Introduction to digestive physiology

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Bio 122 2013

University of Zurich
Vetsuisse Faculty

Clinic
of Zoo Animals, Exotic Pets and Wildlife

getting the food

-

the availability of sufficient amounts of available packages

Getting the food

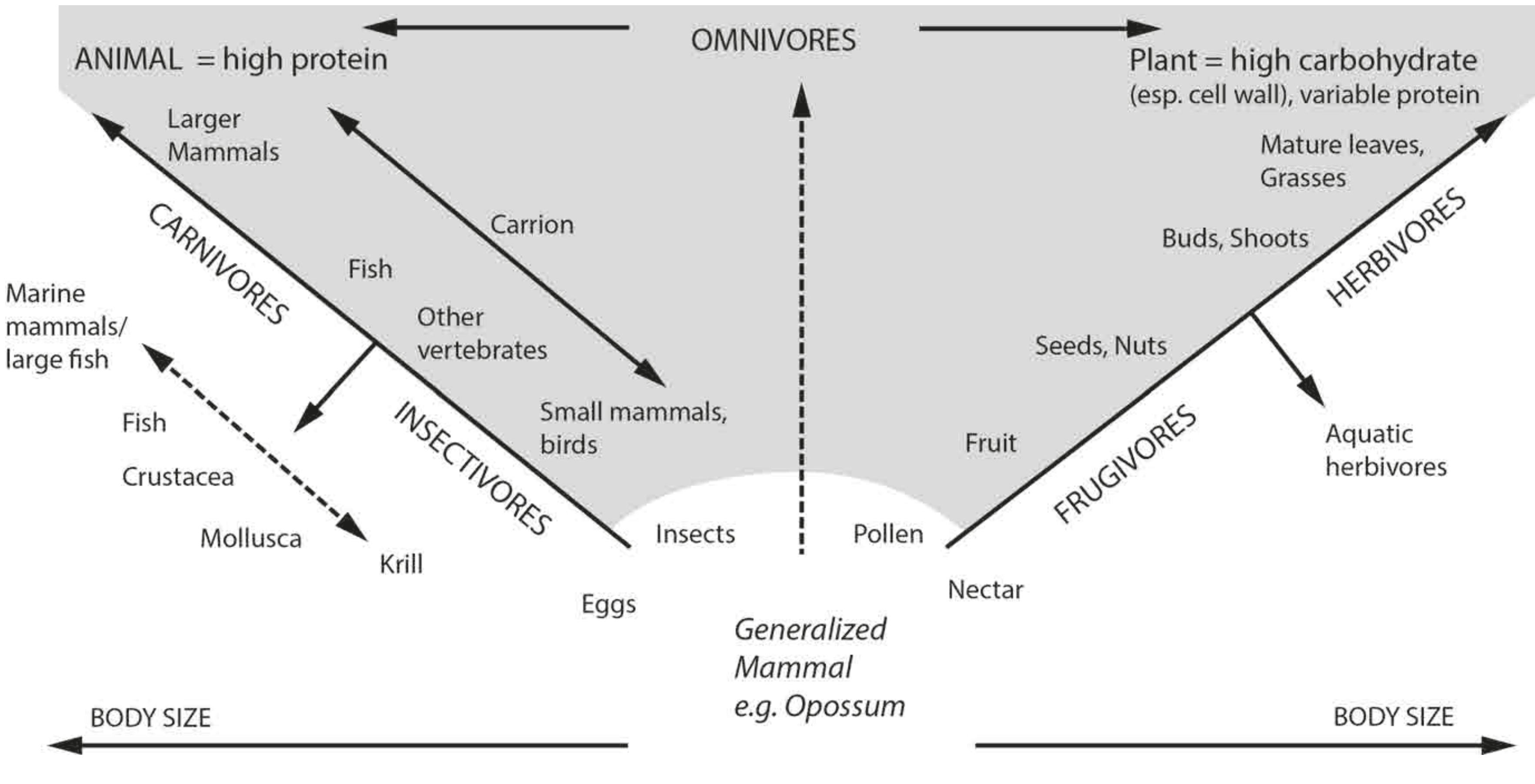
- *Catching prey is (often) the hard part!*



- *Catching plants is (mostly) easy!*

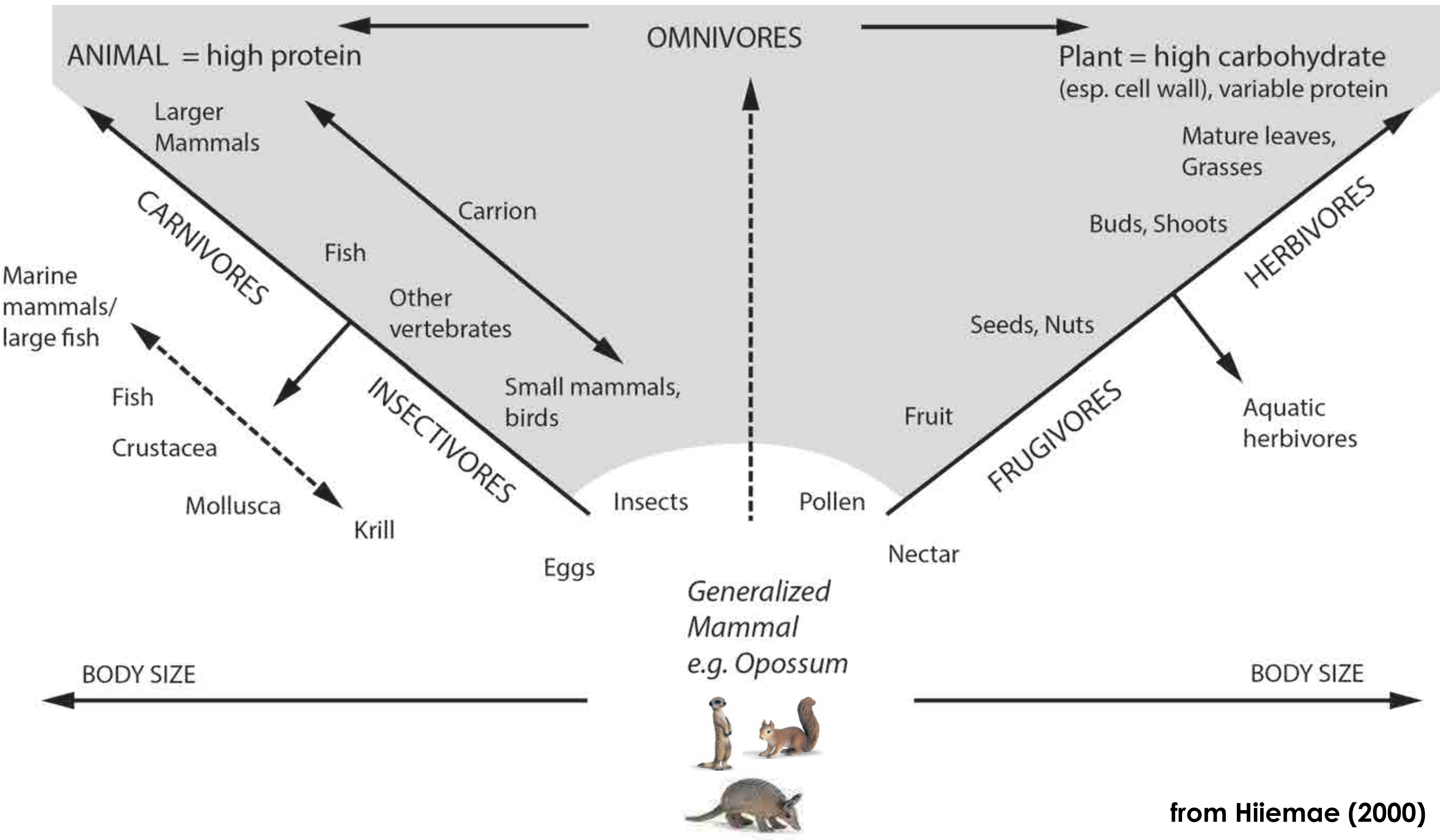


Sufficient amounts of available packages



from Hiiemae (2000)

Sufficient amounts of available packages



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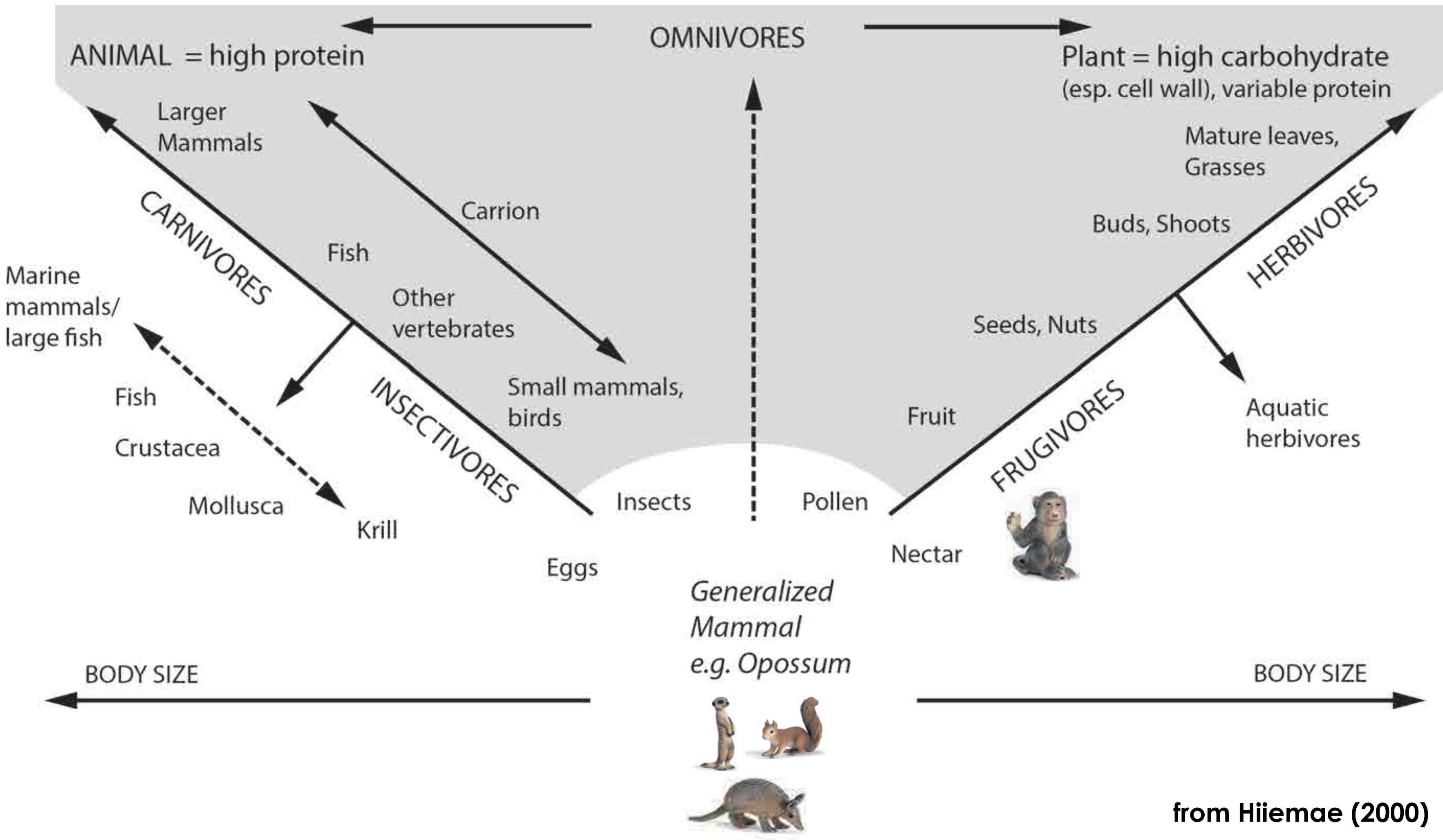

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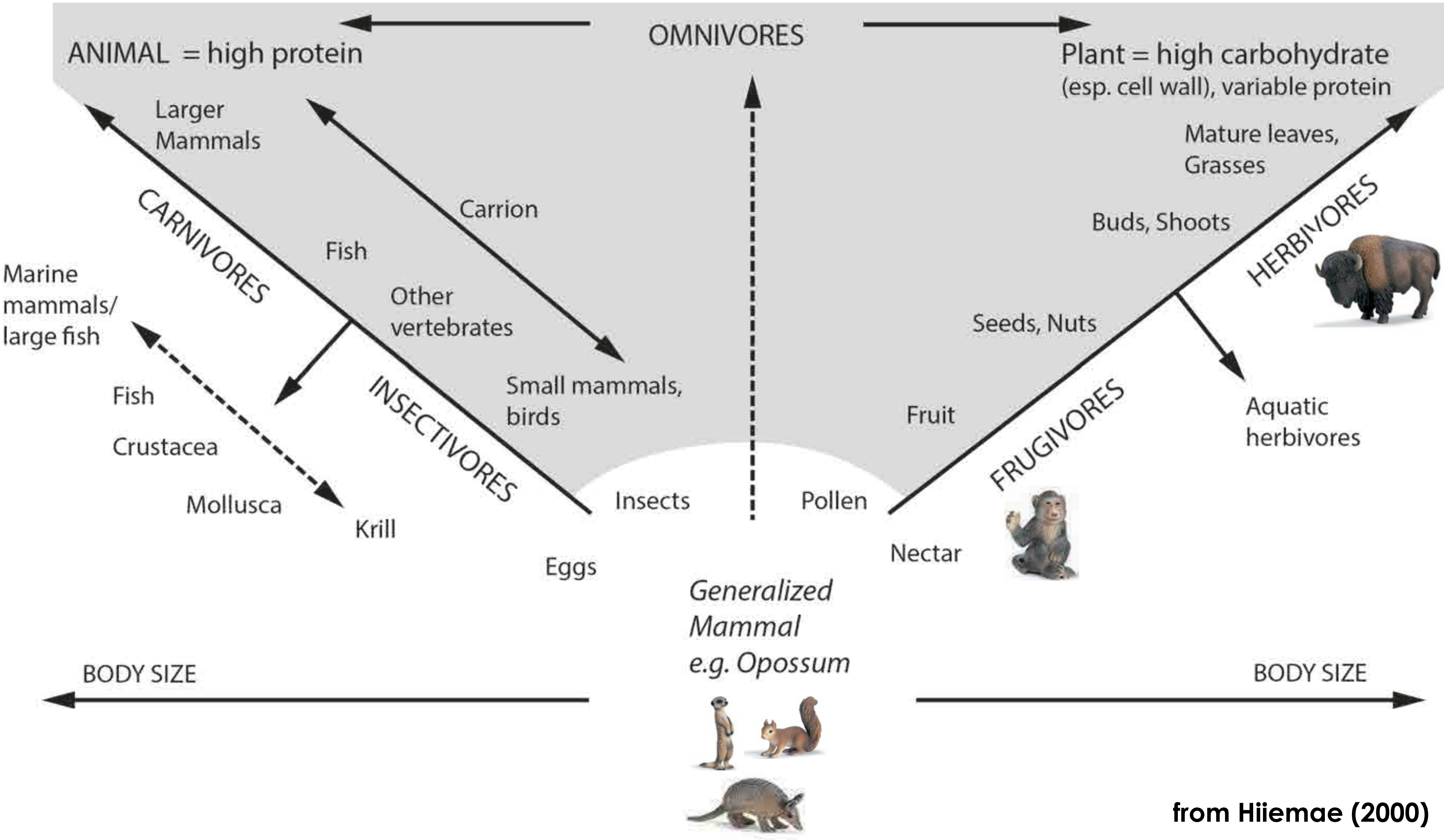

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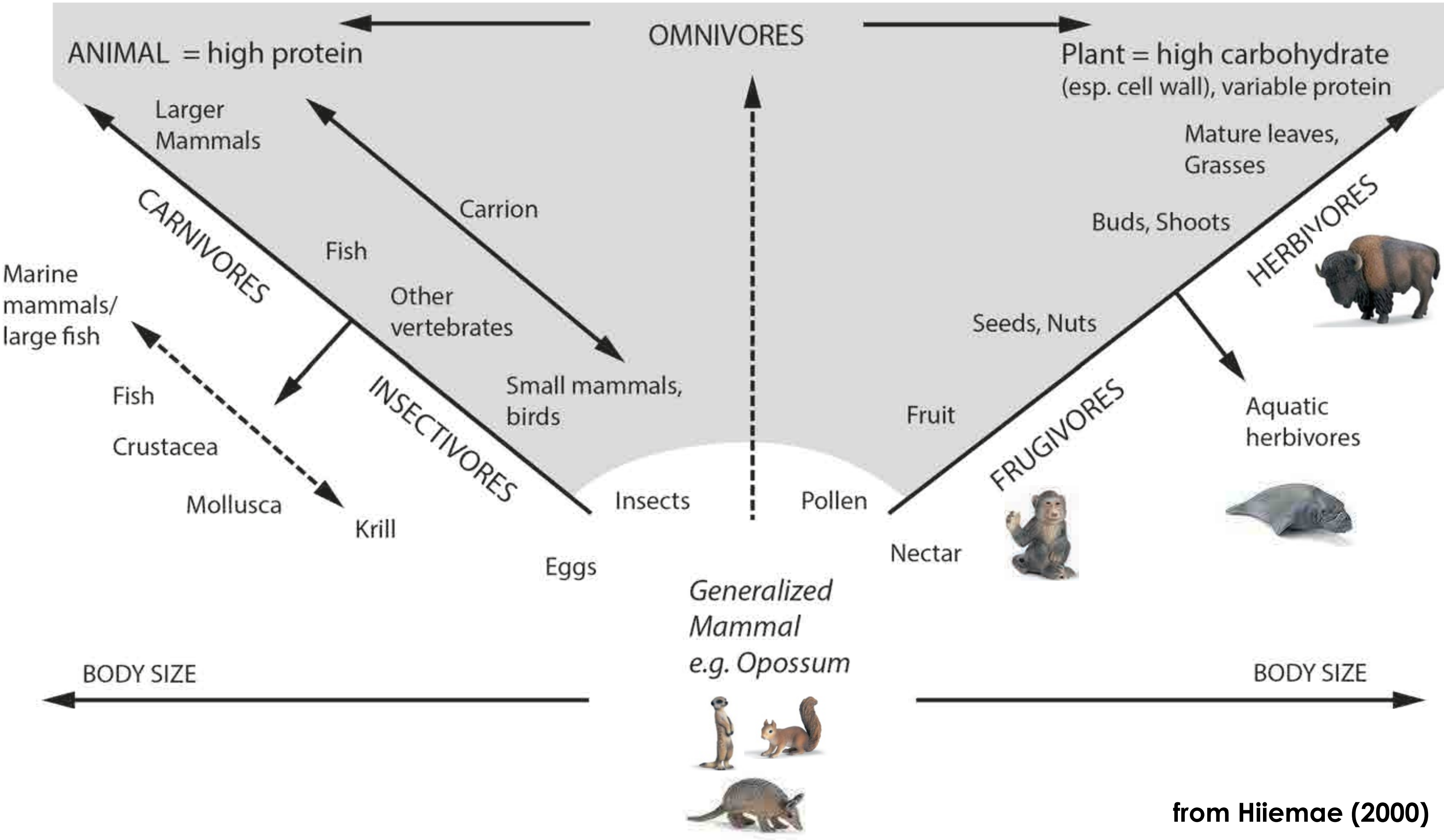

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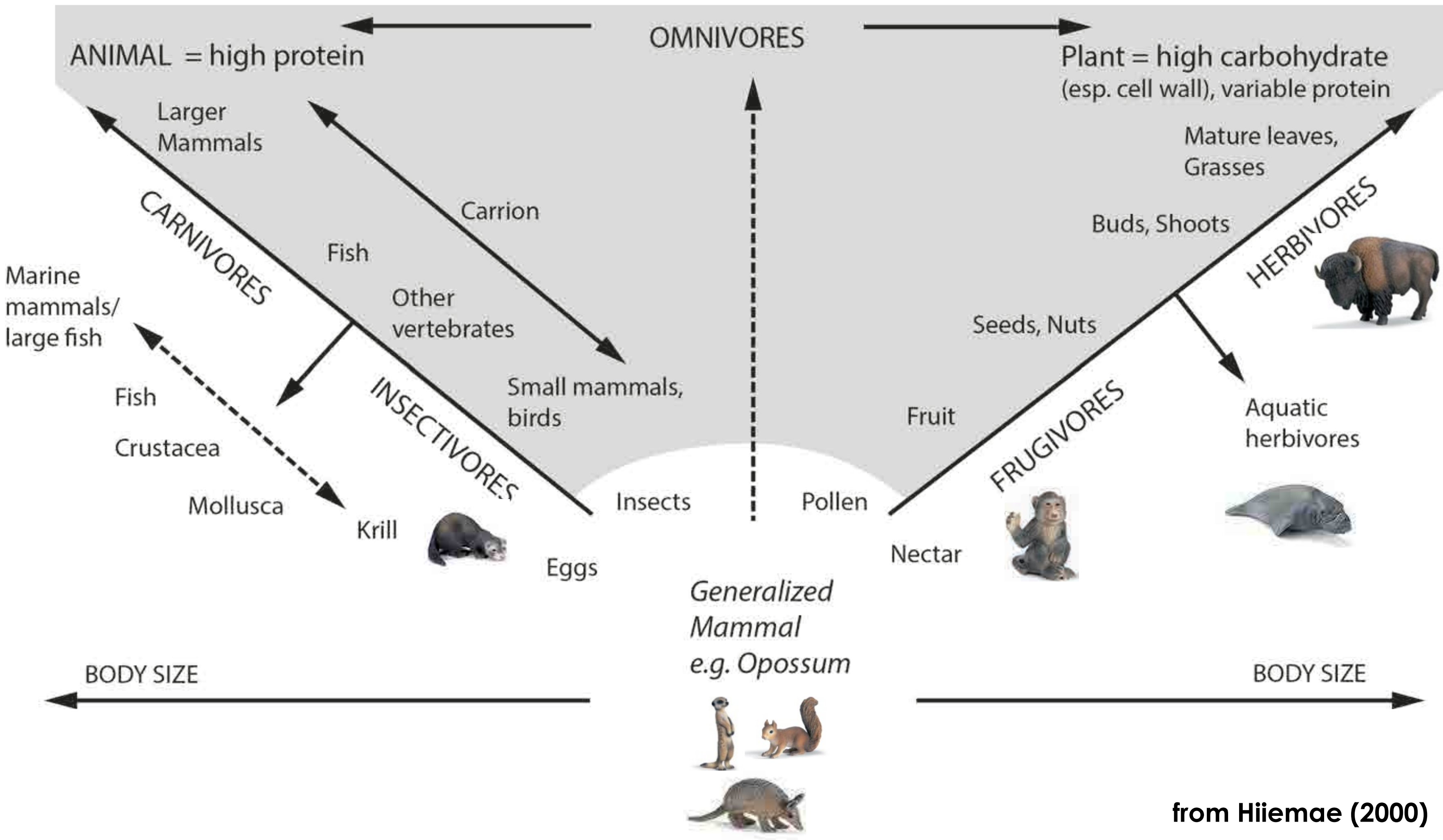

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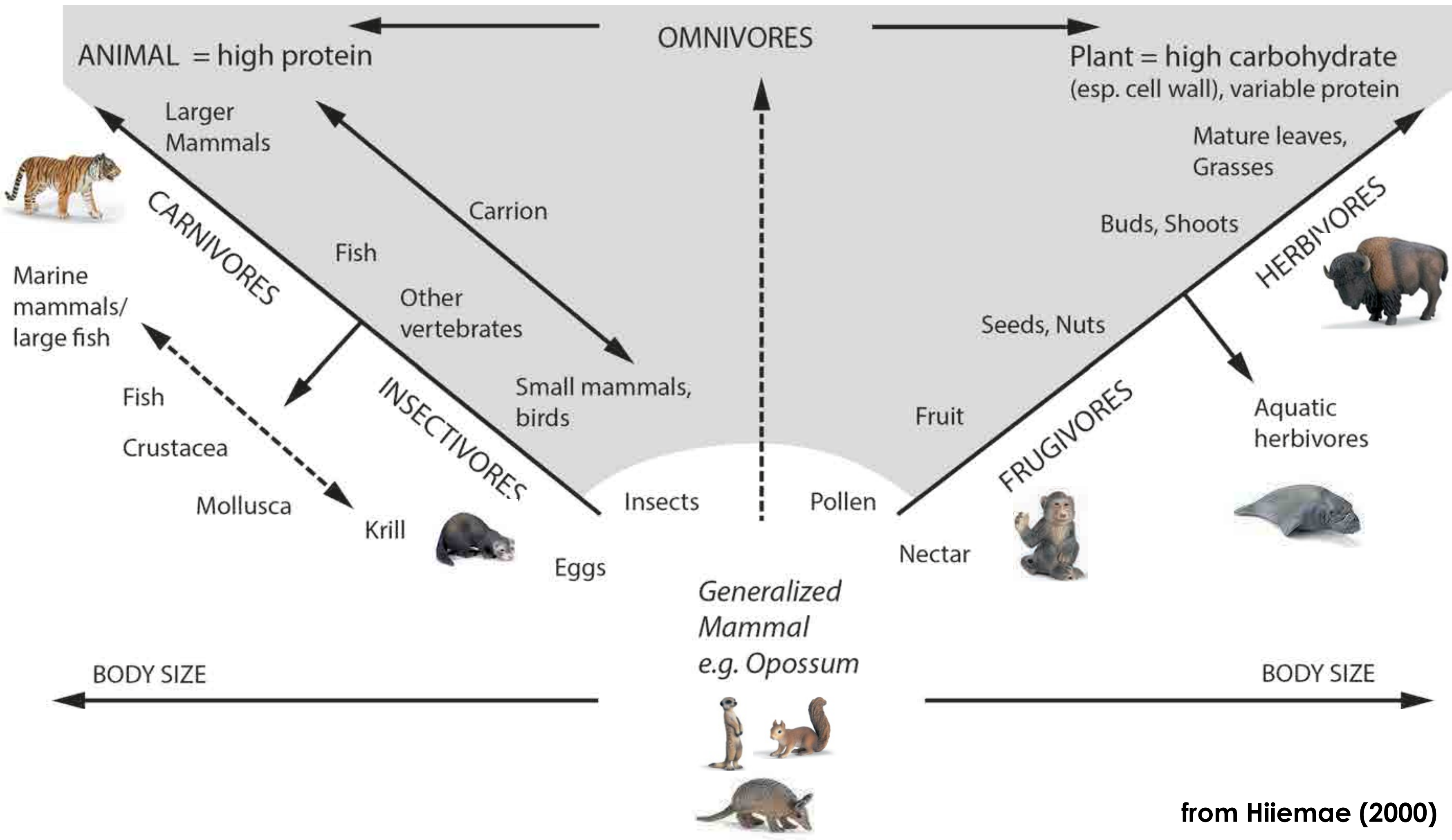

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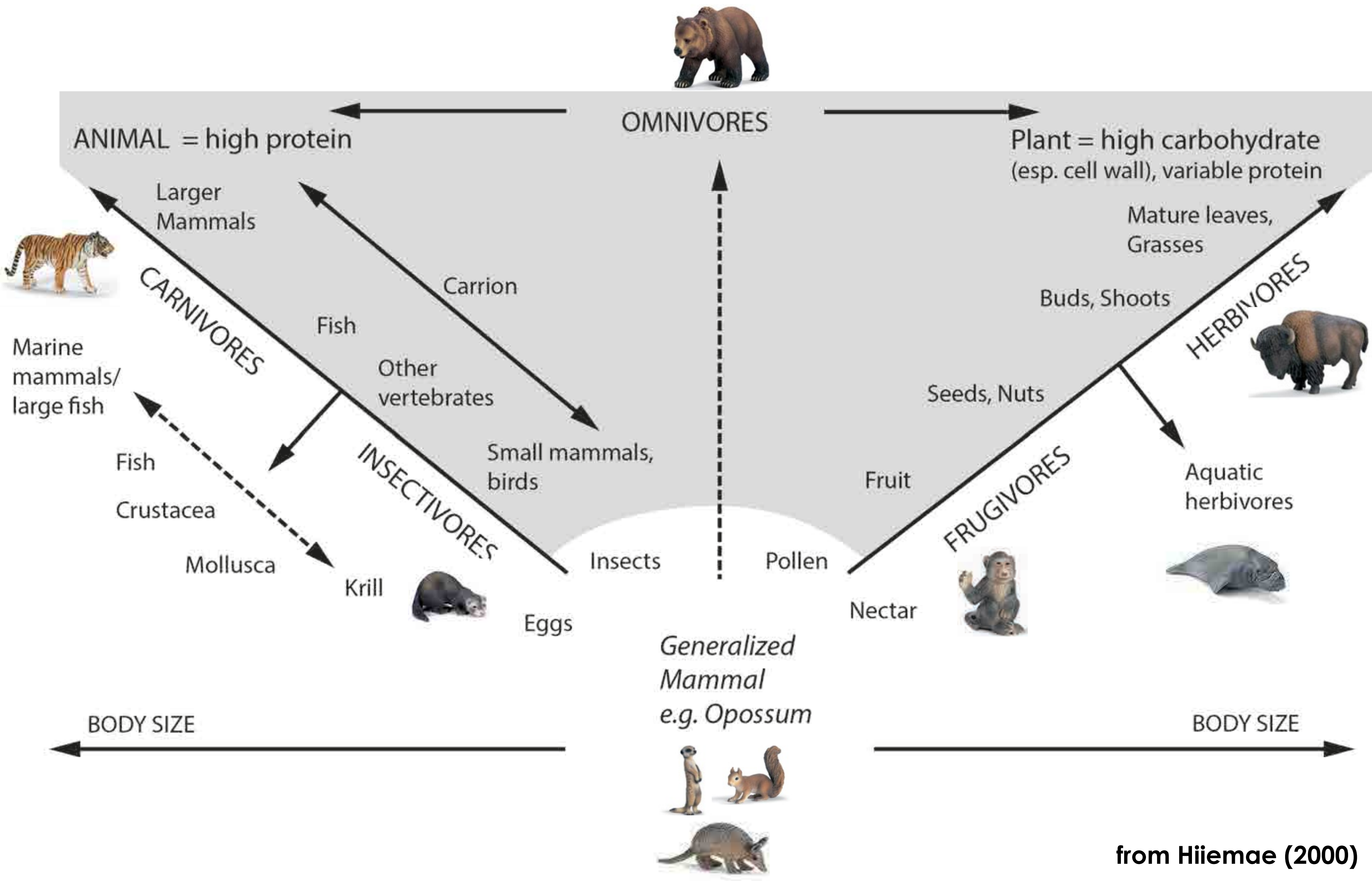

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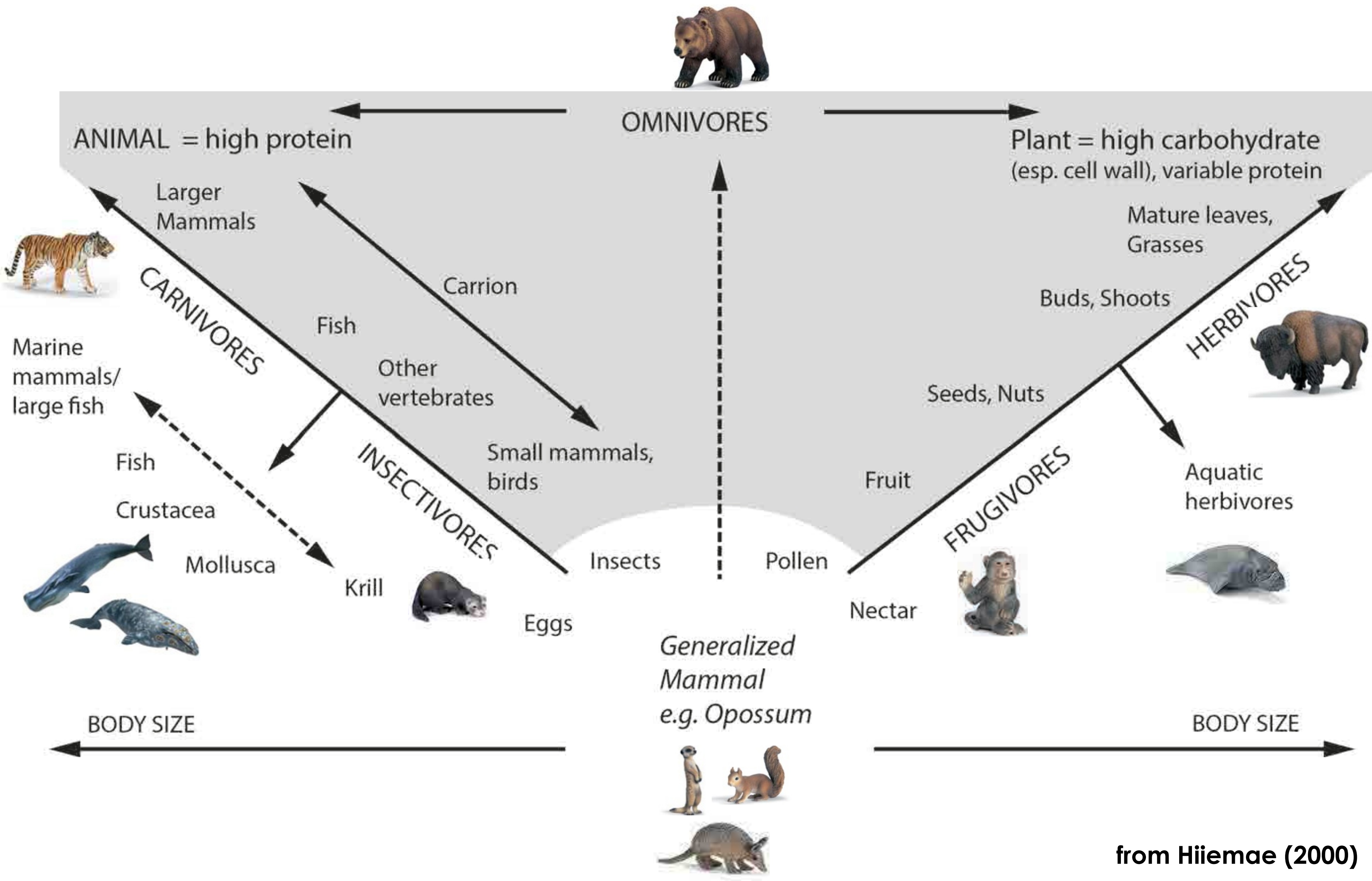


from Hiiemae (2000)

Herbivory and Carnivory

-

Physiological Challenge

and

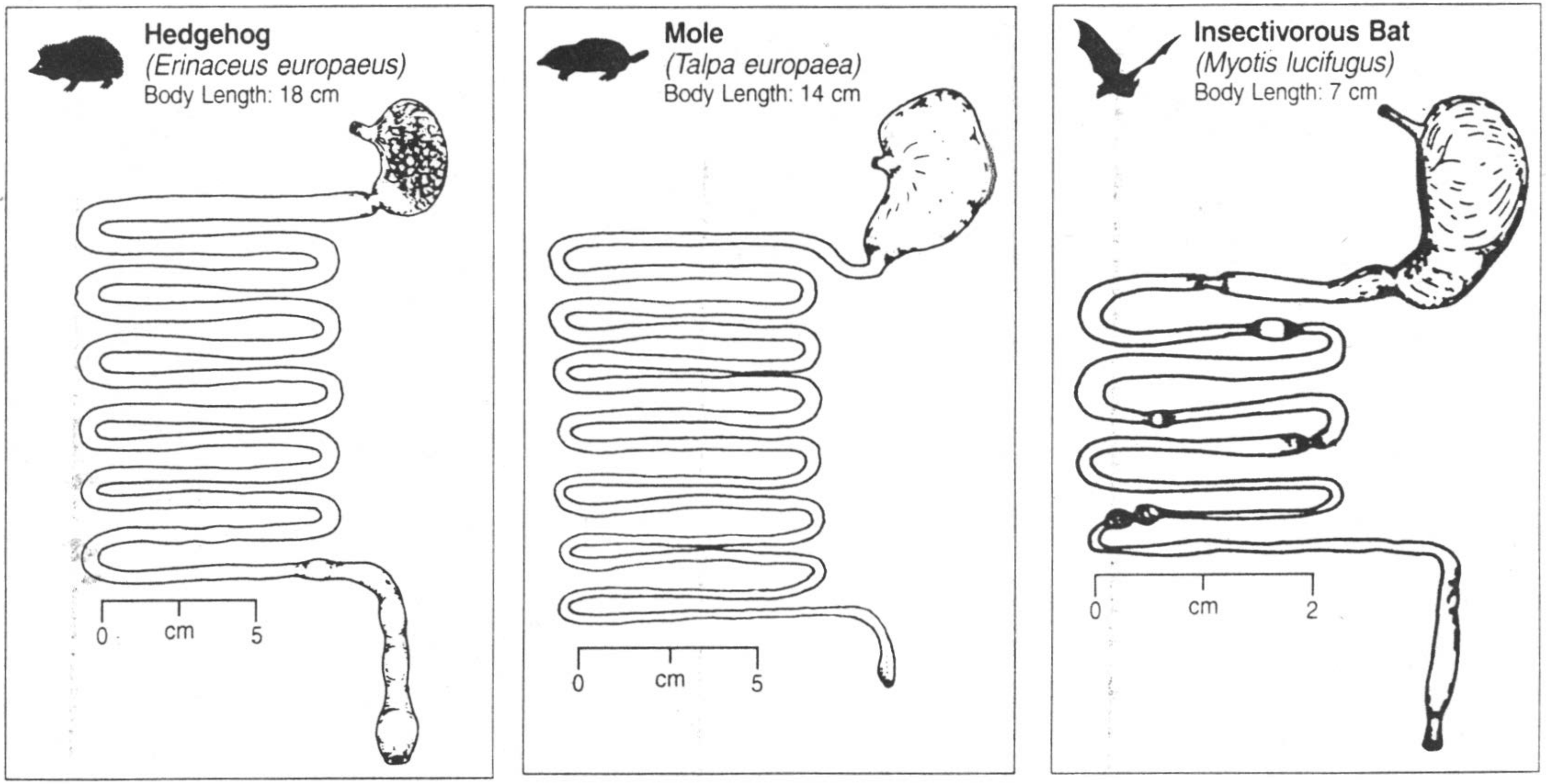
Physiological Opportunity

Carnivory ...

