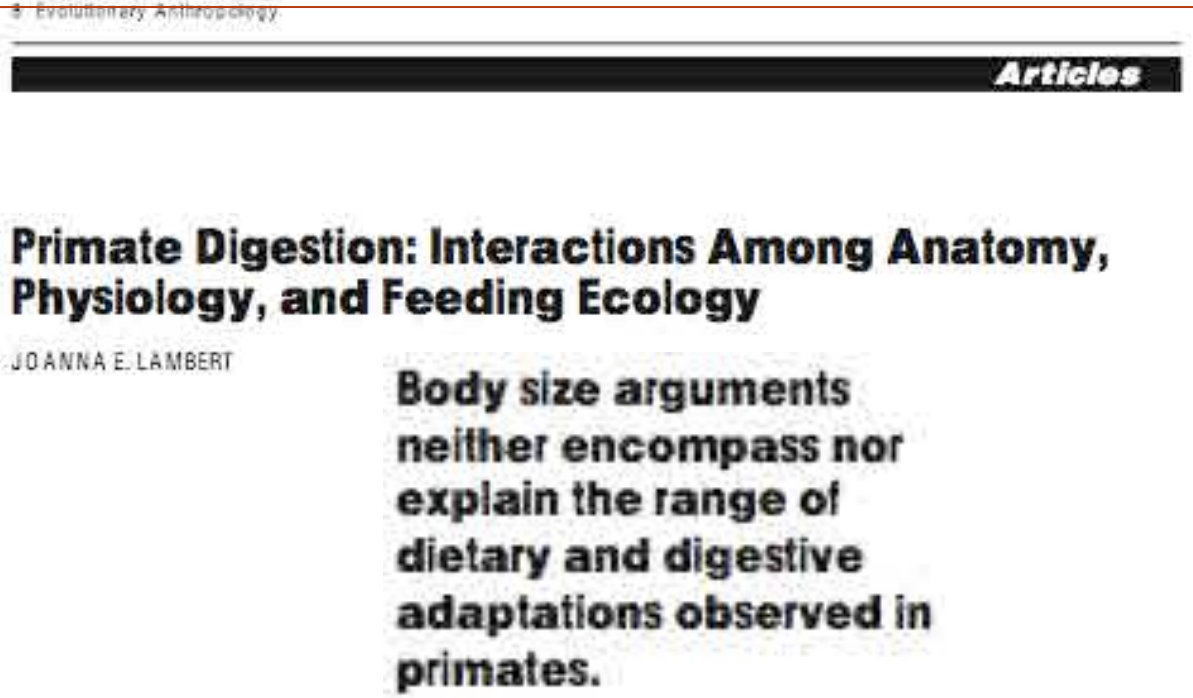


Fig. 2. Results of a least-squares regression of dq (as defined by equation 2) on log (body weight). The regression is significant ($p < .001$), and 43.3% of the variance is explained.

from Sailer et al. (1985)

Body size and primate digestion



Evolutionary Anthropology

Articles

Primate Digestion: Interactions Among Anatomy, Physiology, and Feeding Ecology

JOANNA E. LAMBERT

Body size arguments neither encompass nor explain the range of dietary and digestive adaptations observed in primates.

- Body size effects on digestive physiology might explain the advantage of a holwer monkey over a marmoset in terms of fibre fermentation, but it cannot be used to construe a digestive advantage of a gorilla over a howler!

Jarman-Bell

- Rather than stating "Large body size confers the advantage of being able to use more abundant food of lower quality", try:
- "At any body size, the food of the abundance necessary for the body size in question can be digested appropriately."

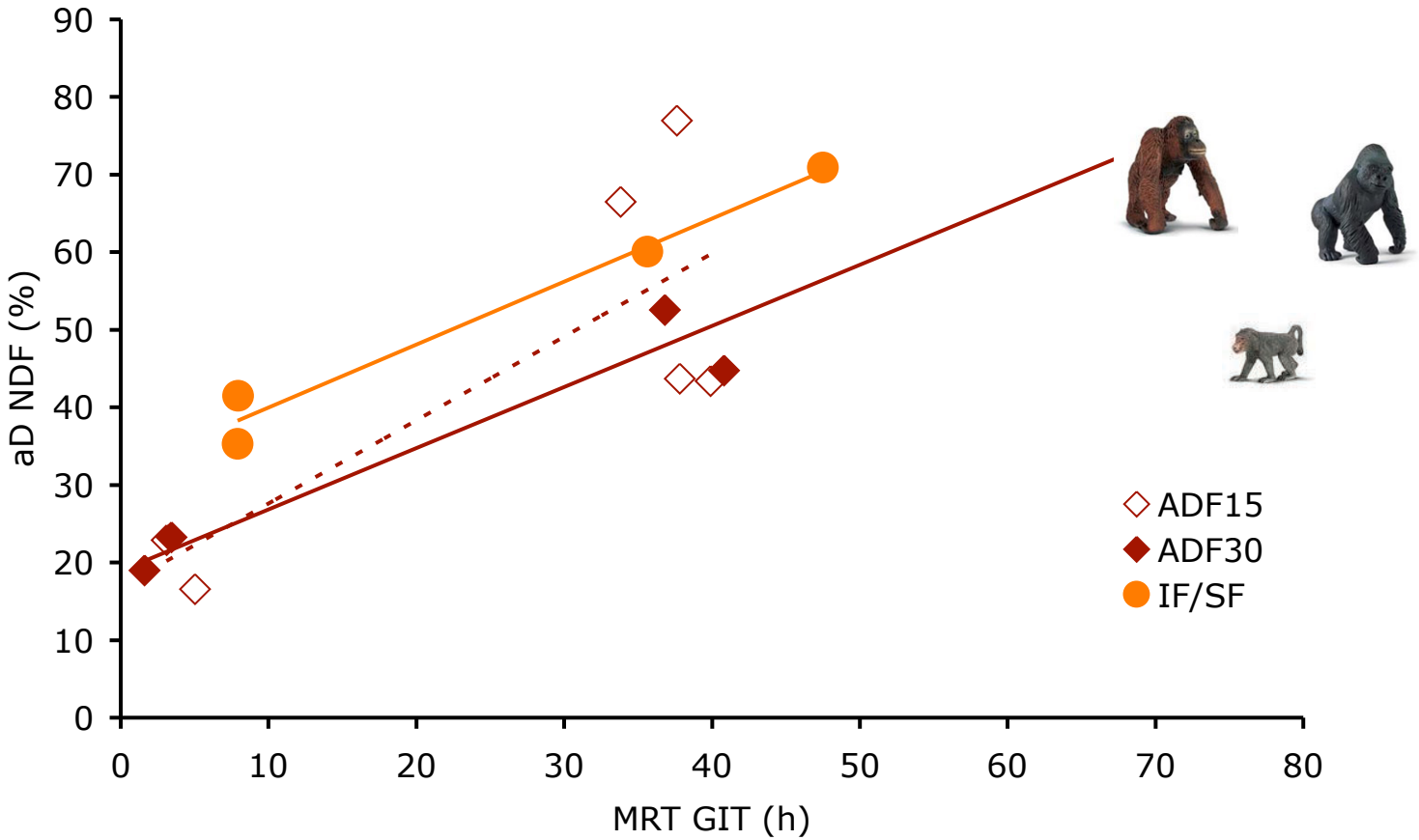
- Or, in other words:

  Rather than stating "Larger animals digest more efficiently", try:
- "Larger animals often have to ingest food of lower quality (but that's no problem)."

Digestive constraint II:

Generally low ‘digesta washing’ in primates?

Relevance of ingesta passage



from Clauss et al. (2008)