- *... is no physiological challenge*
- *... but a biomechanical and logistical one!*

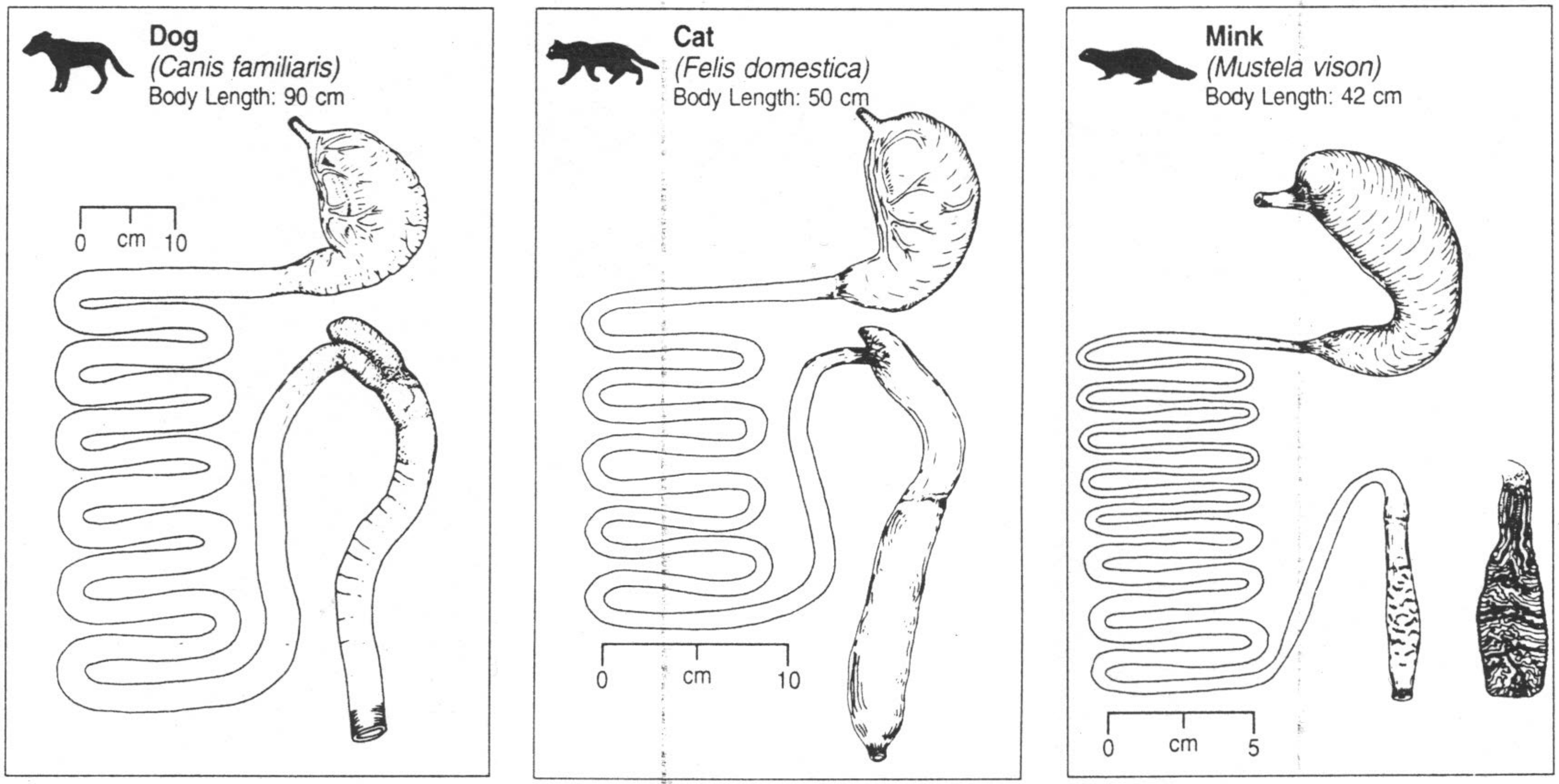
- ***Digesting prey is easy - catching prey is the hard part!***

Insectivores



from Stevens und Hume (1995)

Carnivores



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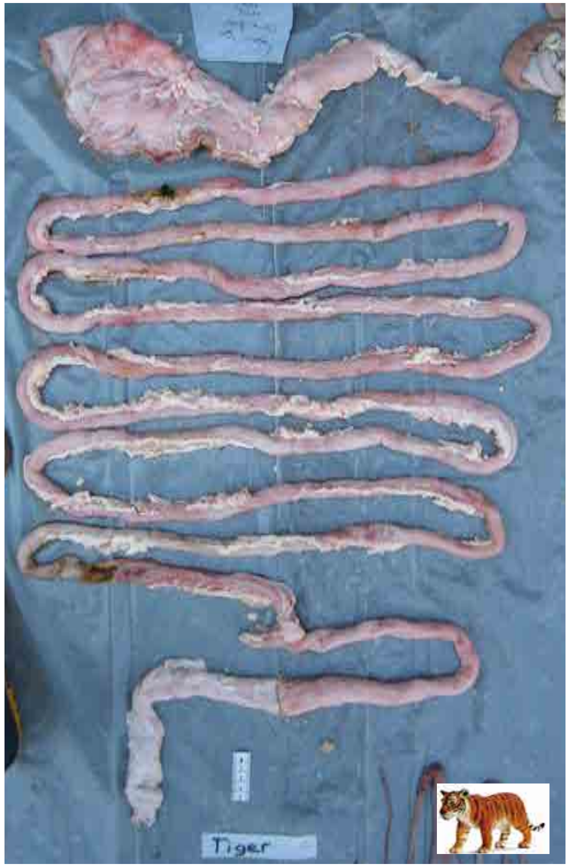
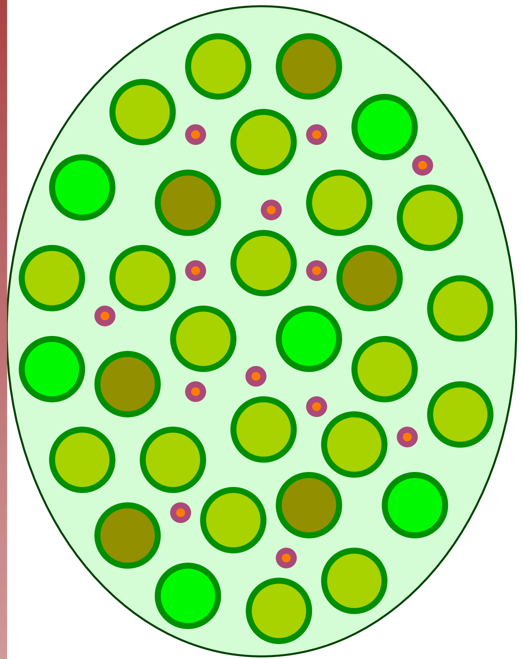


Food



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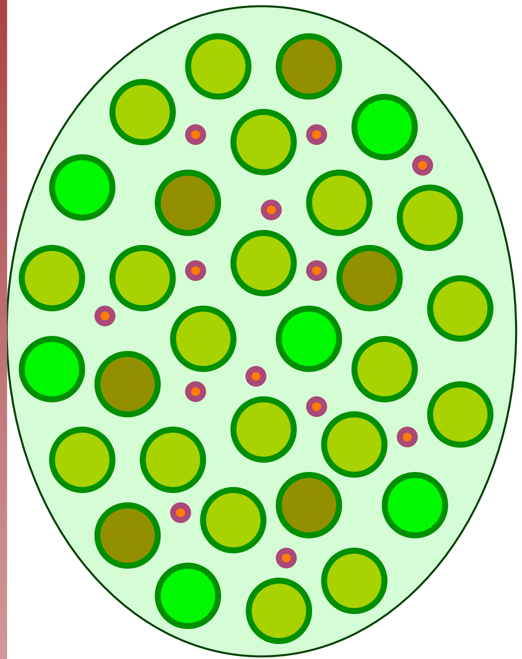
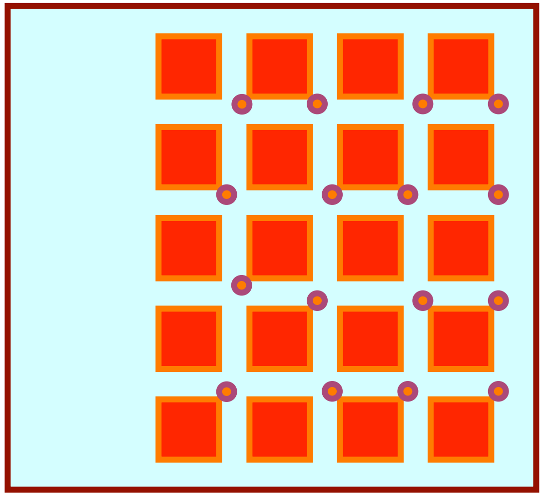
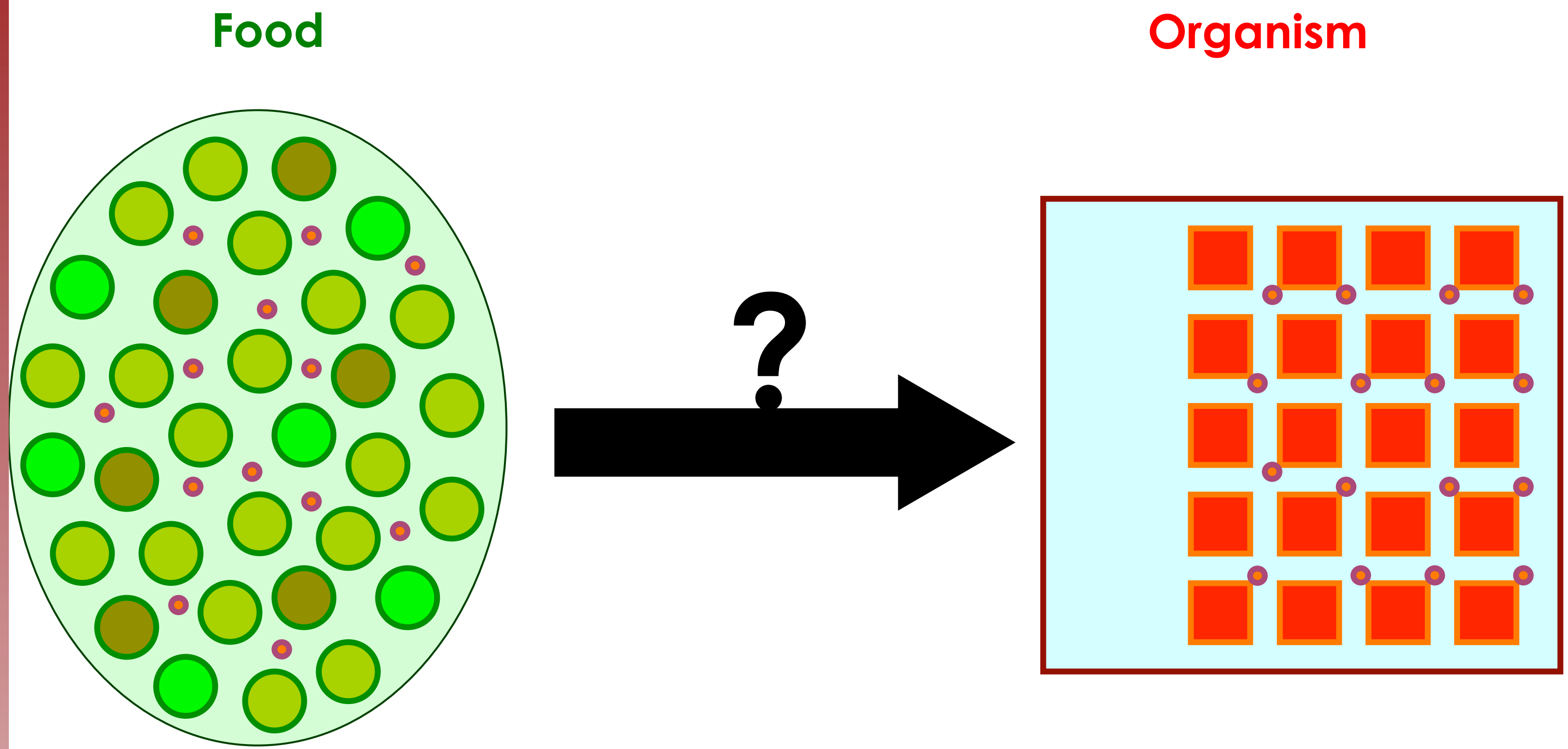
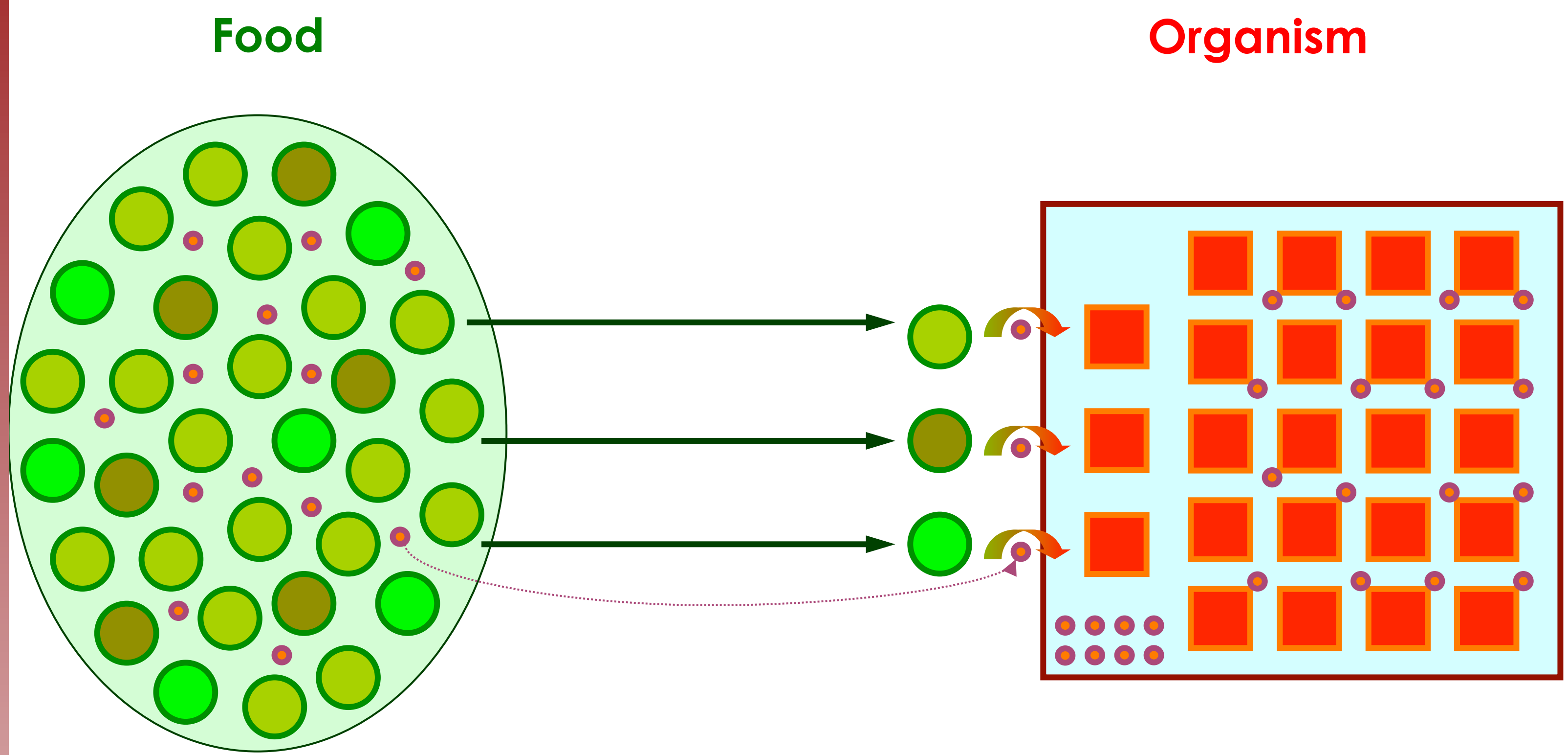


Organism




Food
Organism
?


Food
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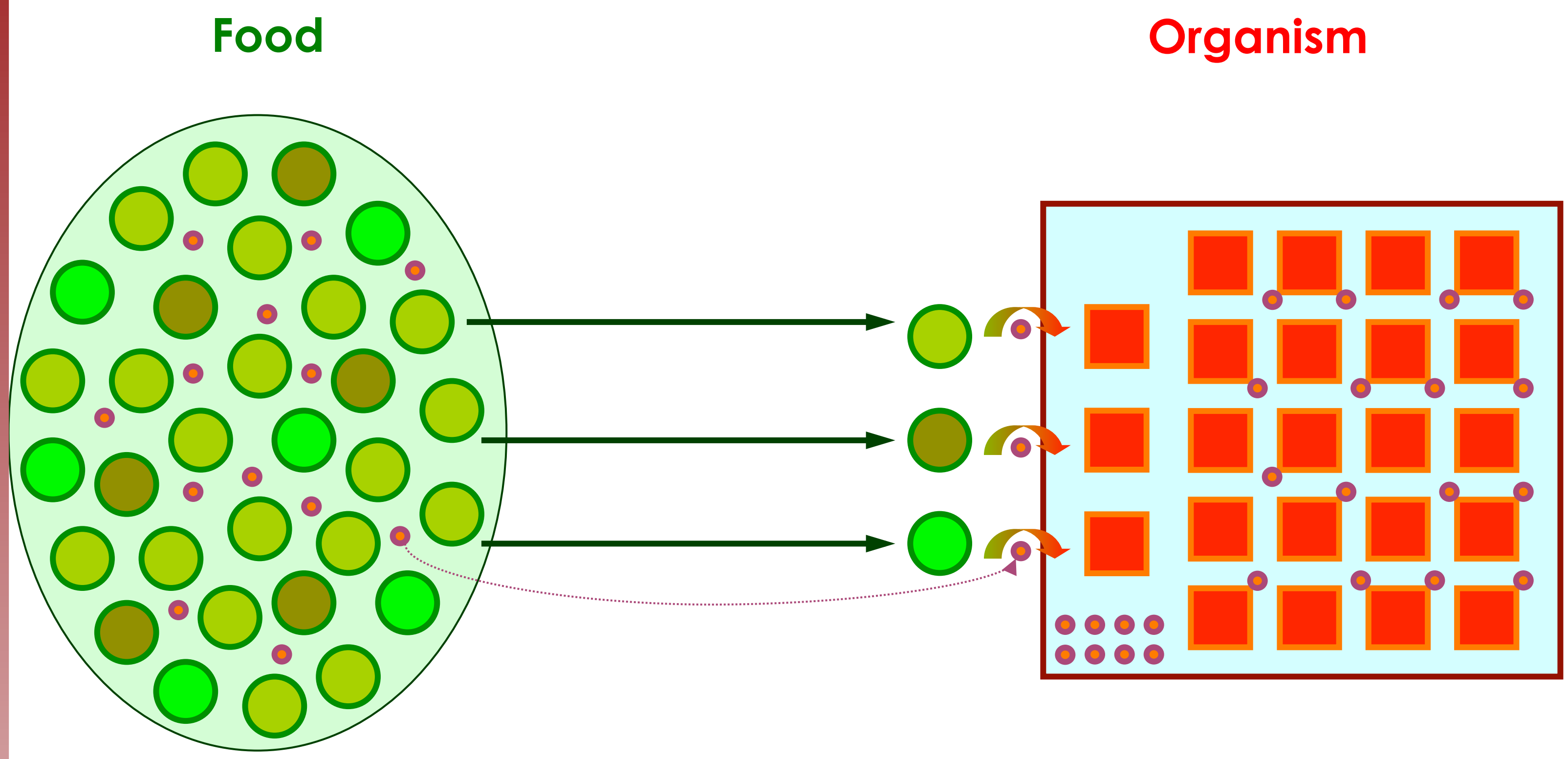
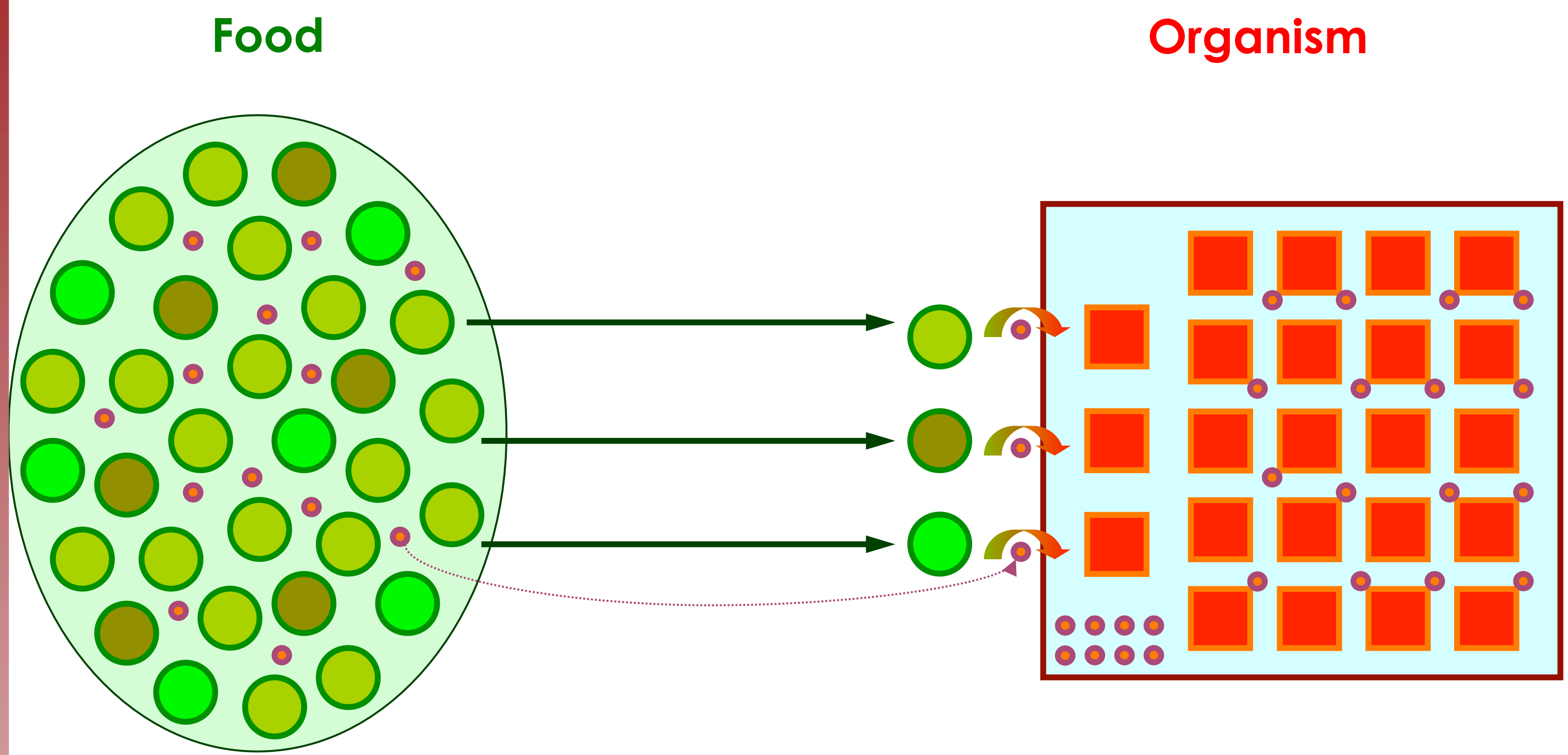
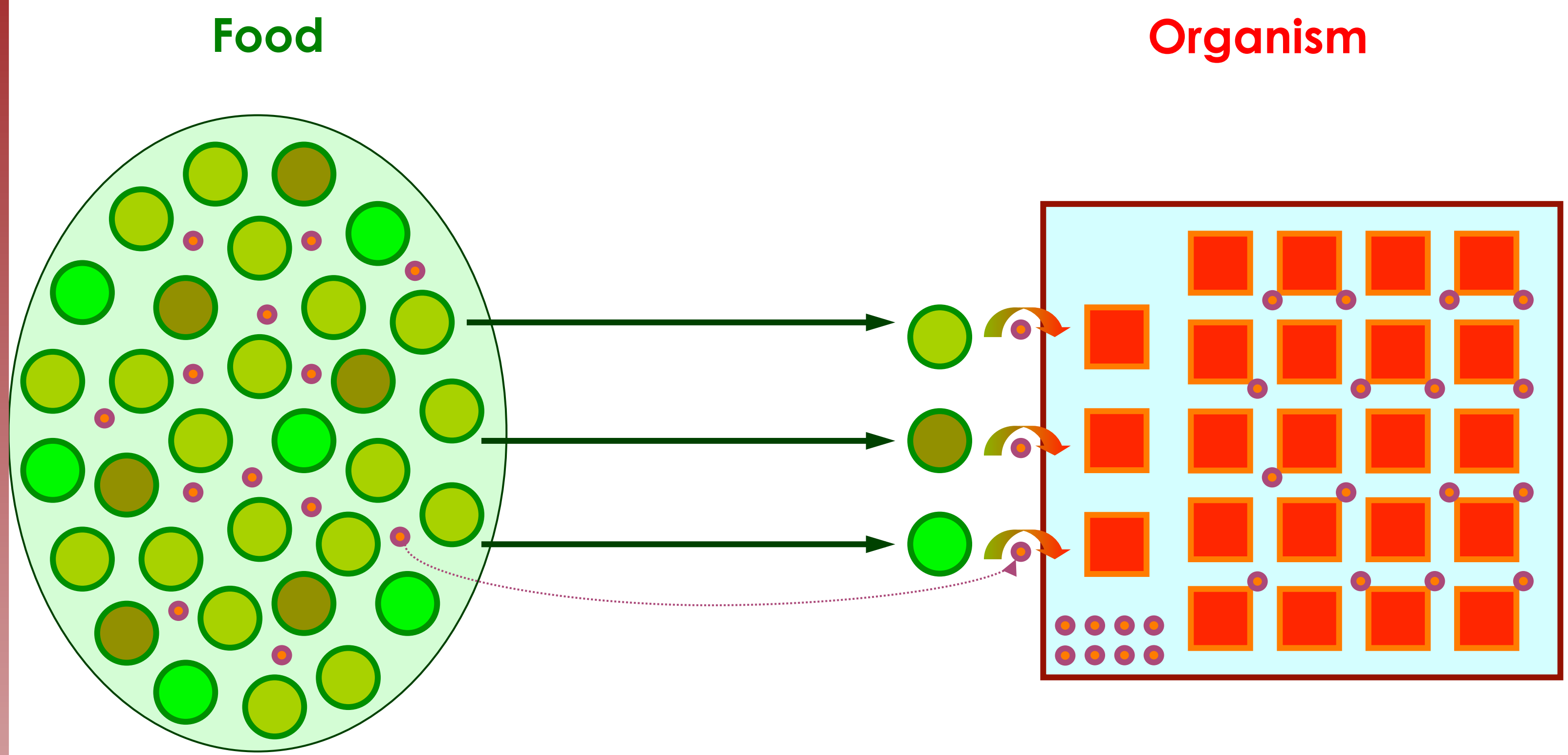


Essential food components (minerals, vitamins, amino acids, fatty acids)



Essential food components (minerals, vitamins, amino acids, fatty acids)

Non-essential food components (fuels and precursors of self-synthetized substances)



Ecophysiological challenge

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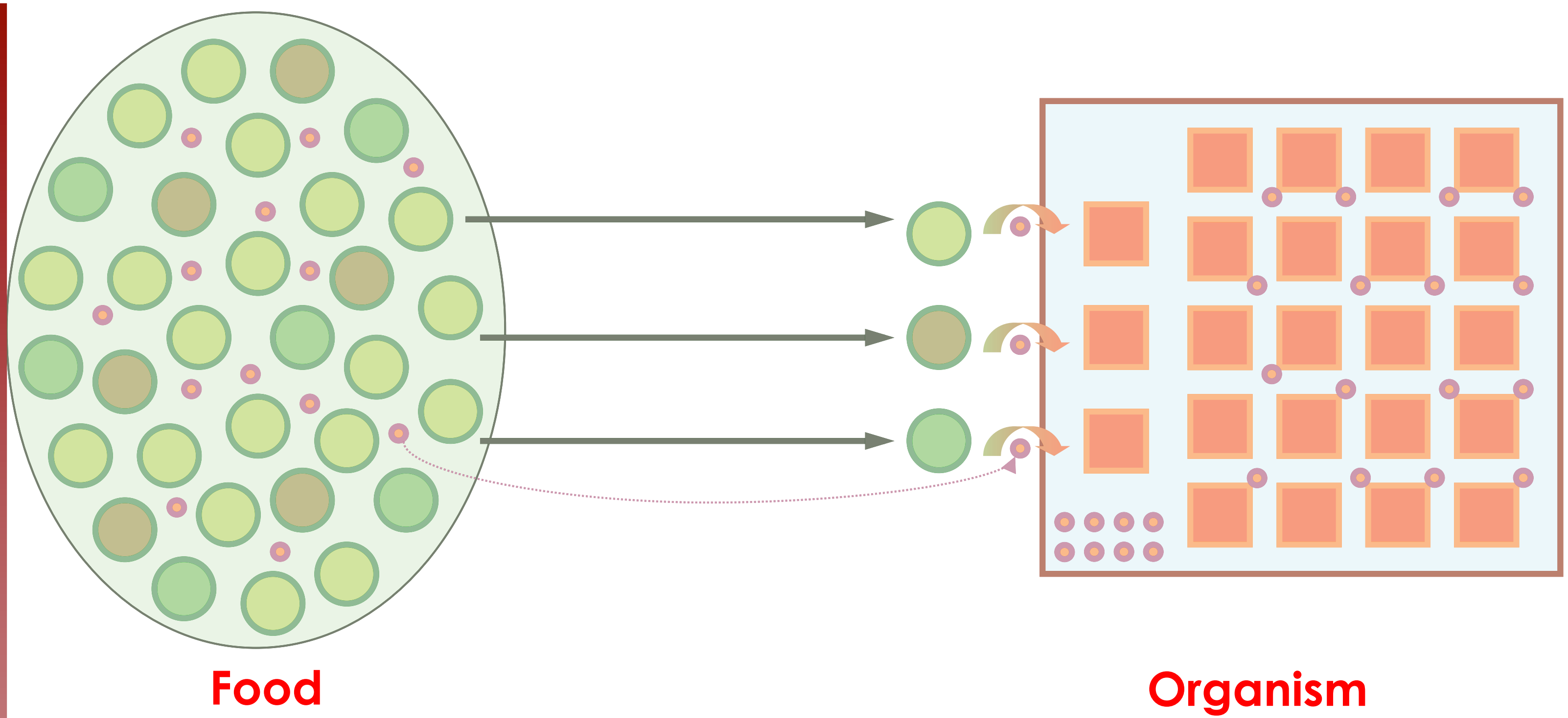
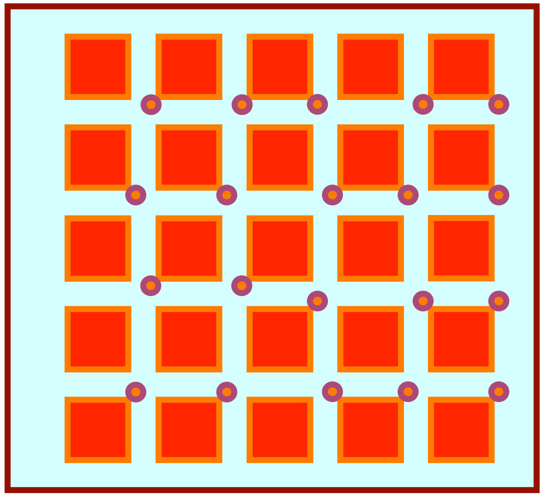
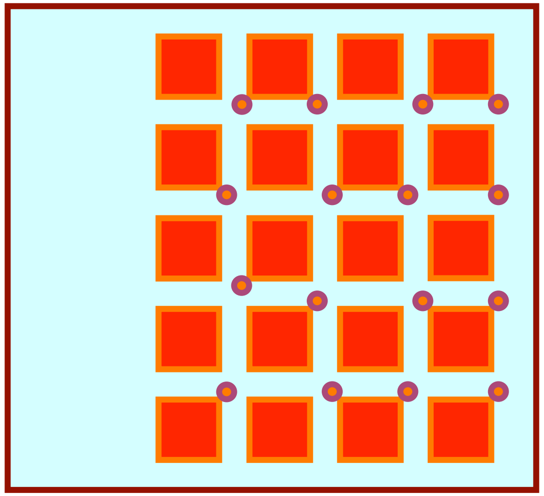
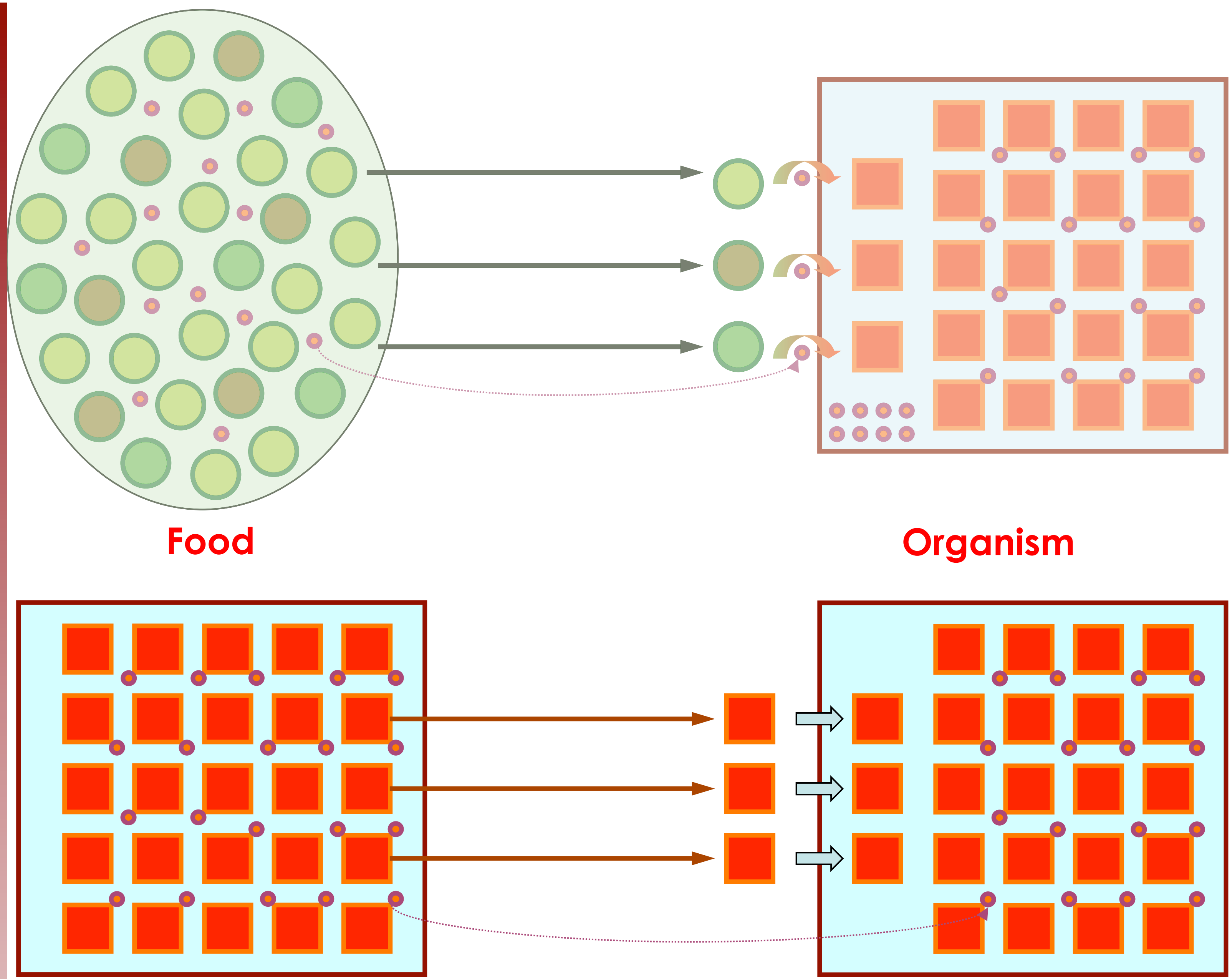
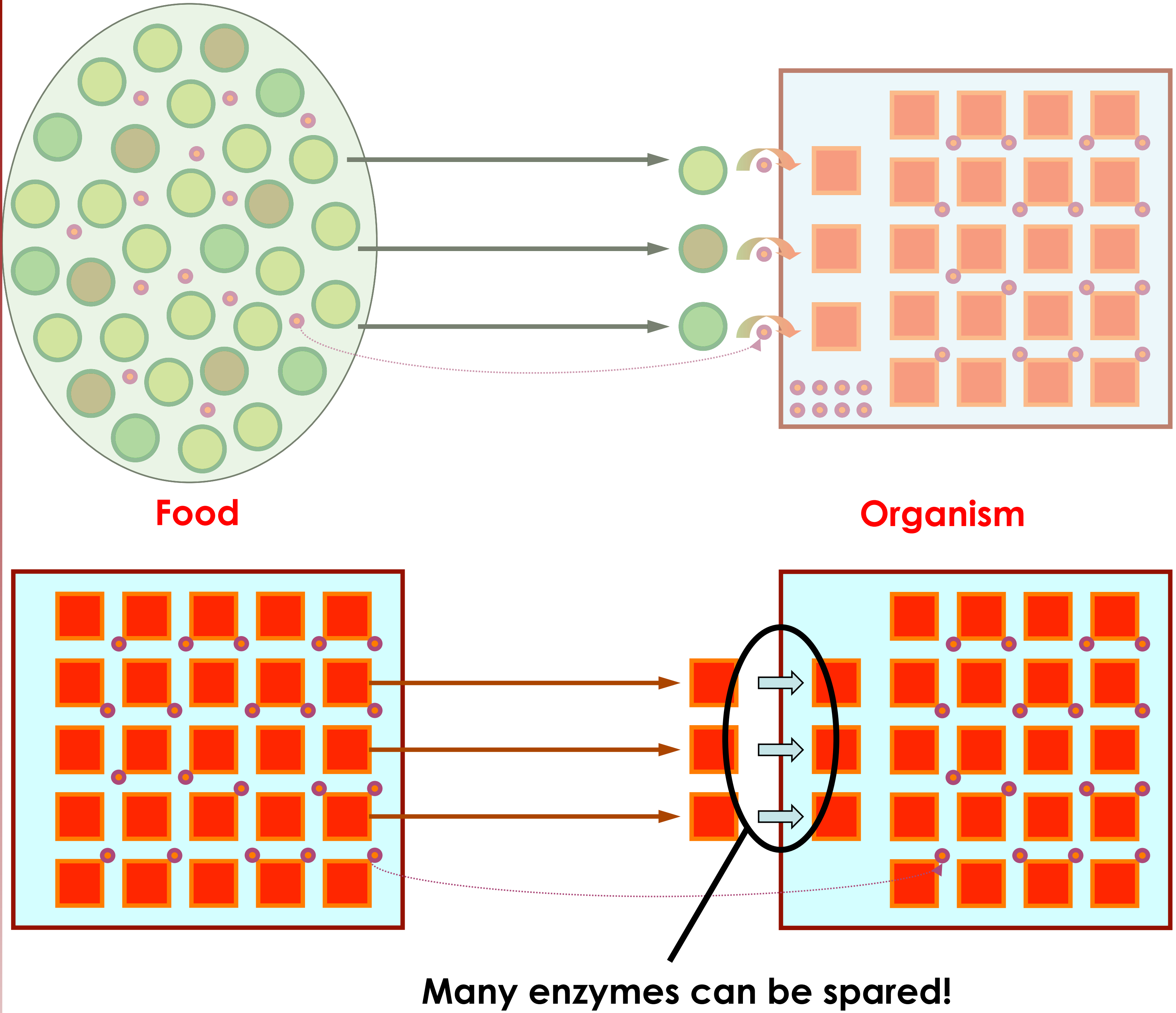

Food
Organism

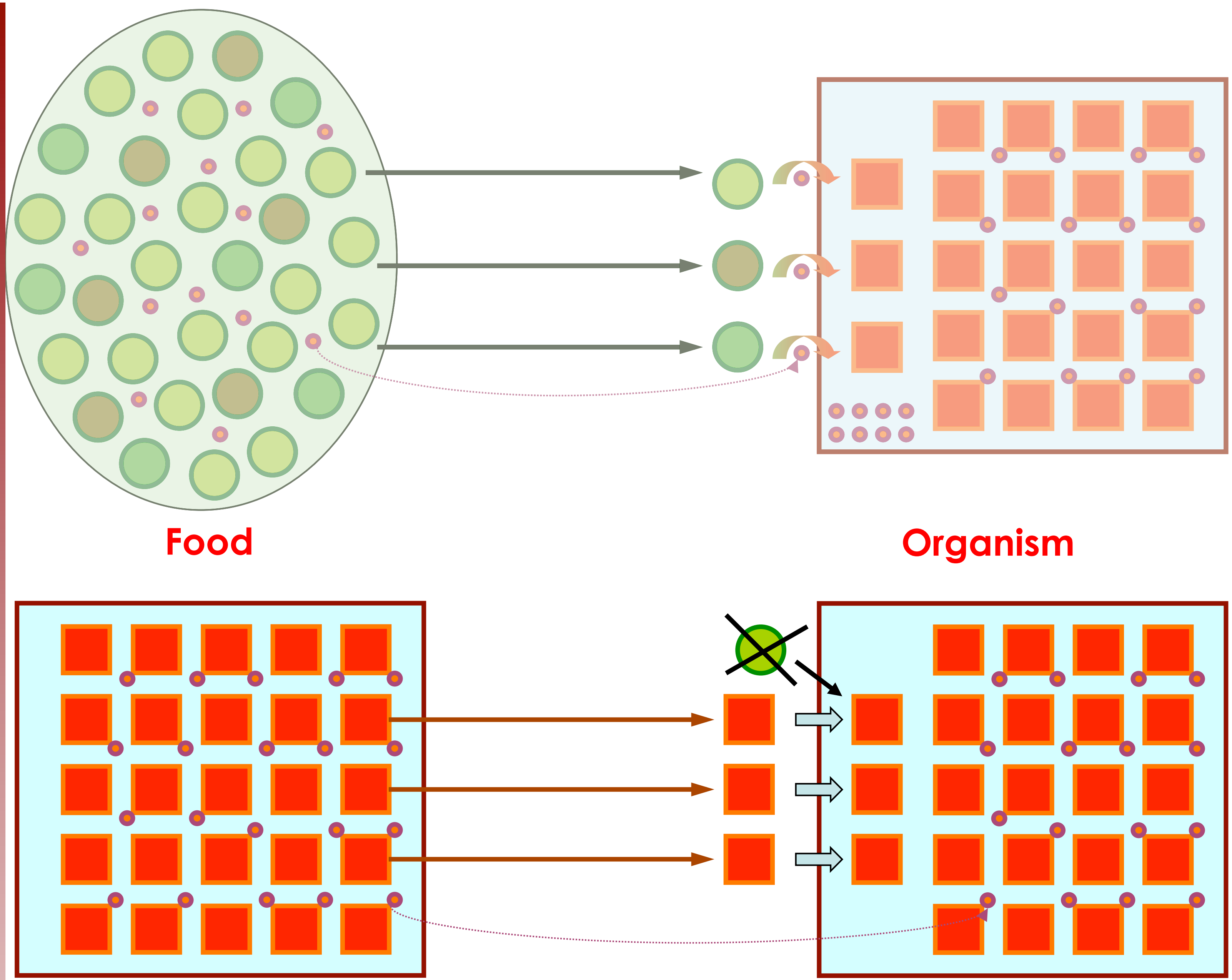





Food
Organism



Food
Organism
Many enzymes can be spared!



but: more essential food components (minerals, vitamins, amino acids, fatty acids)!