Body size and transit time

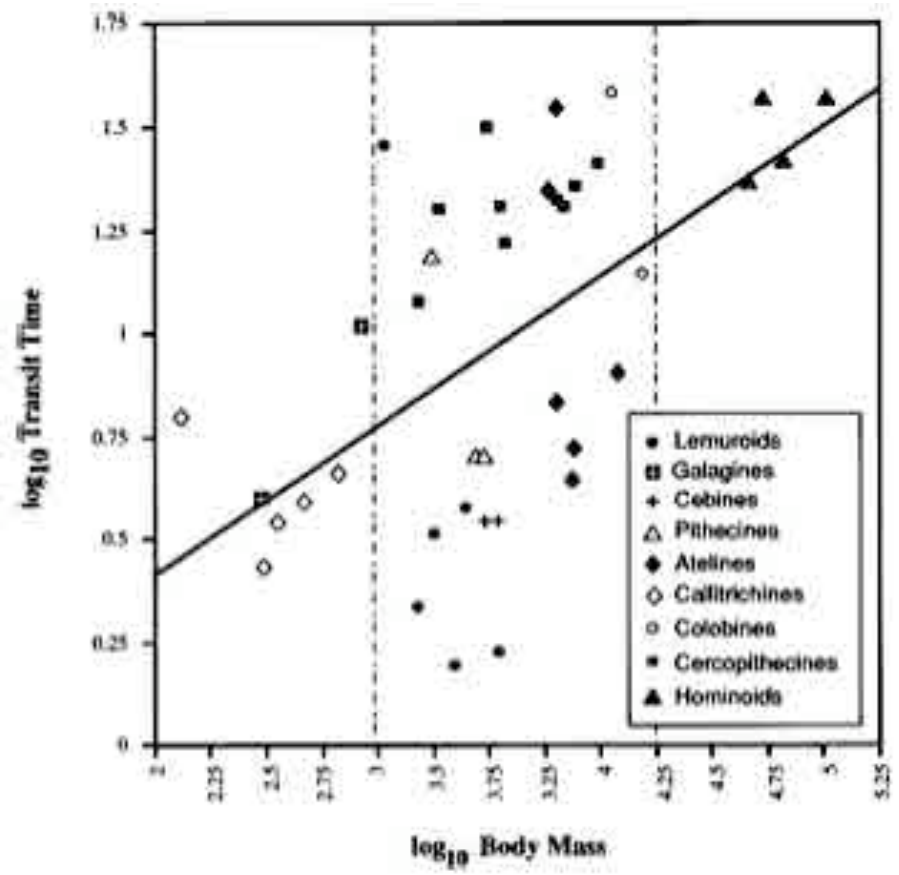
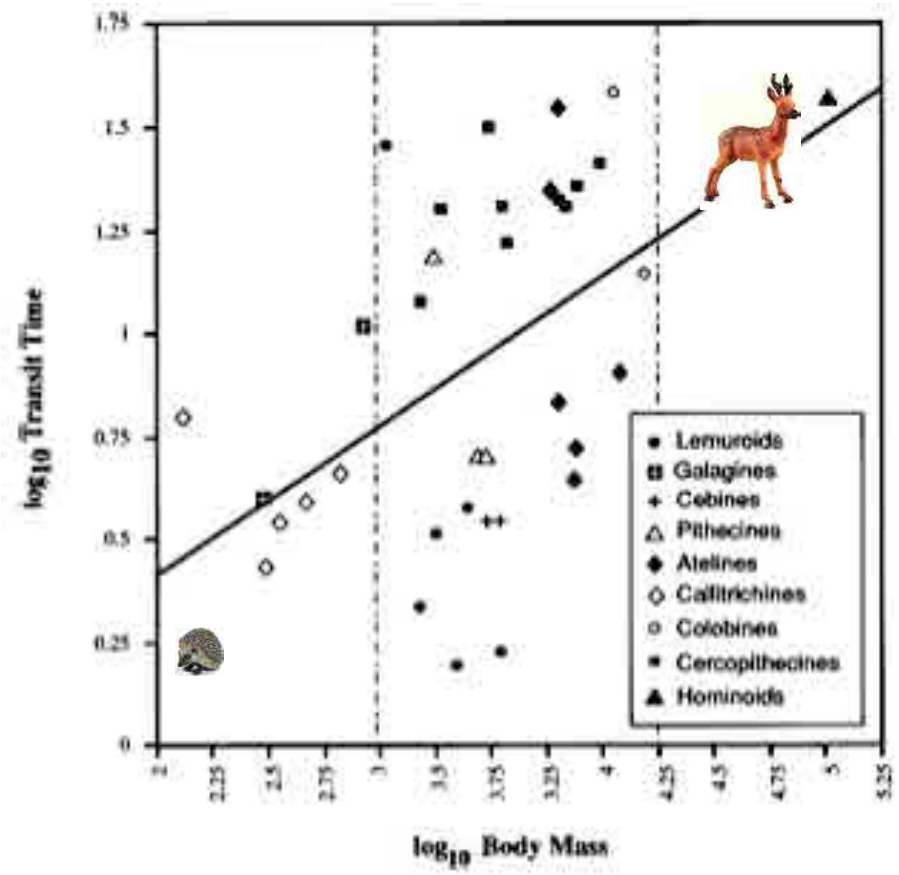


Figure 3 Relationship between body mass and digestive transit times across the primate order. Although there is a slight positive relationship between the two variables, the best fit line explains only 31% of the variance ($y = 0.36x - 0.31$, $r^2 = 0.31$), suggesting that some factor (e.g., diet) other than body size, or some combination of factors (e.g., absorption and processing constraints), more strongly influences transit times in primates. When the smallest (callitrichines, galagines) and largest (hominoids) primates are removed (as indicated by dotted line), note the variance in transit times within a given body mass range.

from Lambert (1998)

Body size and transit time



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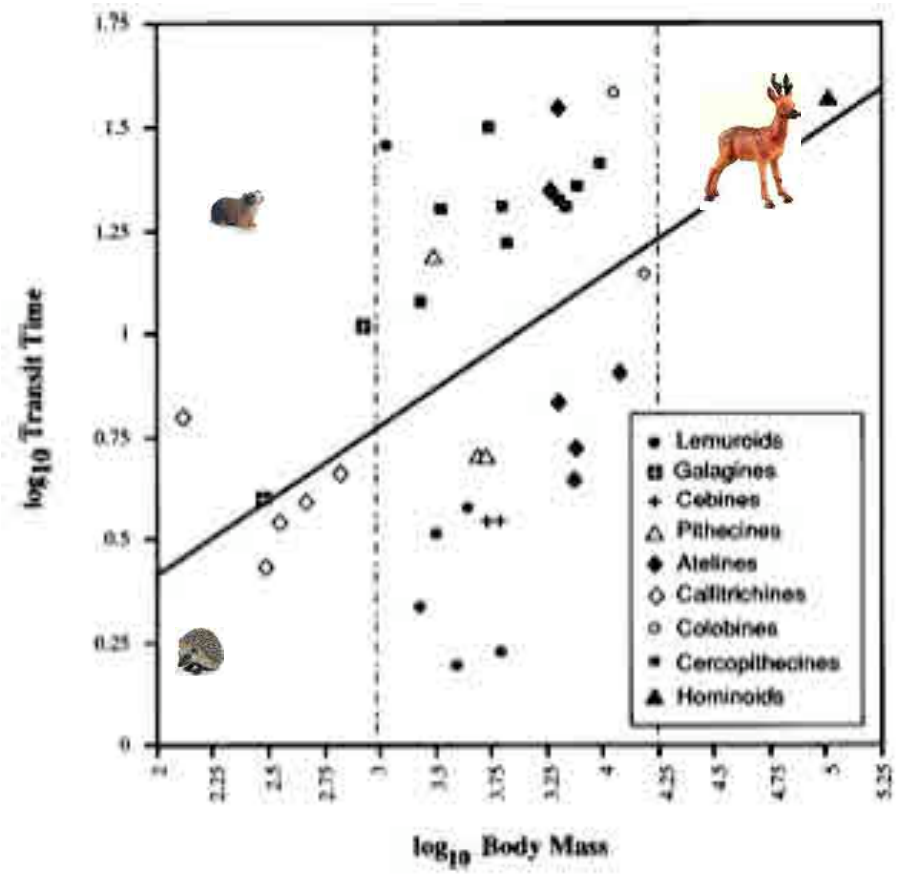

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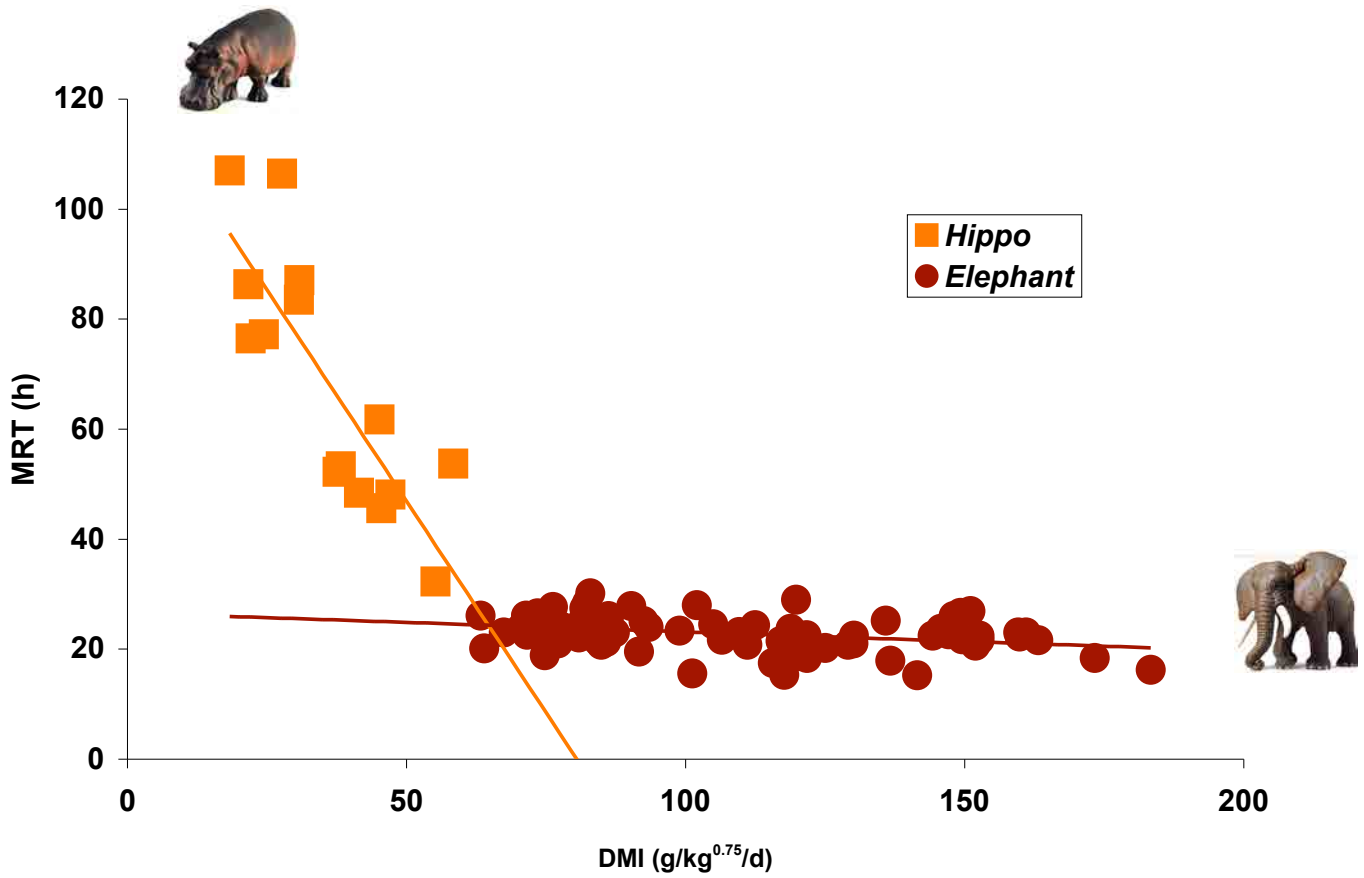
Retention time is not a fixture



Clauss et al. (2007)

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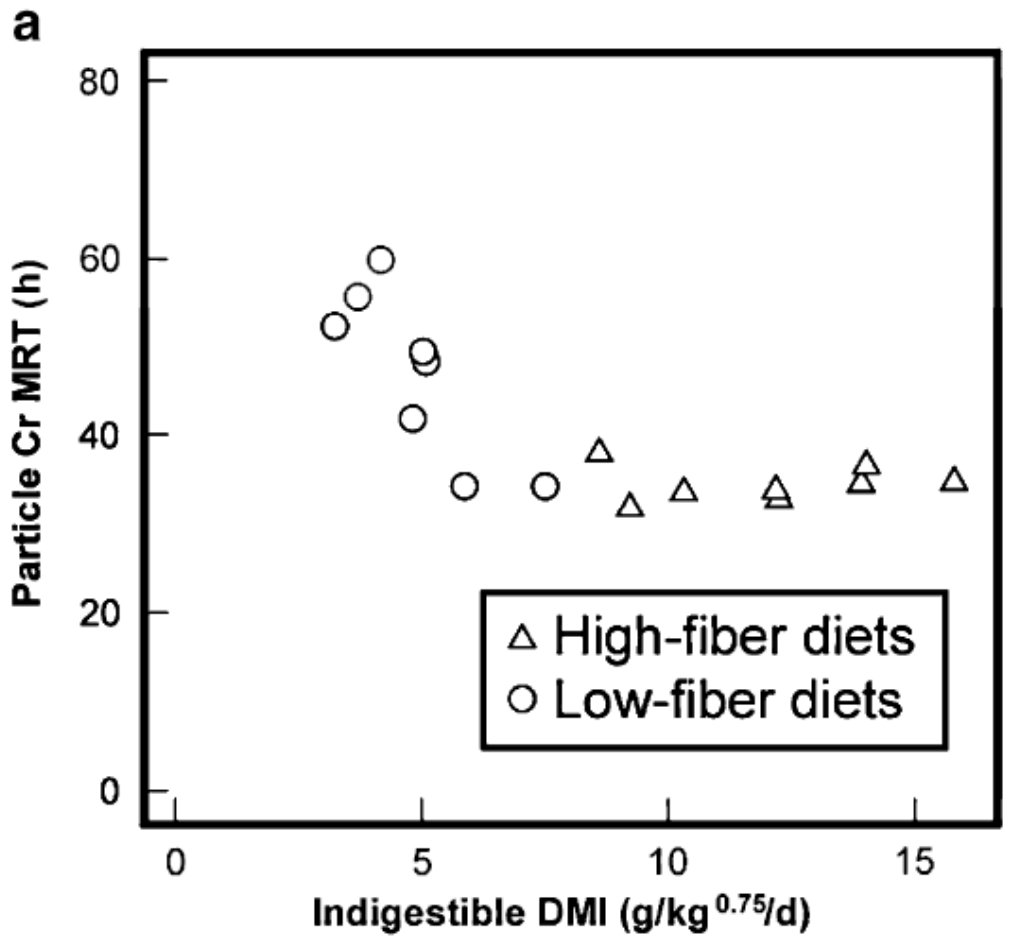
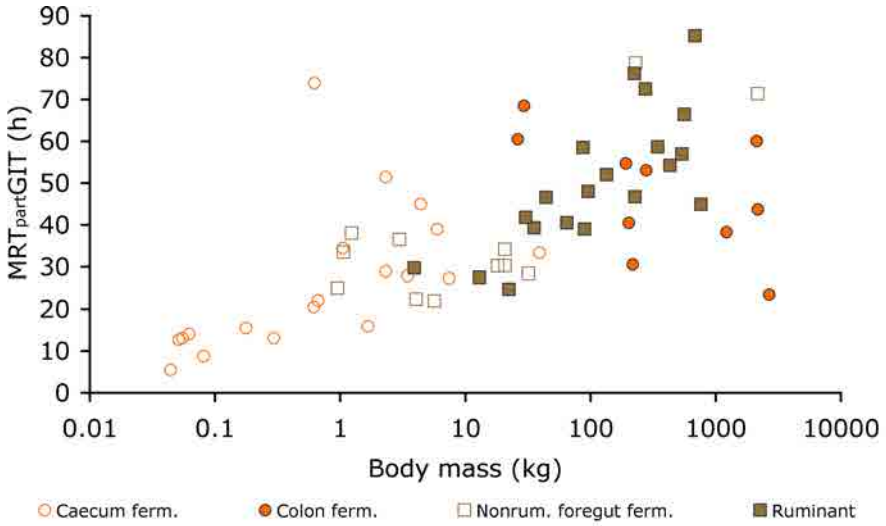
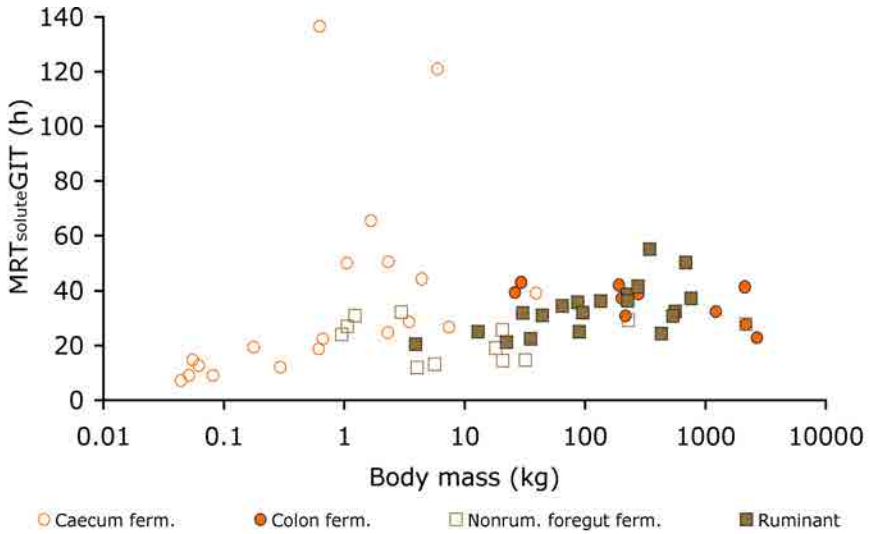


from Sawada et al. (2010)

Digesta passage patterns





from Müller et al. (2011)

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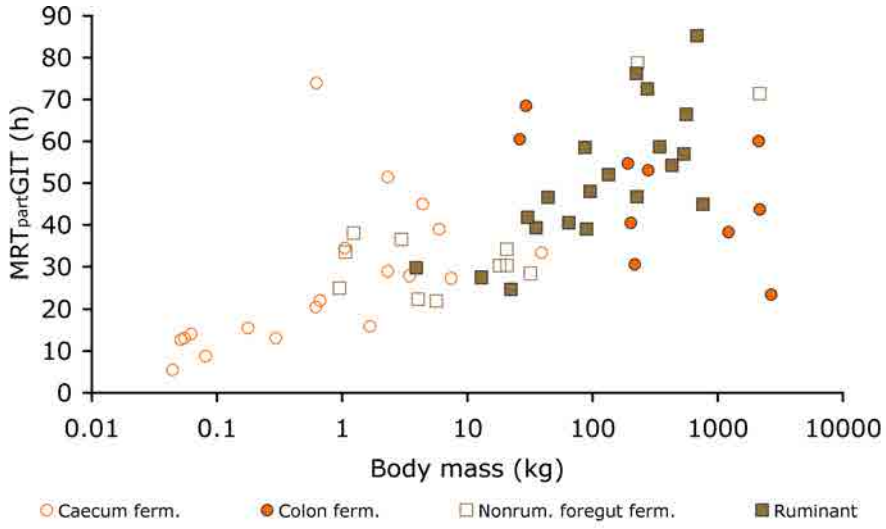