Nutrition Research Reviews (2002), **15**, 153–168

DOI: 10.1079/NRR200238

Idiosyncratic nutrient requirements of cats appear to be diet-induced evolutionary adaptations*

James G. Morris

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James G. Morris

Ecological opportunity adaptation

Particuliarities of the cat

- High protein requirement: amino acid catabolism cannot be reduced even in deficiency

  similar enzyme patterns in trout, alligators, vultures, barn owls

Particuliarities of the cat

- **High protein requirement: amino acid catabolism cannot be reduced even in deficiency**
- **Arginine is essential**

also in mink and ferrets

Particuliarities of the cat

- High protein requirement: amino acid catabolism cannot be reduced even in deficiency
- Arginine is essential
- Taurine is essential: cannot be synthetized in sufficient amount from cysteine and methionine

deficiencies observed in zoo felids, maned wolves, foxes, merkats, anteaters

Particuliarities of the cat

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- Taurine is essential: cannot be synthetized in sufficient amount from cysteine and methionine
- Arachidonic acid is essential: cannot be synthetized in sufficient amount from linoleic acid; docosahexaenoic acid also essential

also in lions, cheetahs and mosquitoes

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- limited tolerance of carbohydrates: CH-digesting enzymes have low activity and cannot be up-regulated

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- ß-carotine has no effect: vit. A cannot be synthetized from ß-carotine

also in foxes

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- ß-carotine has no effect: vit. A cannot be synthetized from ß-carotine
- Vitamin D is essential: no synthesis even in UV-light
- Niacin is essential: cannot be synthetized from tryptophane

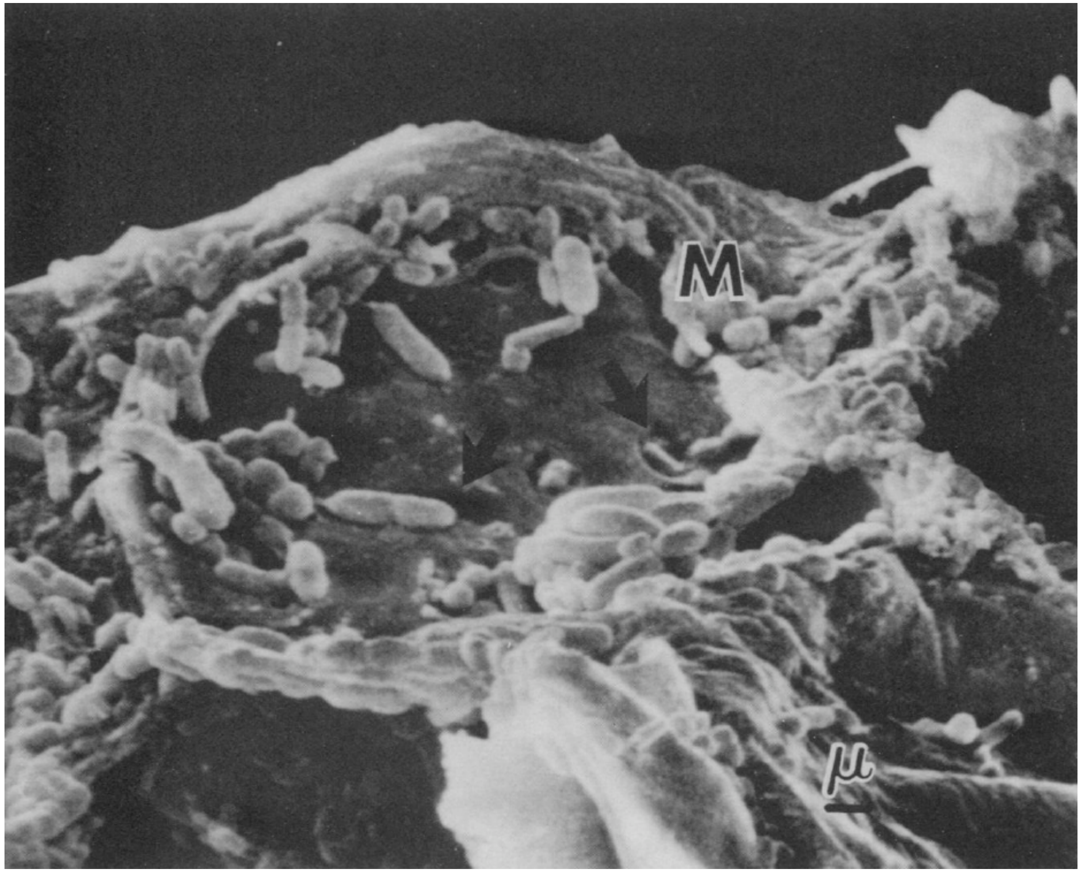
also in trout and salmon

Food chains

A green world

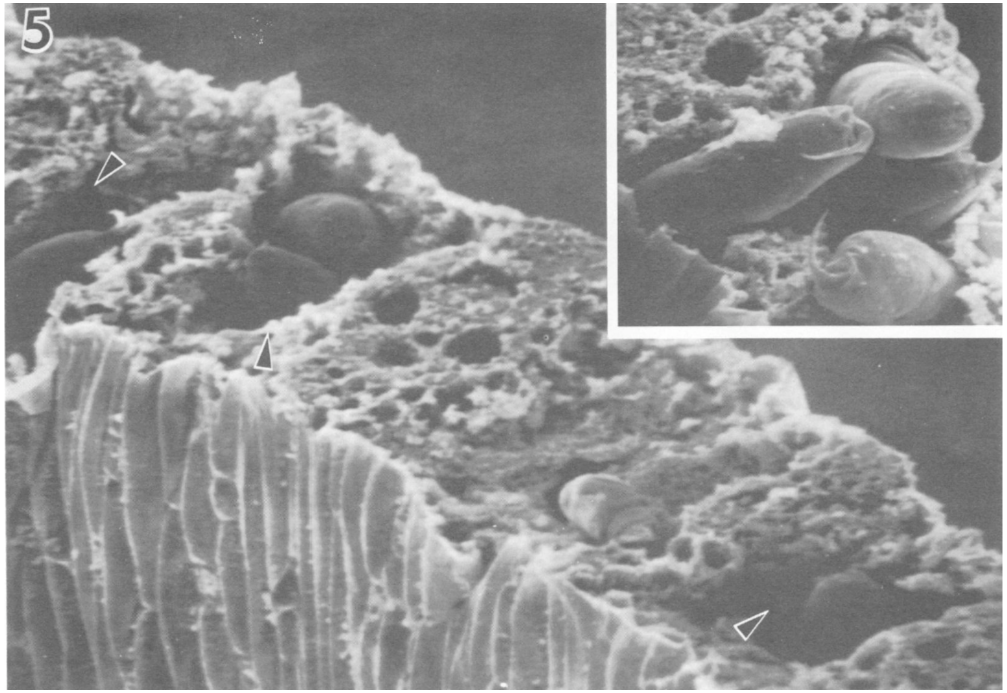
Primary consumers

Primary consumers



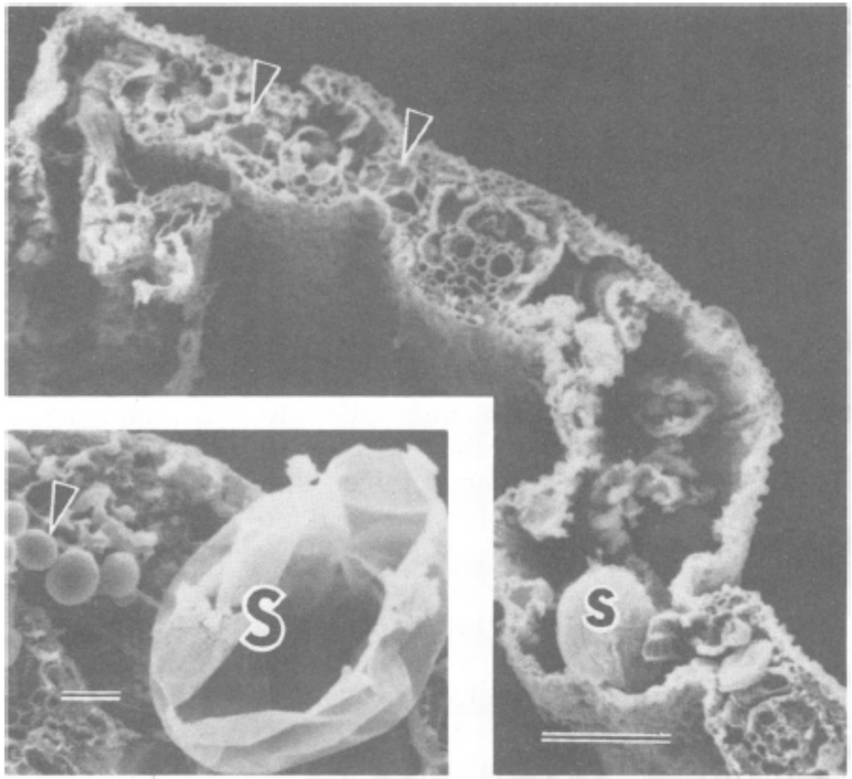
from Akin & Amos (1975)

Primary consumers



from Amos & Akin (1978)

Primary consumers



from Akin & Benner (1988)

Primary consumers

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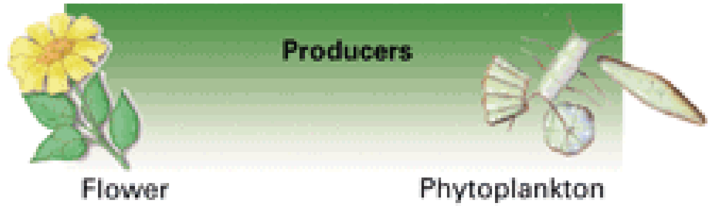
Primary consumers

Food chains

A terrestrial food chain

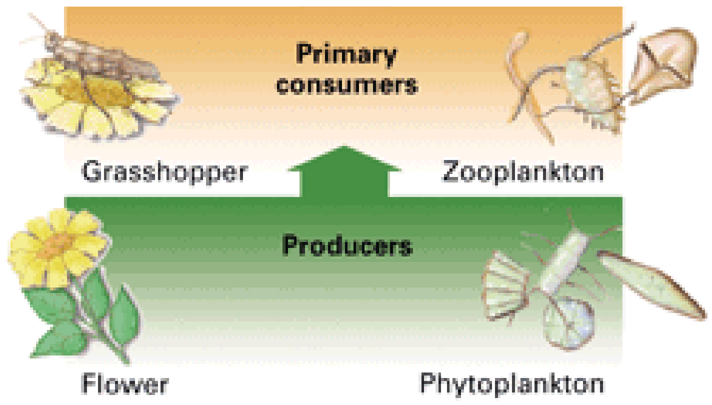
A marine food chain



Food chains

A terrestrial food chain

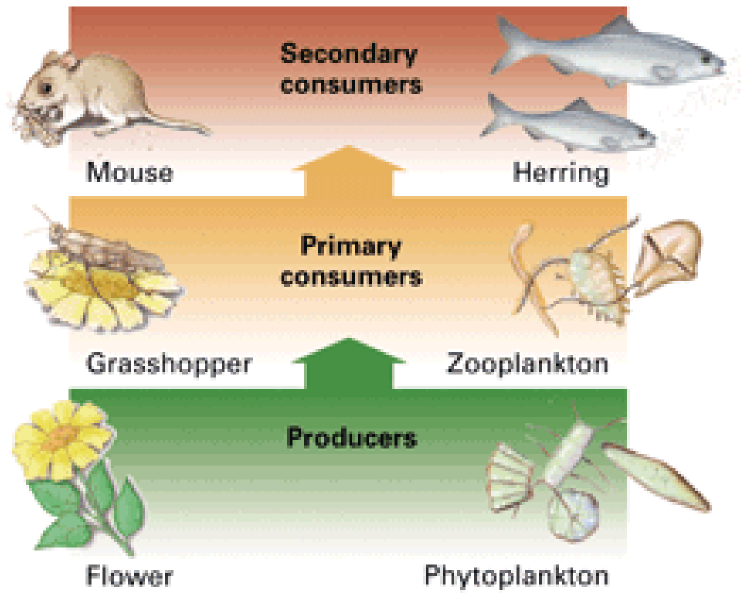
A marine food chain



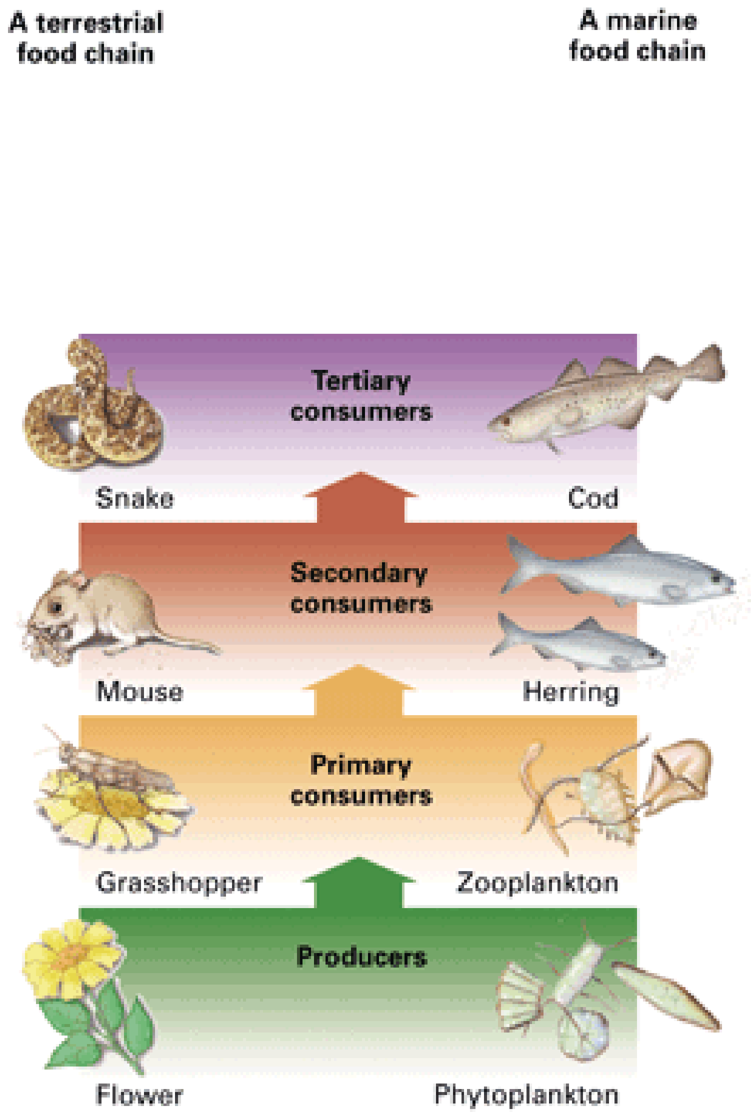
Food chains

A terrestrial food chain

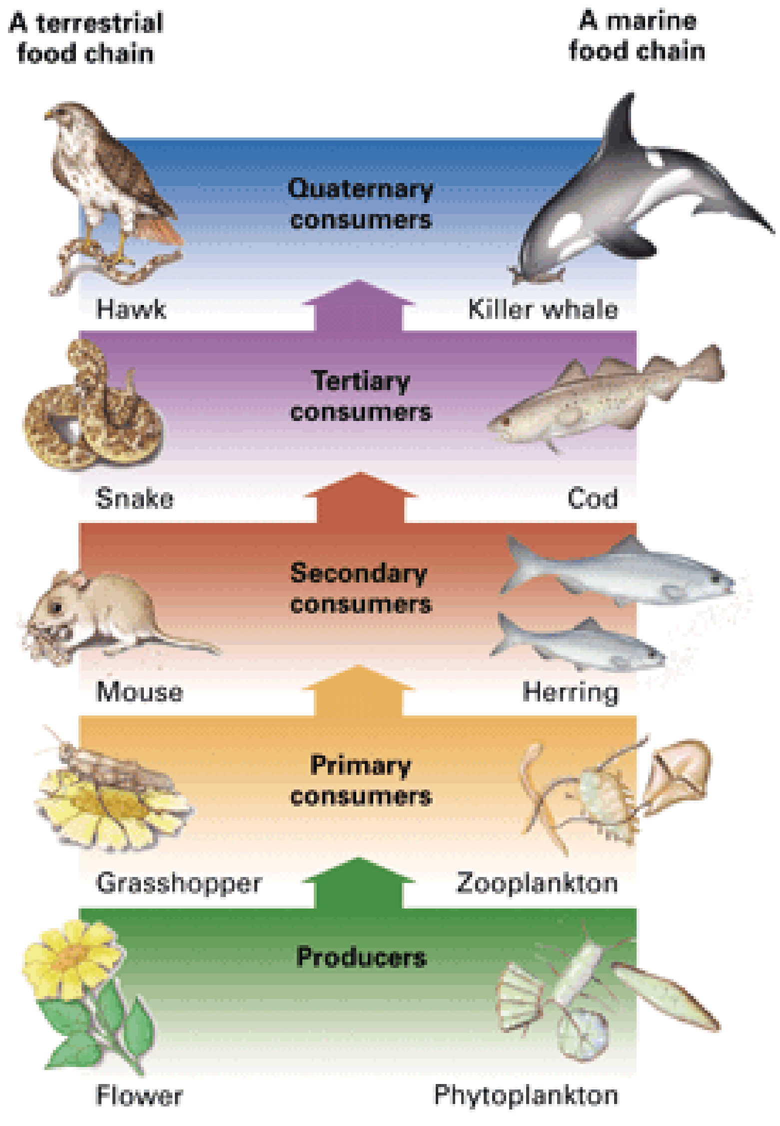
A marine food chain



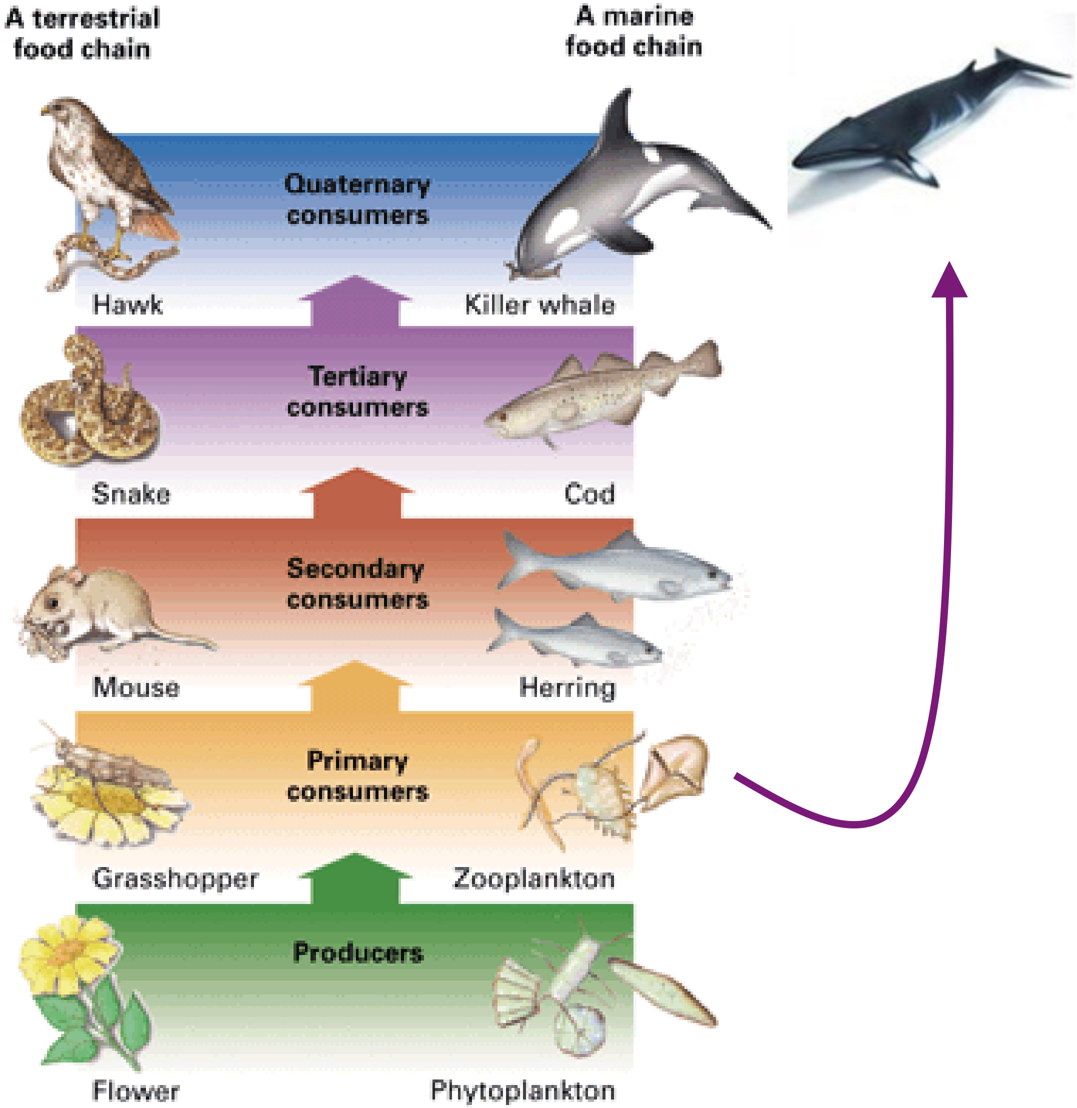
Food chains


A terrestrial food chain
A marine food chain
Tertiary consumers
Snake
Cod
Secondary consumers
Mouse
Herring
Primary consumers
Grasshopper
Zooplankton
Producers
Flower
Phytoplankton

Food chains

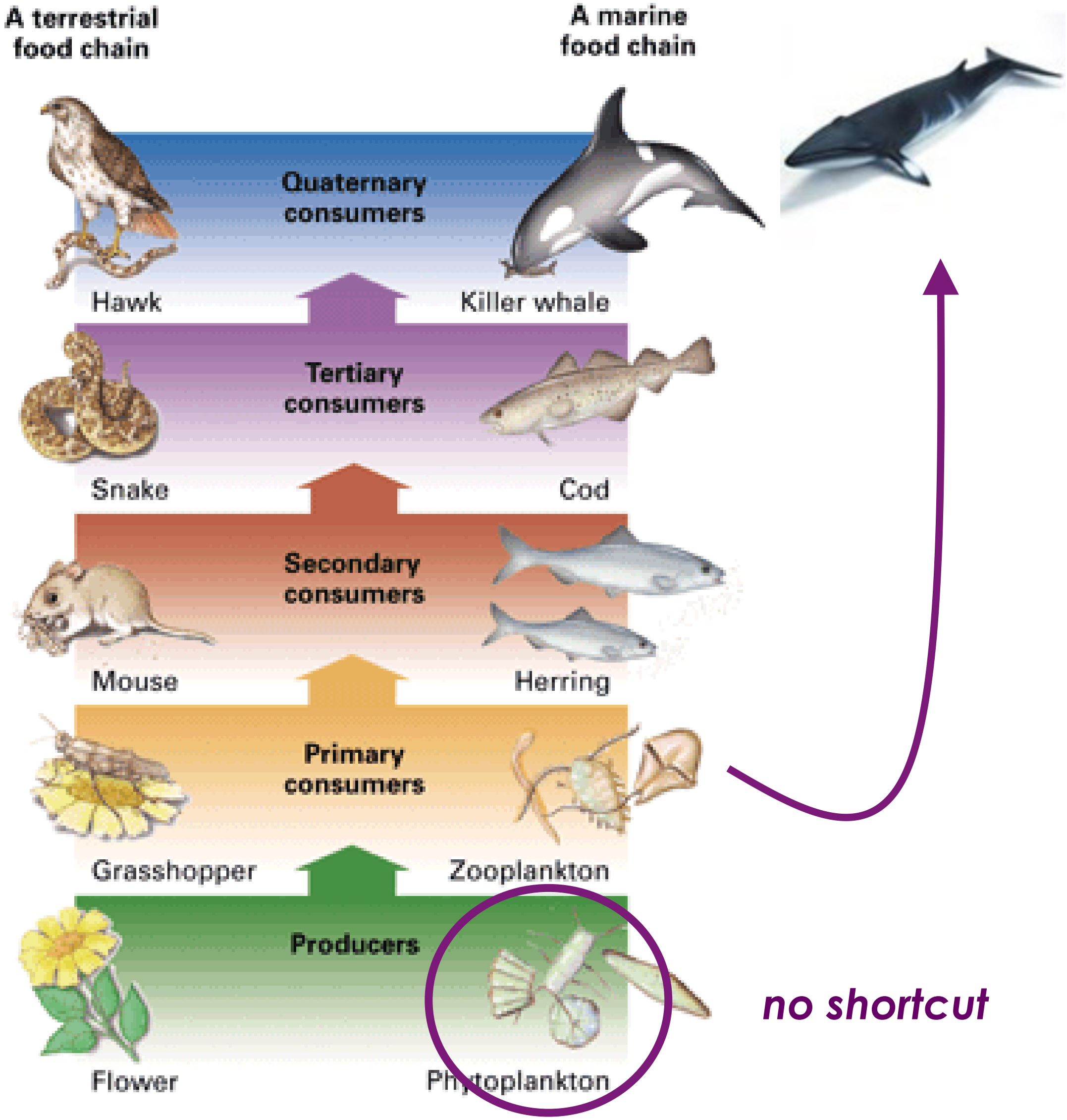

A terrestrial food chain
A marine food chain
Quaternary consumers
Hawk
Killer whale
Tertiary consumers
Snake
Cod
Secondary consumers
Mouse
Herring
Primary consumers
Grasshopper
Zooplankton
Producers
Flower
Phytoplankton

Food chains - and shortcuts

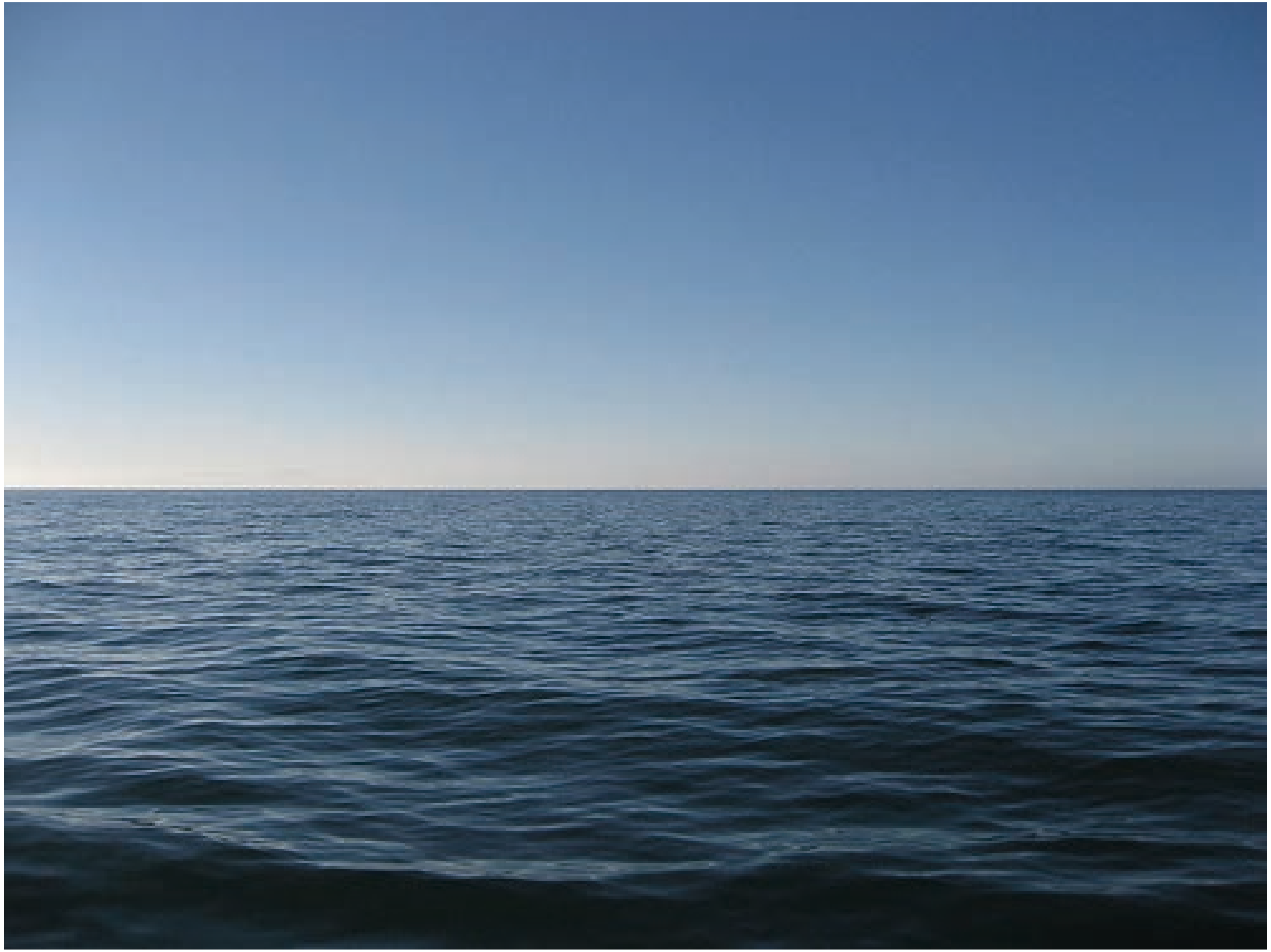


Easy-to-harvest packages of tiny invertebrates – krill clouds

Food chains - and shortcuts



Productive yet minute packages of plant food in marine systems



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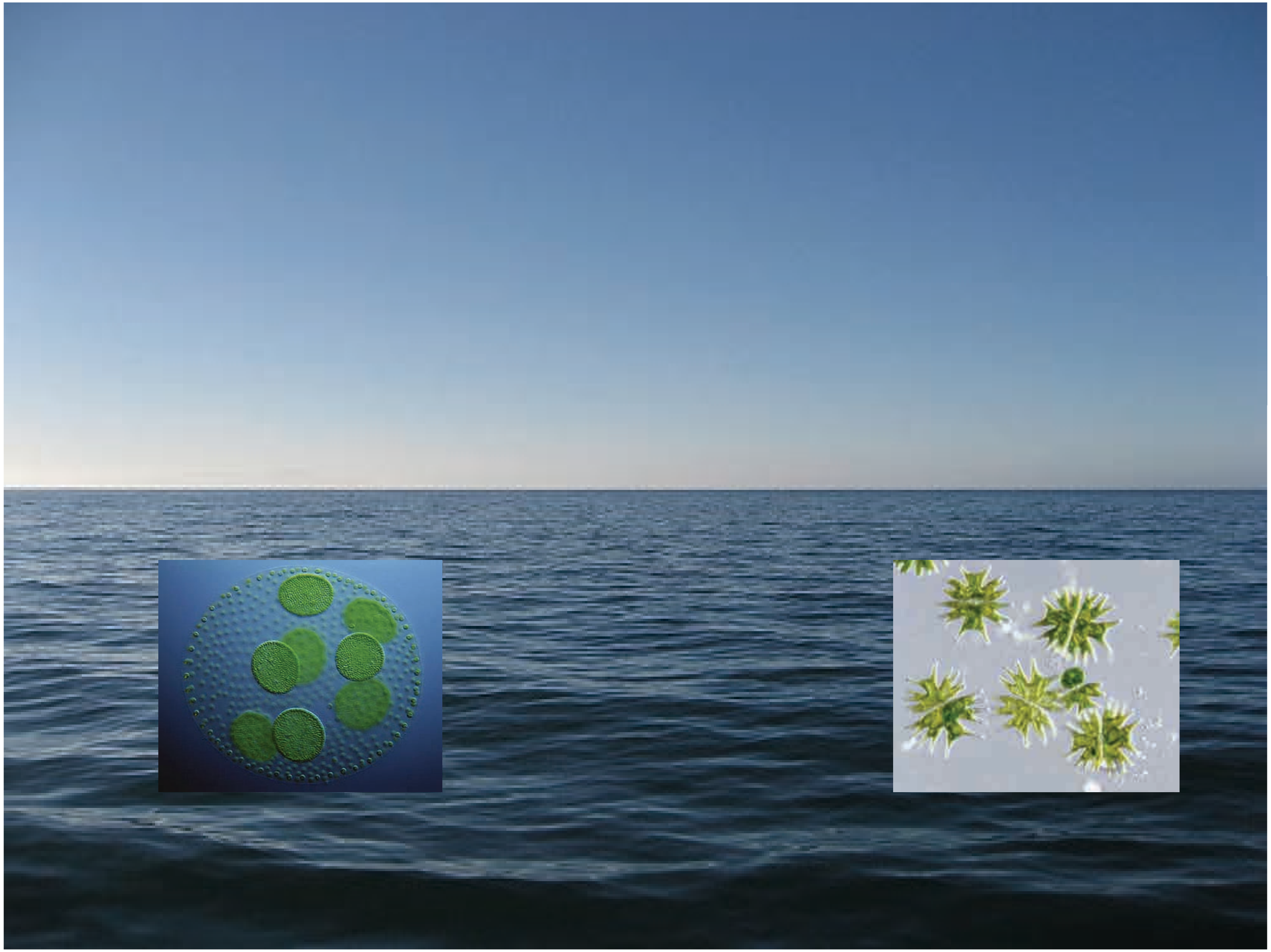
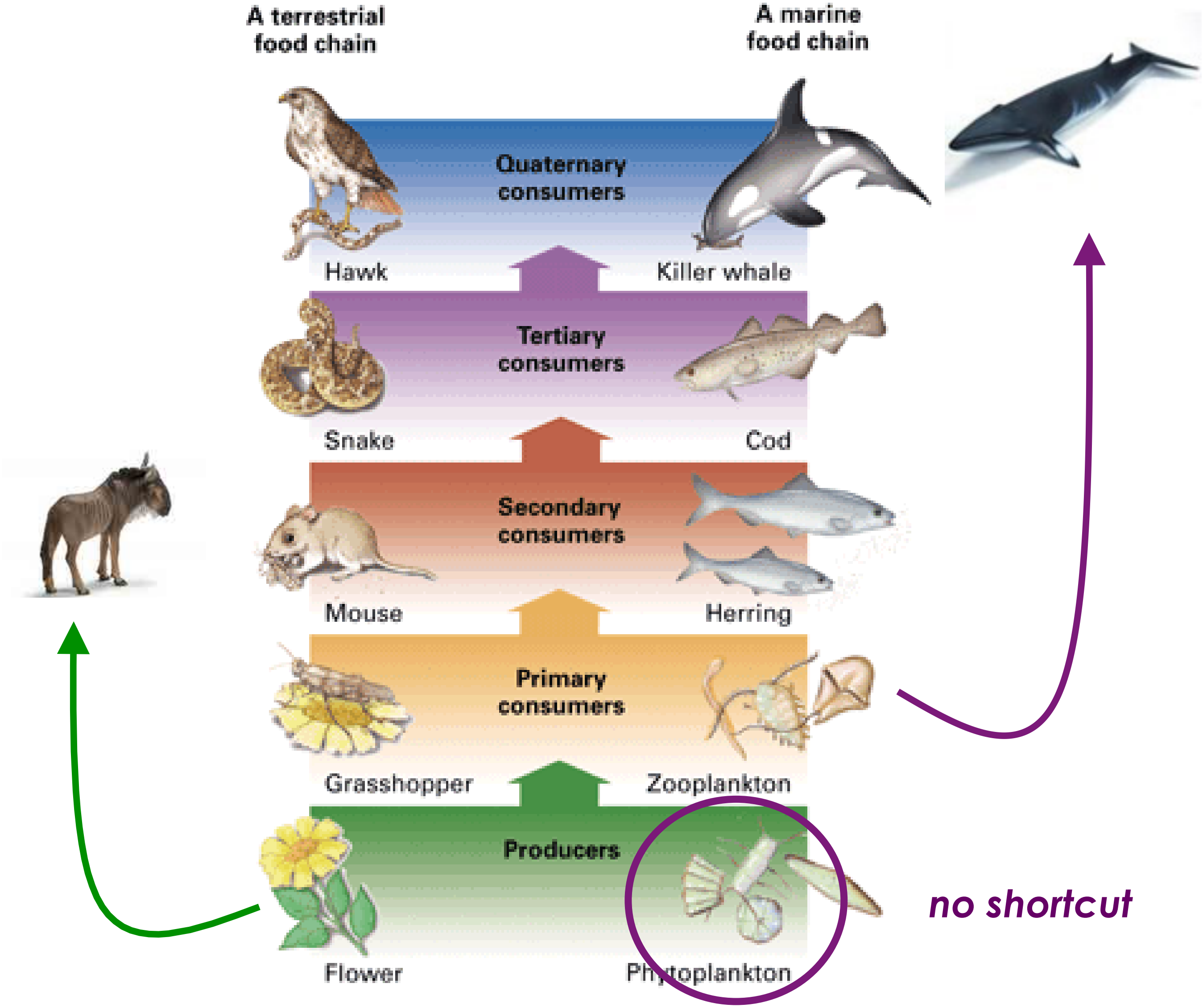