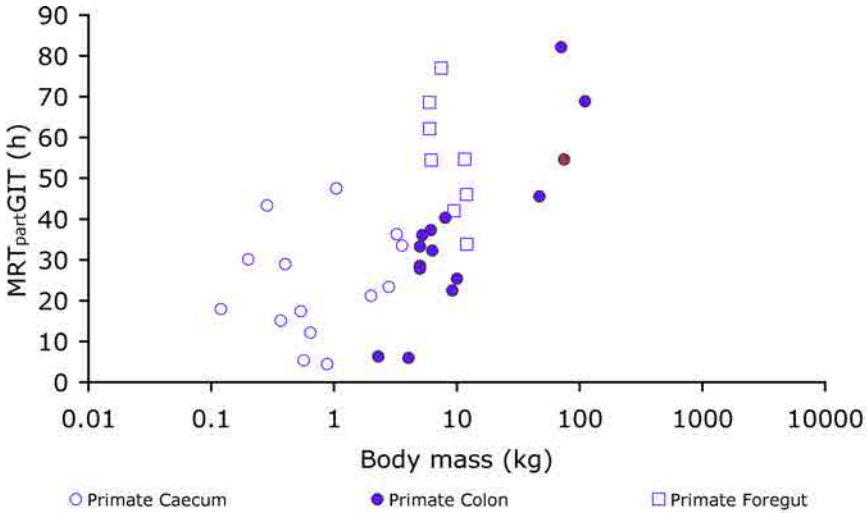

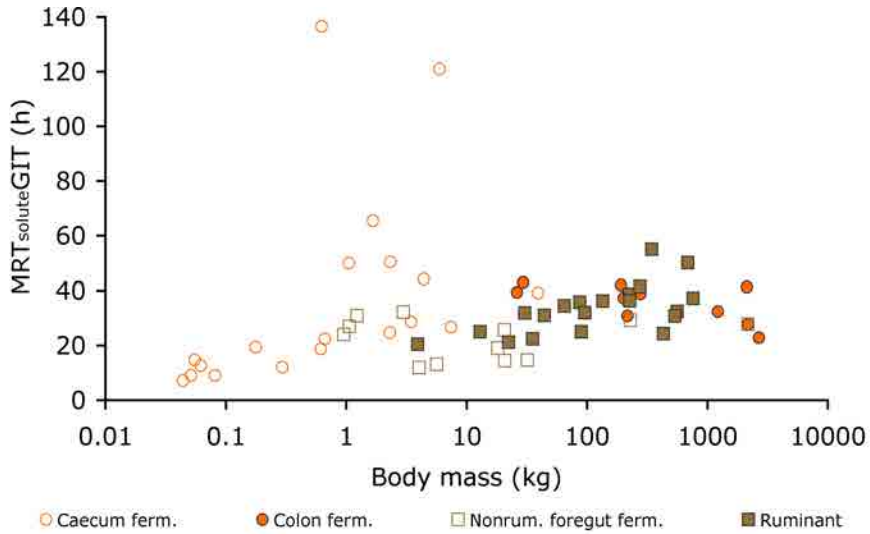

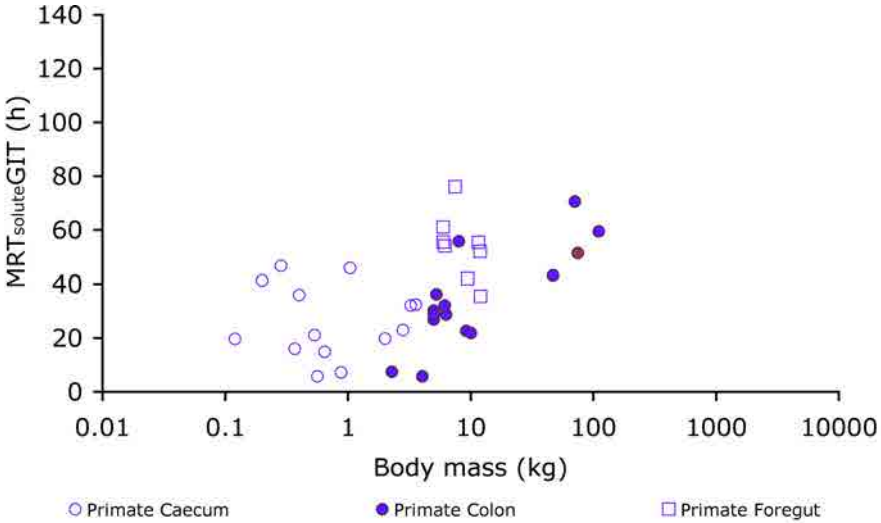

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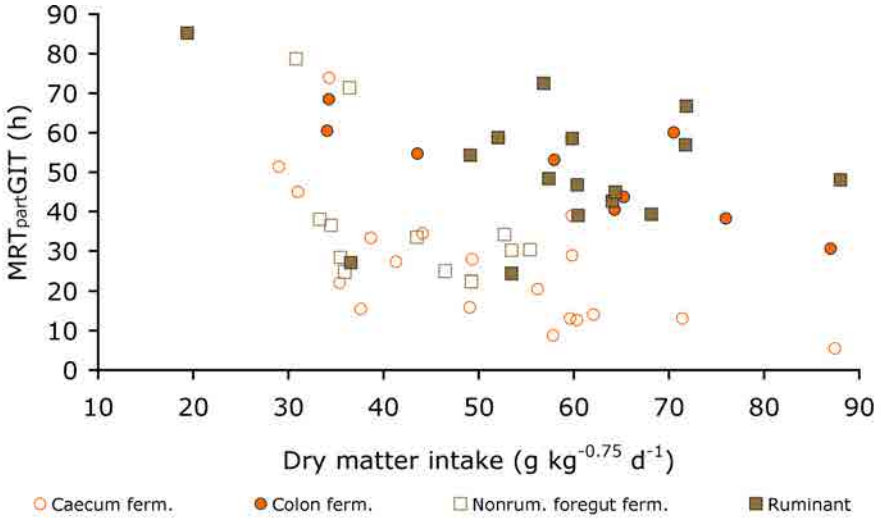

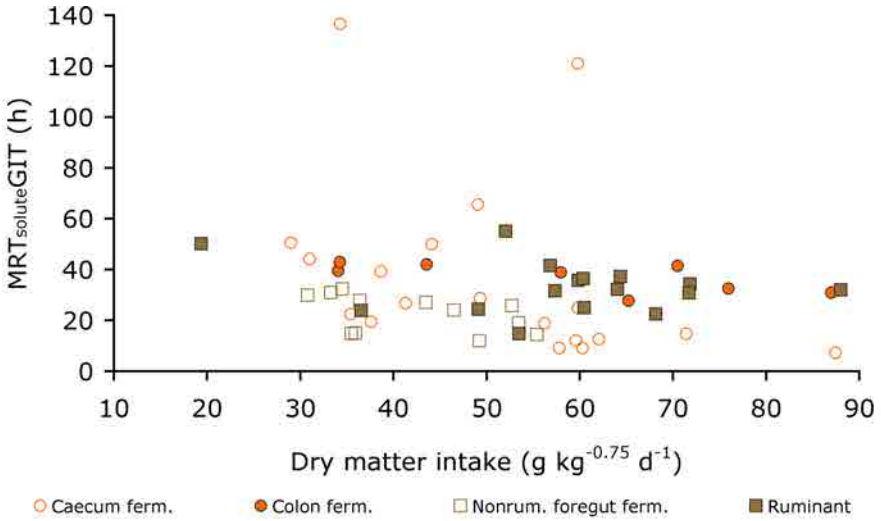

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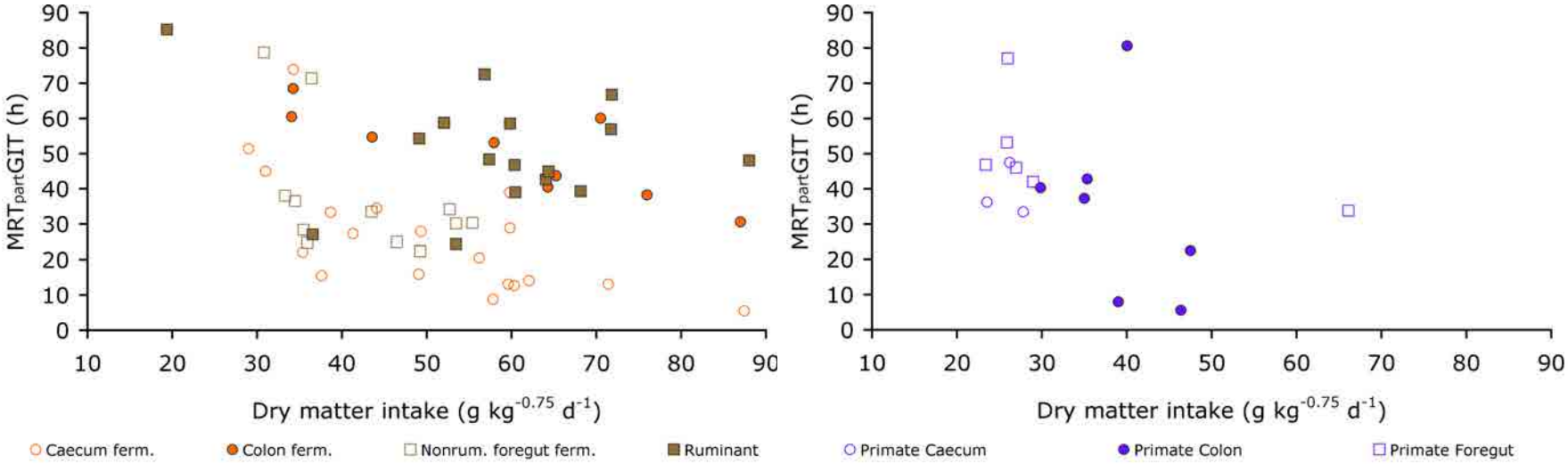