Rare large marine herbivores

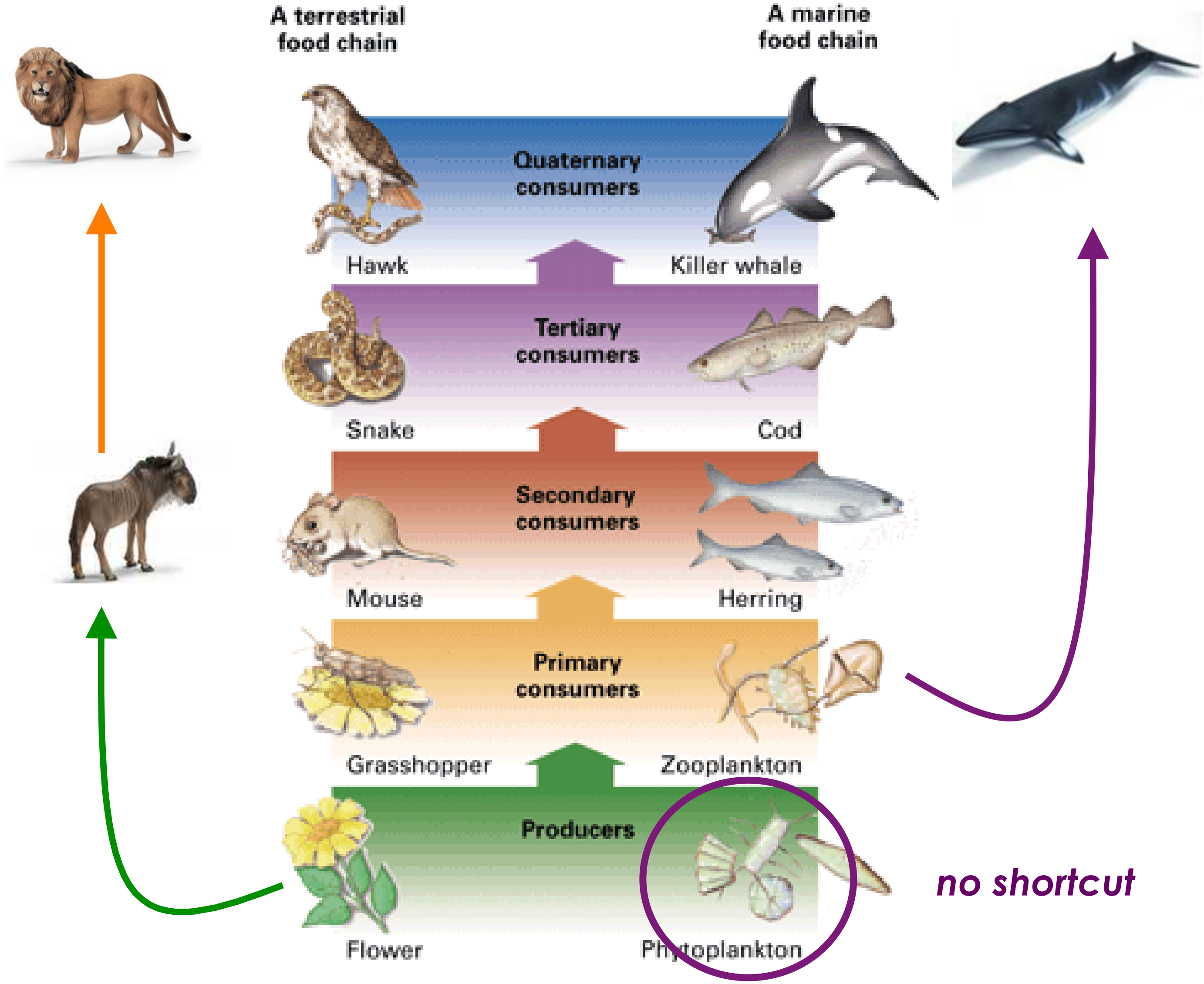
Rare large marine herbivores

Food chains - and shortcuts

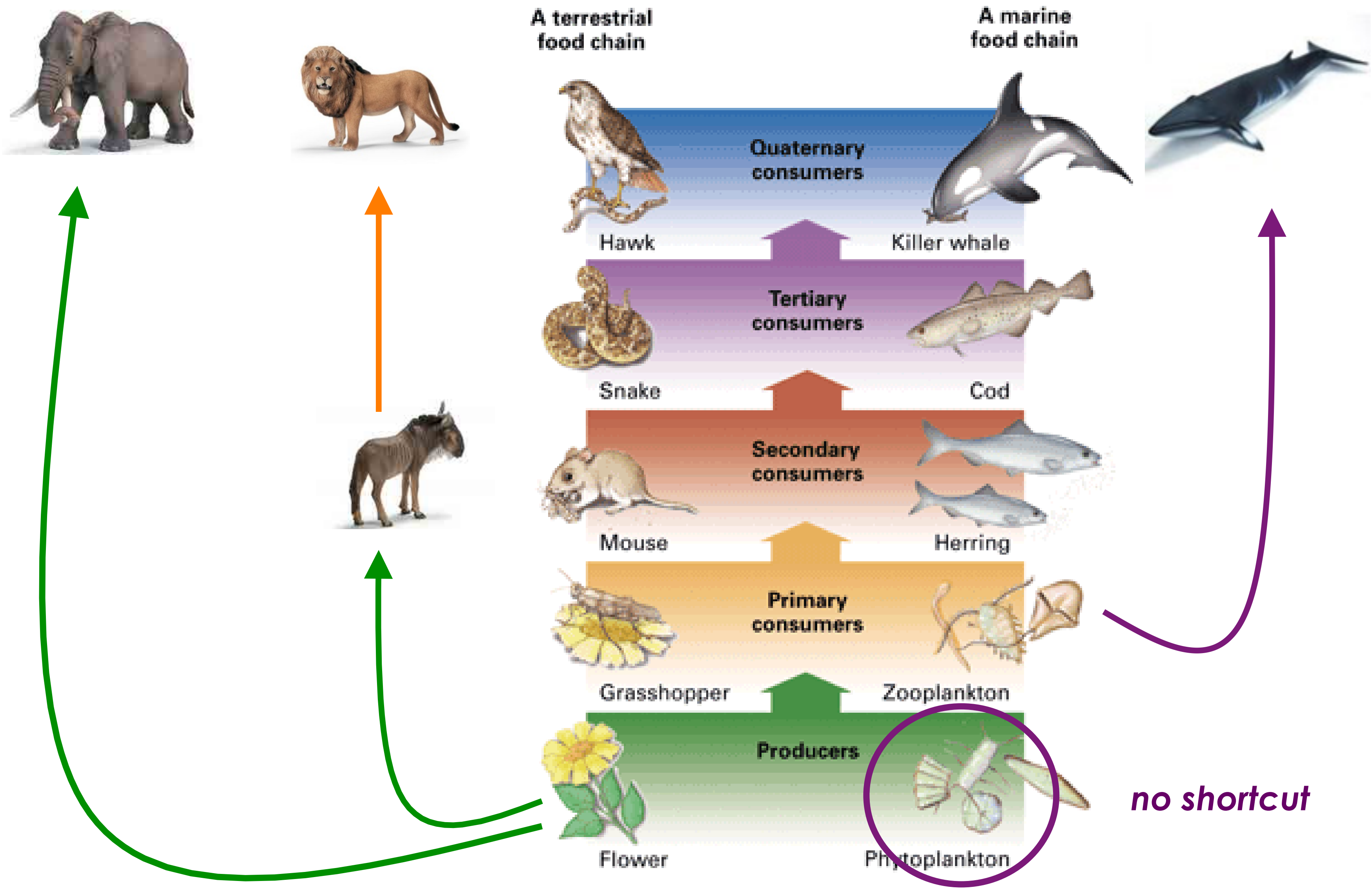


Ubiquitous dense large packages of plant food in terrestrial systems

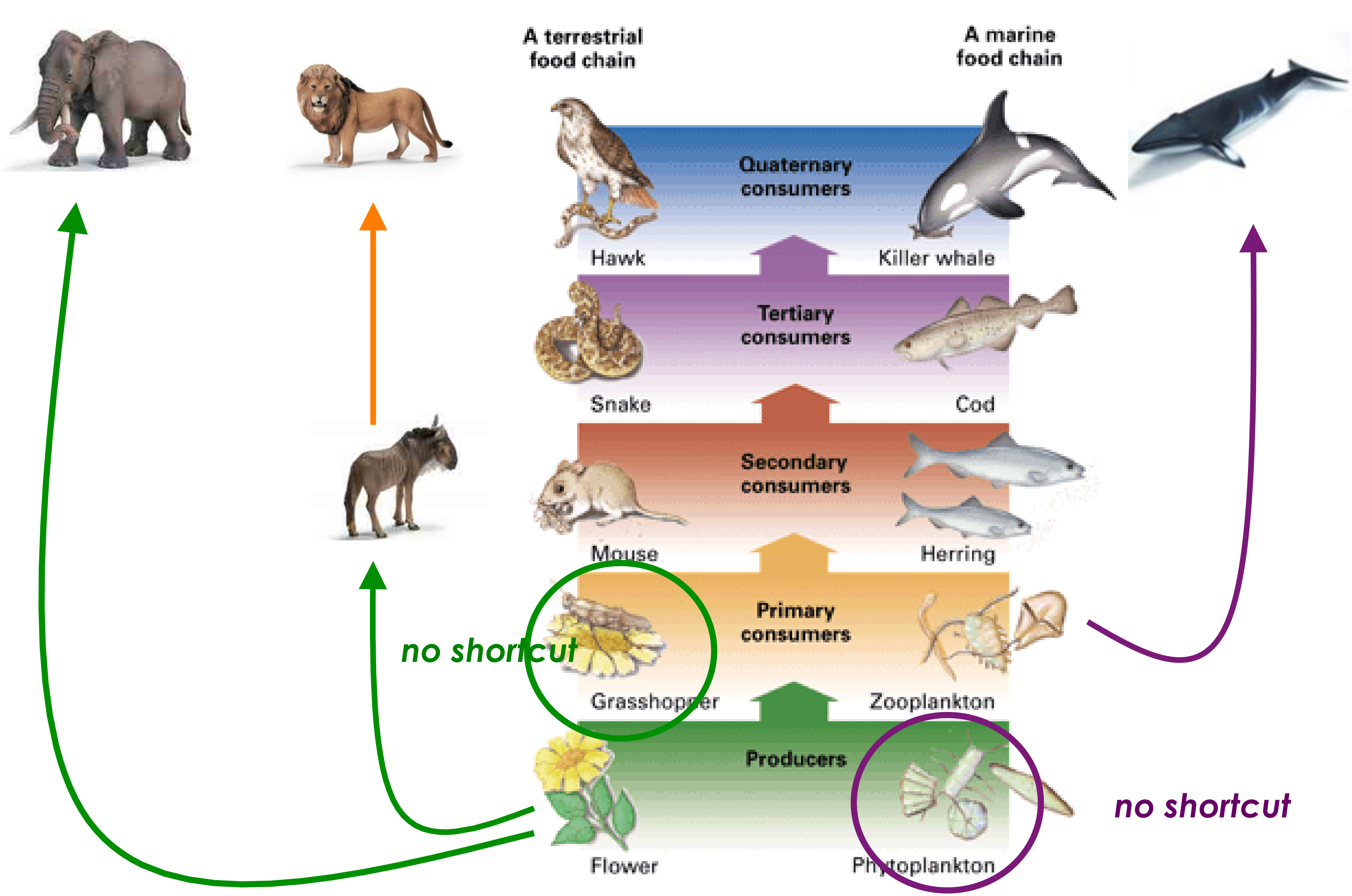
Food chains - and shortcuts



Food chains - and shortcuts



Food chains - and shortcuts



No easy-to-harvest packages of tiny invertebrates

Herbivory

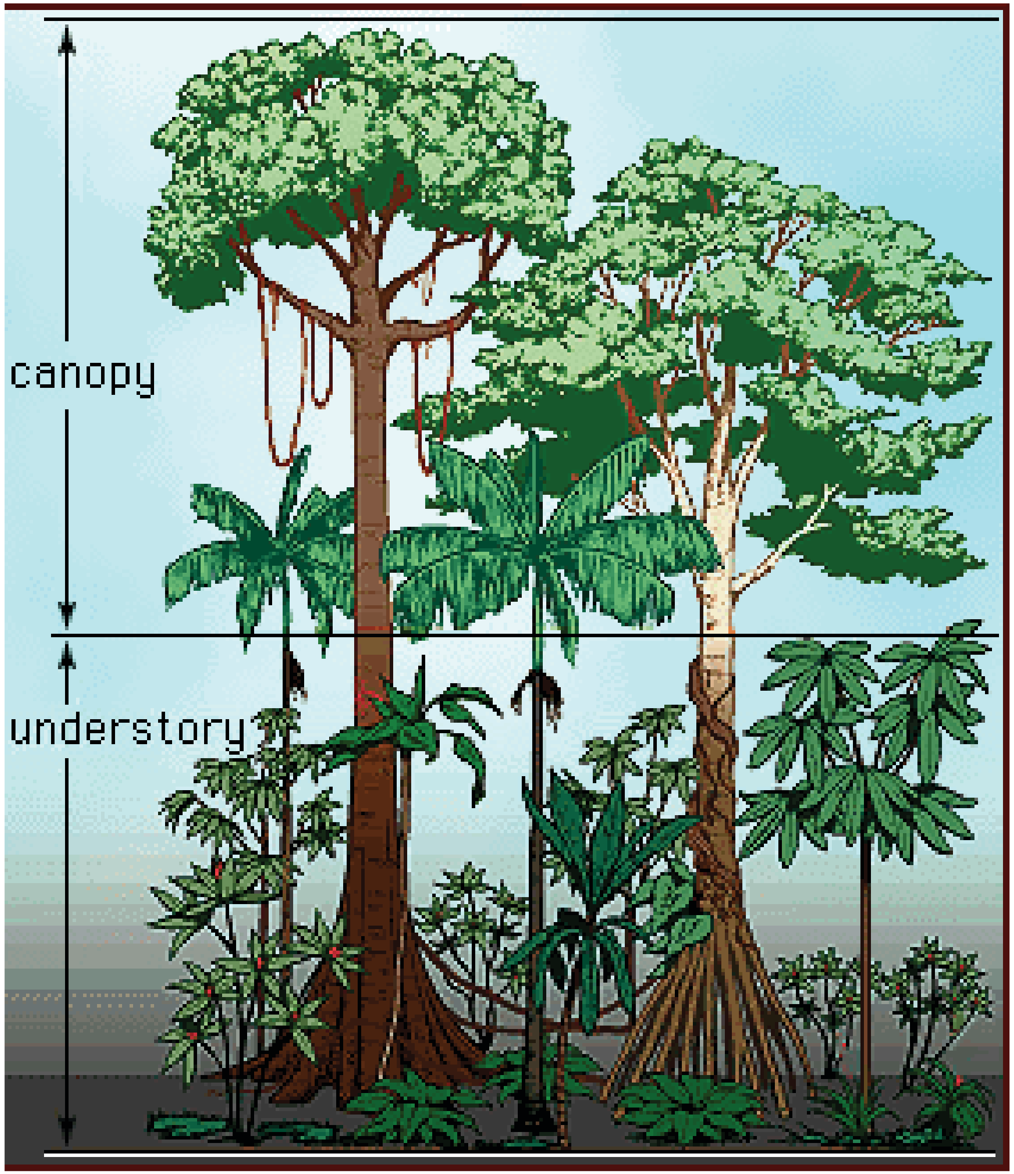
-

Principles

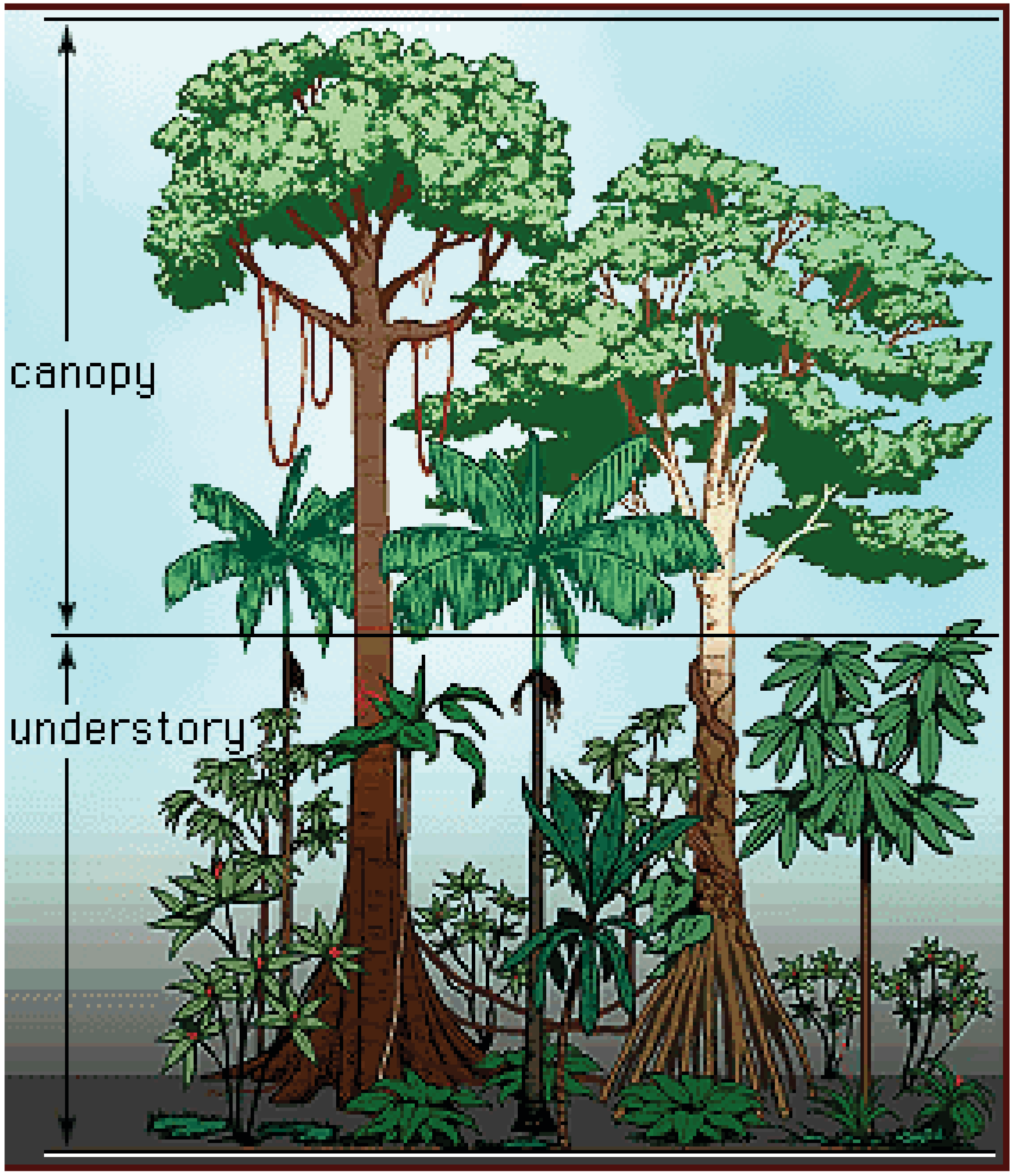
(fibre digestion)

Competition for light ...

Competition for light ...

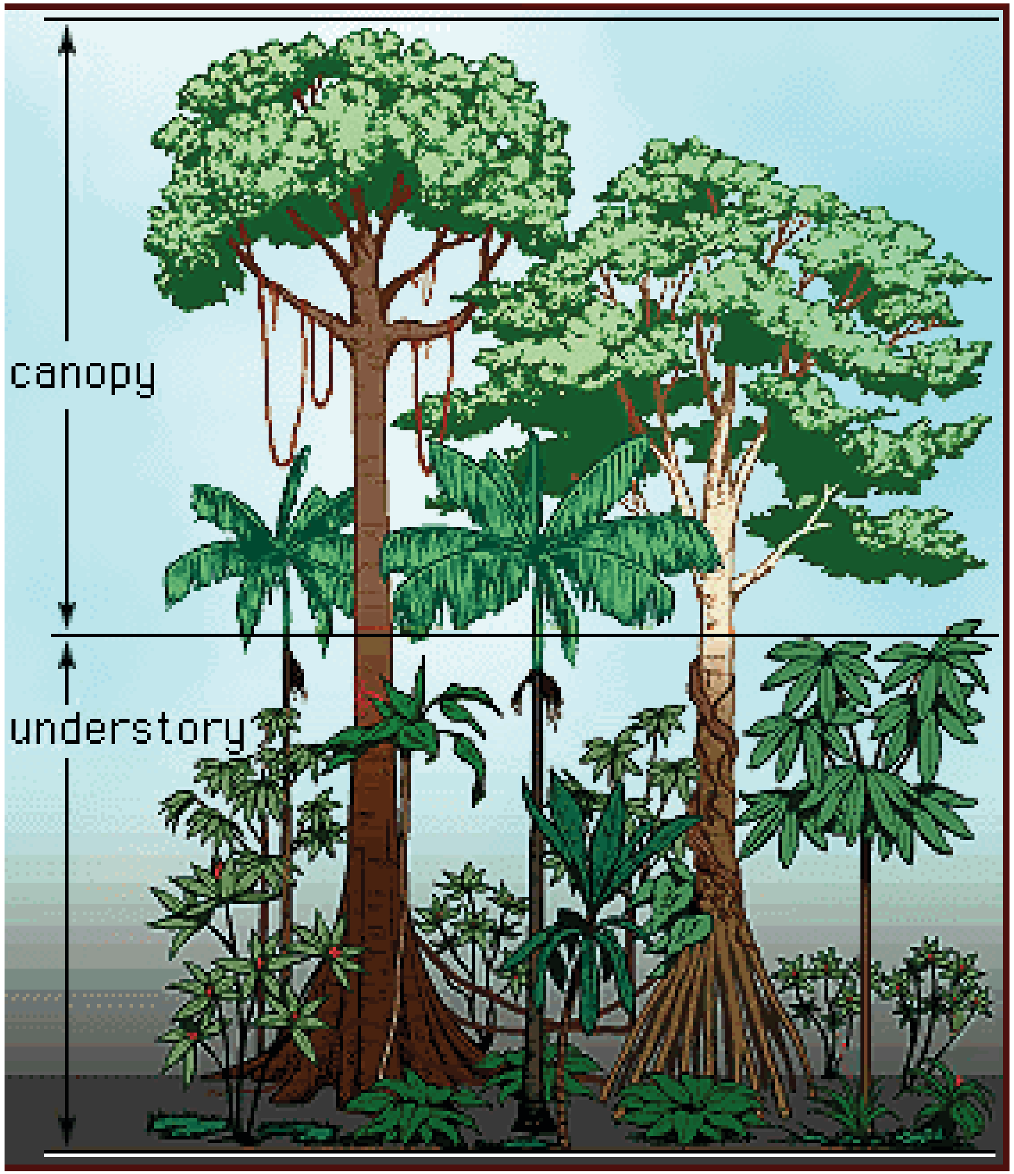


Competition for light ...



... results in a struggle against gravity in terrestrial systems:

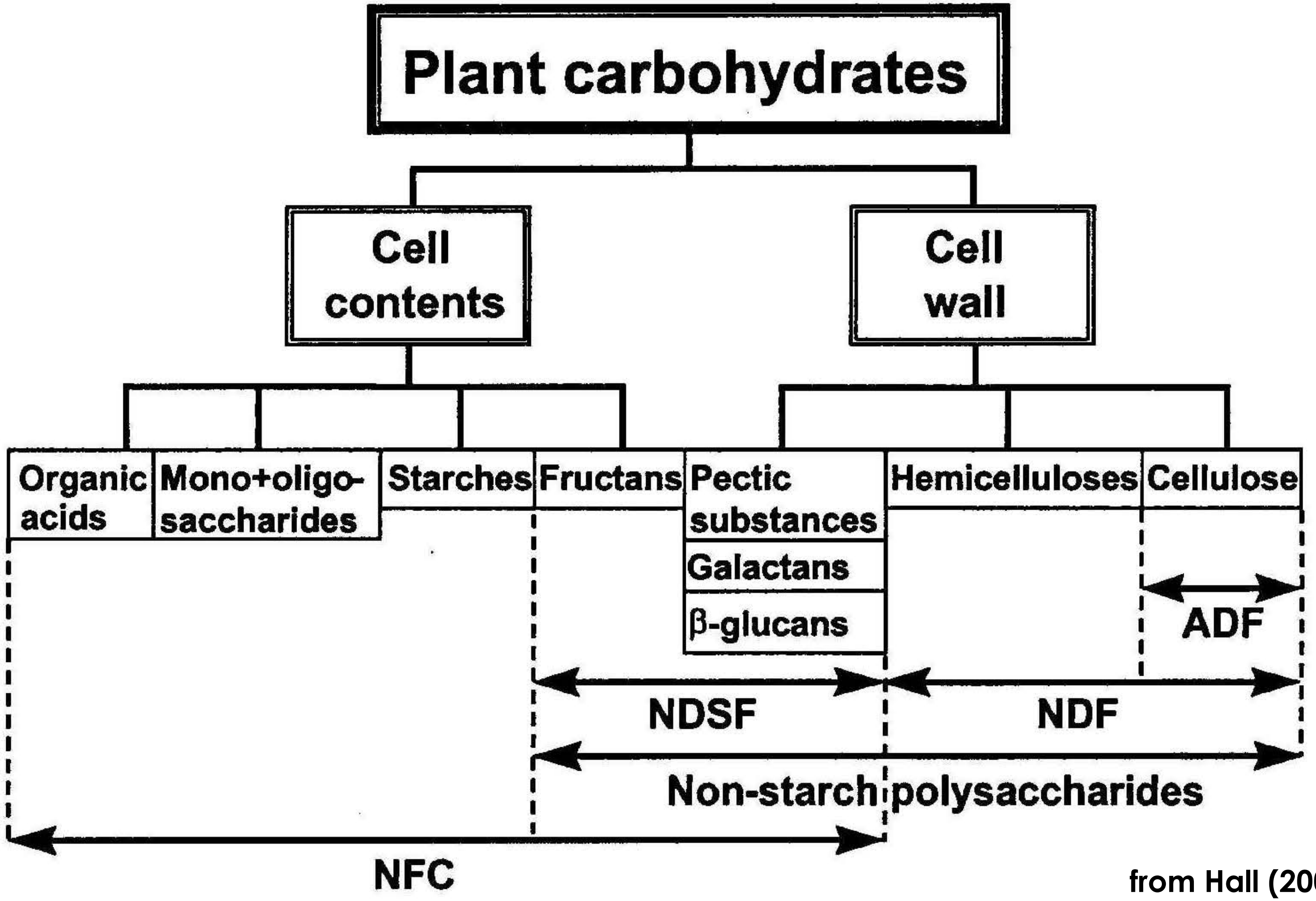
Competition for light ...



... results in a struggle against gravity in terrestrial systems:

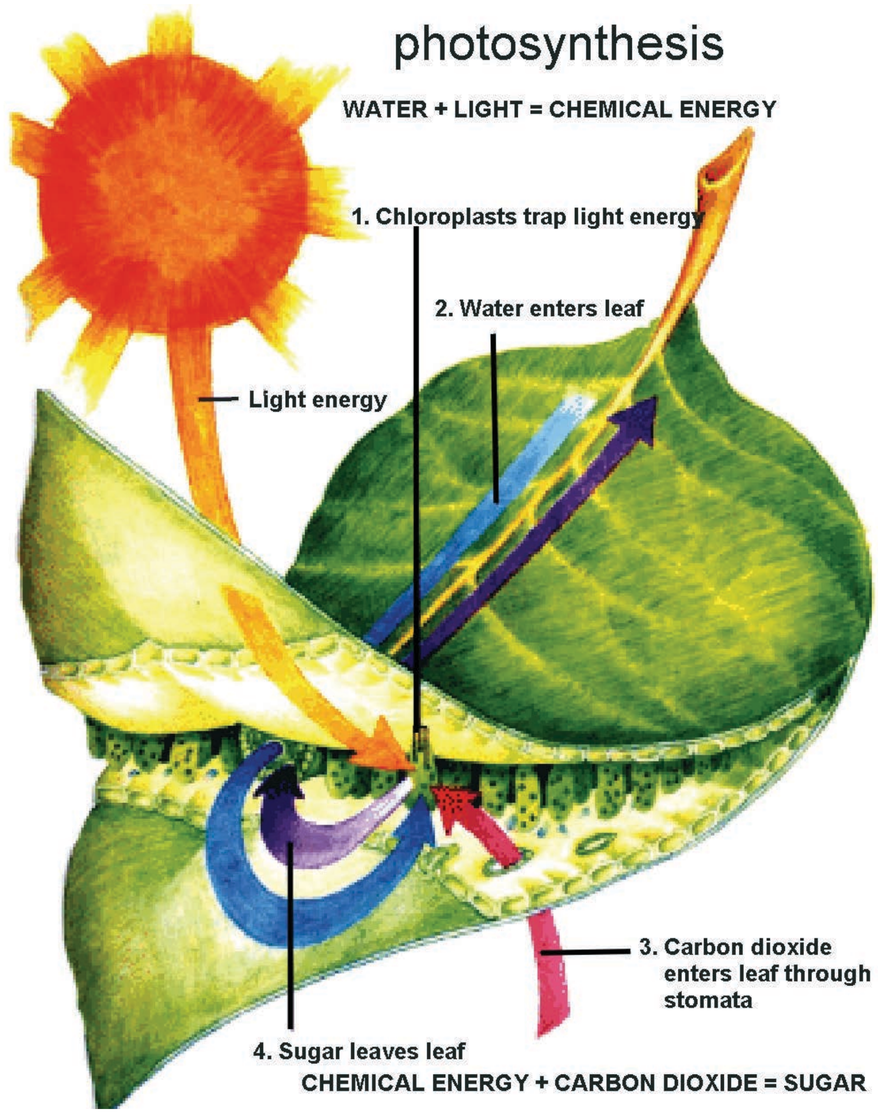
the evolution of 'fibre'

Fibre analysis



from Hall (2003)

Photosynthesis



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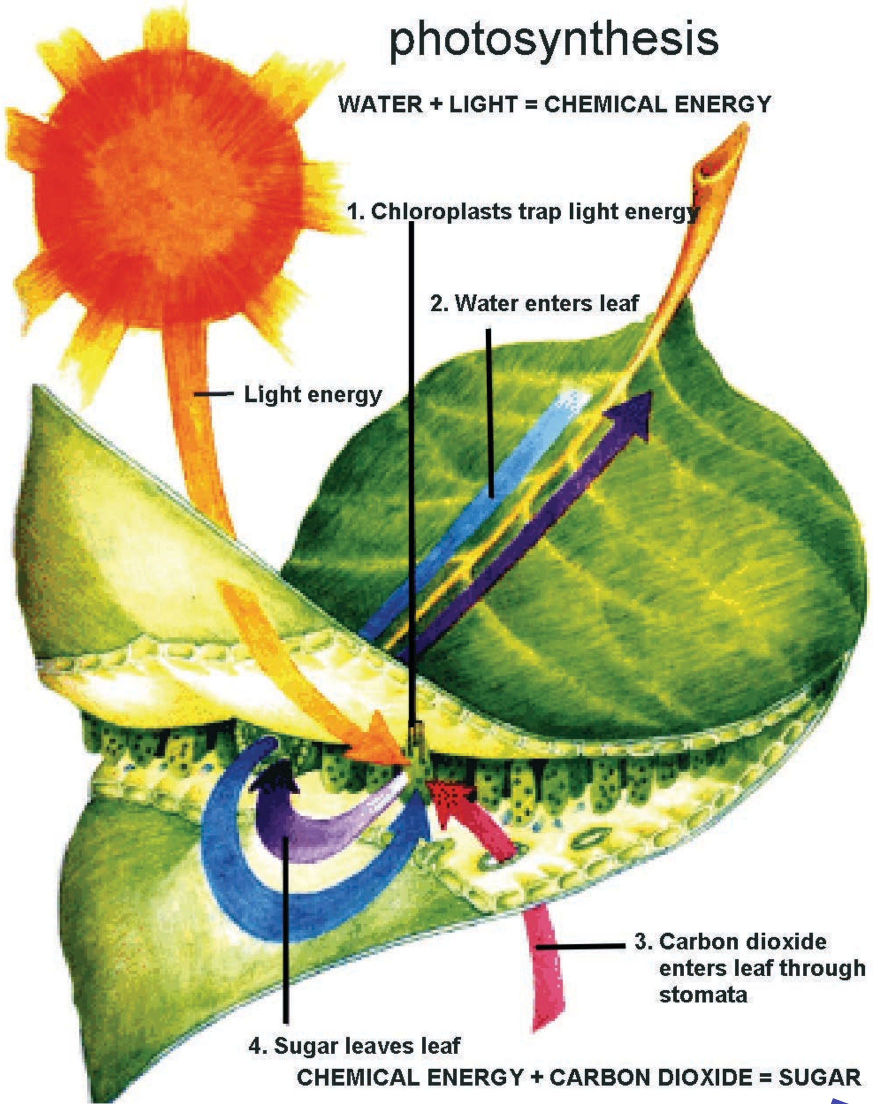

O_2

First fundamental question

Do you want to use plant fibre or only the plant cell contents?

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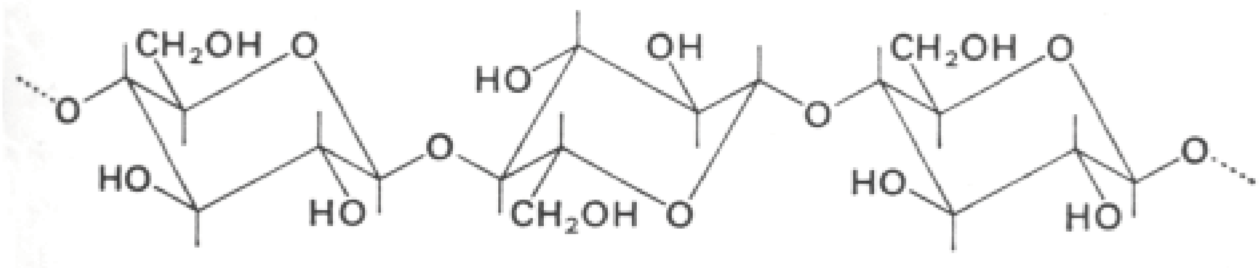
Fibre digestion

Organic polymers
(cellulose, hemicellulose)



from Karasov & Martinez del Rio (2007)

Fibre digestion

Organic polymers
(cellulose, hemicellulose)

↓

Hydrolysis
(soluble sugars)

from Karasov & Martinez del Rio (2007)

Fibre digestion

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Primary fermentation
(lactate, succinate)

from Karasov & Martinez del Rio (2007)

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Secondary fermentation

acetate, propionate, butyrate | **H_2** | **CO_2**

from Karasov & Martinez del Rio (2007)

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Removal ('sinks')?

from Karasov & Martinez del Rio (2007)

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↓

Hydrolysis
(soluble sugars)

↓

Primary fermentation
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Secondary fermentation

acetate, propionate, butyrate | **H_2** | **CO_2**

↓

Methanogenesis
(CH_4, H_2O)

from Karasov & Martinez del Rio (2007)

Fibre digestion

Organic polymers
(cellulose, hemicellulose)

Hydrolysis
(soluble sugars)

Primary fermentation
(lactate, succinate)

Secondary fermentation

acetate, propionate, butyrate

H_2 CO_2

Acetogenesis
($C_2H_3O_2$, H_2O)

Methanogenesis
(CH_4, H_2O)

from Karasov & Martinez del Rio (2007)

Fibre digestion

Organic polymers
(cellulose, hemicellulose)

↓

Hydrolysis
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↓

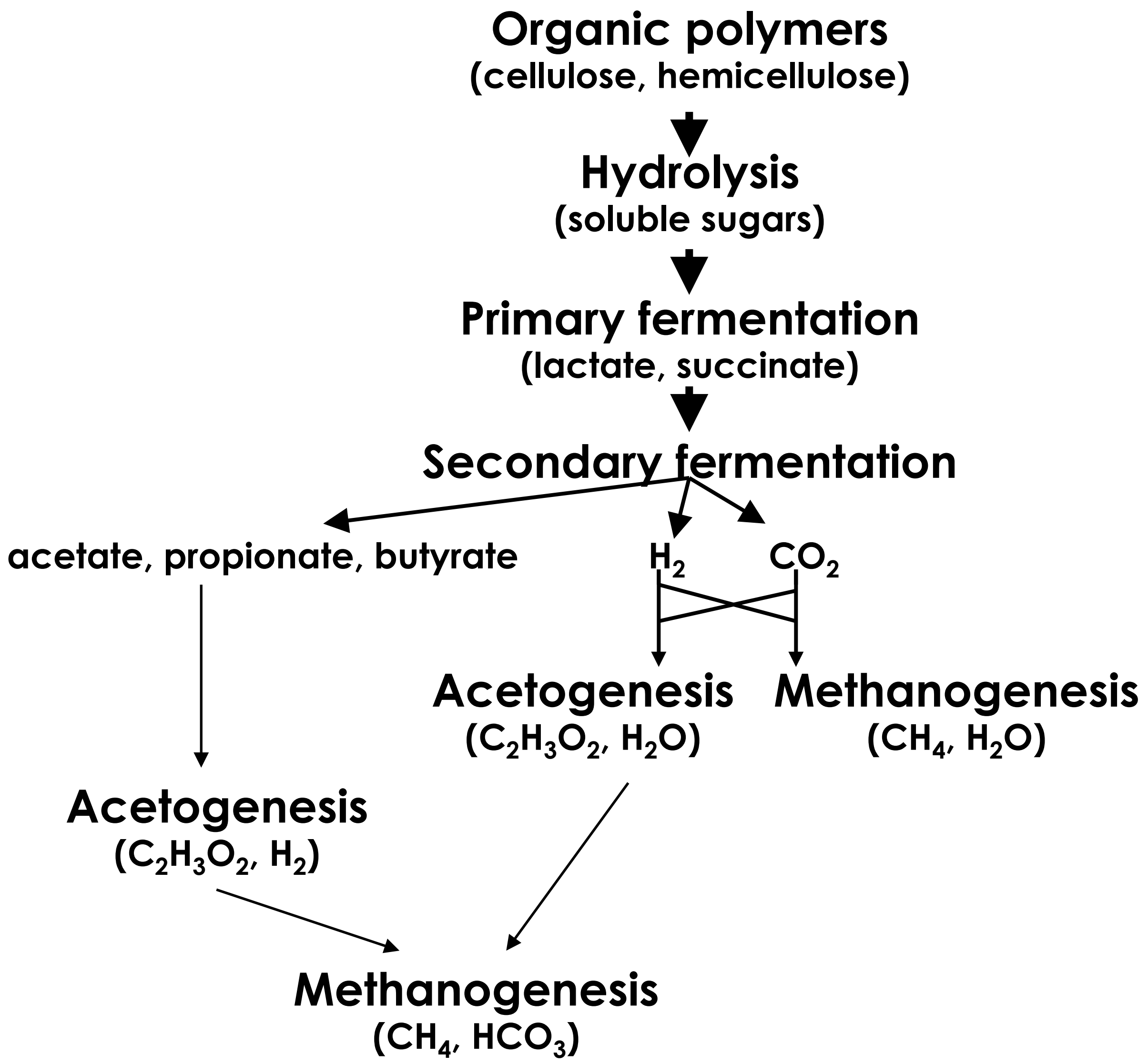
Secondary fermentation

acetate, propionate, butyrate → **Acetogenesis** **($C_2H_3O_2$, H_2)**

H_2 CO_2 → **Acetogenesis** **($C_2H_3O_2$, H_2O)**, **Methanogenesis** **(CH_4, H_2O)**

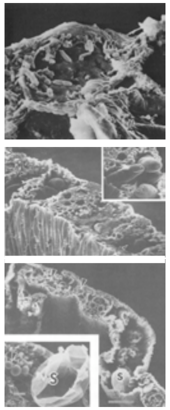
from Karasov & Martinez del Rio (2007)

Fibre digestion



from Karasov & Martinez del Rio (2007)

Fibre digestion



Organic polymers
(cellulose, hemicellulose)

Hydrolysis
(soluble sugars)

Primary fermentation
(lactate, succinate)

Secondary fermentation

acetate, propionate, butyrate

H_2 **CO_2**

Acetogenesis
($C_2H_3O_2$, H_2O)

Methanogenesis
(CH_4, H_2O)

Acetogenesis
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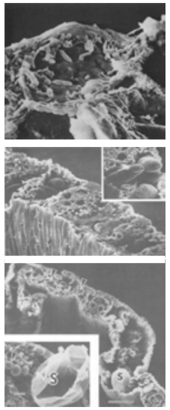
(CH_4, HCO_3)

from Karasov & Martinez del Rio (2007)

Fibre digestion



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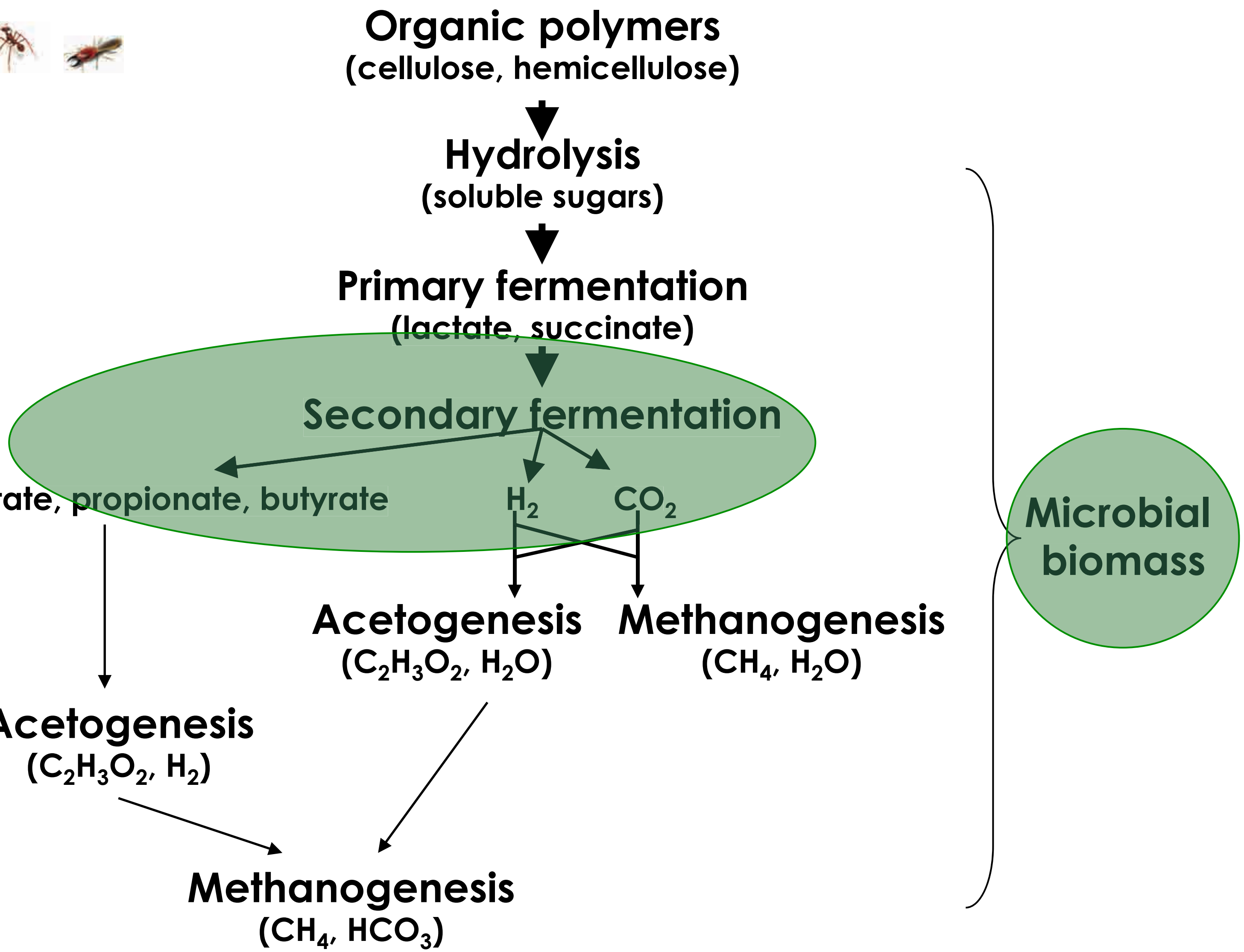
Microbial biomass

from Karasov & Martinez del Rio (2007)

Fibre digestion



from Karasov & Martinez del Rio (2007)

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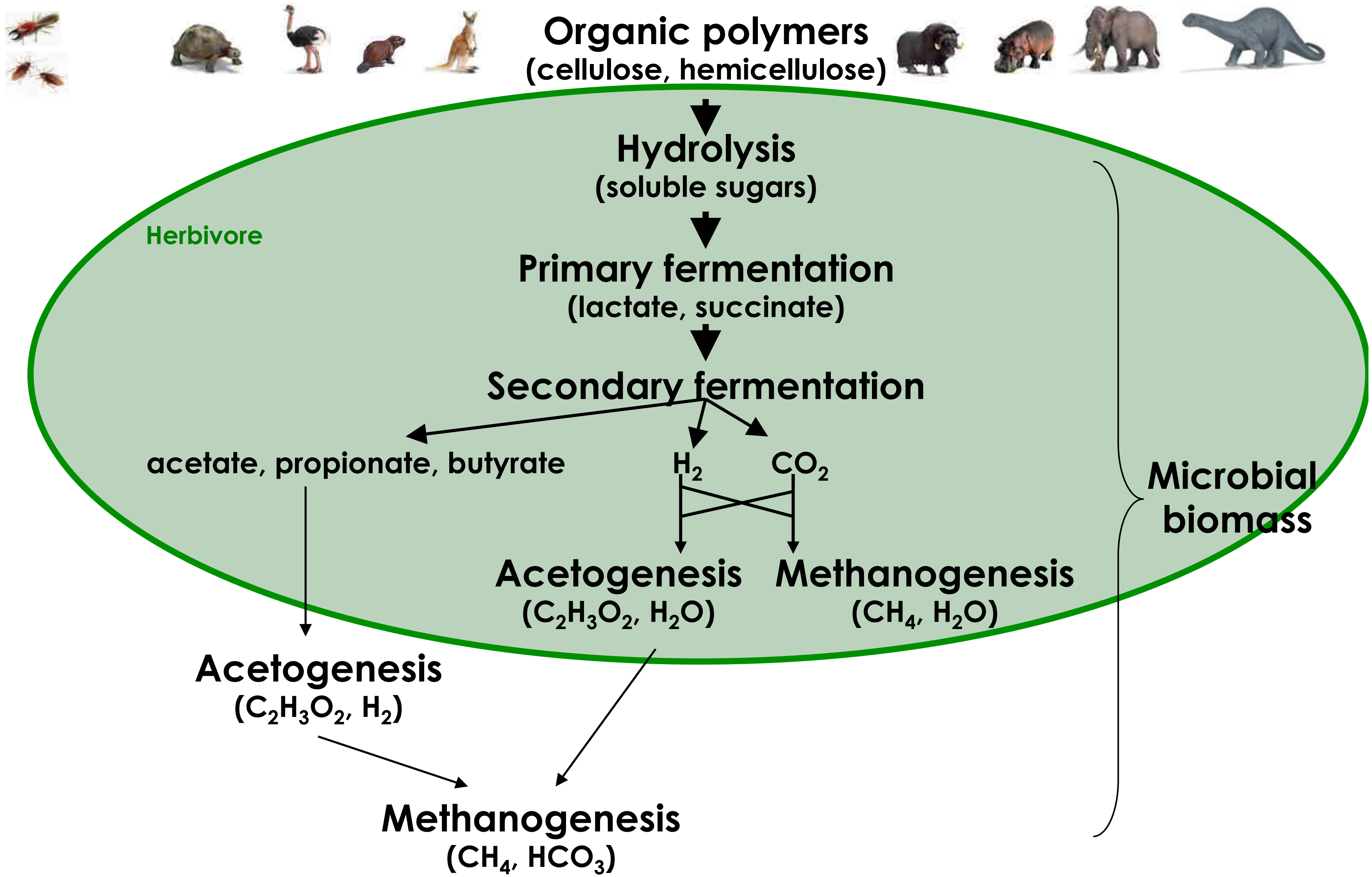

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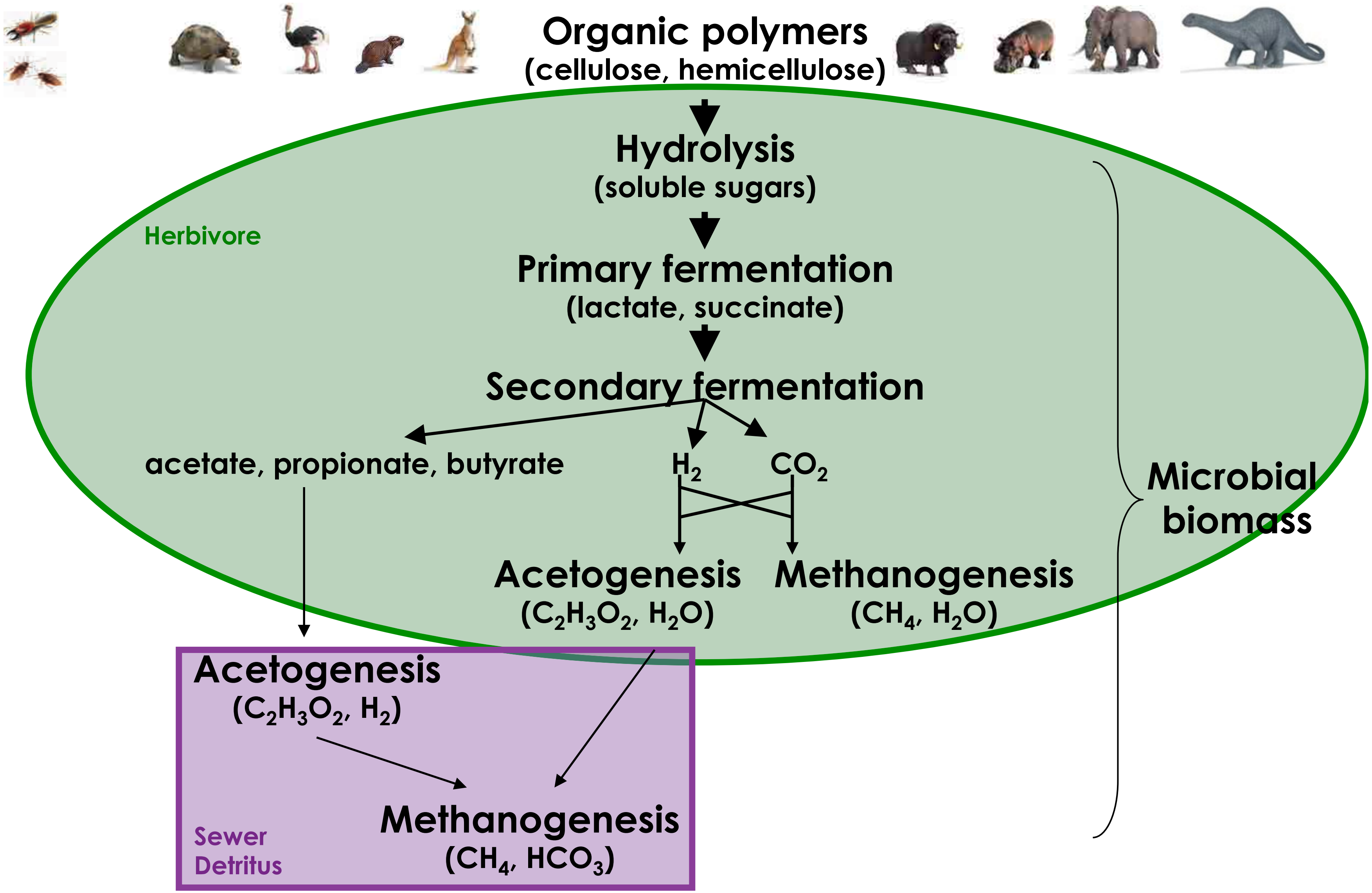

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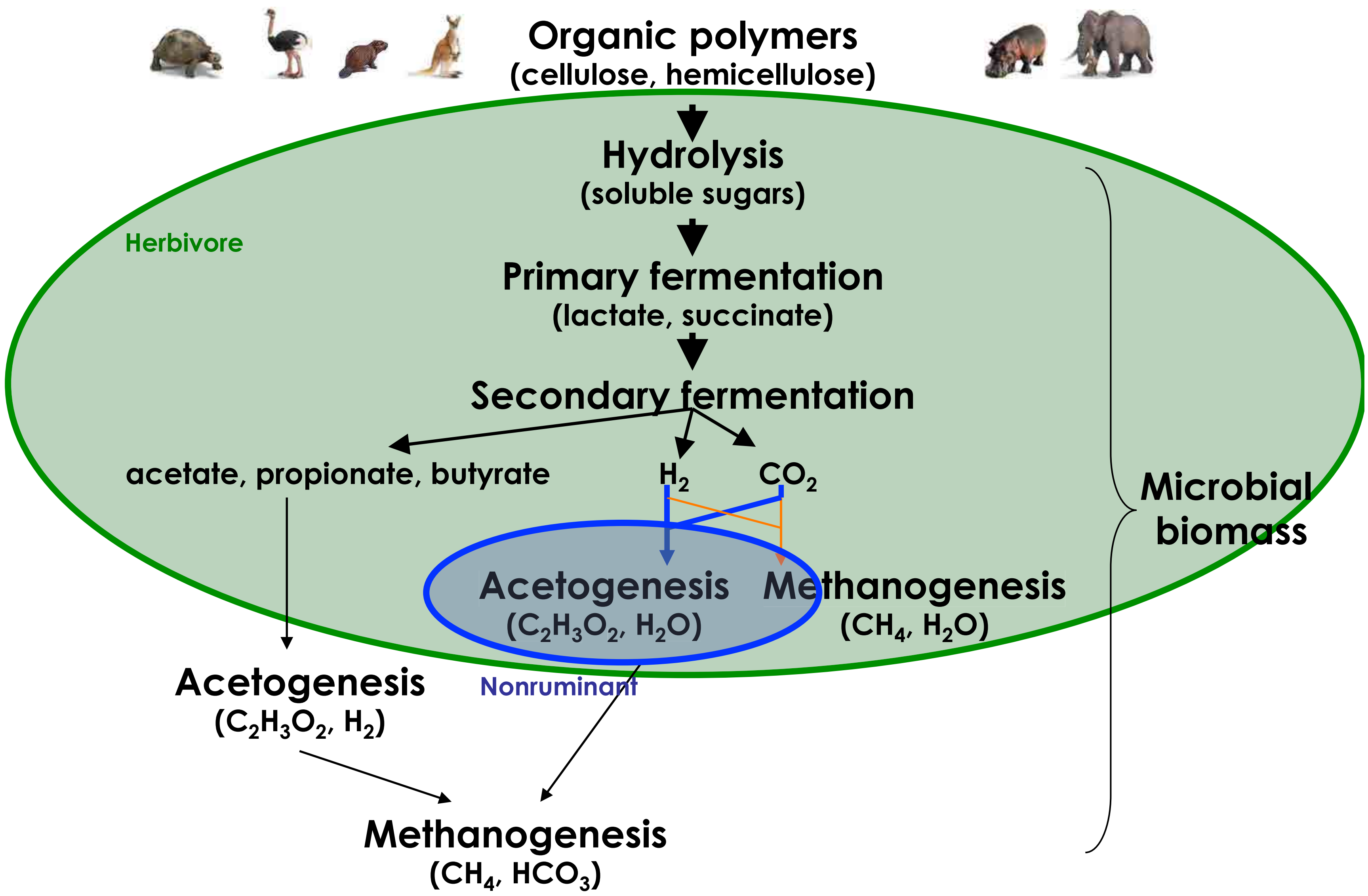

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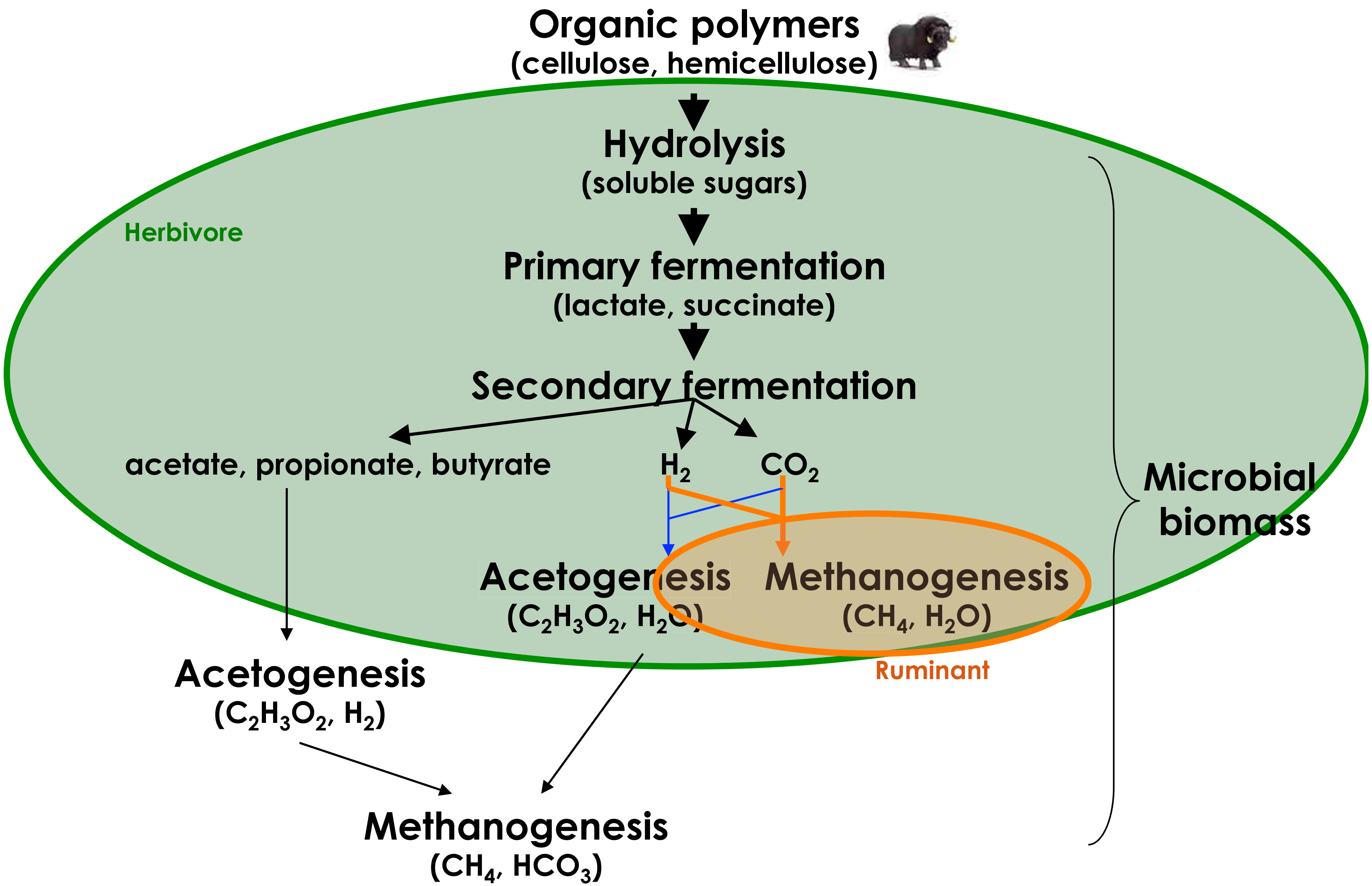
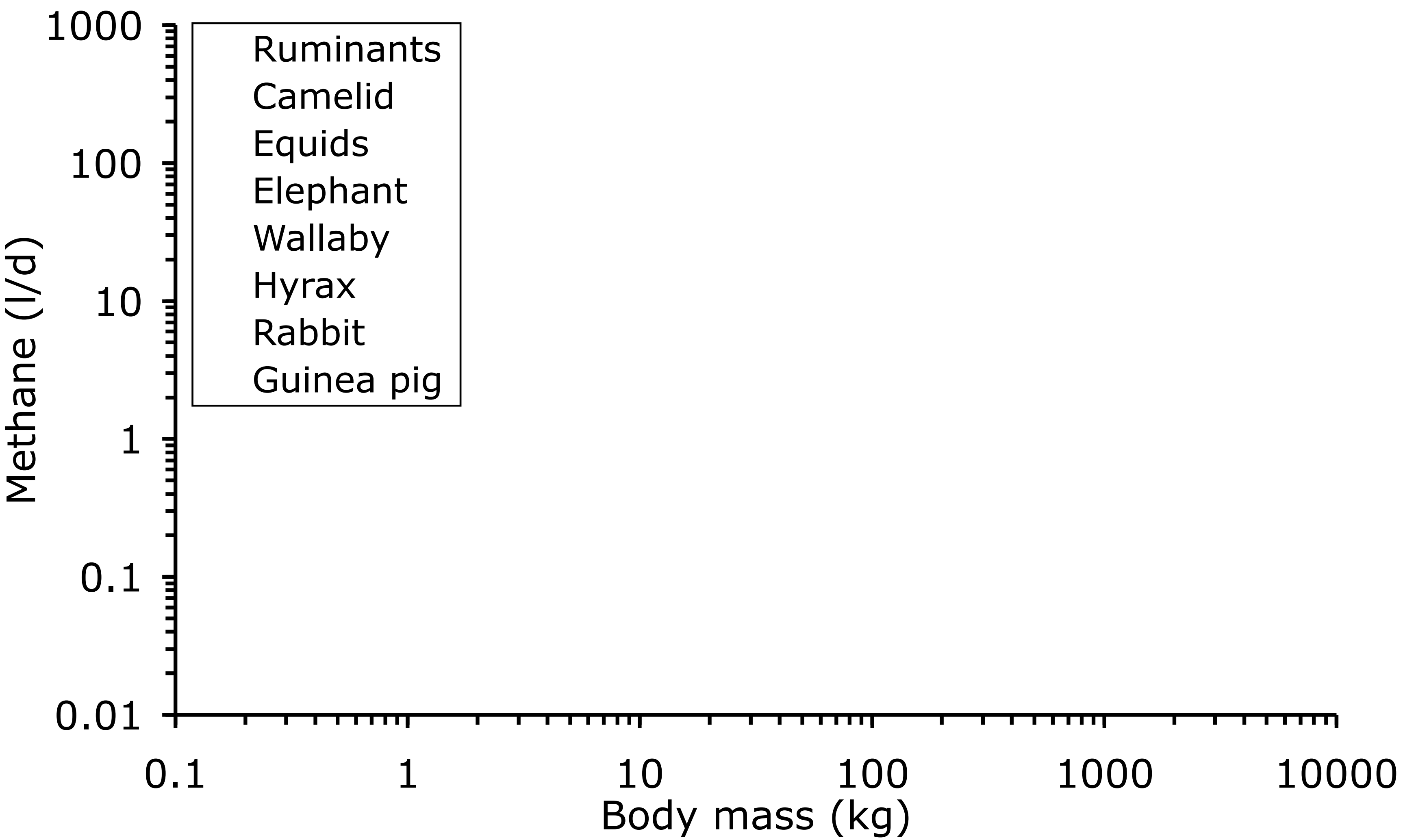
Fibre digestion



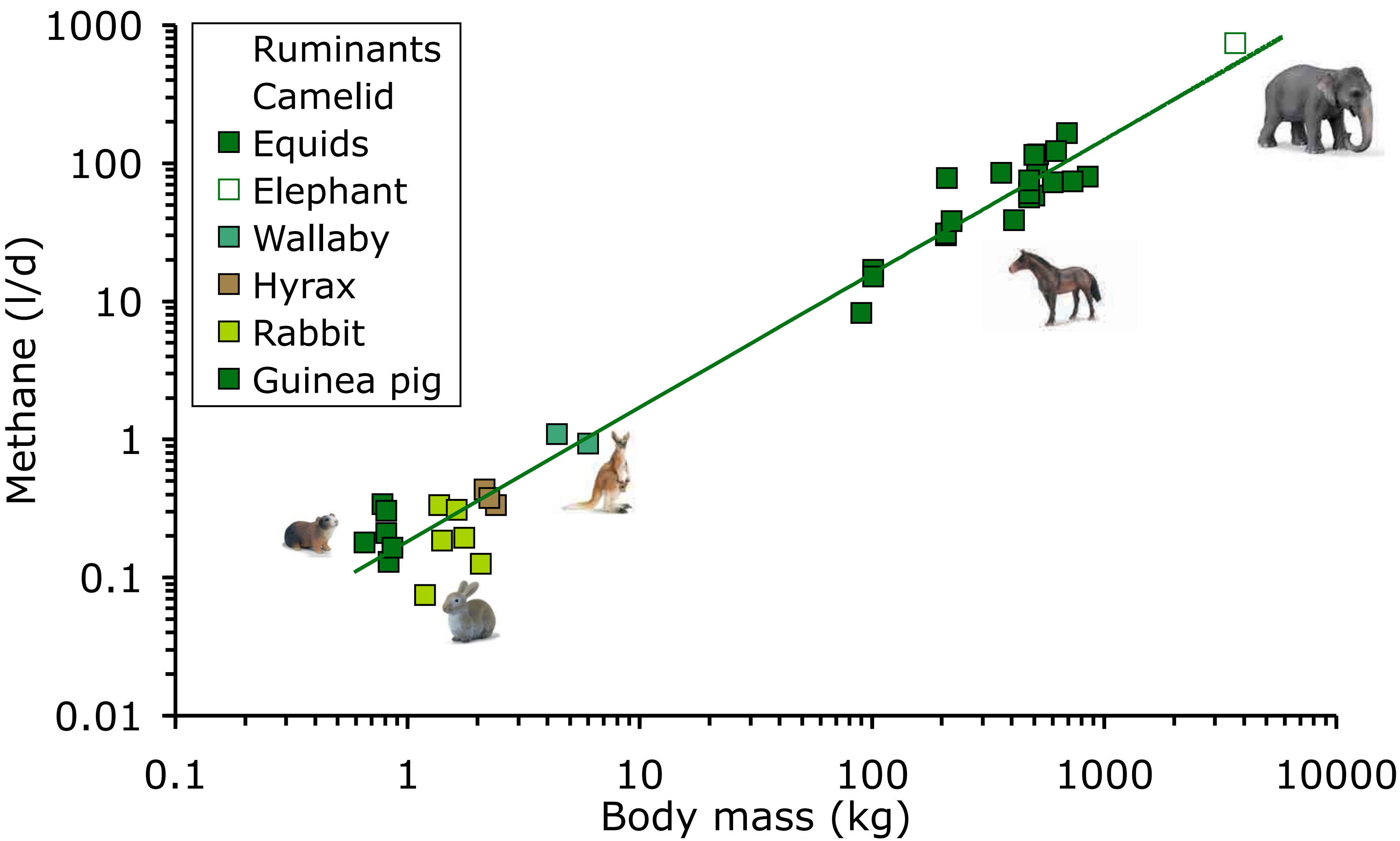
from Karasov & Martinez del Rio (2007)

Methane allometry in herbivores



from Franz et al. (2011)

Methane allometry in herbivores



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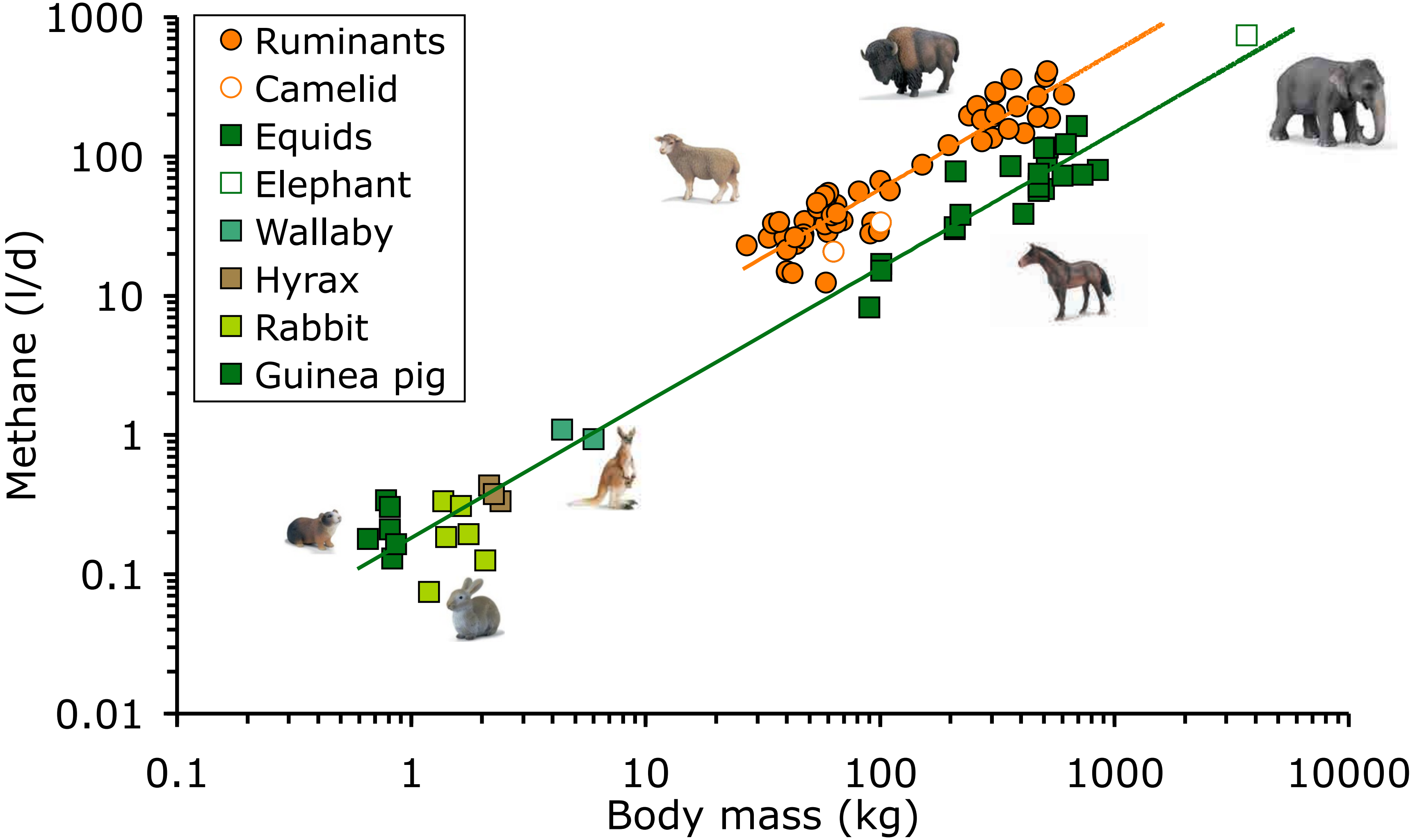

from Franz et al. (2011)

Herbivory

-

Principles

(body size)

Two fundamental questions

1. 'In-house' or outsourcing of fibre digestion?

2. What sequence of fibre digestion and auto-enzymatic digestion?

Two fundamental questions

1. **'In-house' or outsourcing of fibre digestion?**

   'In-house' fibre digestion necessitates anatomical and physiological adaptations that might be costly in some circumstances.

2. **What sequence of fibre digestion and auto-enzymatic digestion?**

Detritivory, coprophagy, and the evolution of digestive mutualisms in Dictyoptera

C. A. Nalepa[1], D. E. Bignell[2] and C. Bandi[3]

Insectes soc. 48 (2001) 194–201

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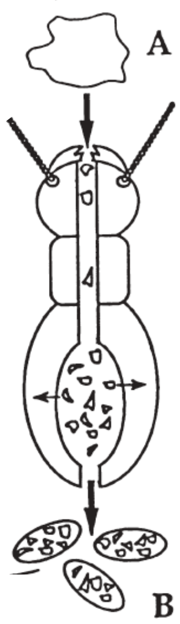

Refractory
food item

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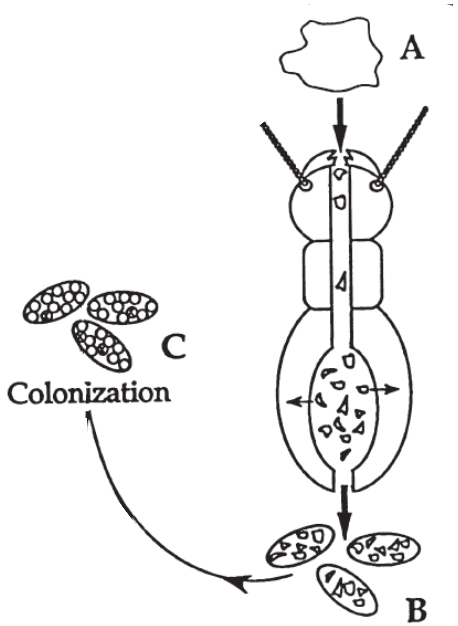

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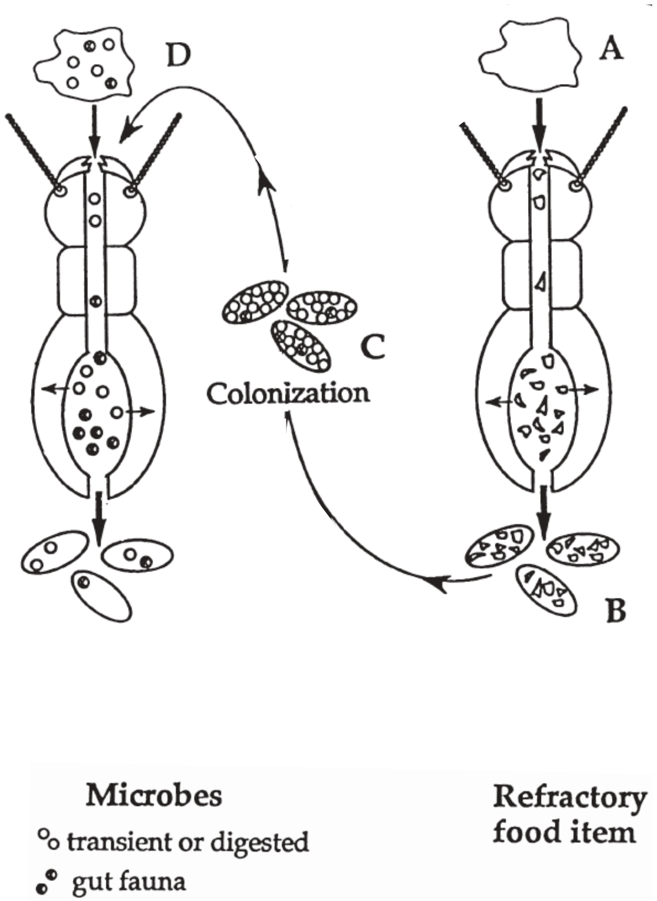

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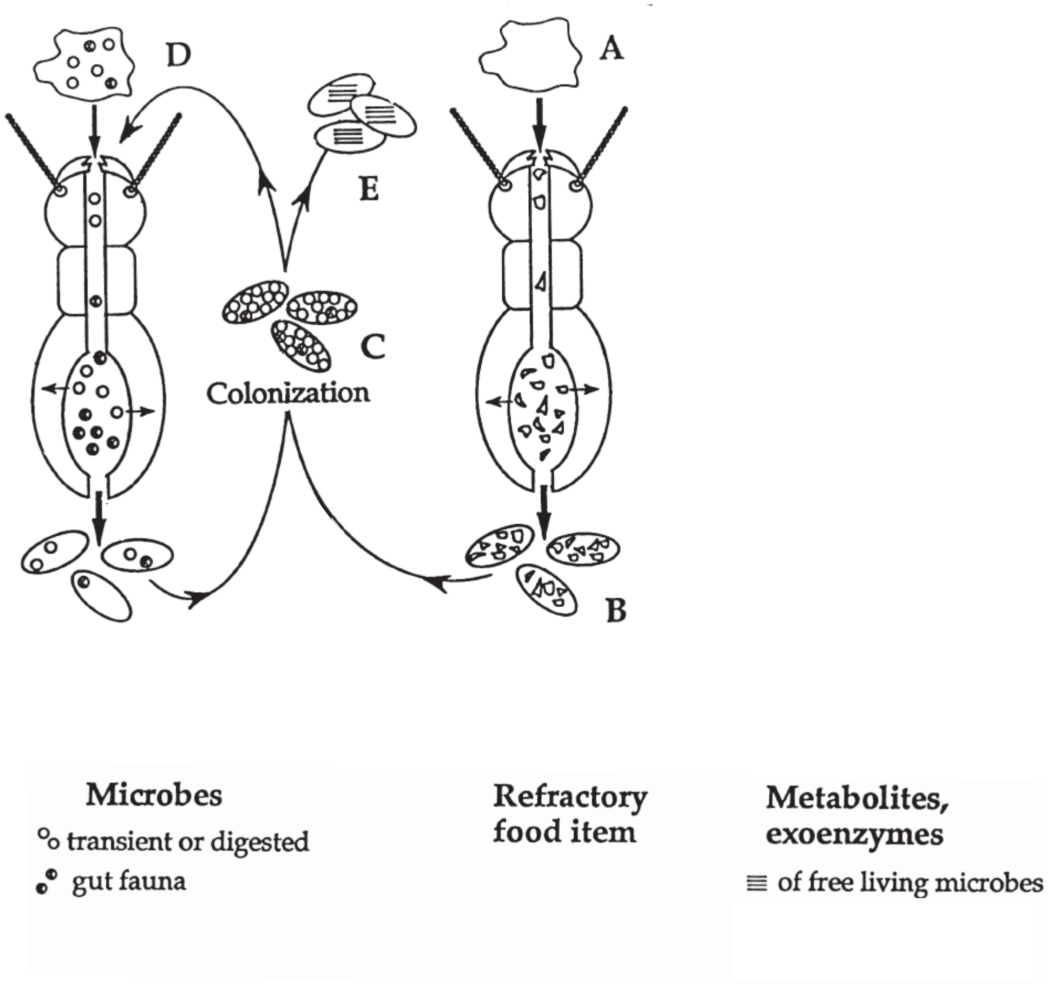

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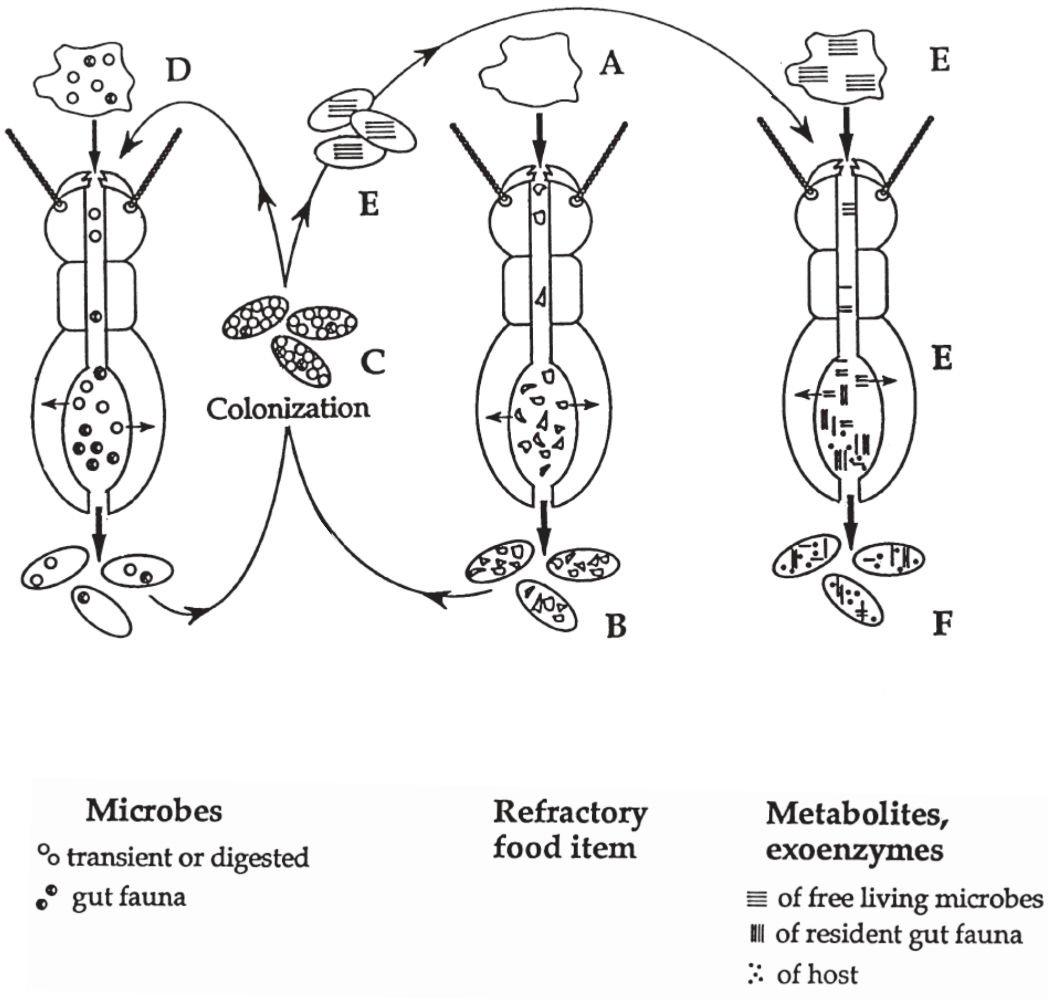

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C. A. Nalepa[1], D. E. Bignell[2] and C. Bandi[3]

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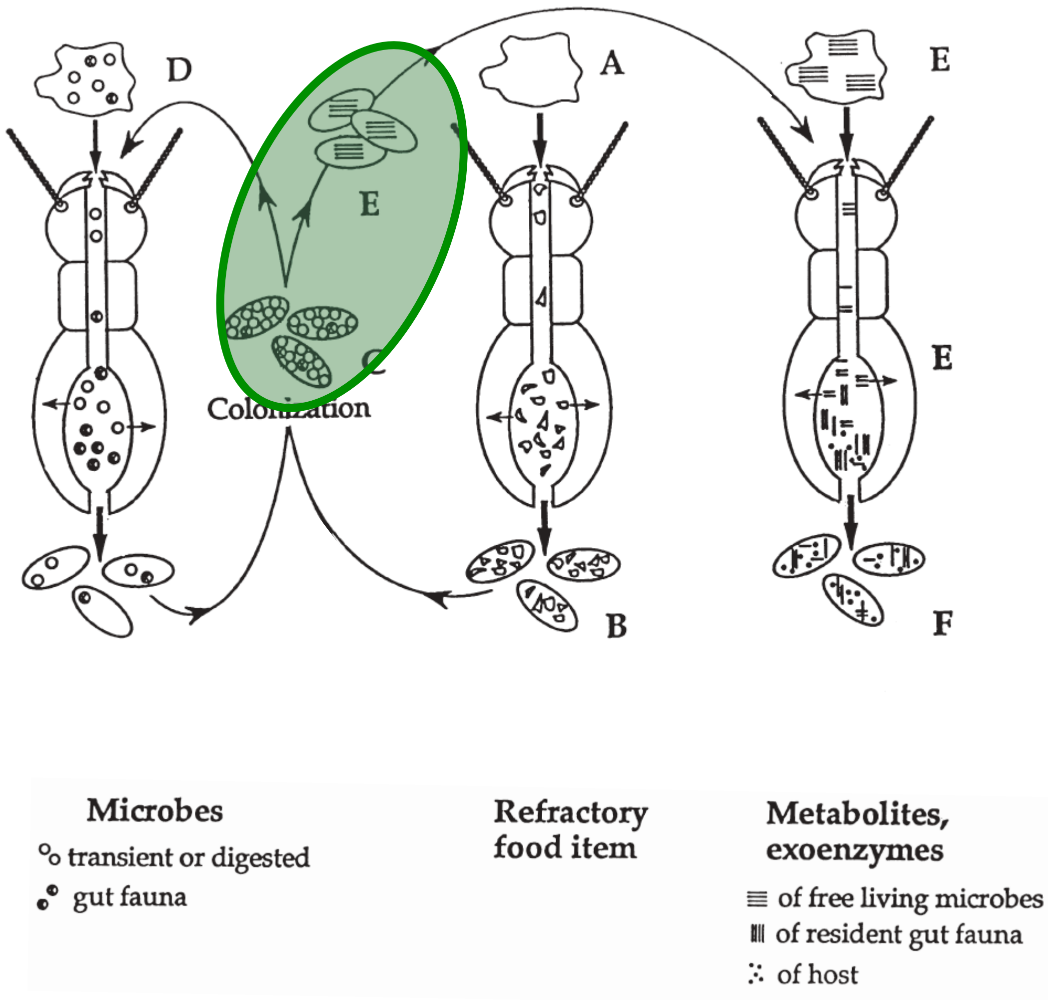
"external rumen"



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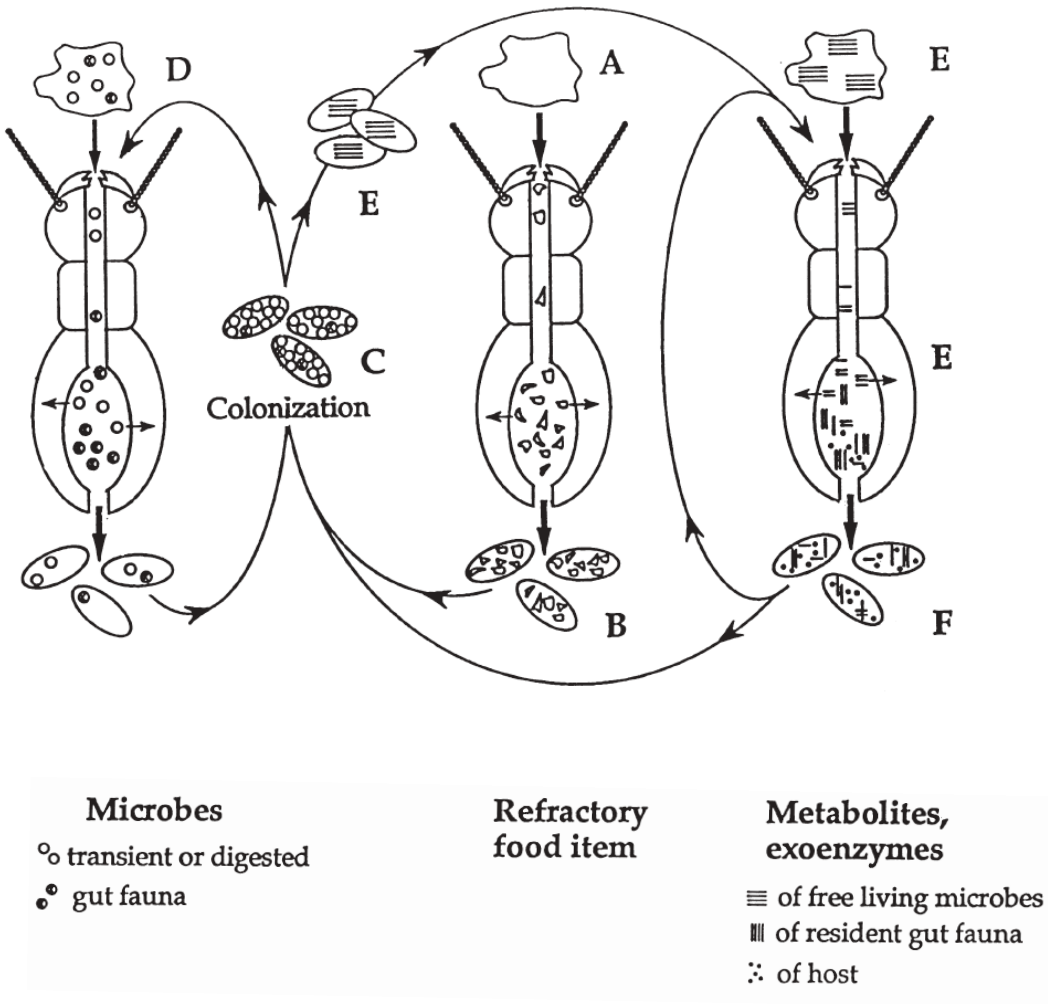
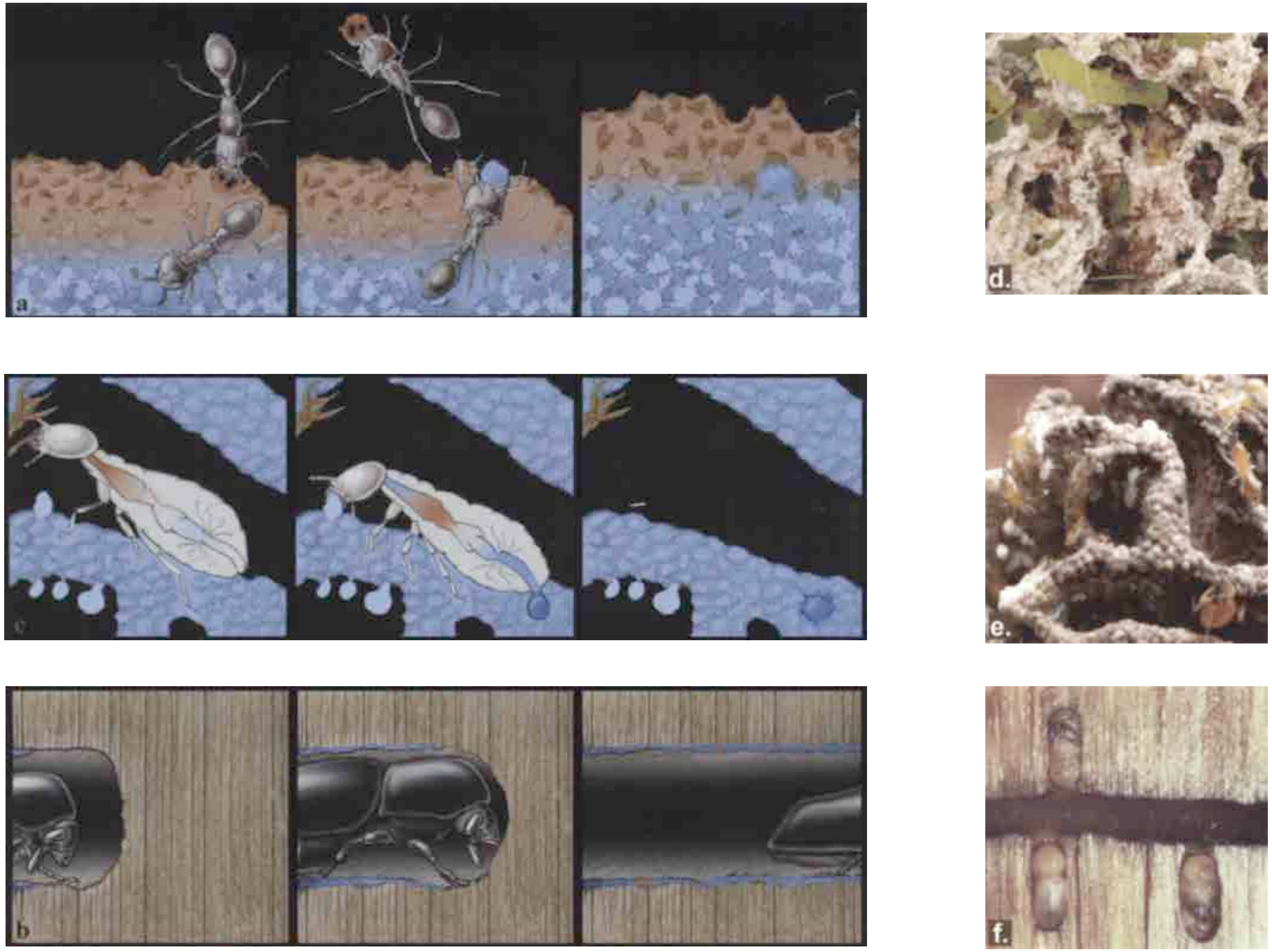


The Evolution of Agriculture in Insects

Ulrich G. Mueller,[1,2] Nicole M. Gerardo,[1,2,3]
Duur K. Aanen,[4] Diana L. Six,[5] and Ted R. Schultz[6]

Annu. Rev. Ecol. Evol. Syst. 2005. 36:563–95

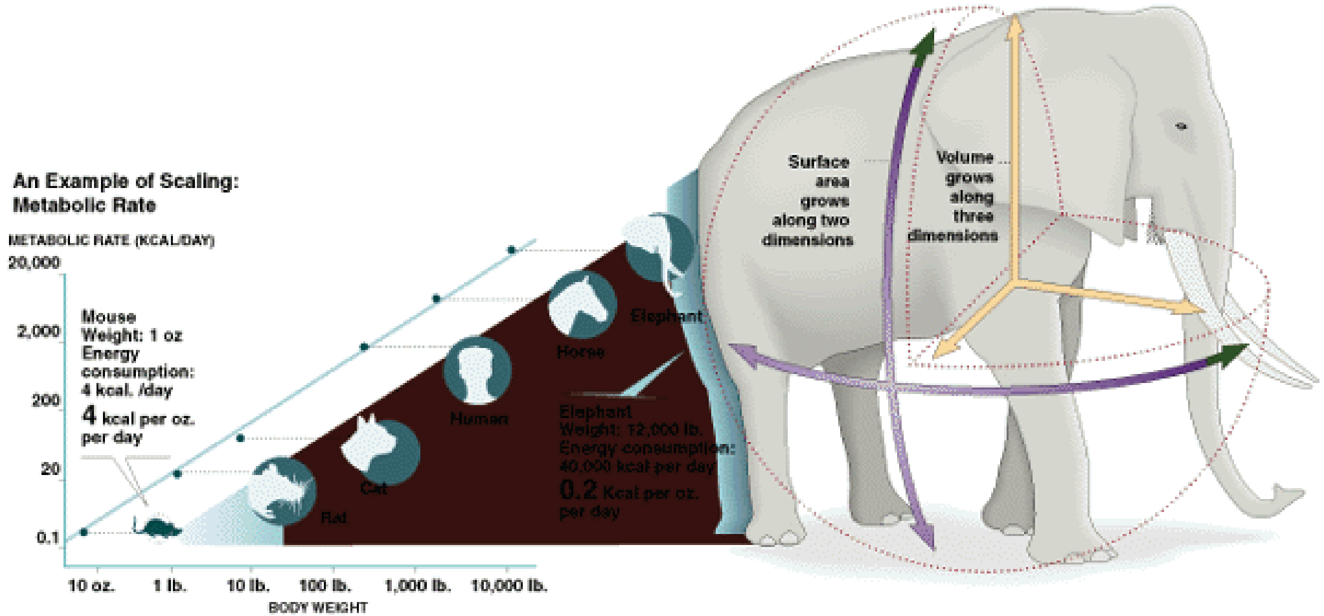


Body size

Most biologists consider body mass the most important characteristic of an organism. It is also (mostly) easy to measure.

All morphological and physiological traits scale somehow with body mass.

"Scaling is interesting because, aside from natural selection, it is one of the few laws we really have in biology." John Gittleman



Two fundamental questions

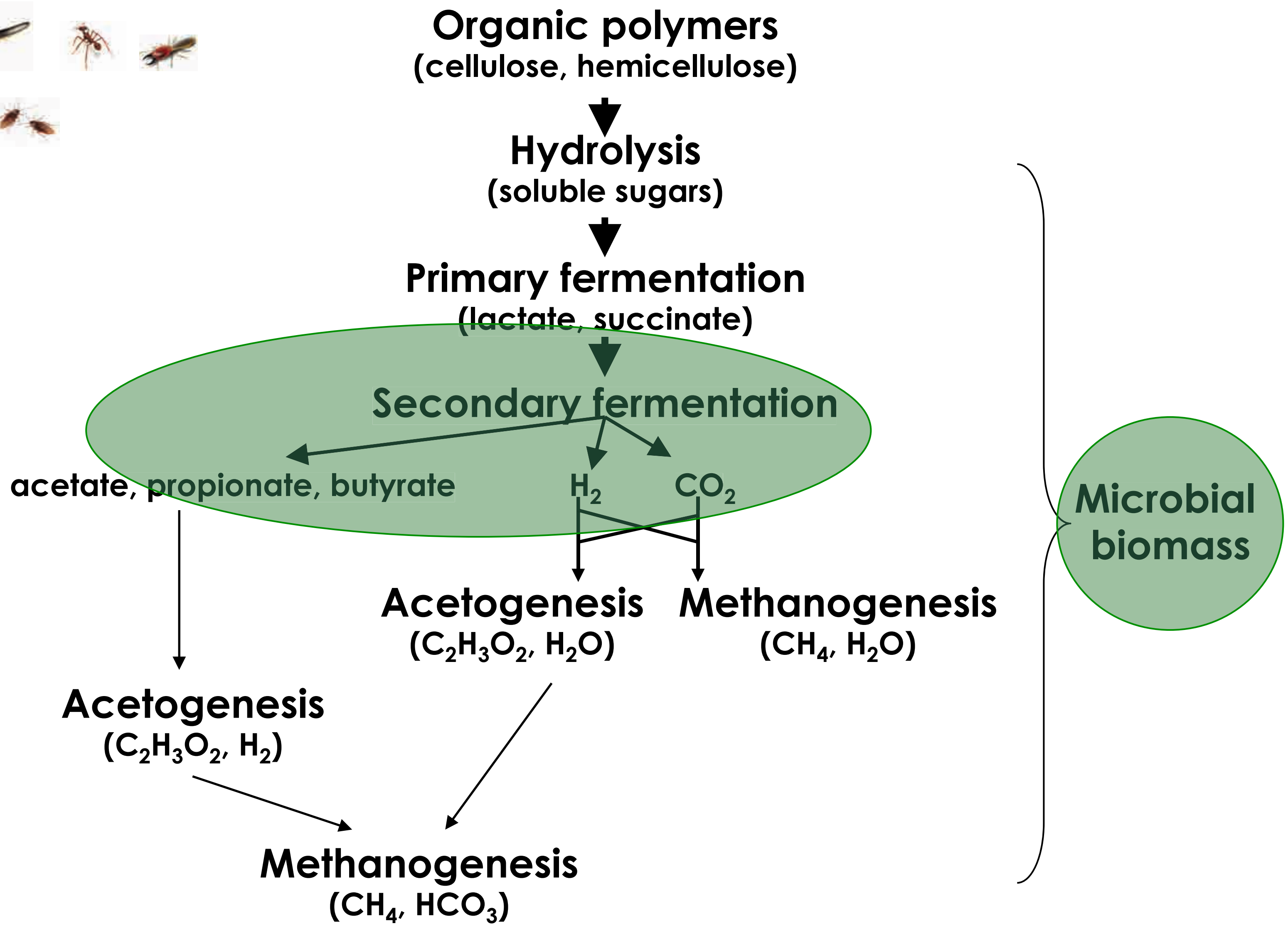
1. 'In-house' or outsourcing of fibre digestion?

'In-house' fibre digestion necessitates anatomical and physiological adaptations that might be costly in some circumstances.

Outsourcing is only feasible at small body sizes where you have high encounter rates with nutritionally relevant amounts of microorganisms.