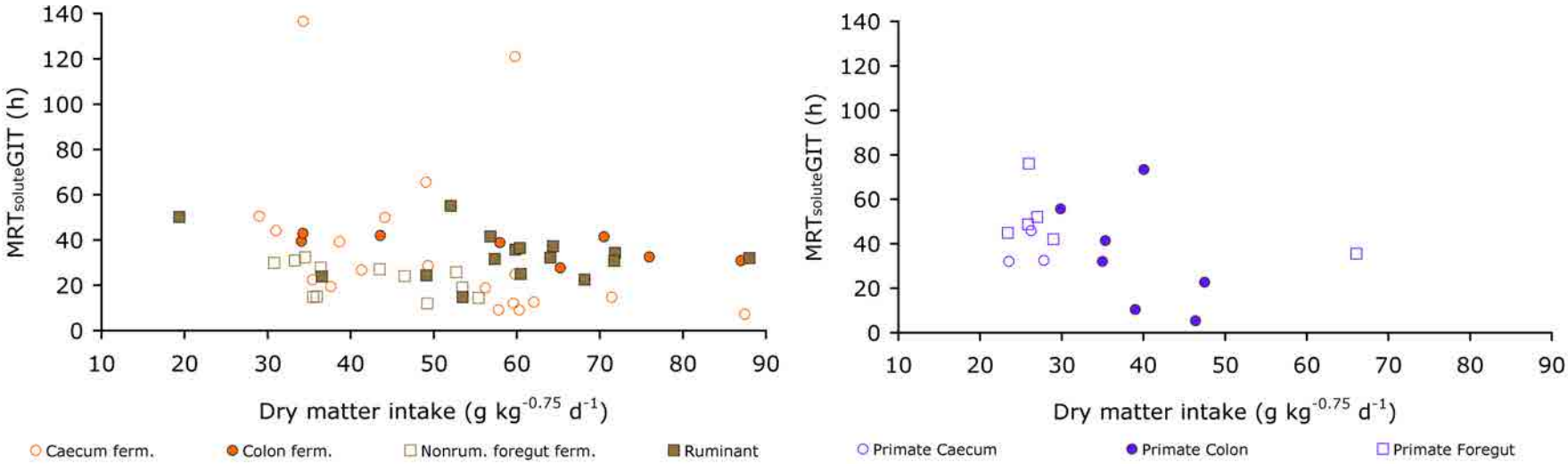

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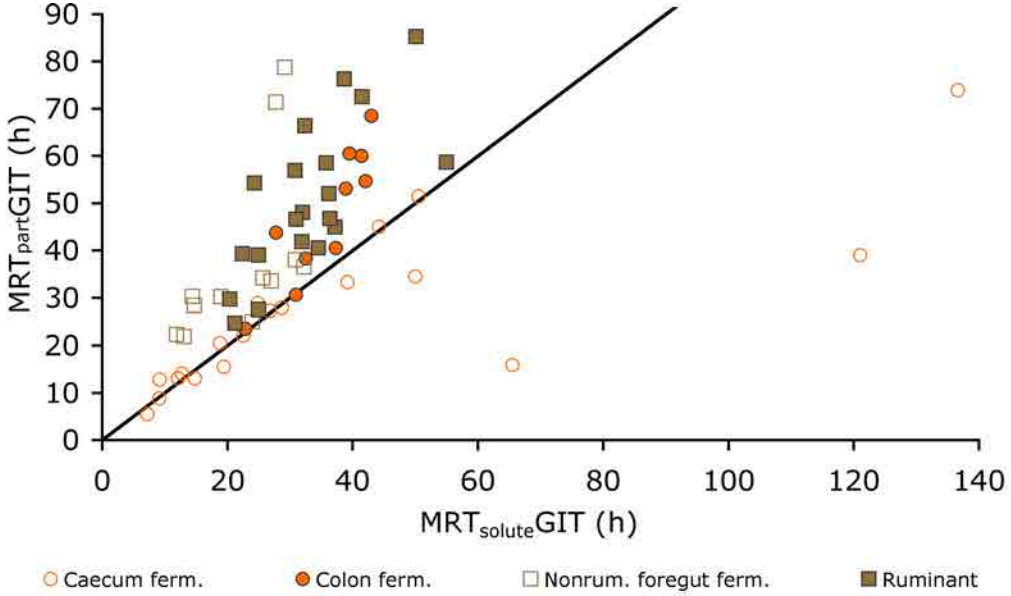
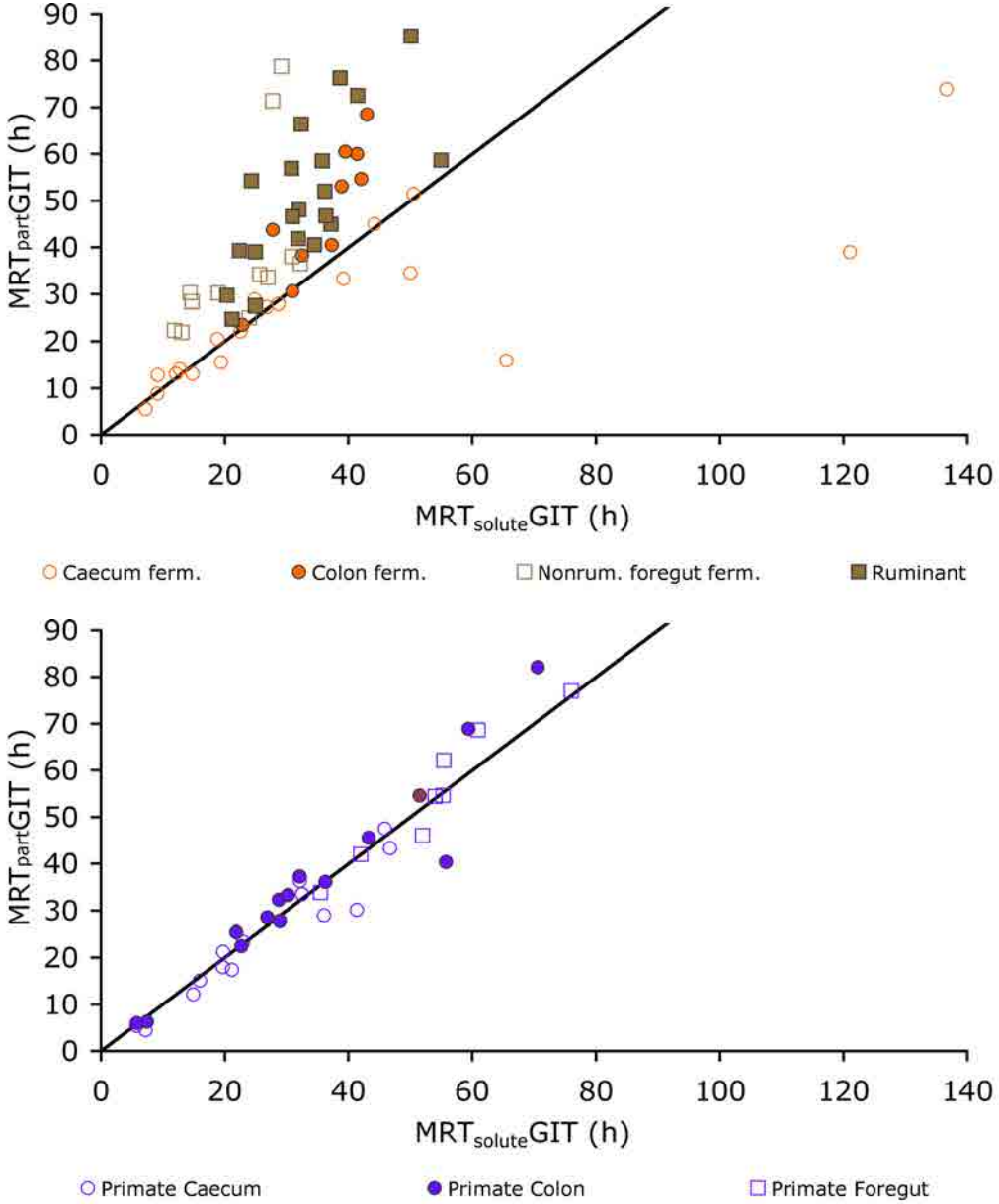
Digesta passage patterns



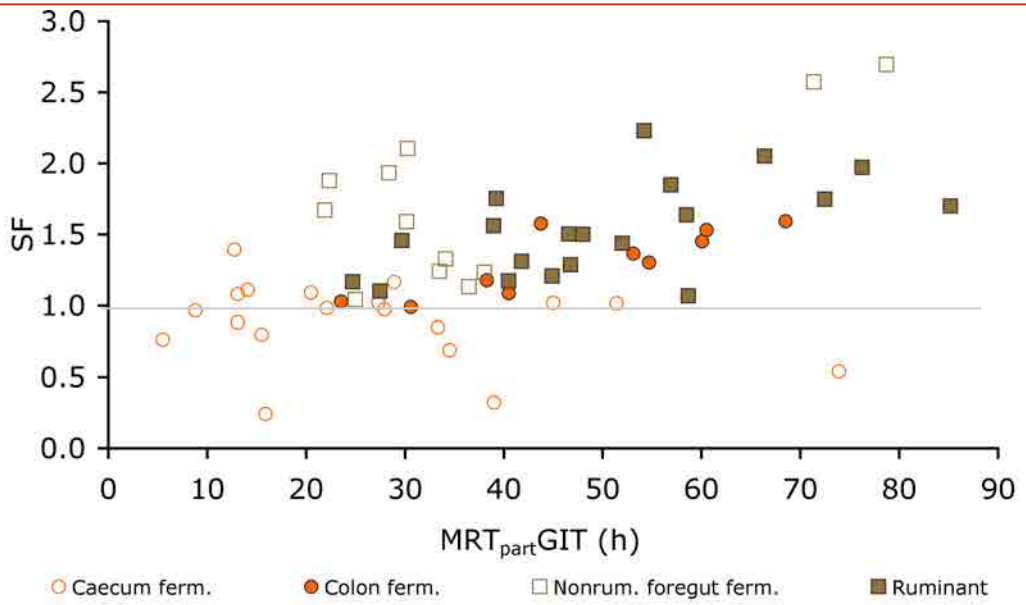
from Müller et al. (2011)

Digesta passage patterns



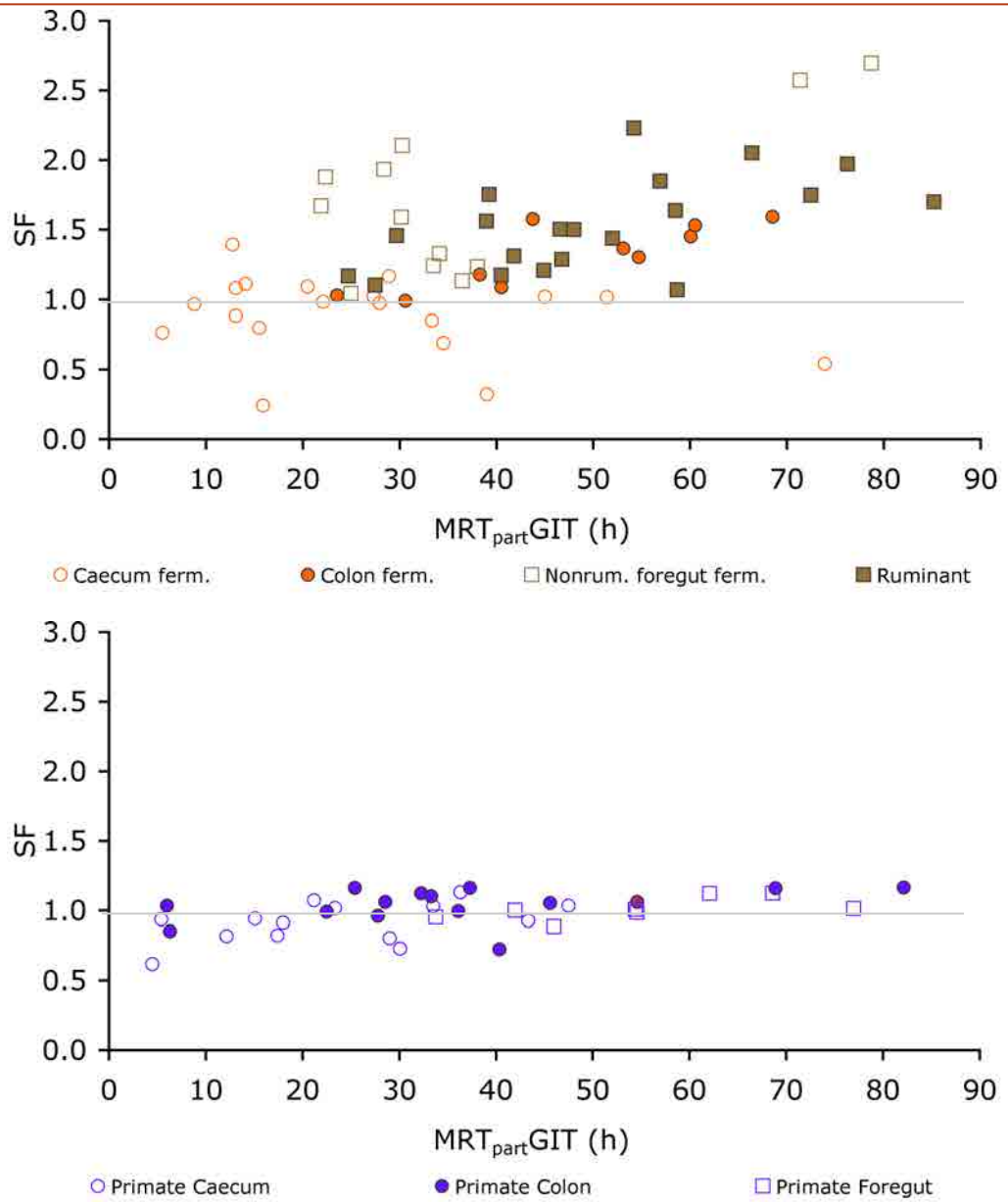
from Müller et al. (2011)

Digesta passage patterns



from Müller et al. (2011)

Digesta passage patterns



from Müller et al. (2011)

Digesta passage patterns

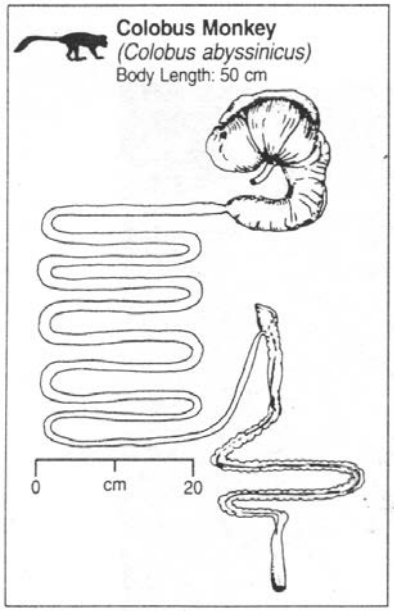
1. Primates appear to be limited in their digestive physiology insofar as they do not achieve a separation of fluid and particle movement in the gut ('digesta washing').
2. Digesta washing is considered an important adaptation to herbivory in groups such as ruminants or caecum fermenters.
3. Digesta washing is particularly considered an adaptation to grass-dominated diets.
4. Does the absence of digesta washing represent an evolutionary constraint in primates?