(although there are billions of microorganisms in this room, their mass is not enough to meet the daily energy requirements of a single member of the audience)

Fibre digestion



from Karasov & Martinez del Rio (2007)

Fibre digestion

Organic polymers
(cellulose, hemicellulose)

Herbivore

Hydrolysis
(soluble sugars)

Primary fermentation
(lactate, succinate)

Secondary fermentation

acetate, propionate, butyrate

H_2 CO_2

Acetogenesis
($C_2H_3O_2$, H_2O)

Methanogenesis
(CH_4, H_2O)

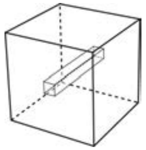
Microbial biomass

Acetogenesis
($C_2H_3O_2$, H_2)

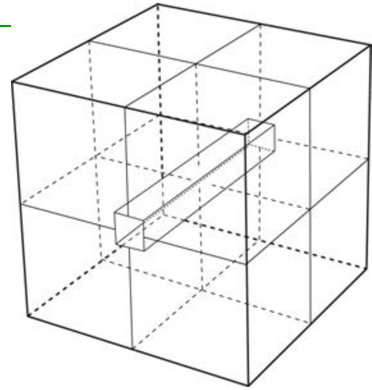
Methanogenesis
(CH_4, HCO_3)

from Karasov & Martinez del Rio (2007)

Surface/volume geometry



6:1



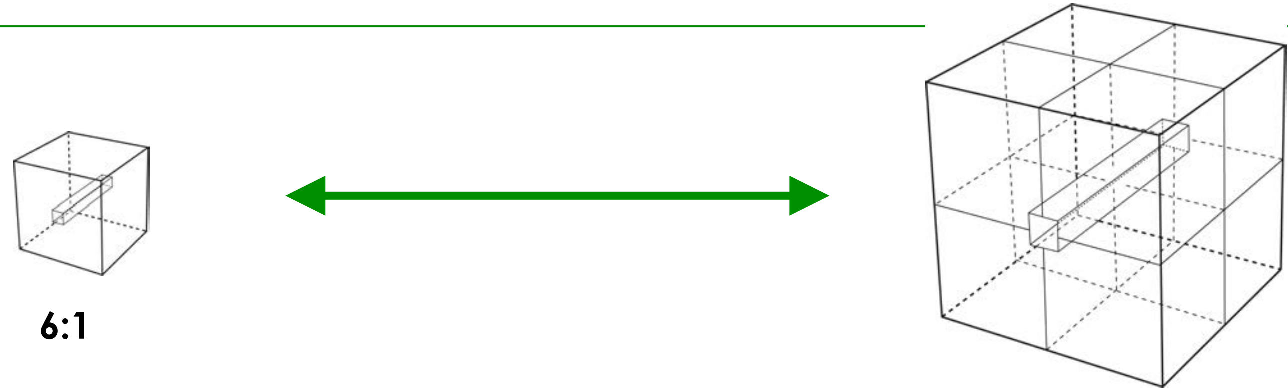
24:8=3:1

... affects all surface-related processes

heat loss - - - - ► **energy requirements** - - - - ► **food intake**

from Clauss & Hummel (2005)

Surface/volume geometry



6:1

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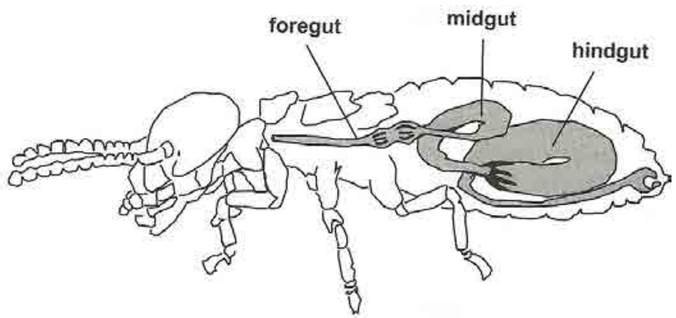

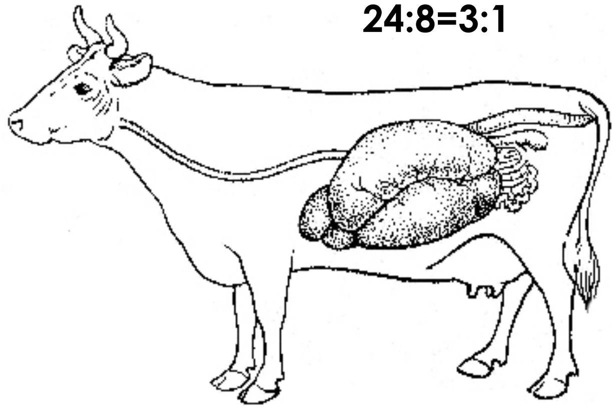

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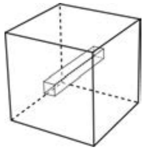

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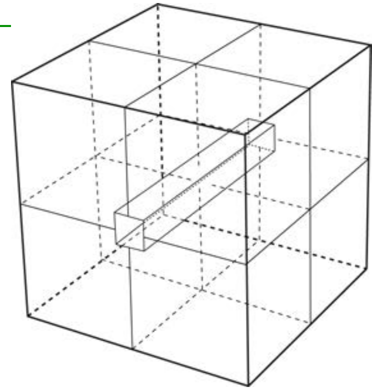

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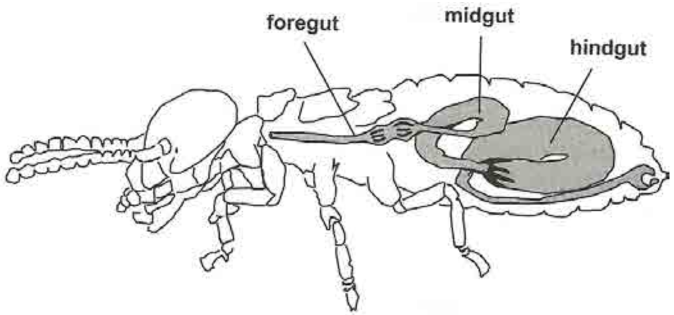

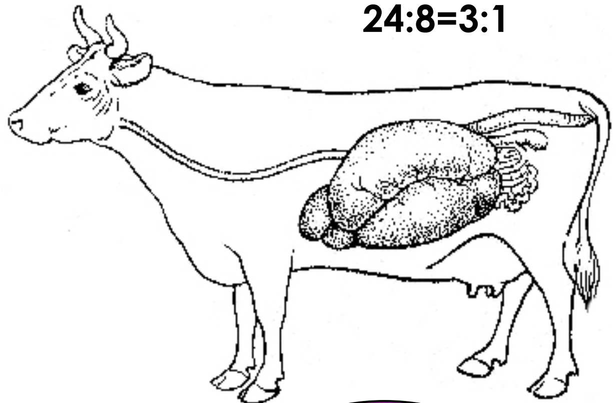

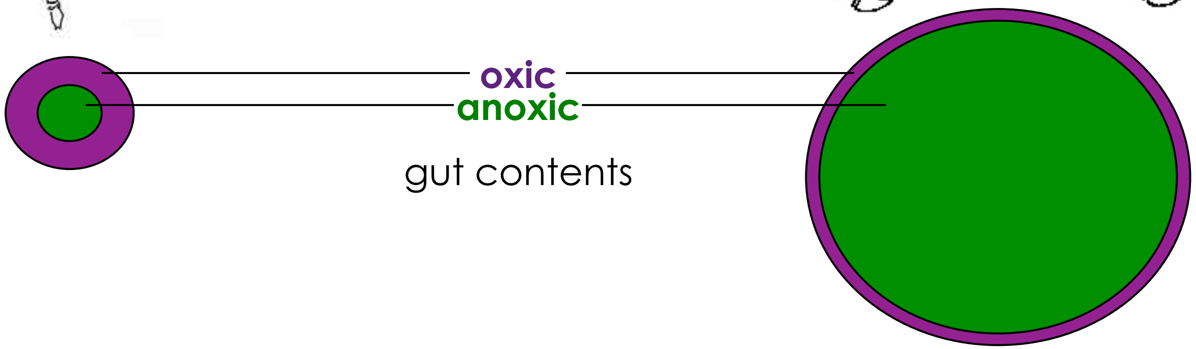

from Karasov & Martinez del Rio (2007)

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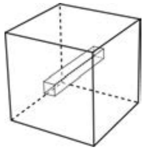

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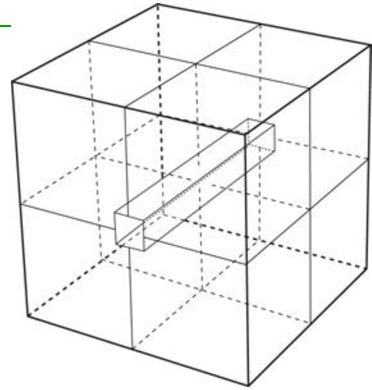

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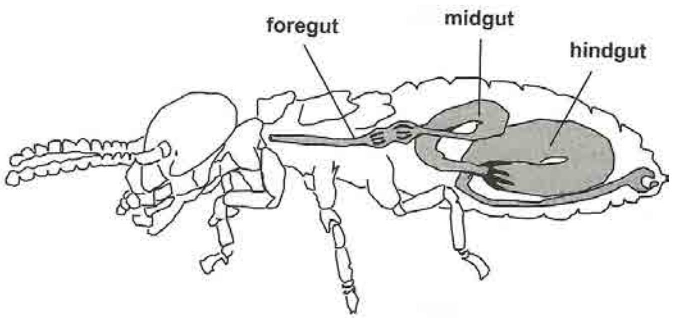
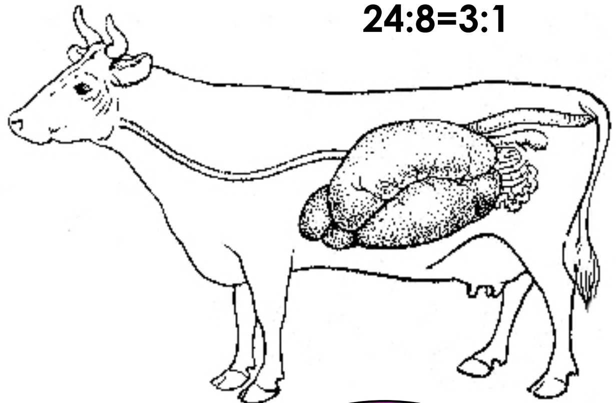
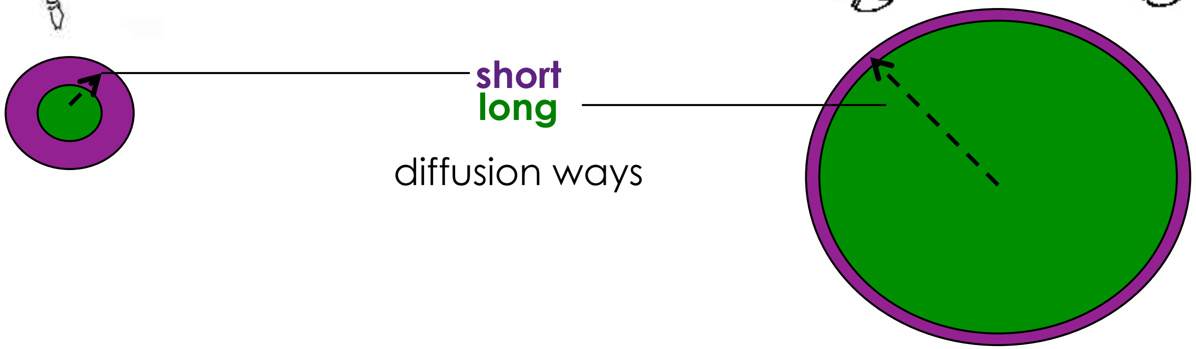
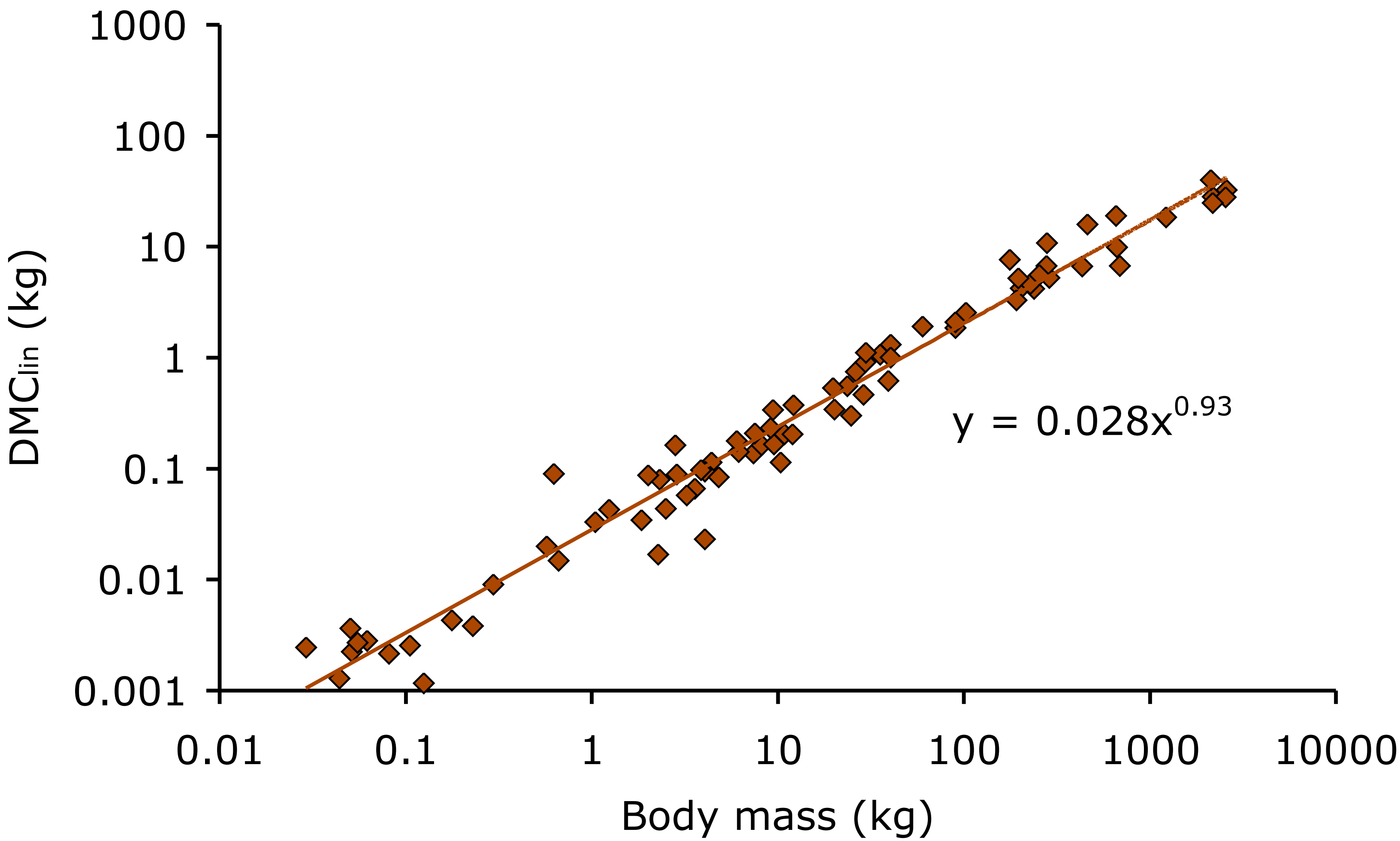






from Karasov & Martinez del Rio (2007)

Gut moisture content



from Müller et al. (2013)

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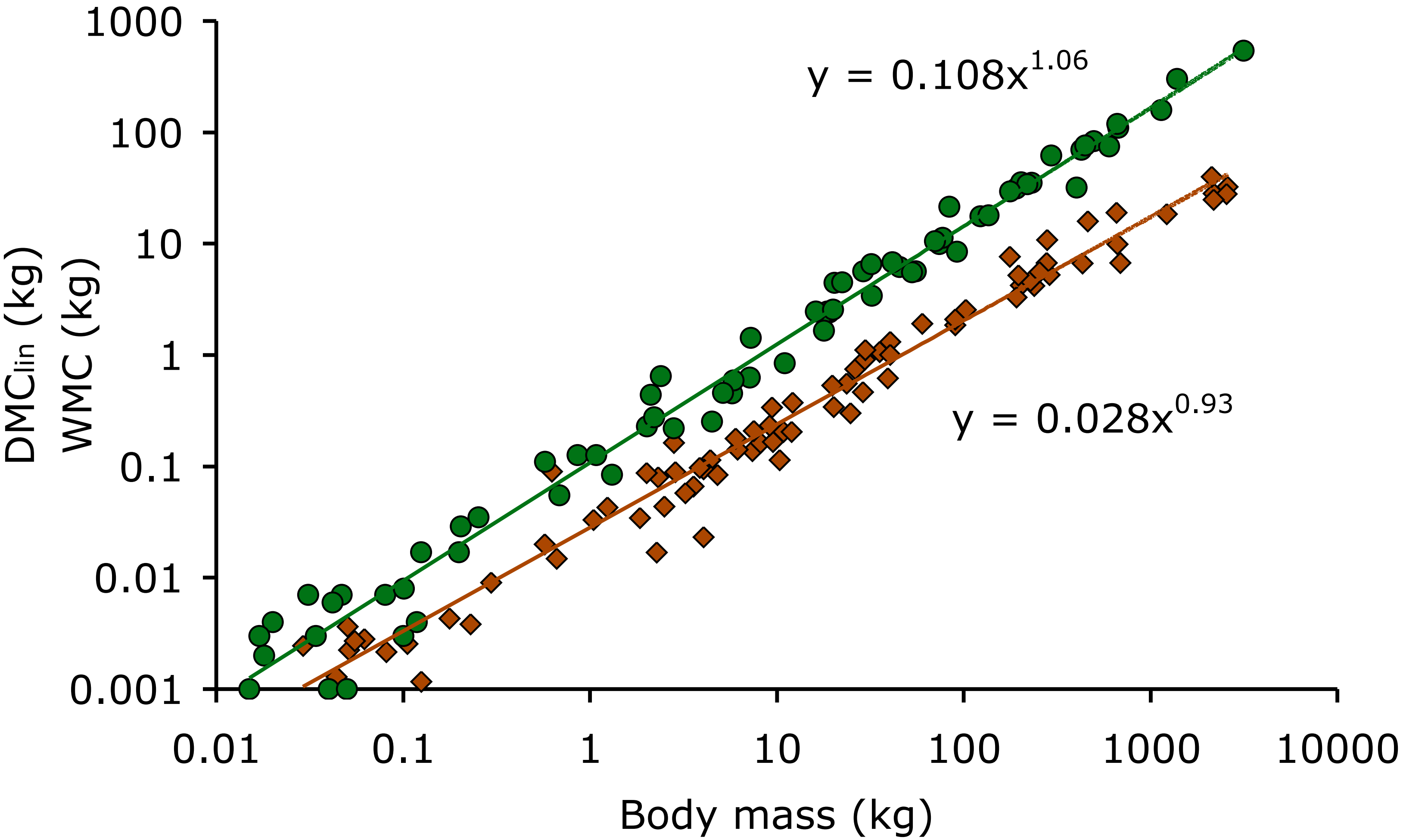

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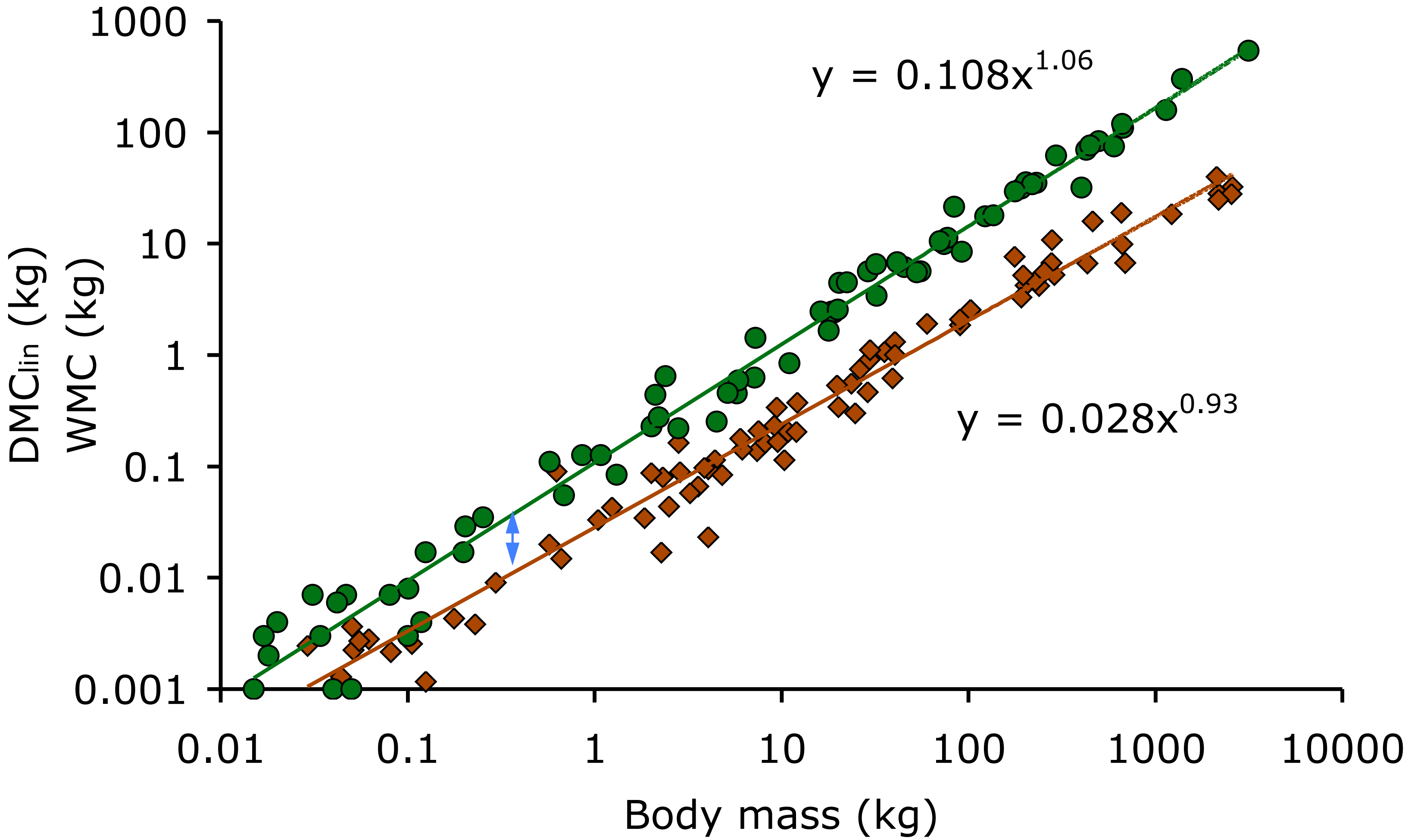

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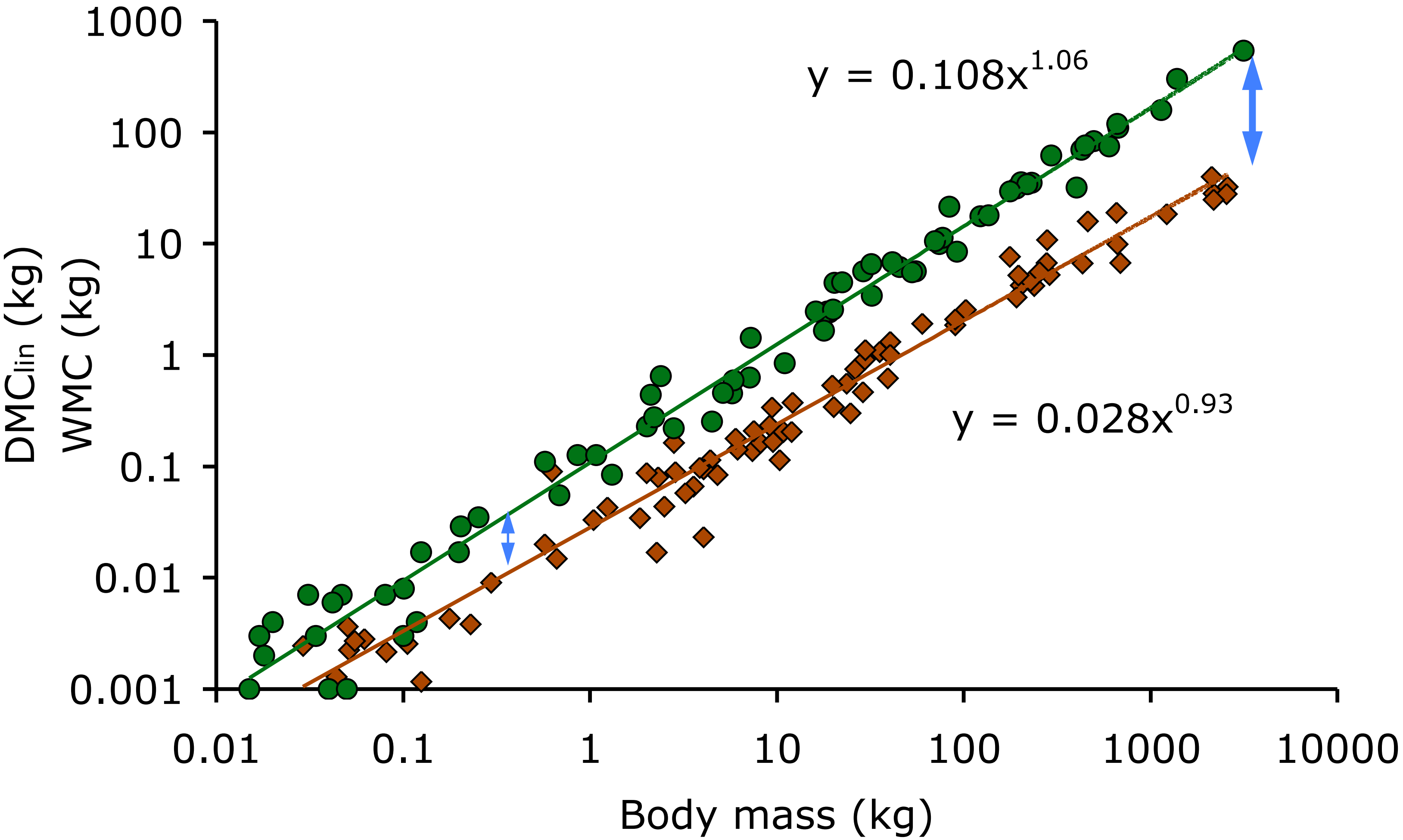

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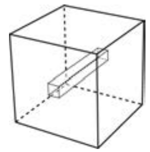
Surface/volume geometry



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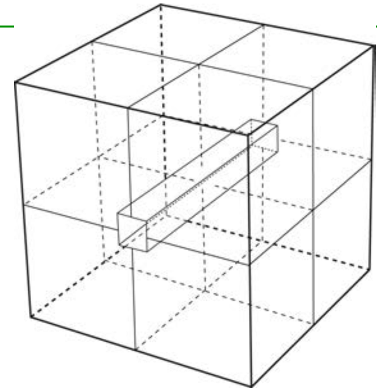

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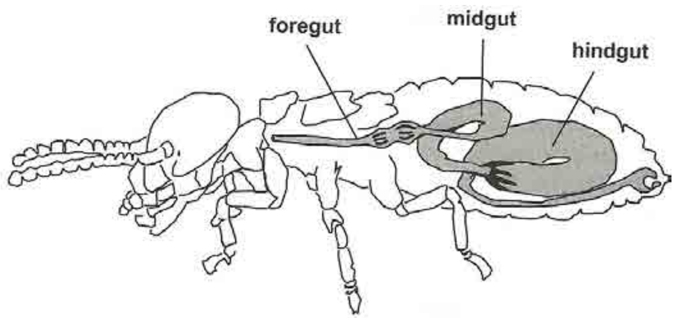
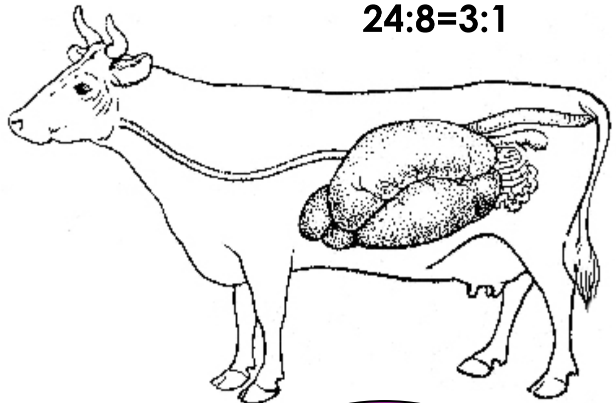
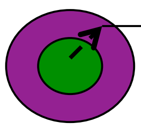
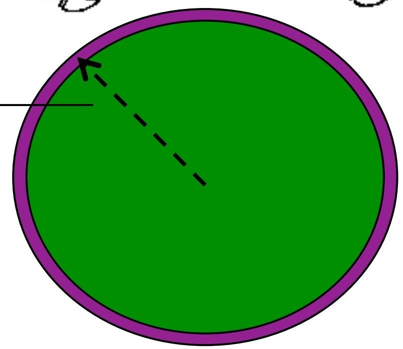






short
long
diffusion ways



from Karasov & Martinez del Rio (2007)

Herbivory
-
Principles
(digestive tracts)

Two fundamental questions

2. What sequence of fibre digestion and auto-enzymatic digestion?

- fibre digestion prior to auto-enzymatic digestion allows the use of bacterial biomass

- bacterial digestion after auto-enzymatic digestion allows more efficient use of those substrates that can be digested auto-enzymatically

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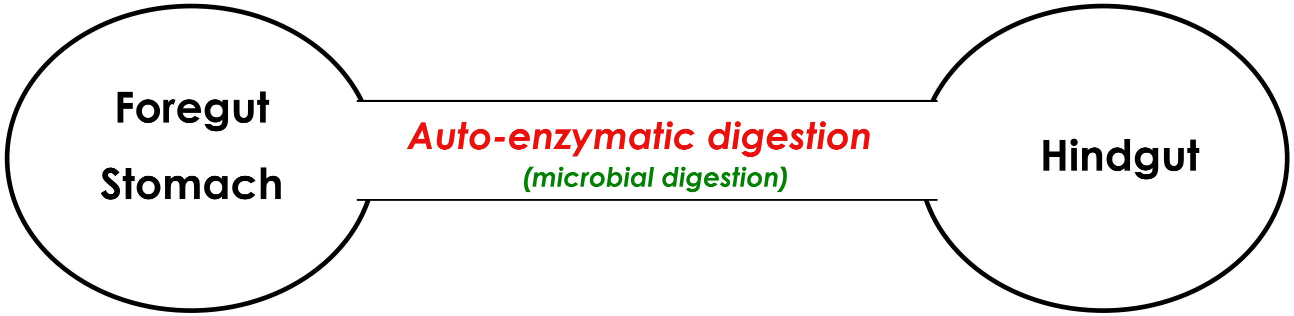

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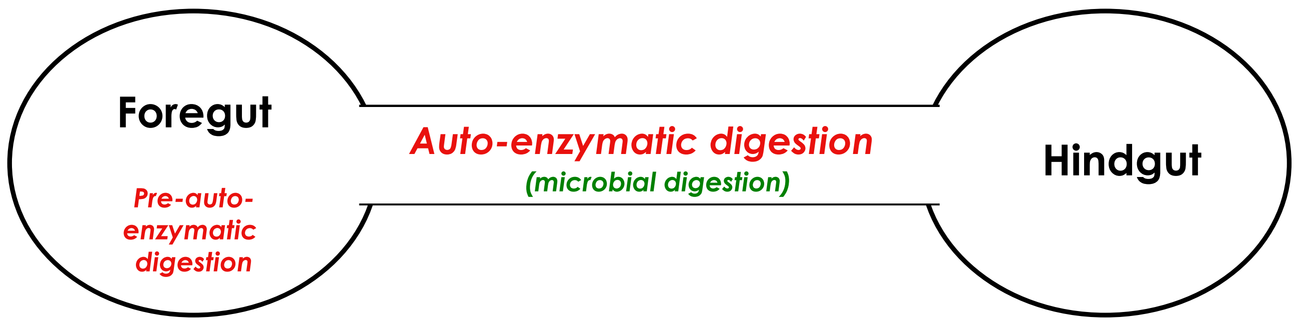

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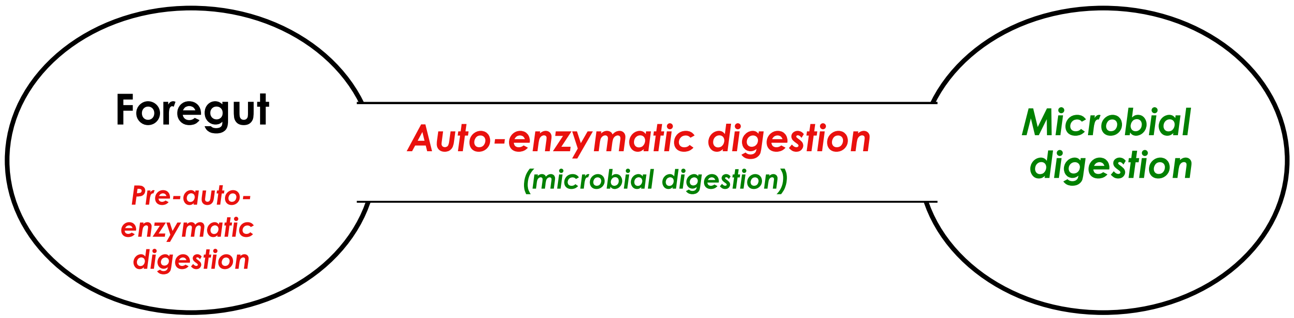

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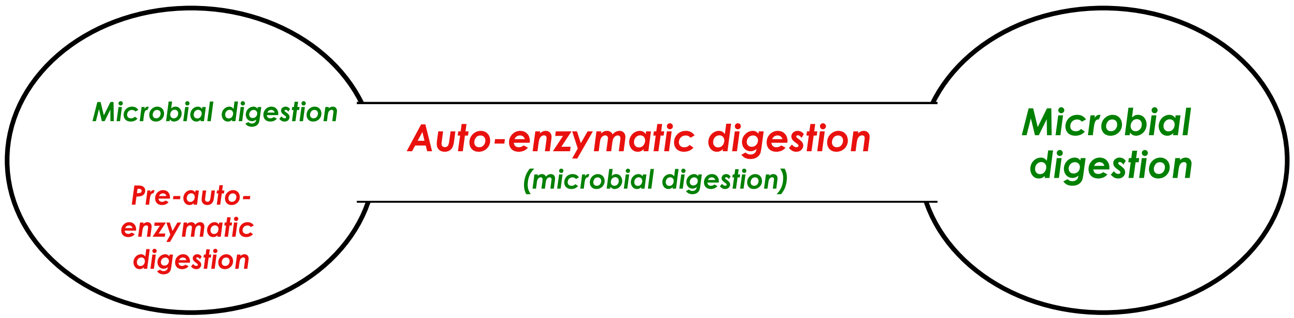

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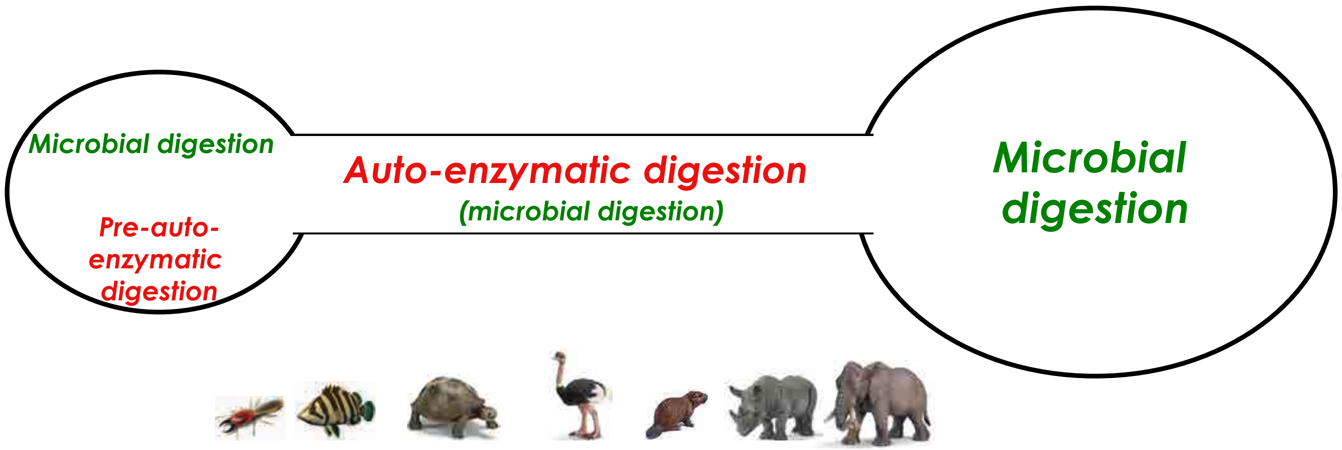

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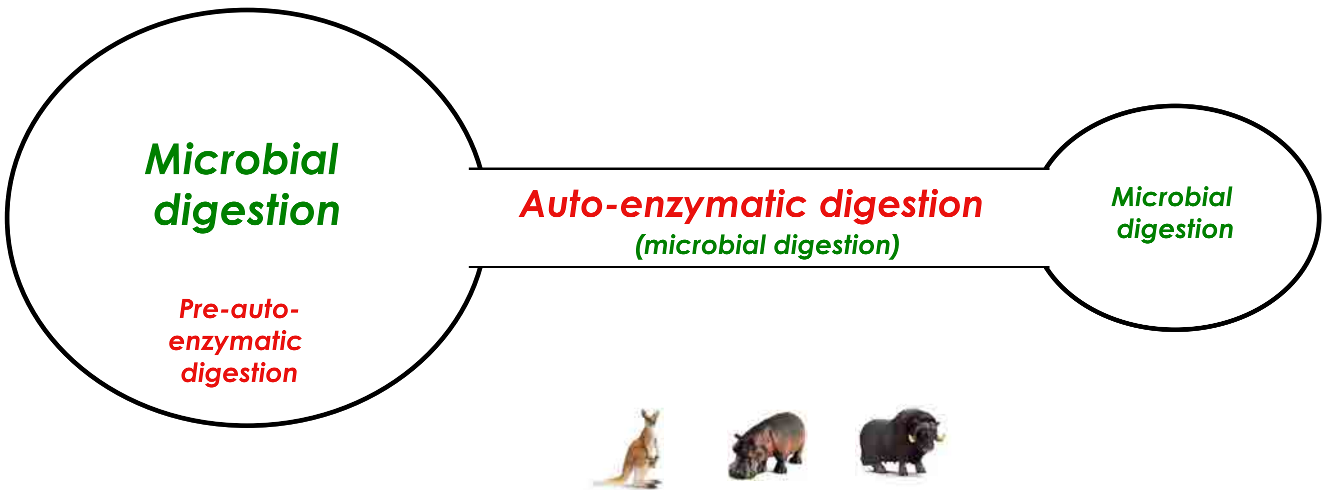

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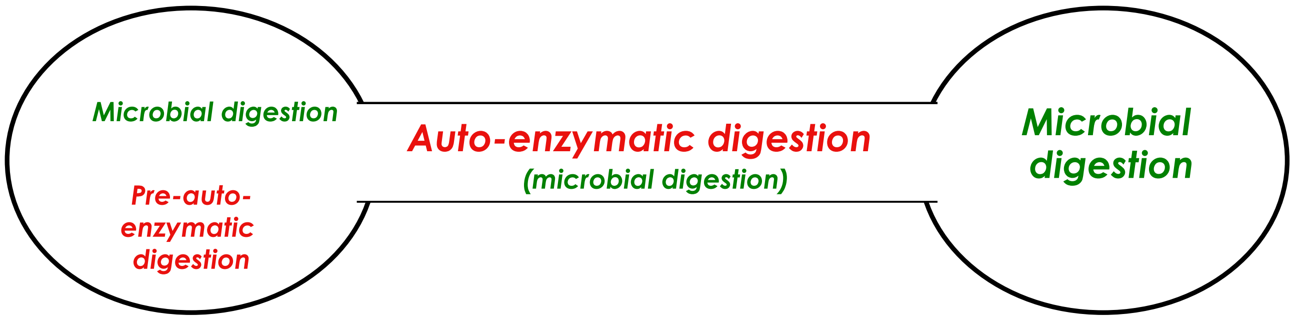

Two fundamental questions

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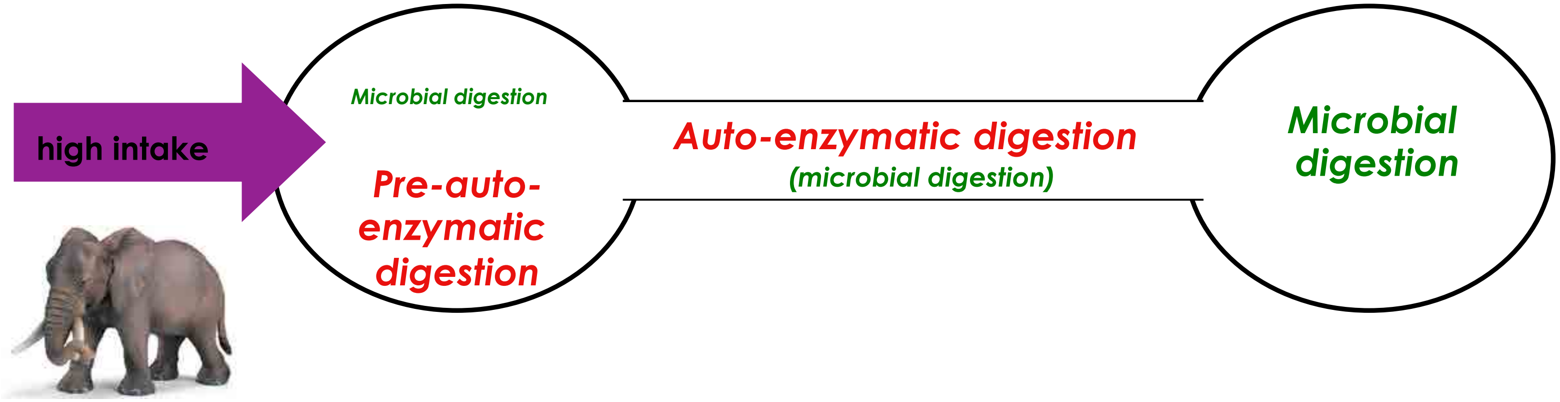
- fibre digestion prior to auto-enzymatic digestion allows the use of bacterial biomass

- bacterial digestion after auto-enzymatic digestion allows more efficient use of those substrates that can be digested auto-enzymatically



Two fundamental questions

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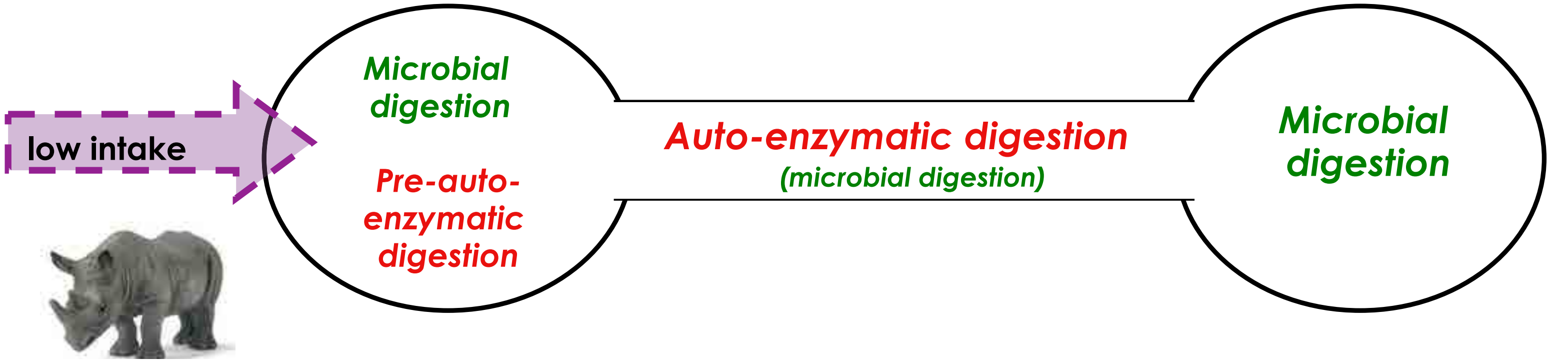
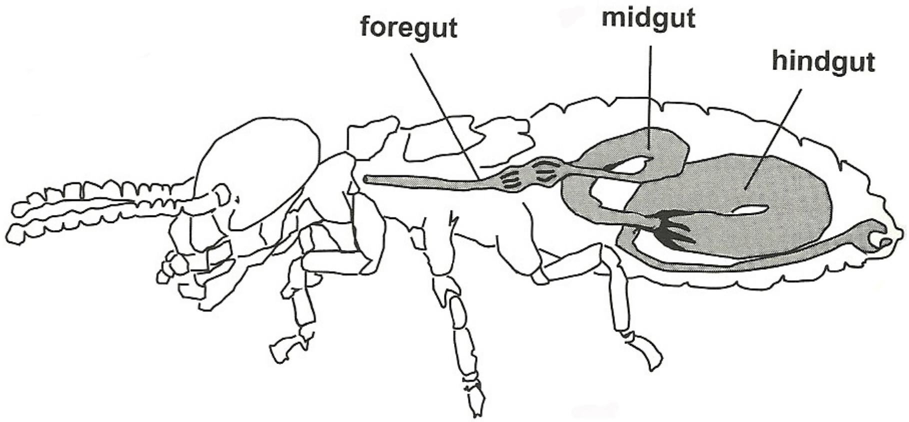
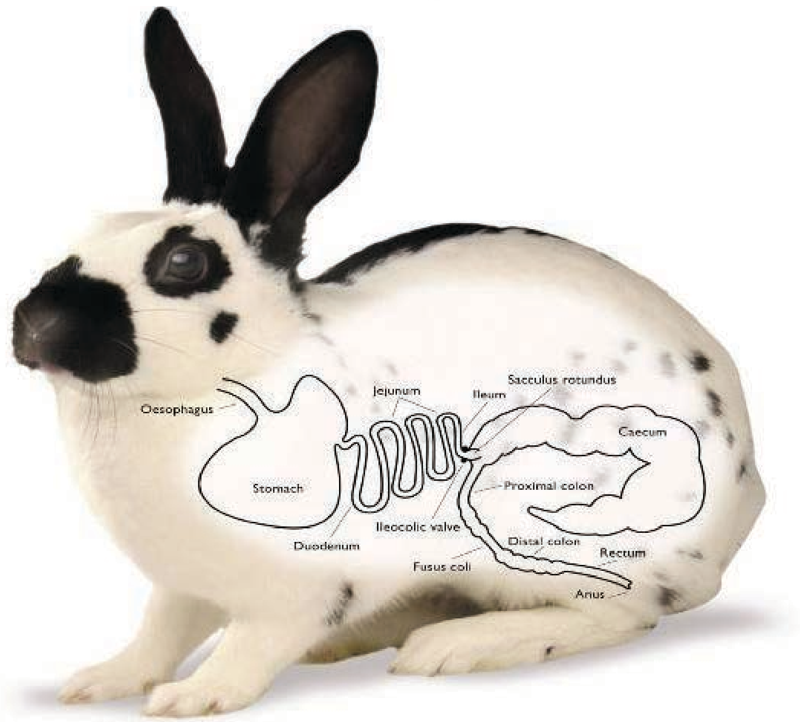


Hindgut fermentation - ‘the conventional approach’

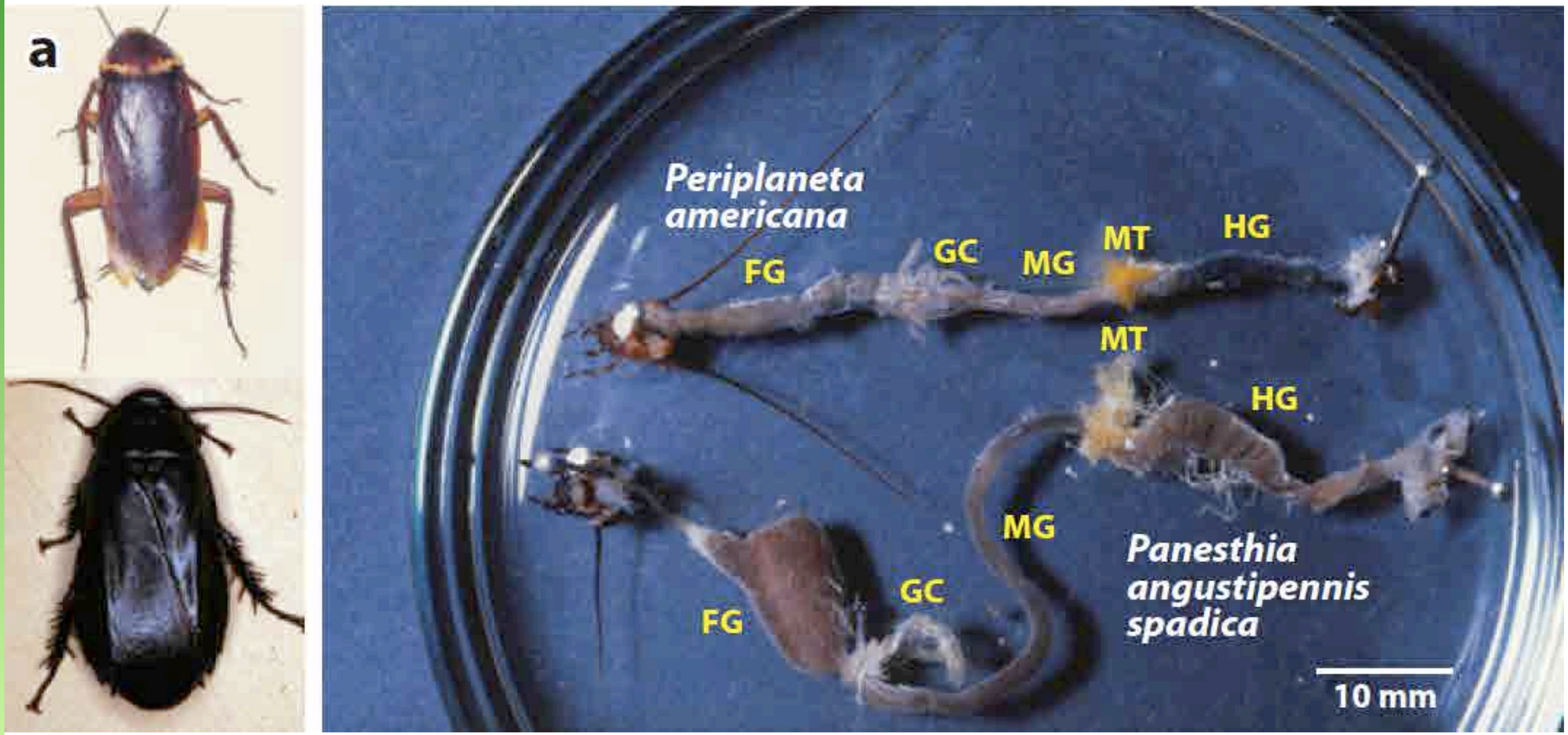




Cellulolytic Systems in Insects

Hirofumi Watanabe[1] and Gaku Tokuda[2]

Annu. Rev. Entomol. 2010. 55:609–32



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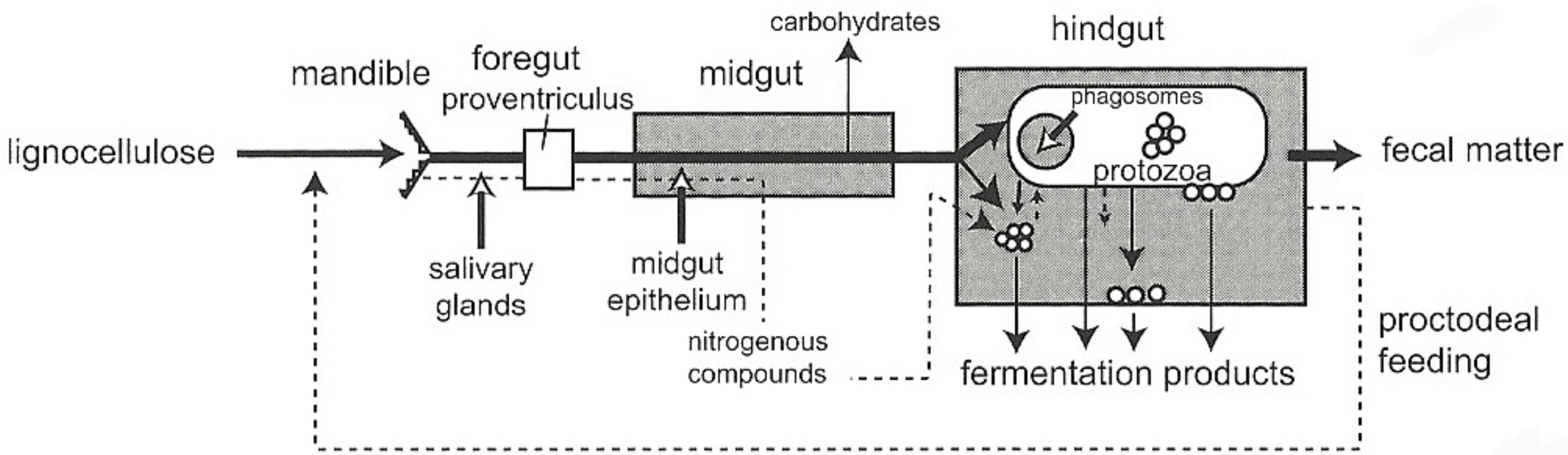
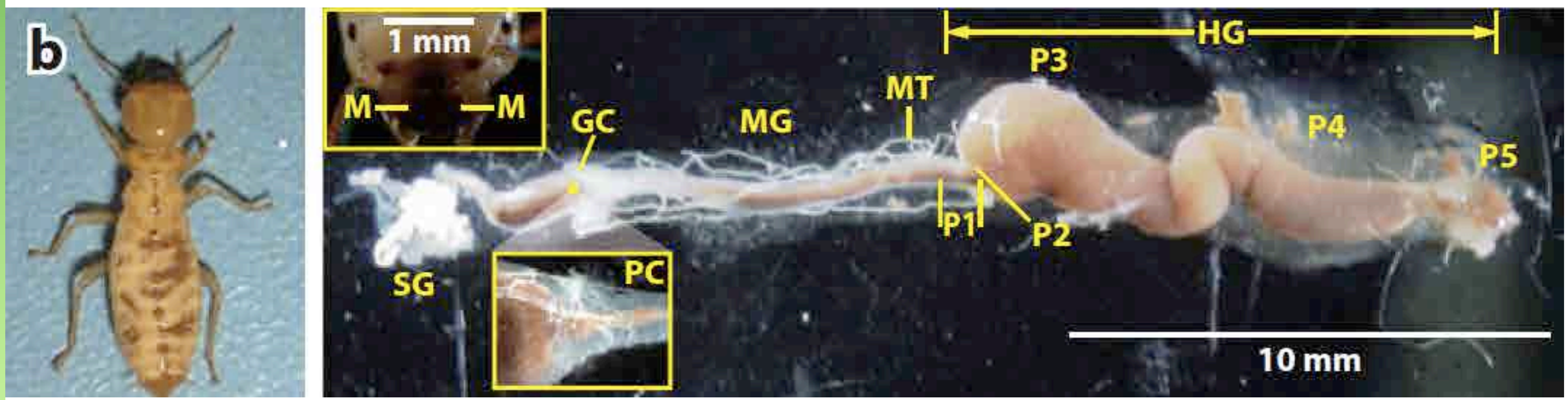




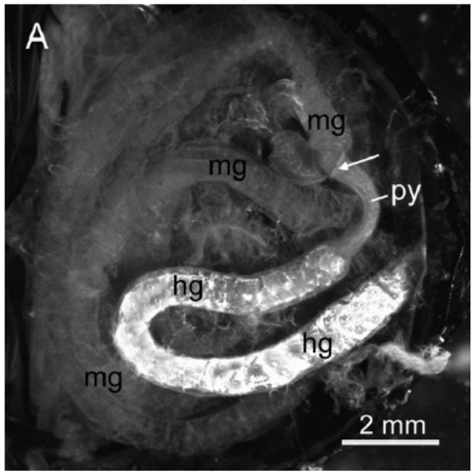
scheme from Karasov & Martinez del Rio (2007)

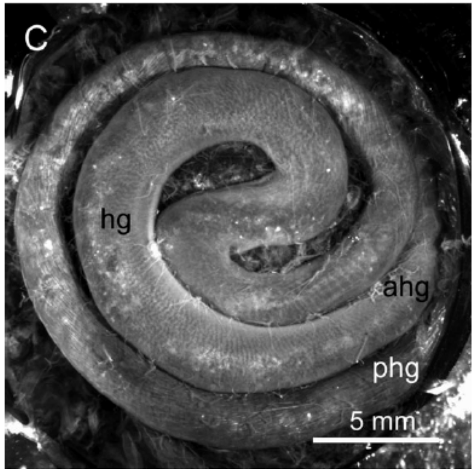
Elongated Hindguts in Desert-Living Dung Beetles (Scarabaeidae: Scarabaeinae) Feeding on Dry Dung Pellets or Plant Litter

Peter Holter[1]* and Clarke H. Scholtz[2]

JOURNAL OF MORPHOLOGY 274:657–662 (2013)

Scarabaeus spp.
(fresh dung)



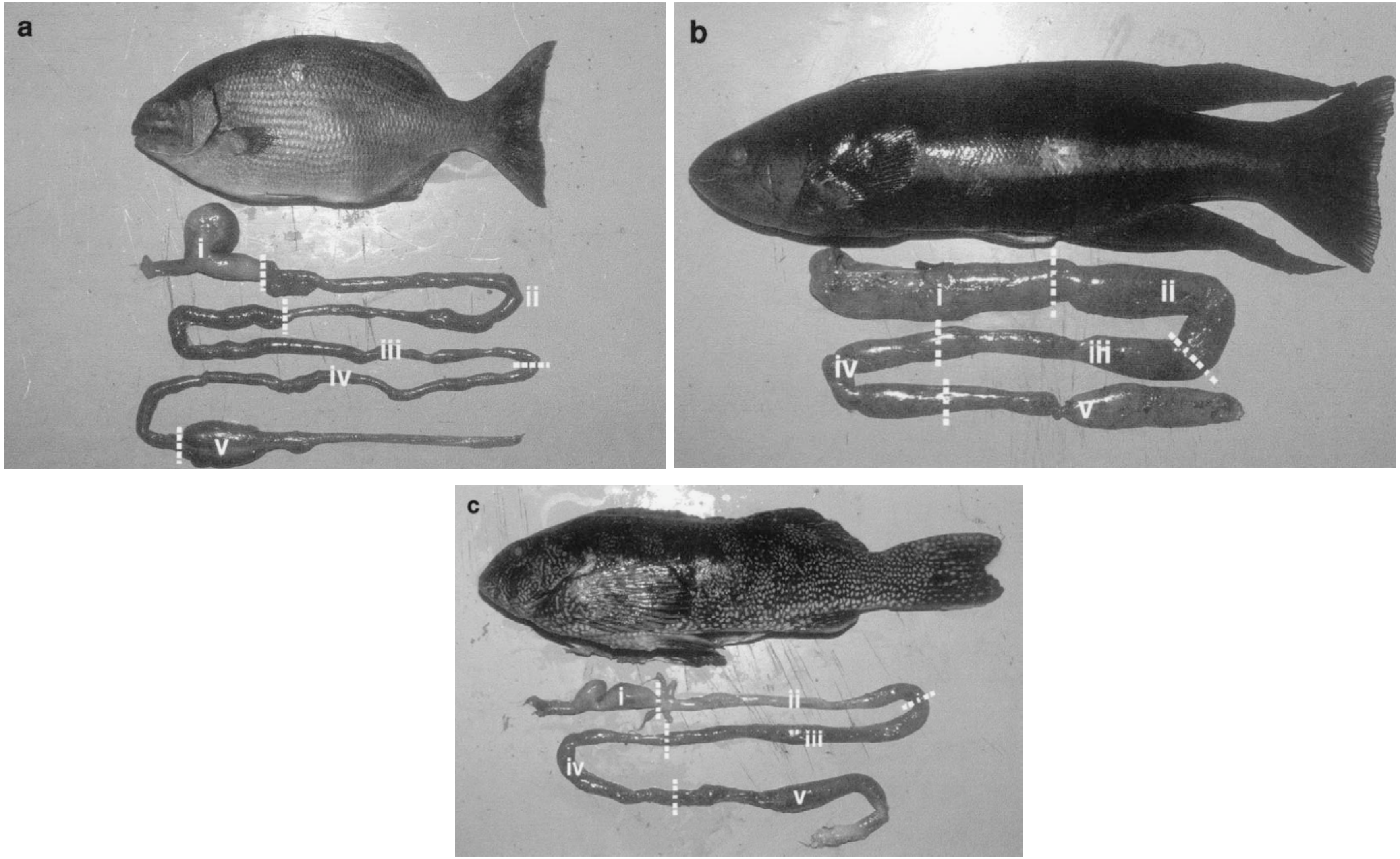


Pachysoma spp.
(plant litter)

Hindgut Fermentation in Three Species of Marine Herbivorous Fish

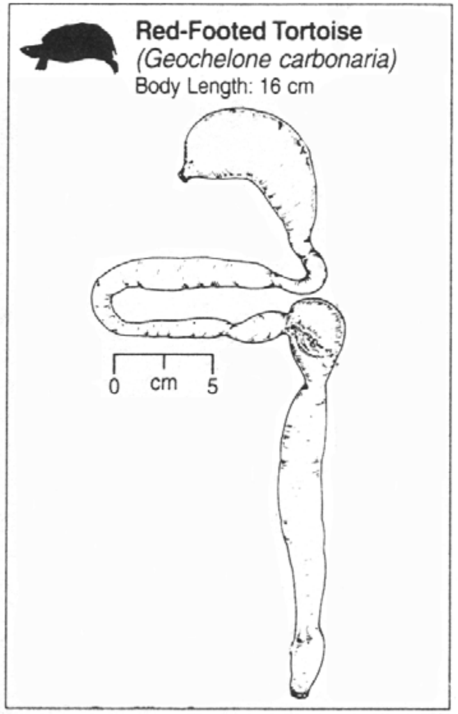
Douglas O. Mountfort,[1*] Jane Campbell,[2] and Kendall D. Clements[2]

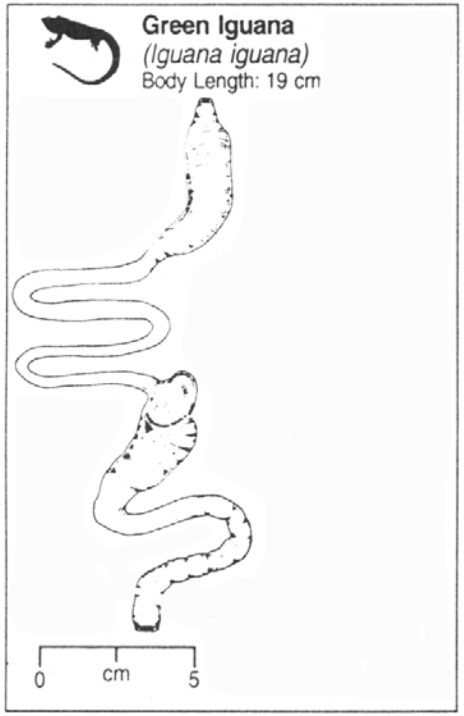
APPLIED AND ENVIRONMENTAL MICROBIOLOGY, Mar. 2002, p. 1374–1380



Herbivorous fish

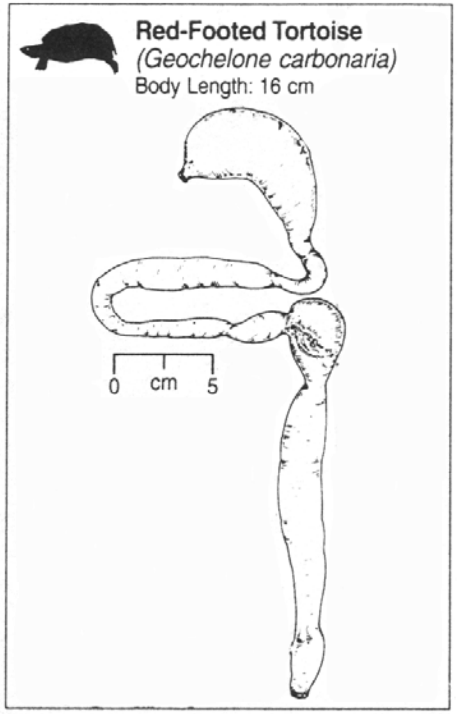
Hindgut Fermentation - Reptiles

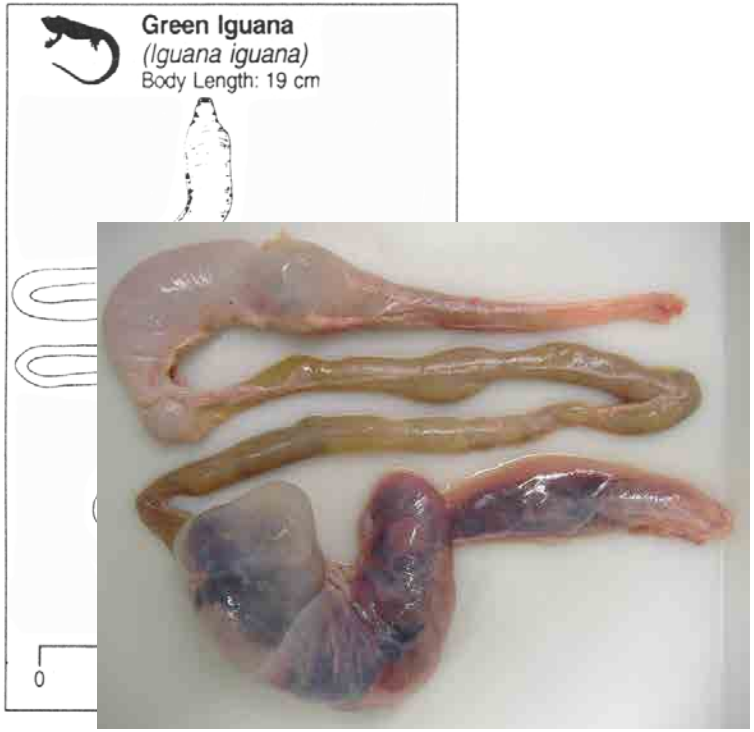




from Stevens & Hume (1995)

Hindgut Fermentation - Reptiles

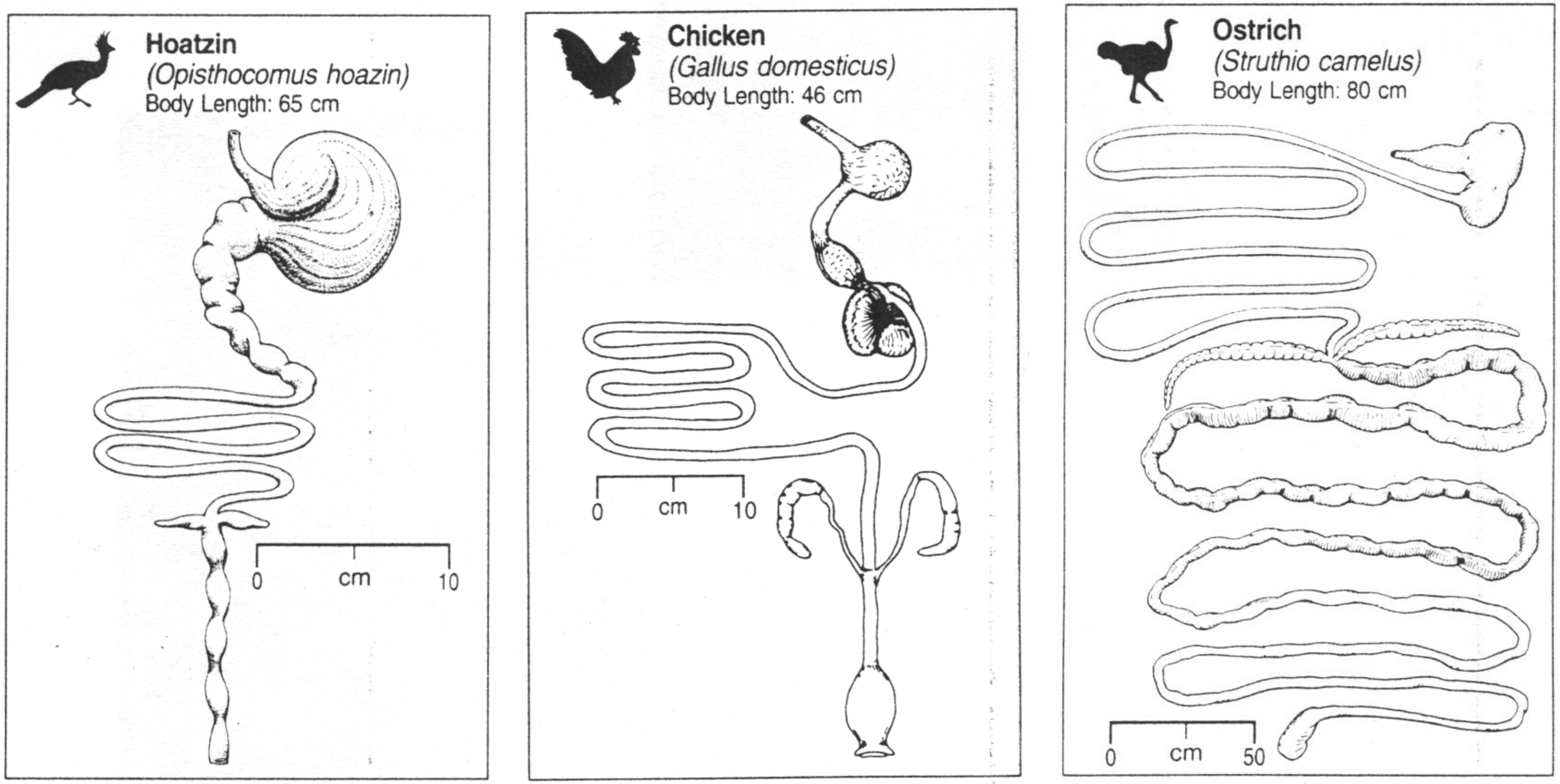




from Stevens & Hume (1995)

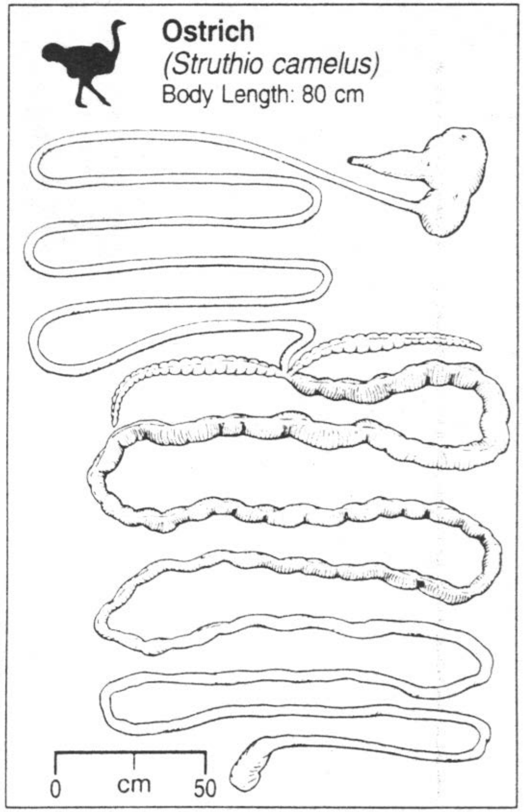
Photo: J. Fritz

Herbivores - Birds



from Stevens und Hume (1995)

Herbivores - Birds

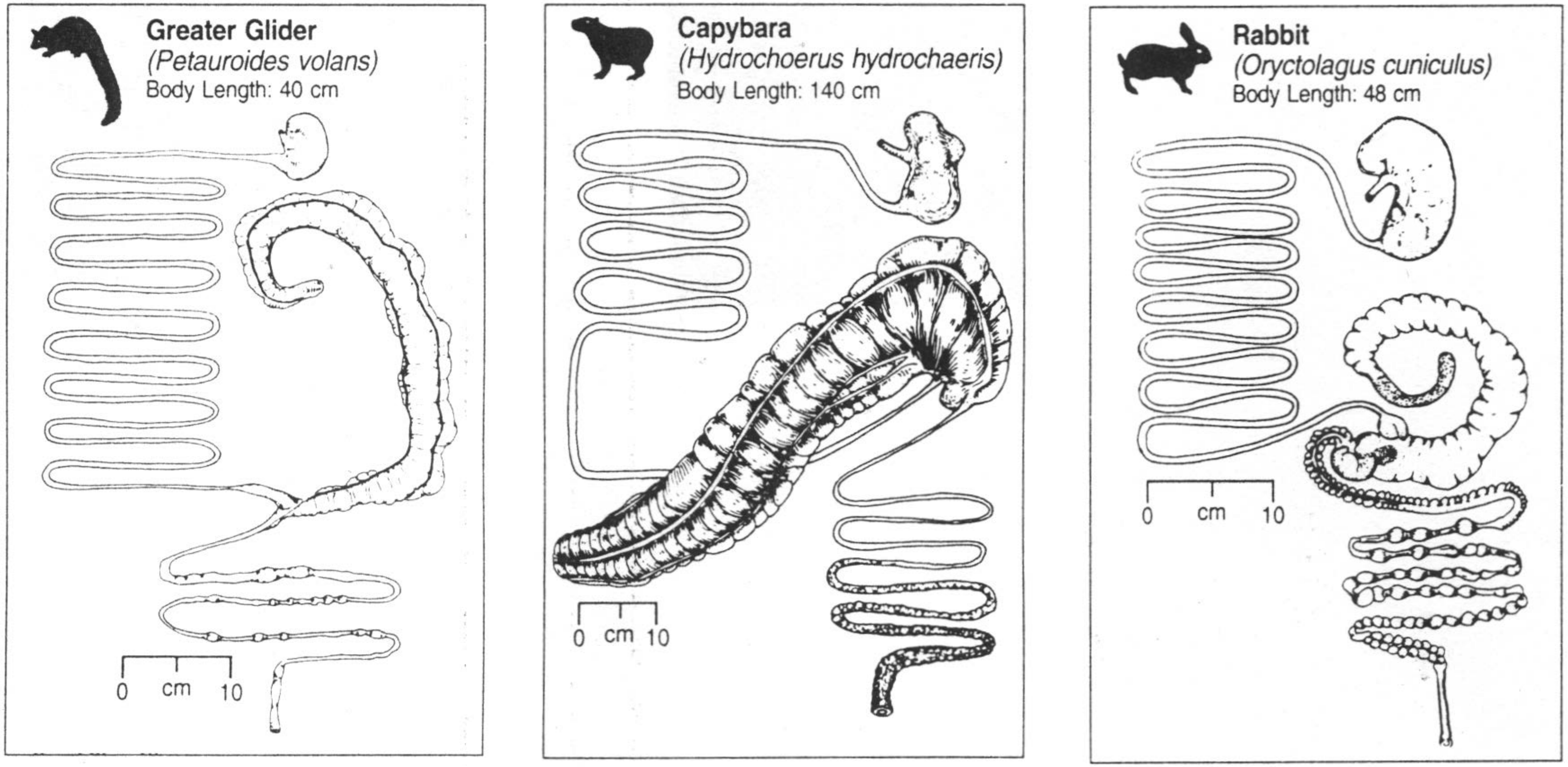


from Stevens und Hume (1995)
Photo: J. Fritz

Herbivores - Birds

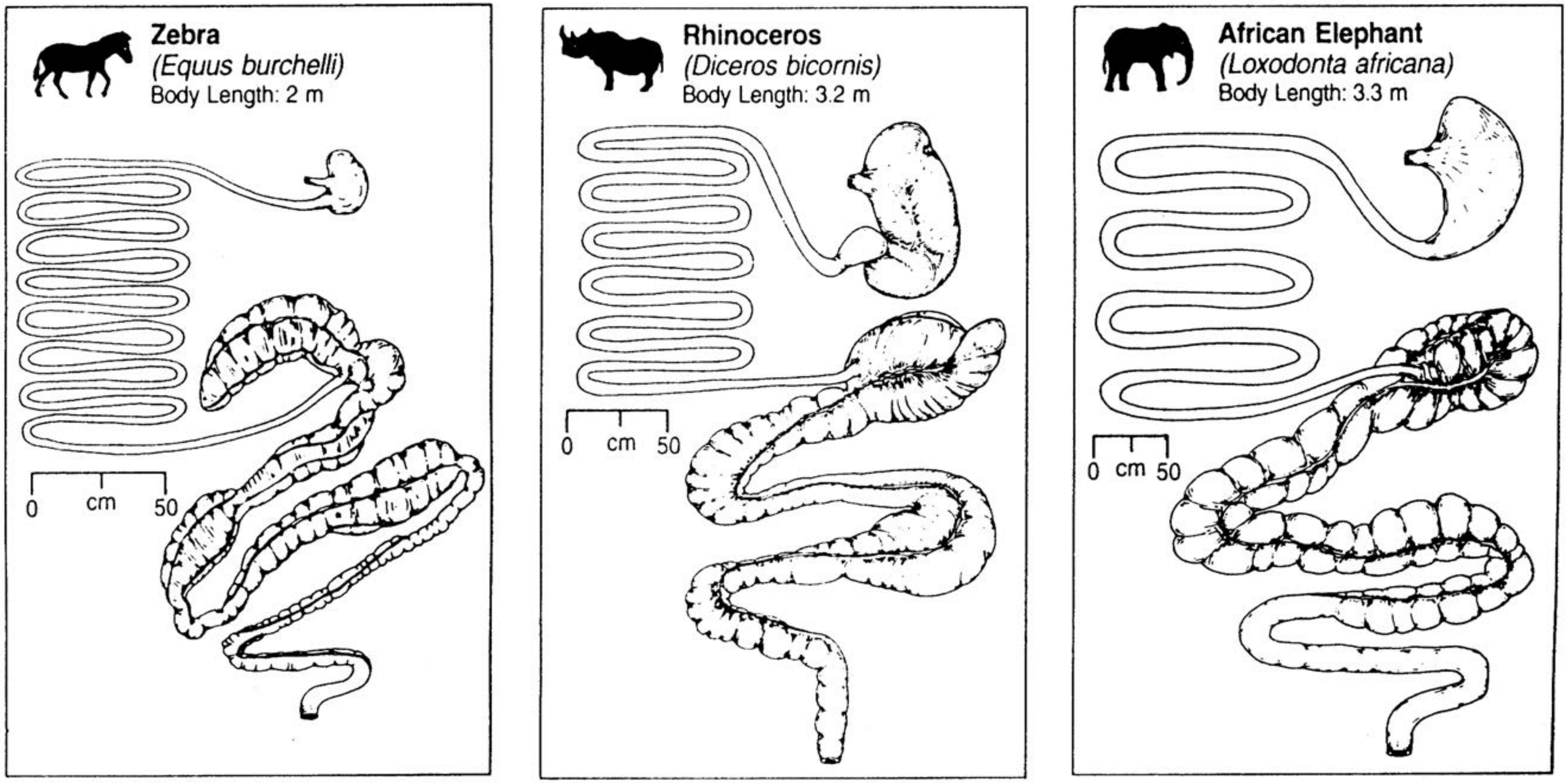
Photos: J. Fritz

Hindgut Fermentation - Caecum



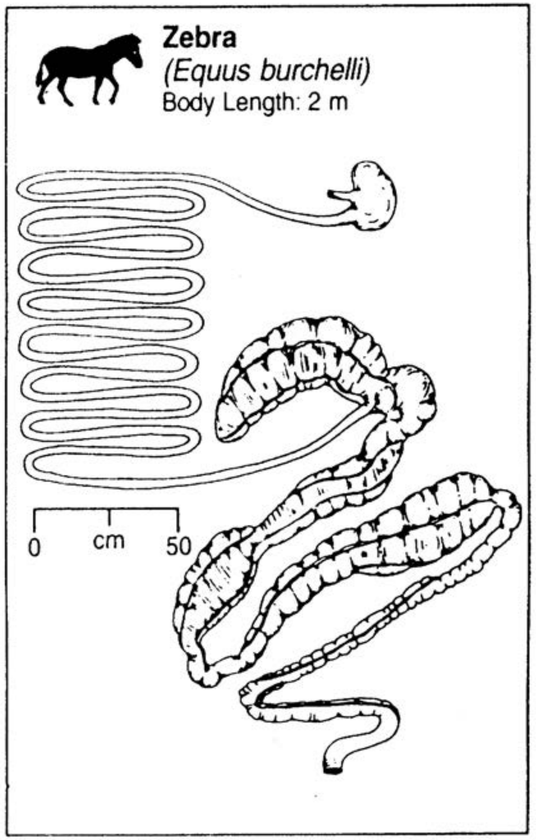
from Stevens & Hume (1995)

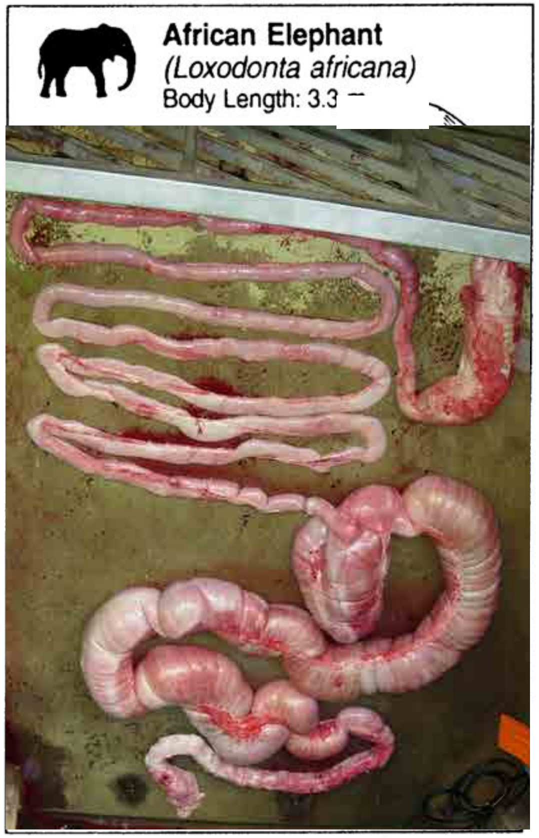
Hindgut Fermentation - Colon



from Stevens & Hume (1995)

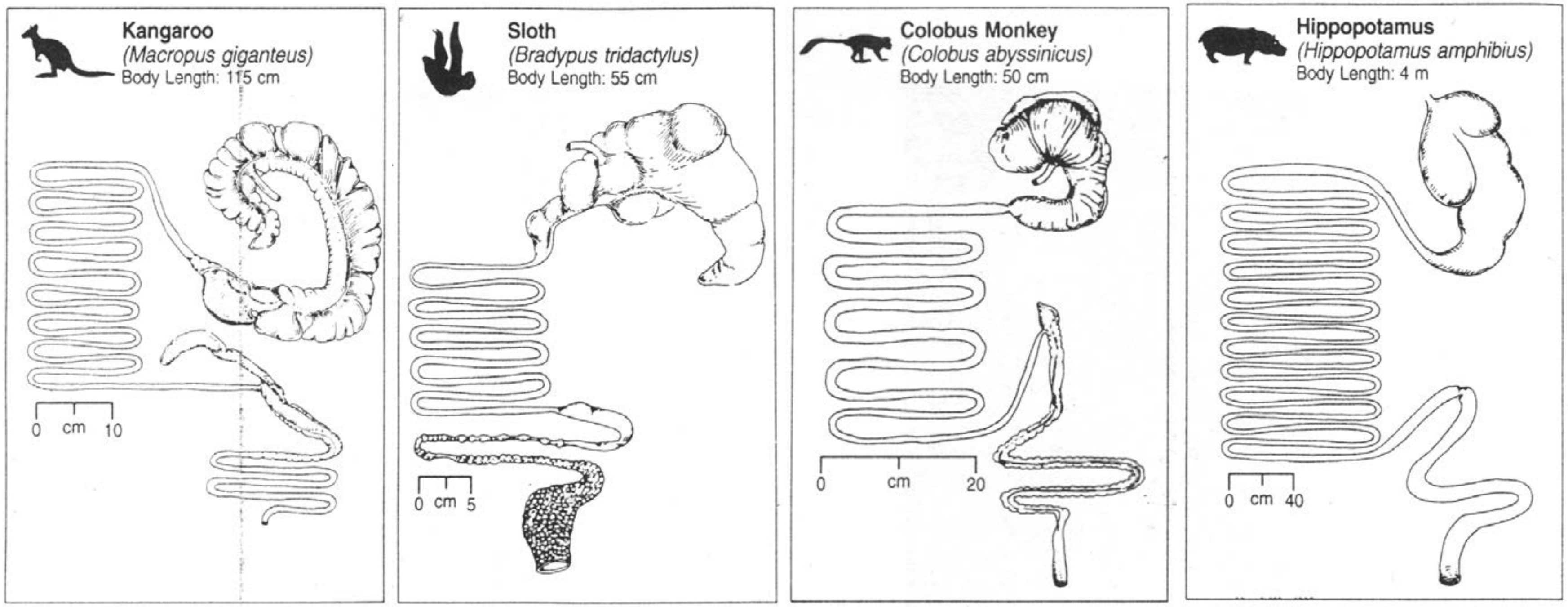
Hindgut Fermentation - Colon





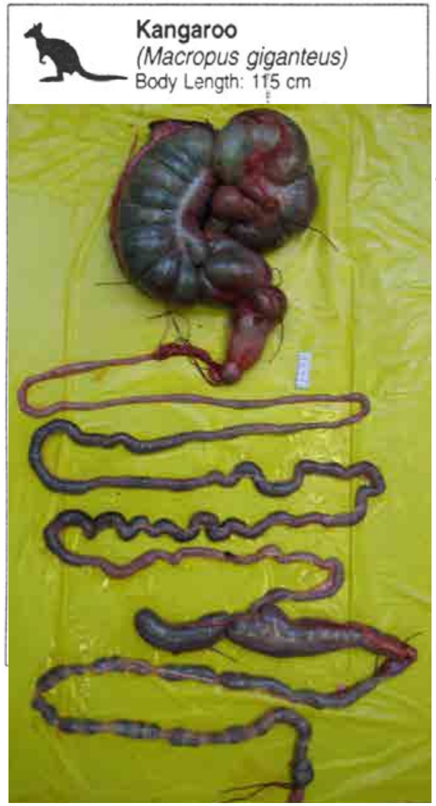
from Stevens & Hume (1995)

Foregut Fermentation



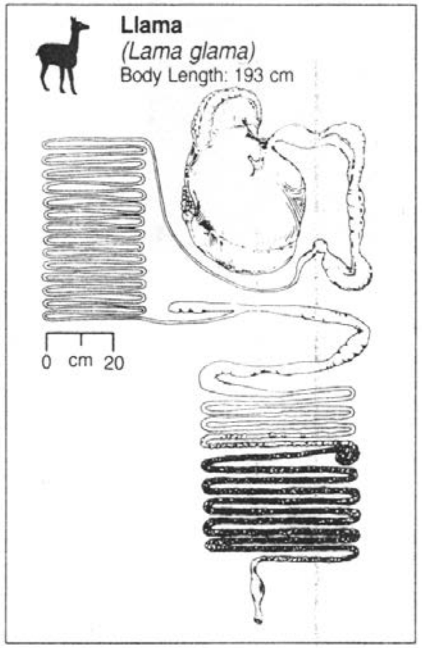
from Stevens & Hume (1995)

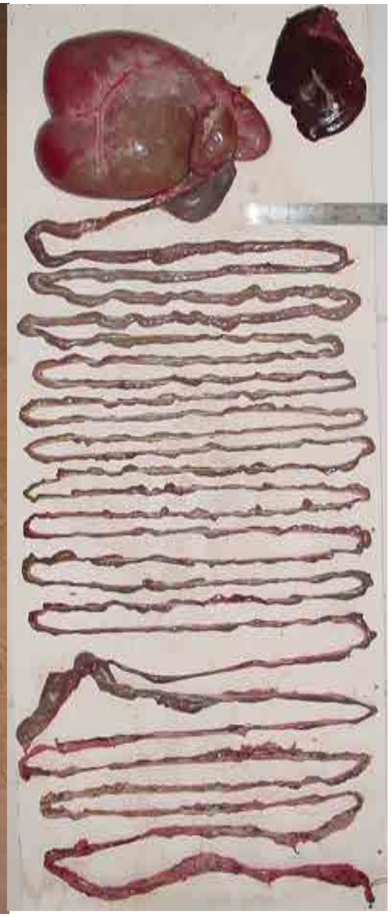
Foregut Fermentation

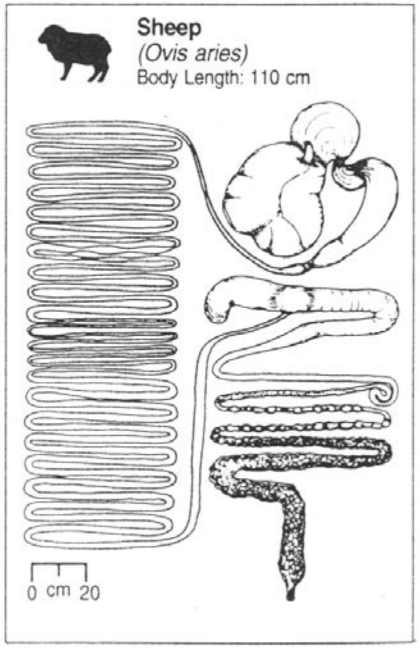


**Photos A. Schwarm/
M. Clauss**

Foregut Fermentation - Ruminant



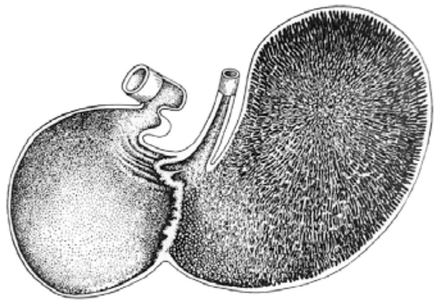




aus Stevens & Hume (1995)
Photo Llama: A. Riek

Foregut/Hindgut Fermenters

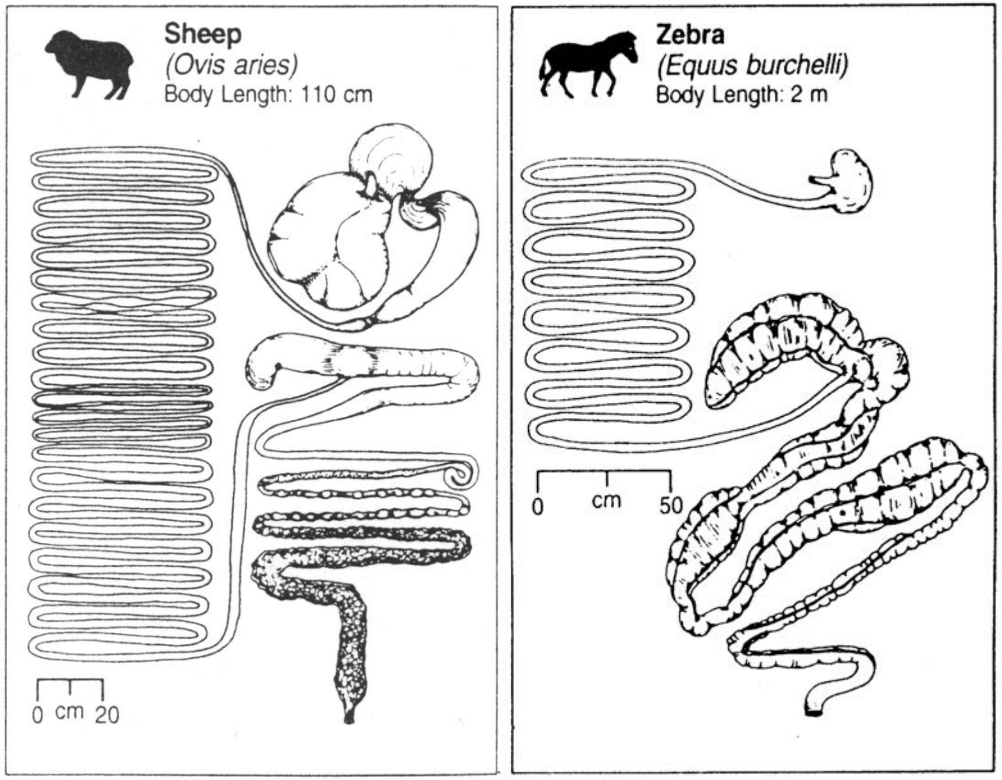
With the majority of rodent species un-studied, we have not grasped the variability, and adaptive significance, of foregut and hindgut fermentation yet.