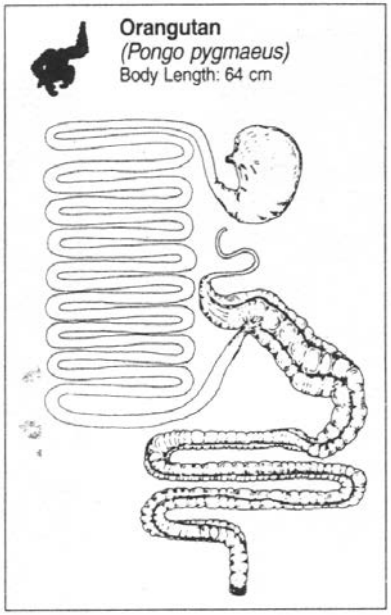
feeding your monkey

Feeding high-sugar/starch diets

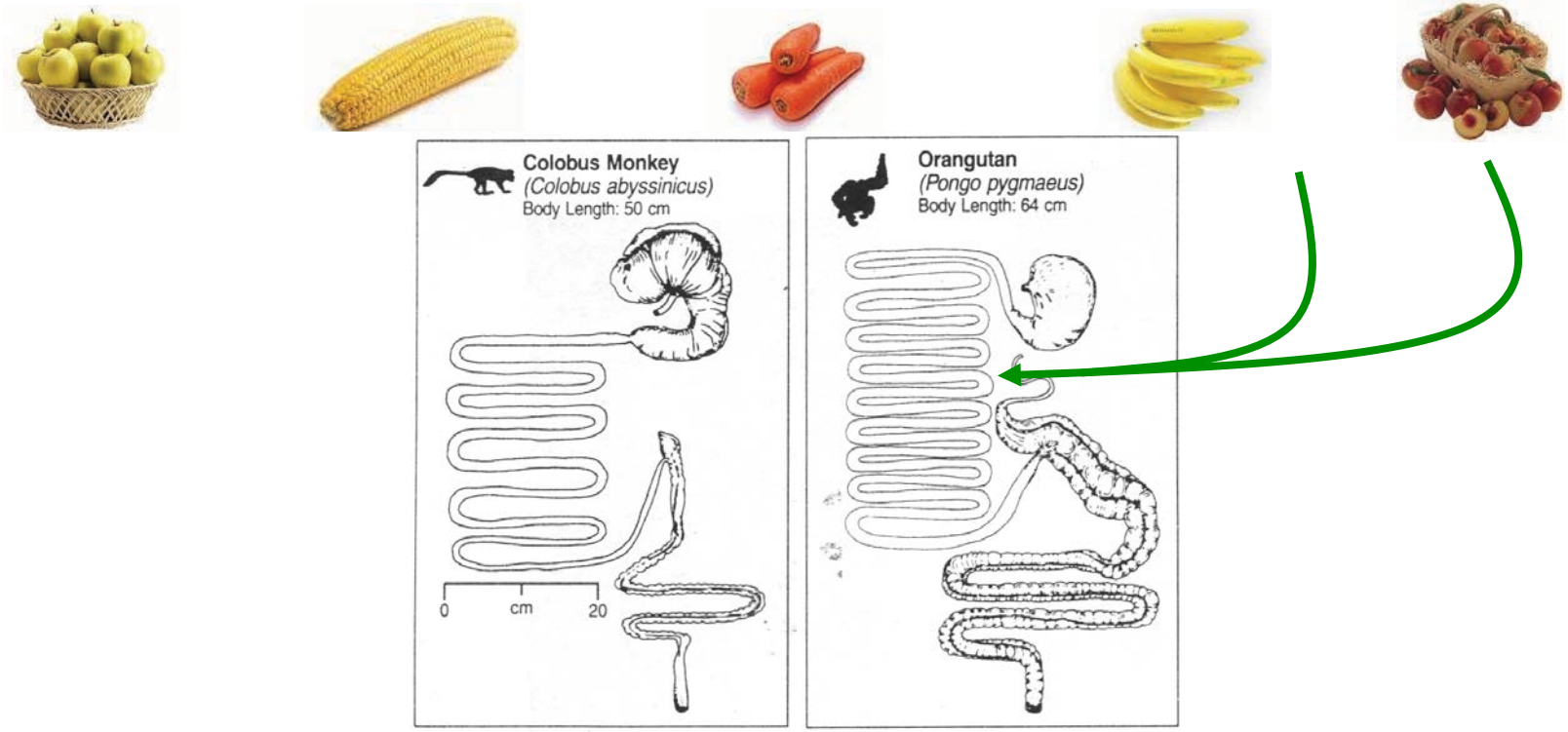








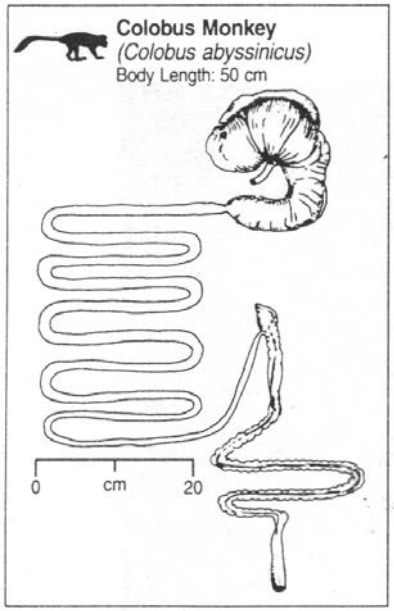
Feeding high-sugar/starch diets

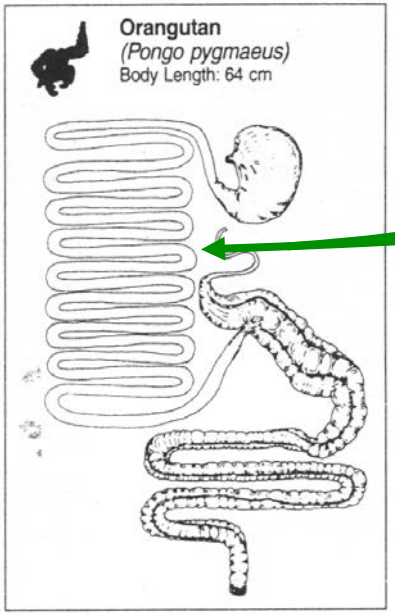


Feeding high-sugar/starch diets



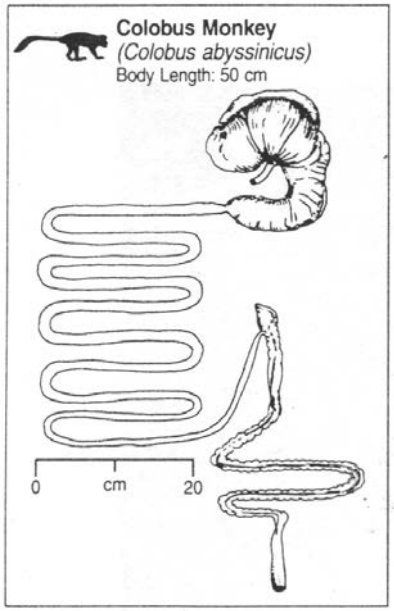


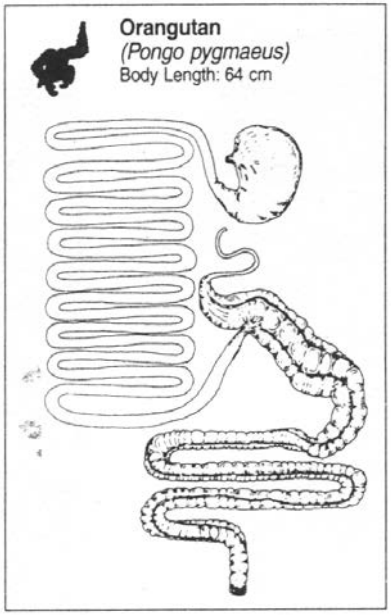


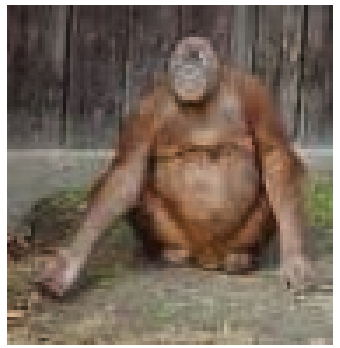


Easily digestible nutrients absorbed in small intestine => obesity

Feeding high-sugar/starch diets







cf. Schwitzer & Kaumanns (2001)

Obesity in primates

Int J Primatol (2007) 28:429–440
DOI 10.1007/s10764-007-9117-9

Factors Influencing the Well-Being and Longevity of Captive Female Orangutans

Leif Cocks

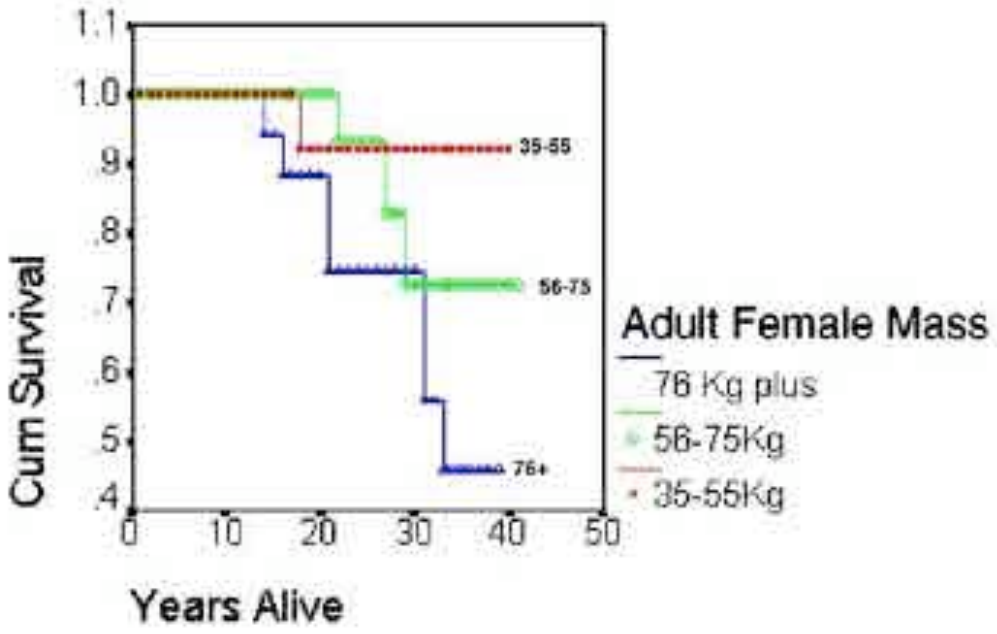
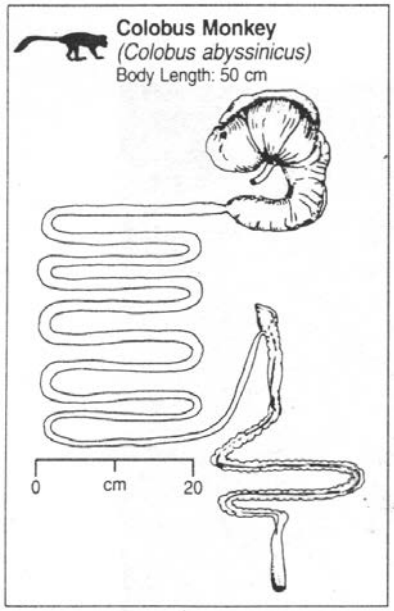


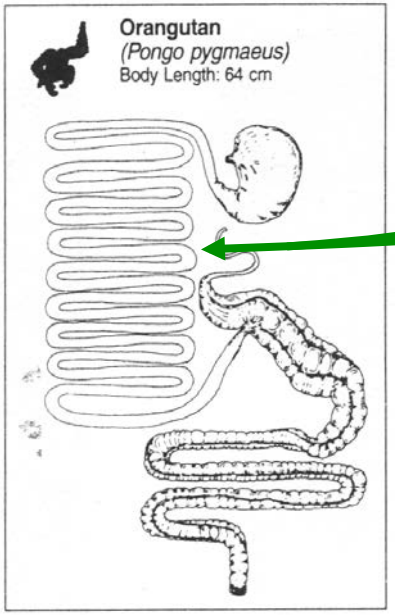
Fig. 12 Survival vs. female weight.

Feeding high-sugar/starch diets









Easily digestible nutrients absorbed in small intestine => obesity

Only at very excessive amounts: 'caecum acidosis', diarrhoea, laminitis

Polymerase chain reaction detection of *Clostridium perfringens* in feces from captive and wild chimpanzees, *Pan troglodytes*

Shiho Fujita[1] & Takashi Kageyama[2]

J Med Primatol **36** (2007) 25–32

Table 2 Detection of *Clostridium perfringens* in feces of captive chimpanzees

Subject	Sex	Age	Birth	No. of samples tested	First PCR	Nested PCR	Not detected
Ai[1]	Female	24 years	Wild	1	1	0	0
Pendesa	Female	23 years	Captive[2]	1	0	0	1
Chloé	Female	19 years	Captive[4]	4	3	1	0
Reo	Male	18 years	Captive[3]	2	0	1	1
Ayumu[1]	Male	5 months	Captive[3]	2	1	1	0
Total (%)				10	5 (50)	3 (30)	2 (20)

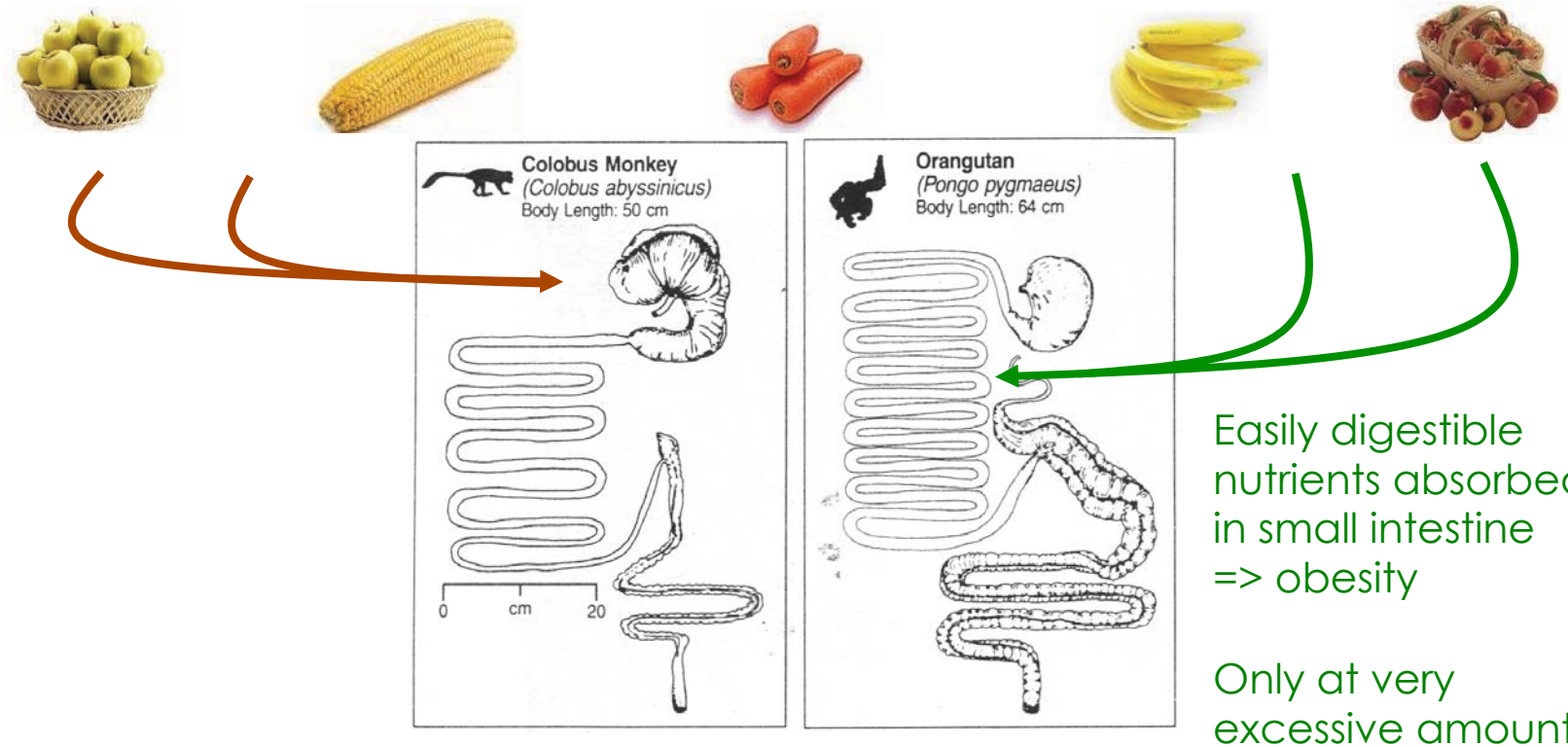
[1]Ai and Ayumu are a mother–infant pair.
[2]Japan Monkey Center.
[3]Primate Research Institute.
[4]Parc Zoologique de Paris.

Table 3 Detection of *Clostridium perfringens* in feces of wild chimpanzees

Site	Season	No. of samples tested	First PCR	Nested PCR	Not detected
Mahale	Dry	16	0 (0.0)[1]	1 (6.3)	15 (93.7)
	Wet (I and II)	65	0 (0.0)	0 (0.0)	65 (100.0)
	Total	81	0 (0.0)	1 (1.3)	80 (98.7)
Bossou	Dry	23	1 (4.3)	2 (8.7)	20 (87.0)
	Wet	30	5 (16.7)	4 (13.3)	21 (70.0)
	Total	53	6 (11.3)	6 (11.3)	41 (77.4)

[1]The values in parentheses show percentages.

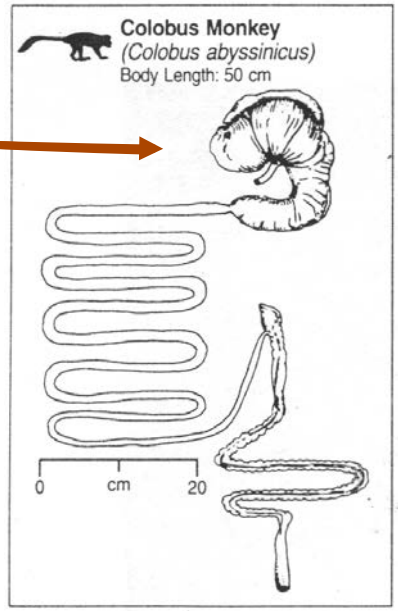
Feeding high-sugar/starch diets

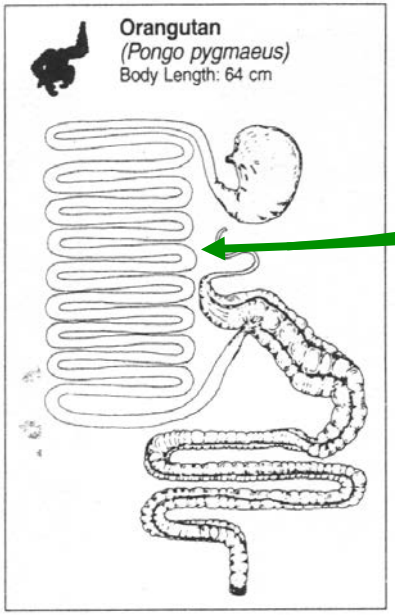


Easily digestible nutrients absorbed in small intestine => obesity

Only at very excessive amounts: 'caecum acidosis', diarrhoea, laminitis

Feeding high-sugar/starch diets



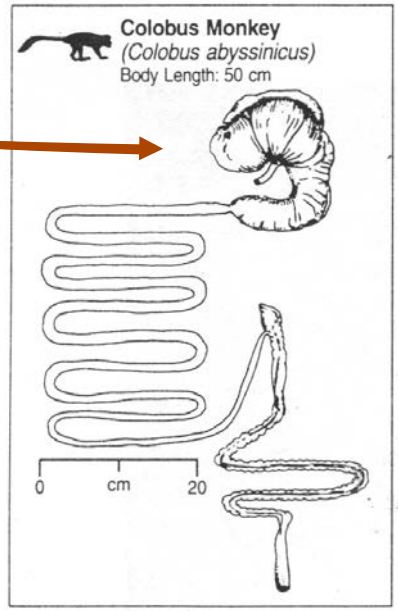


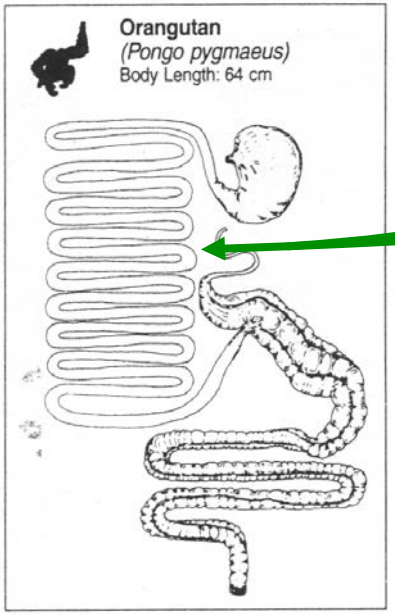
Easily digestible nutrients enter the fermentation chamber
⇒'malfermentation'

Easily digestible nutrients absorbed in small intestine
=> obesity

Only at very excessive amounts: 'caecum acidosis', diarrhoea, laminitis

Feeding high-sugar/starch diets





Easily digestible nutrients enter the fermentation chamber
⇒'malfermentation'

Low food intake
Laminitis
Liver abscess
Reduced lifespan?
Diarrhoea
Oral stereotypies

Easily digestible nutrients absorbed in small intestine
=> obesity

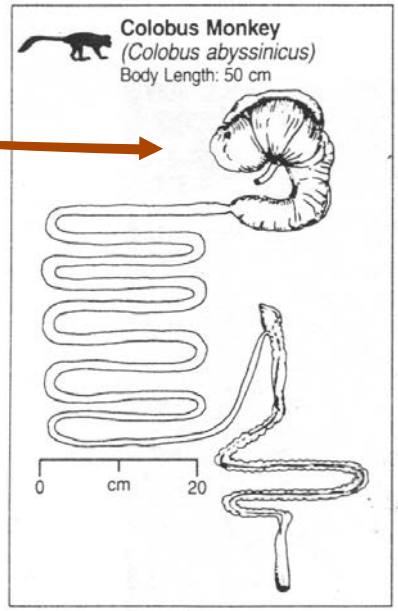
Only at very excessive amounts: 'caecum acidosis', diarrhoea, laminitis

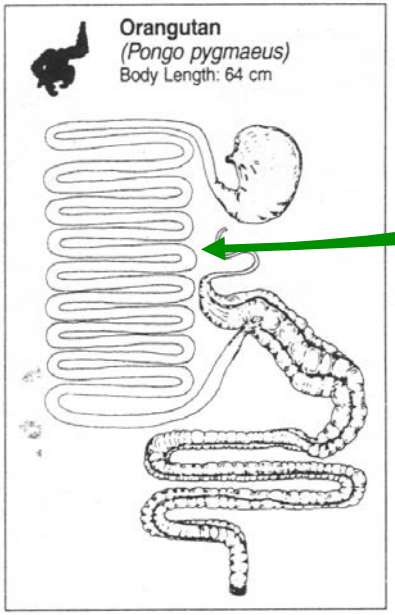
Feeding high-sugar/starch diets





Easily digestible nutrients enter the fermentation chamber
=>
'malfermentation'





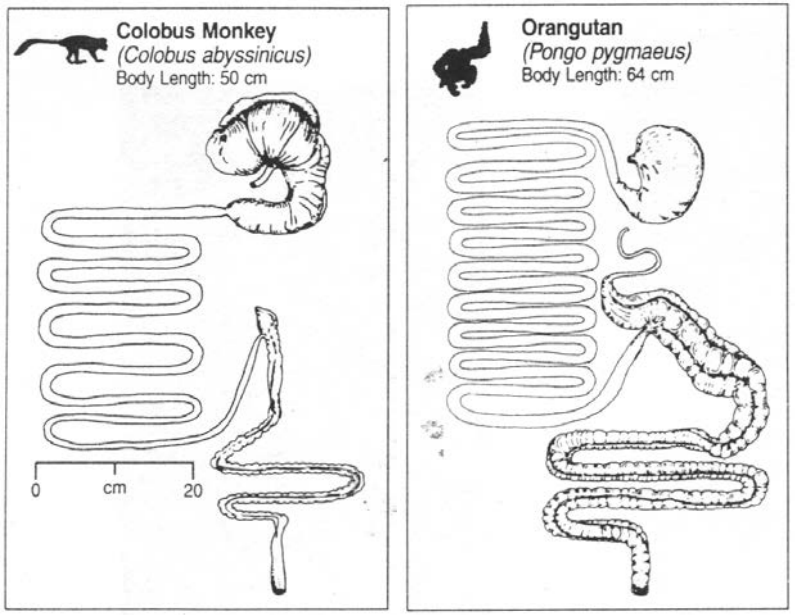
Easily digestible nutrients absorbed in small intestine
=> obesity

Thin, unthrifty langurs

Obese lemurs

cf. Schwitzer & Kaumanns (2001)

Feeding high-sugar/starch diets



Monkey zoo diet 1878

- Milk, sugar and soft bread
- Cooked rice, potatoes, carrots
- Fruits, nuts, almonds
- Tea, coffee, beer, wine
- Fried meat should be investigated!
- 1 cigar

Martin PF (1878) Die Praxis der Naturgeschichte. Weimar

thank you
for your attention