Demon mole rat
(*Tachyoryctes daemon*)
papillated forestomach

from Vrontsov (2003)

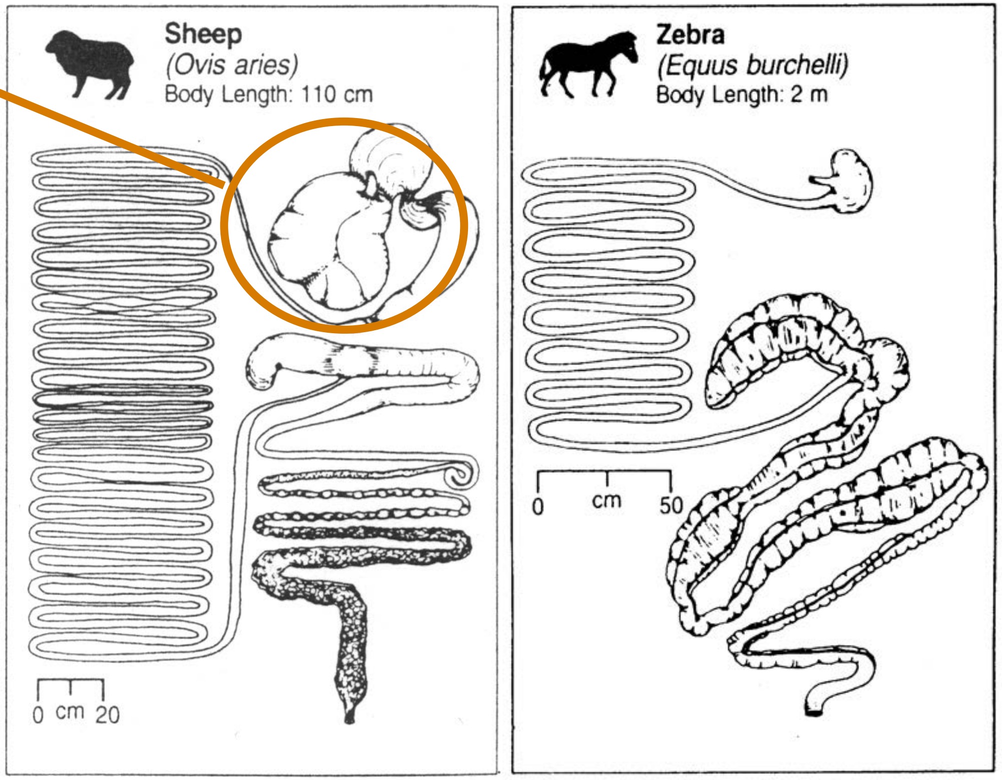
Foregut vs. Hindgut Fermentation



from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation

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

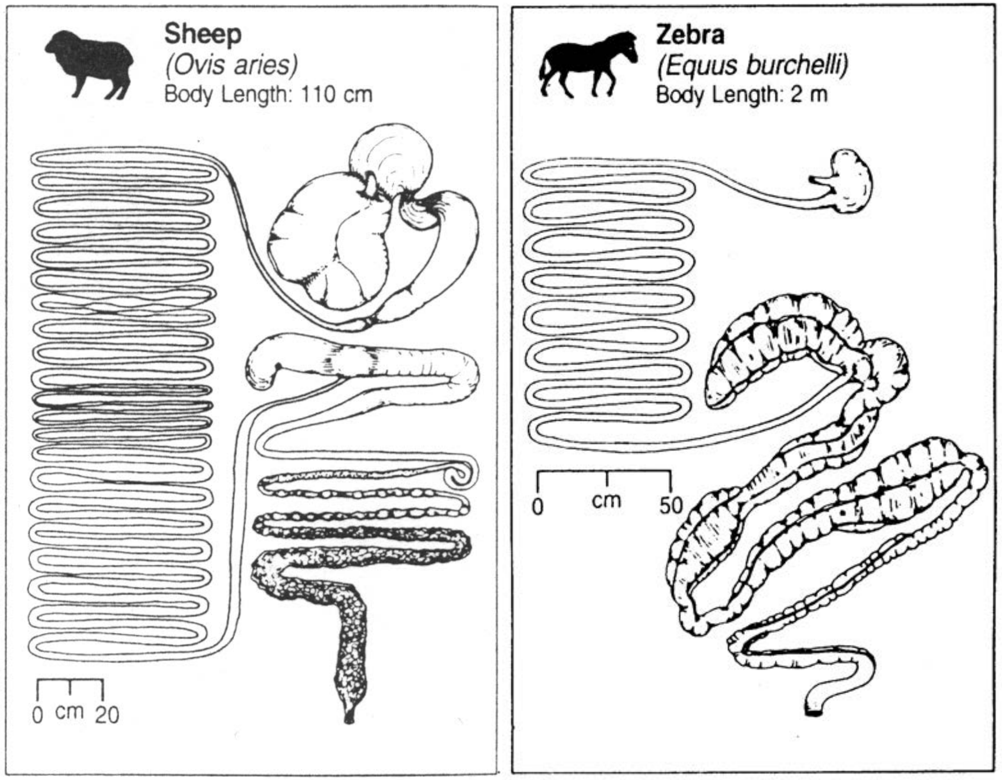


from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation

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

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



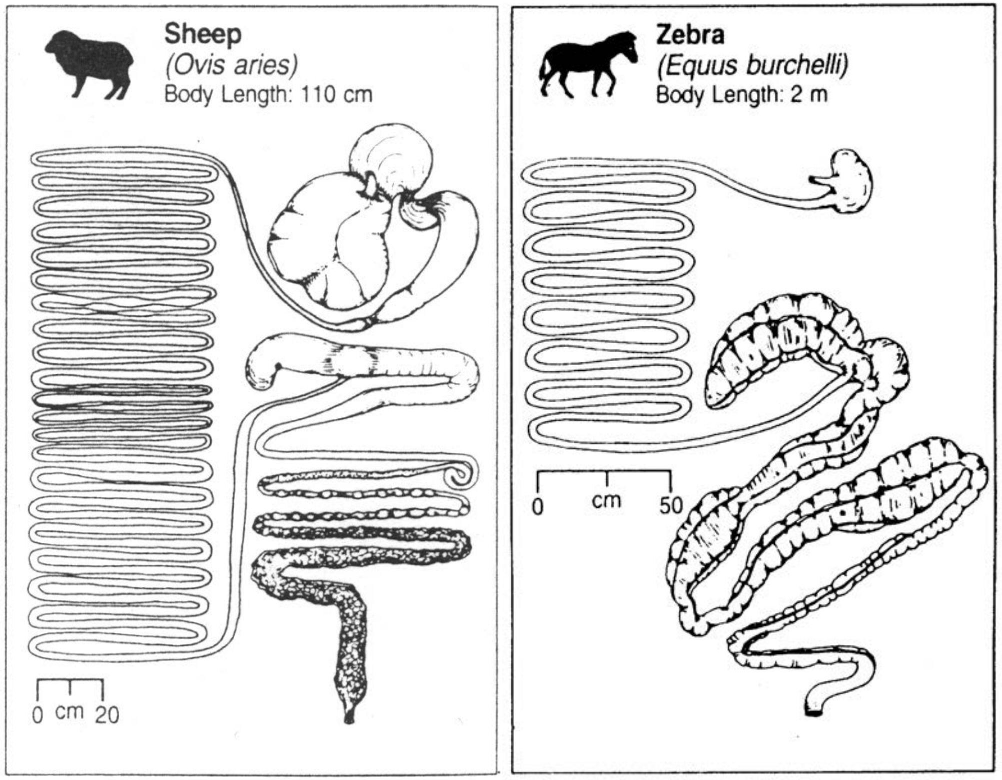
from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation

Fermentation prior to enzymatic digestion and absorption:

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

'Loss' of easily digestible substrates and bacterial modification



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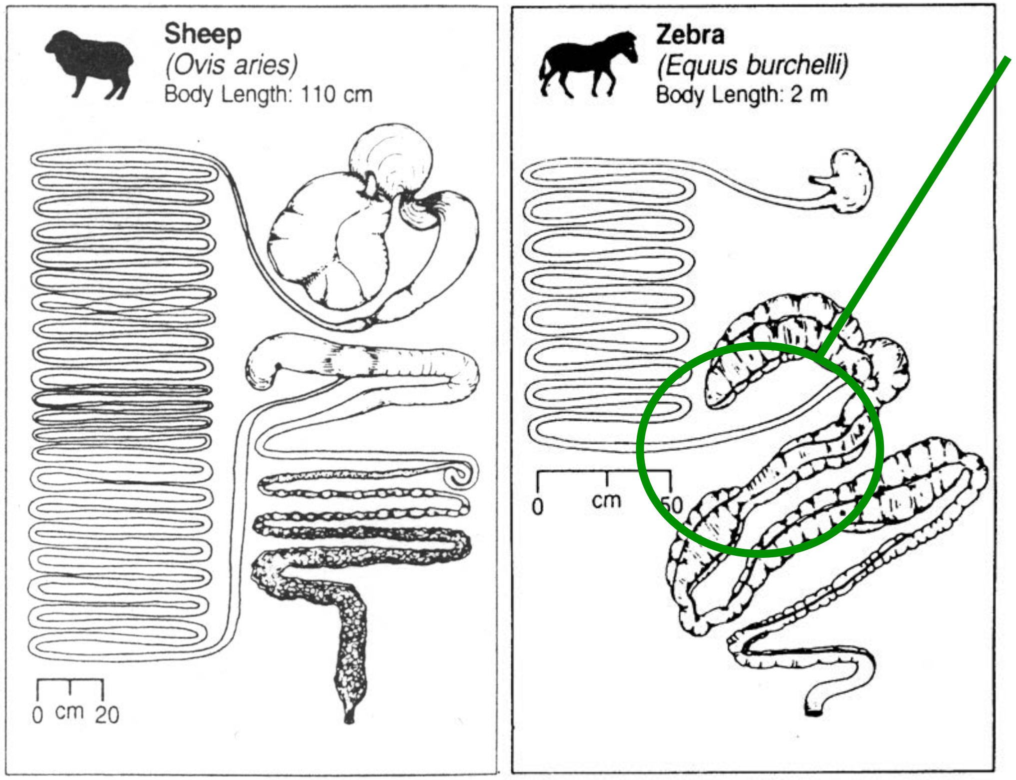

Fermentation after enzymatic digestion and absorption:

from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation

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

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

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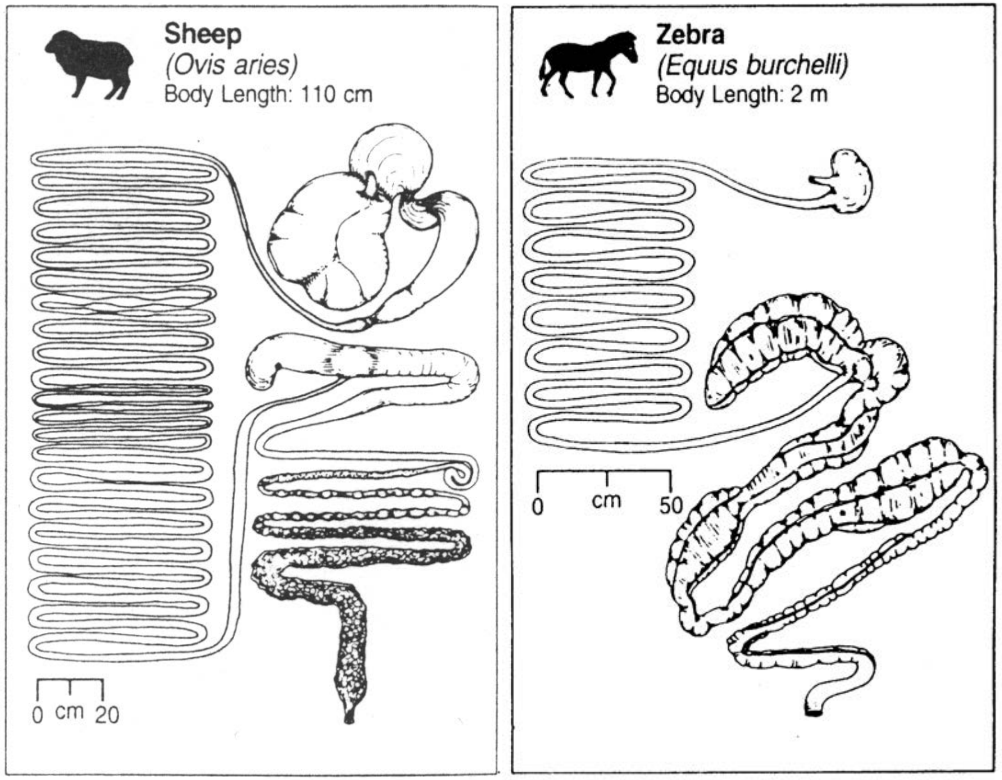


Fermentation <u>after</u> enzymatic digestion and absorption:

<u>Use</u> of easily digestible substances prior to fermentation

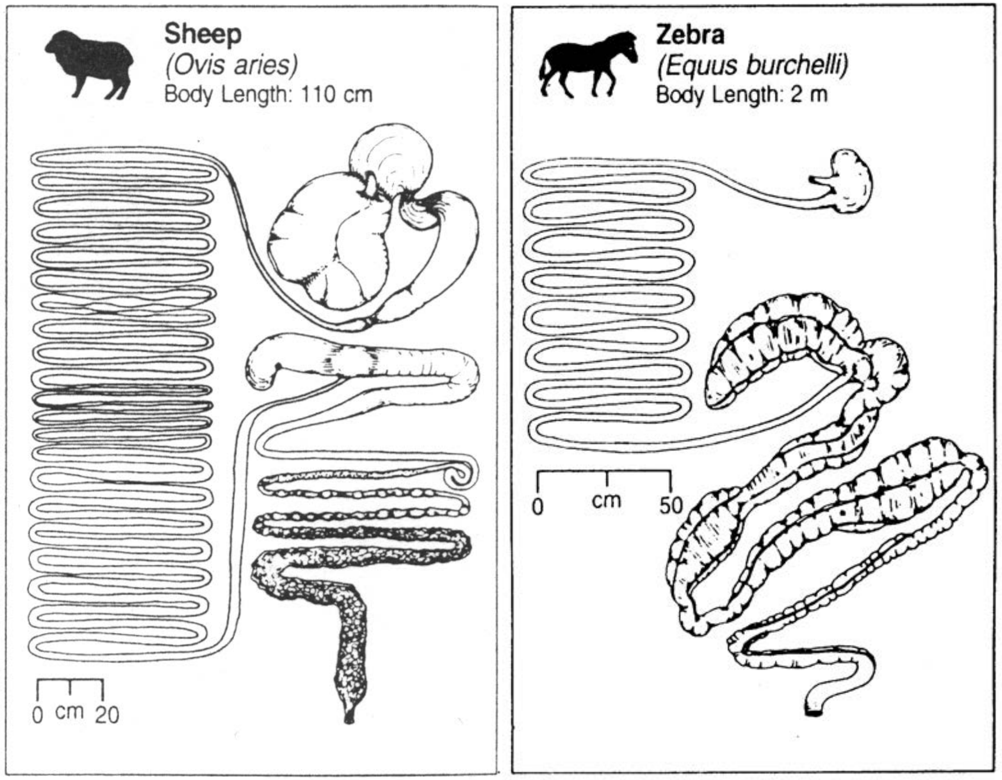
from Stevens & Hume (1995)

Foregut vs. Hindgut Fermentation

Fermentation prior to enzymatic digestion and absorption:

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

'Loss' of easily digestible substrates and bacterial modification



Fermentation after enzymatic digestion and absorption:

Use of easily digestible substances prior to fermentation

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

from Stevens & Hume (1995)

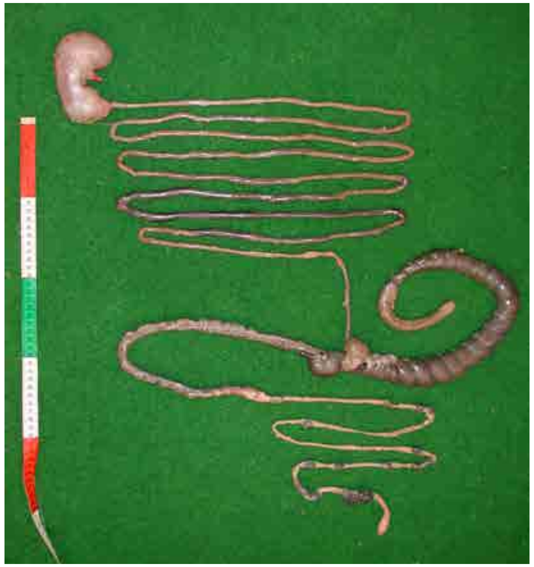
Herbivory

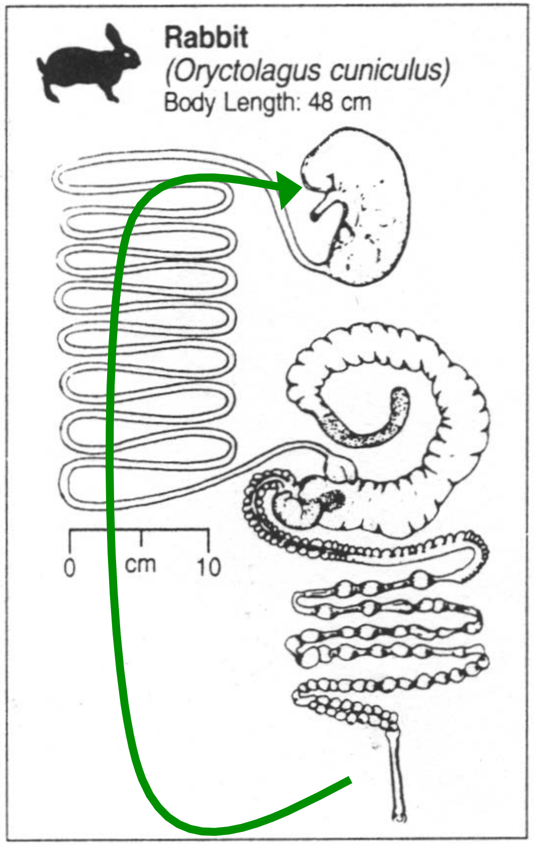
-

Principles

(coprophagy)

‘Backward pass’





Fermentation <u>after</u> sites of aut-enzymatic digestion and absoprtion:

<u>Use</u> of easily digestible substances prior to fermentation

<u>Loss</u> of bacterial protein

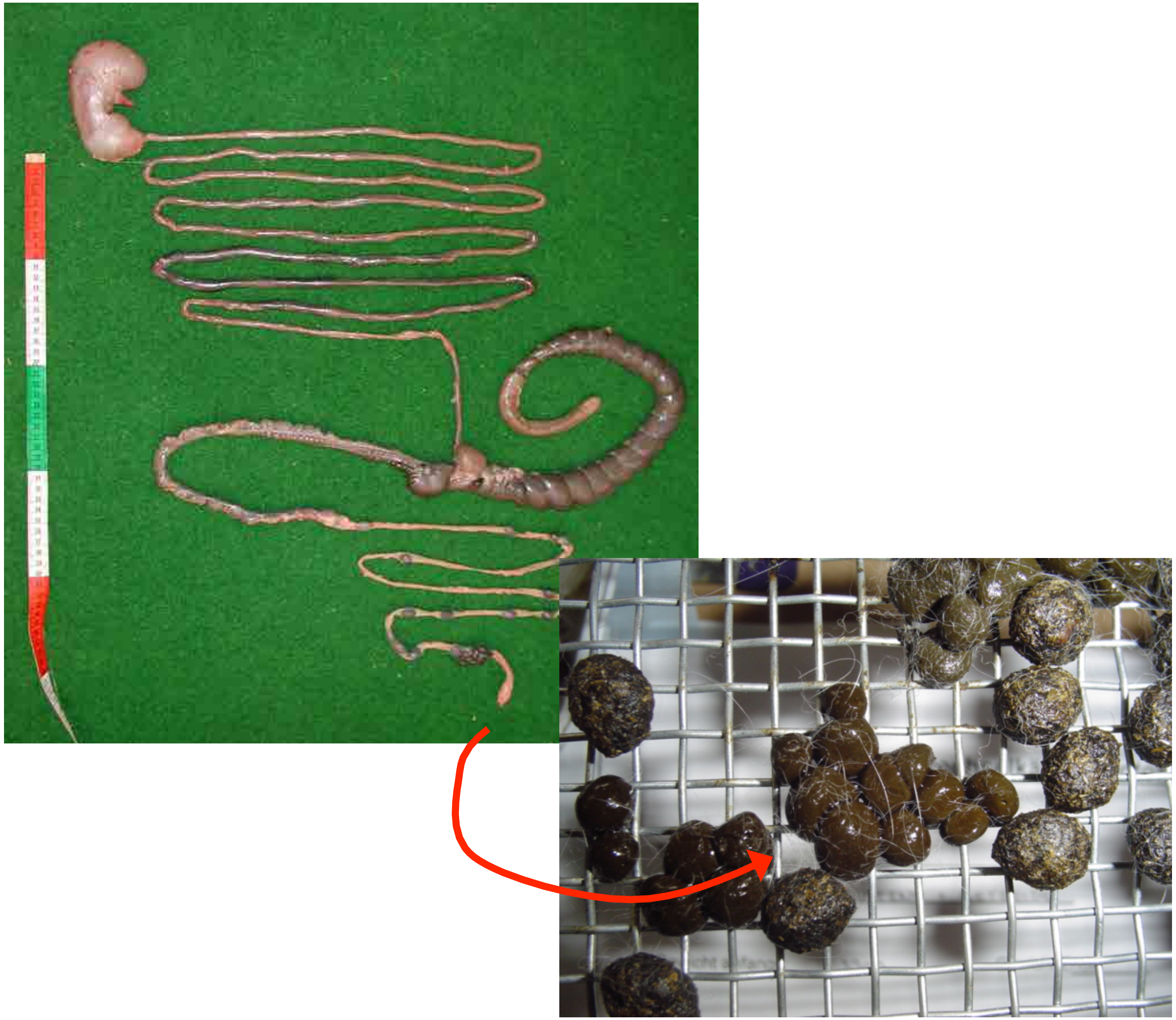
Coprophagy/ Caecotrphy

from Stevens und Hume (1995)
Photo: B. Burger

Coprophagy/Caecotrophy

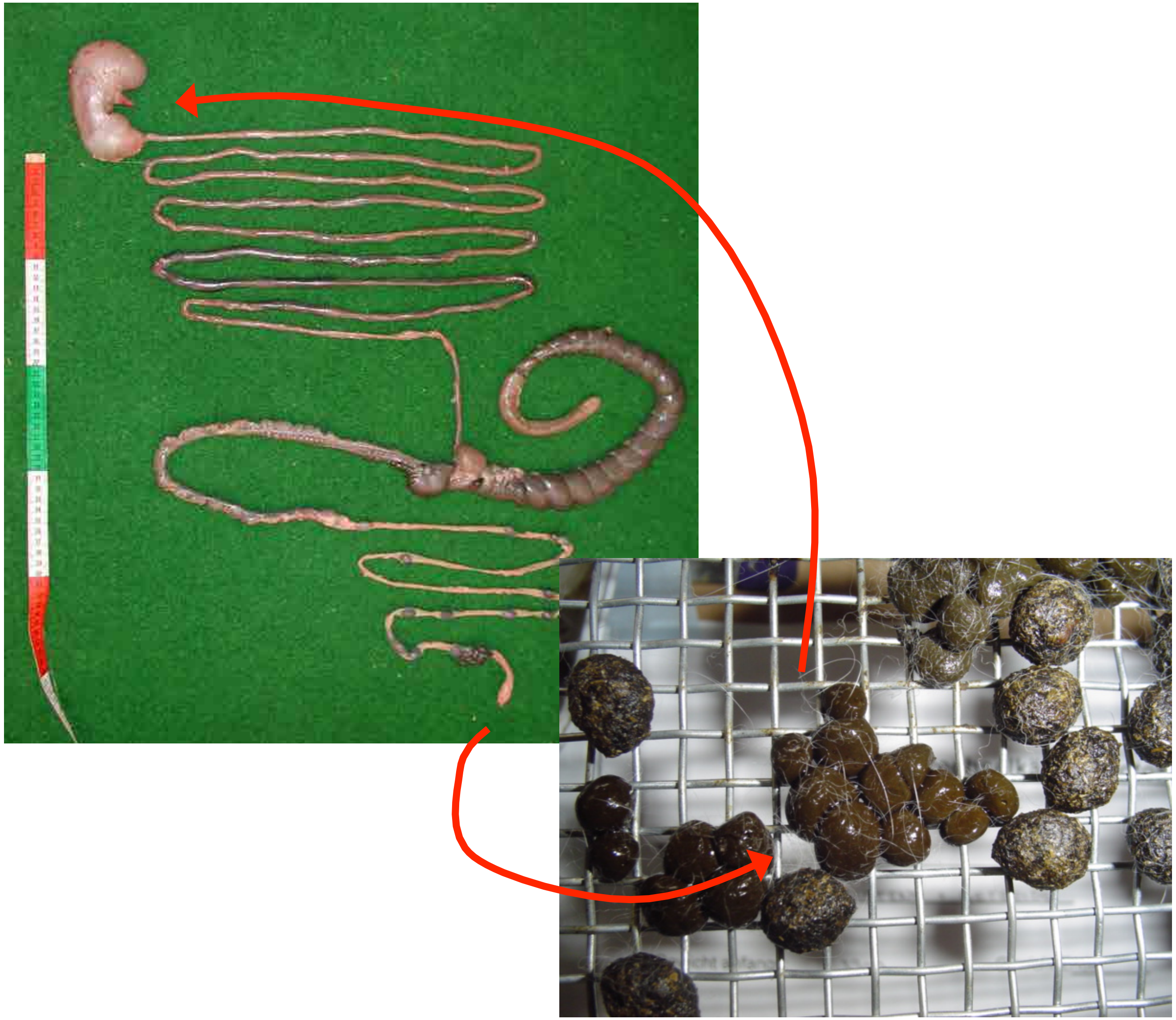
Photos: B. Burger

Coprophagy/Caecotrophy



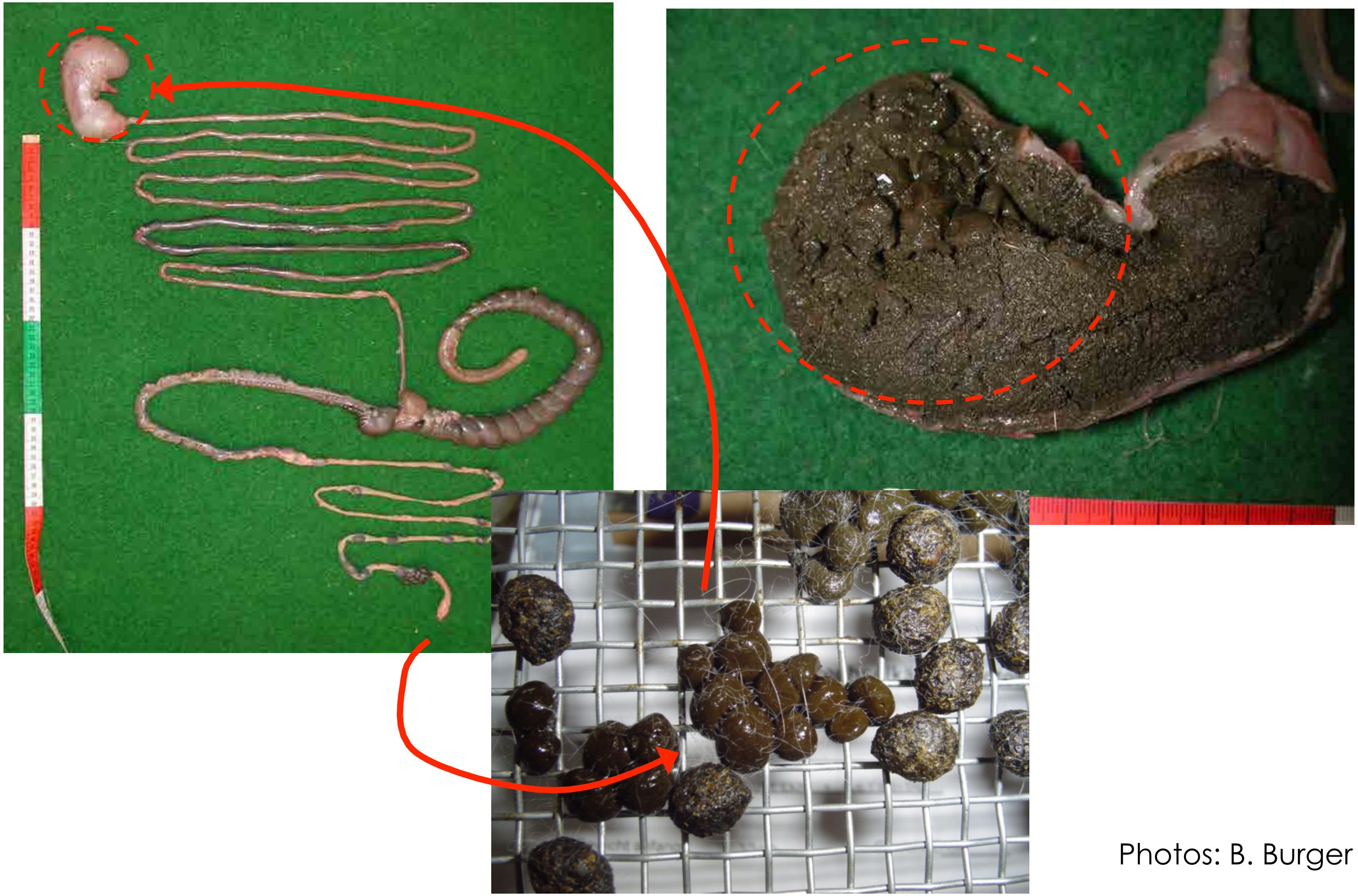
Photos: B. Burger

Coprophagy/Caecotrophy



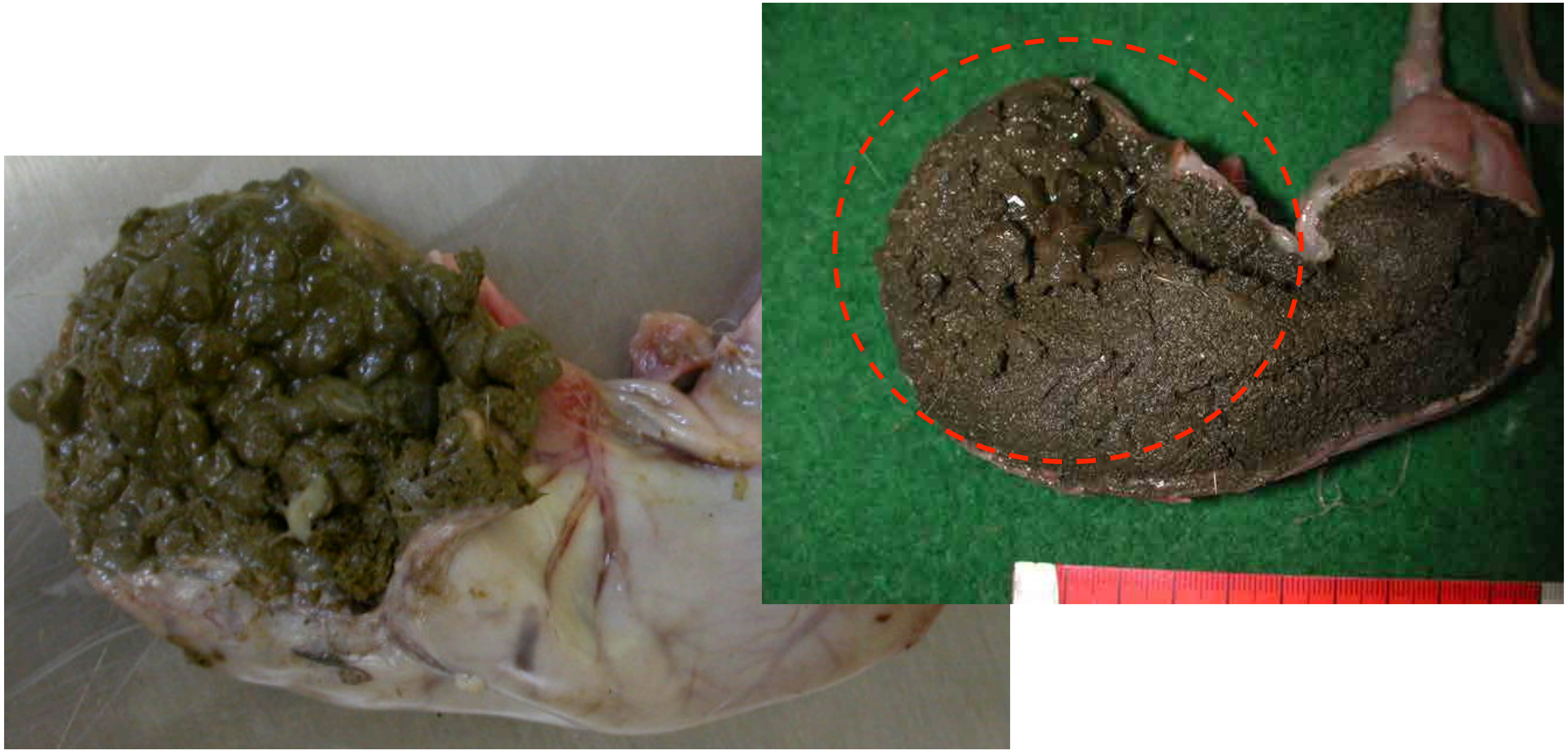
Photos: B. Burger

Coprophagy/Caecotrophy



Photos: B. Burger

Coprophagy/Caecotrophy



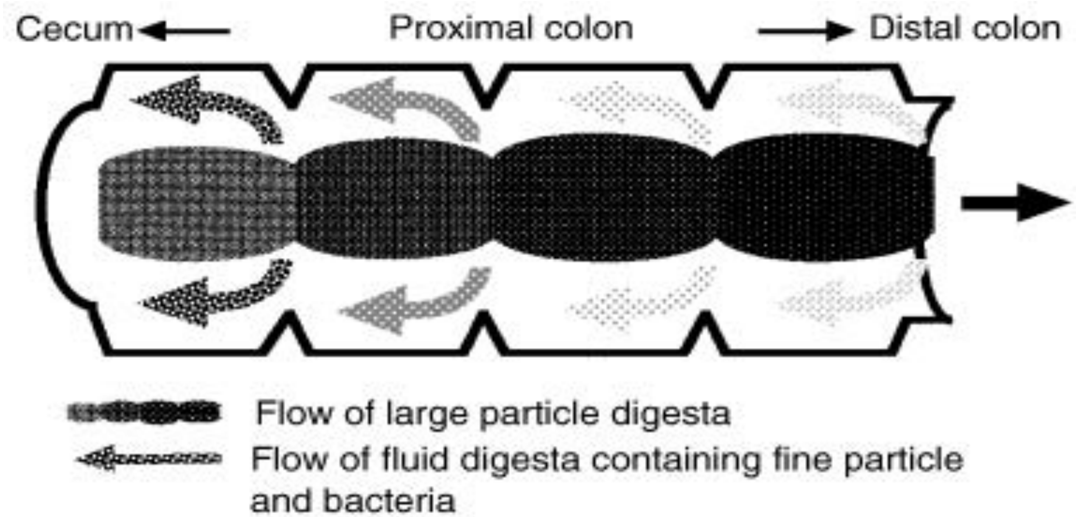
Photos: B. Burger, M. Clauss

Coprophagy/Caecotrophy

Photo: A. Tschudin

Sorting of ingesta for caecotroph formation

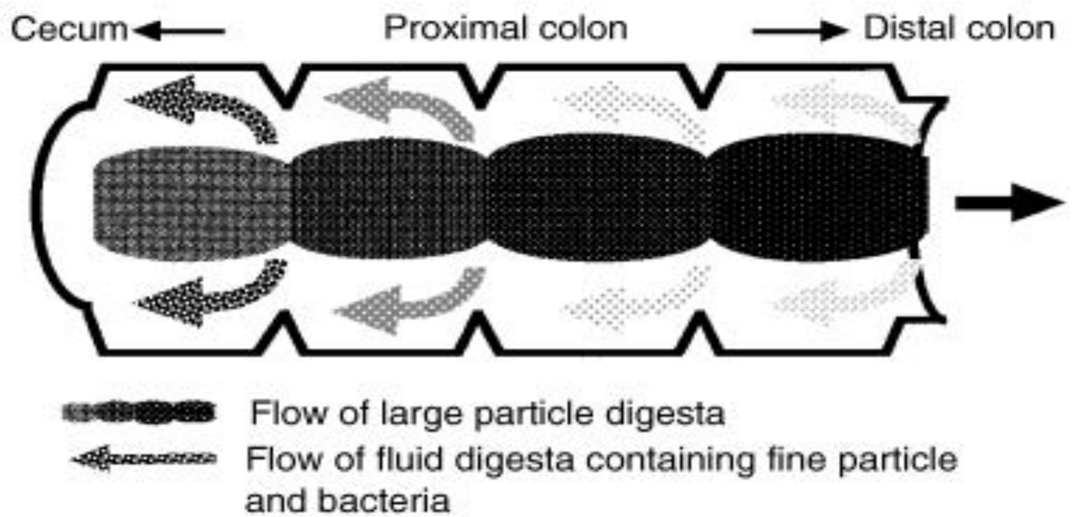
Wash back mechanism (Rabbit)



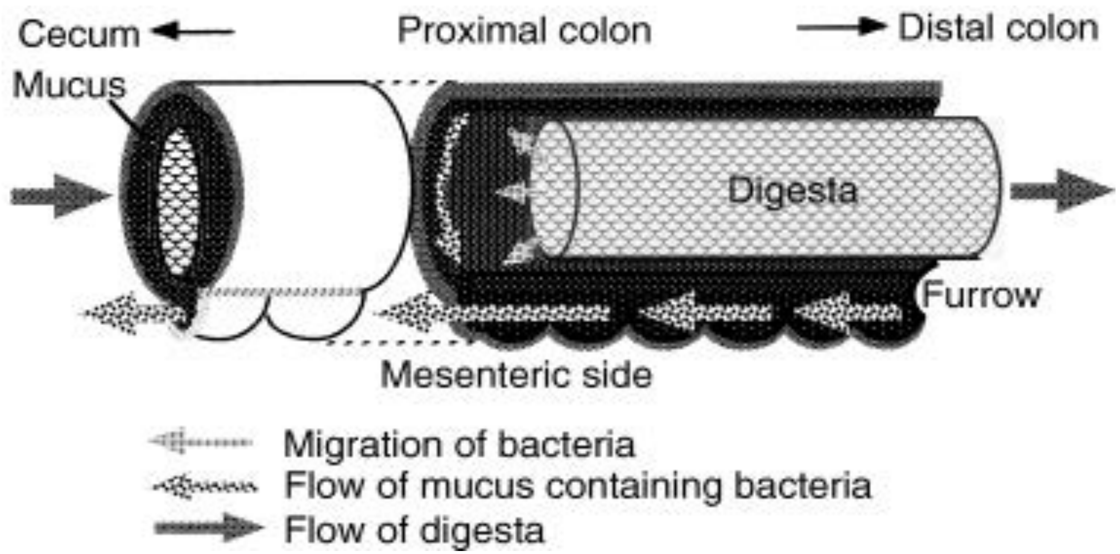
from Sakaguchi (2003)

Sorting of ingesta for caecotroph formation

Wash back mechanism (Rabbit)

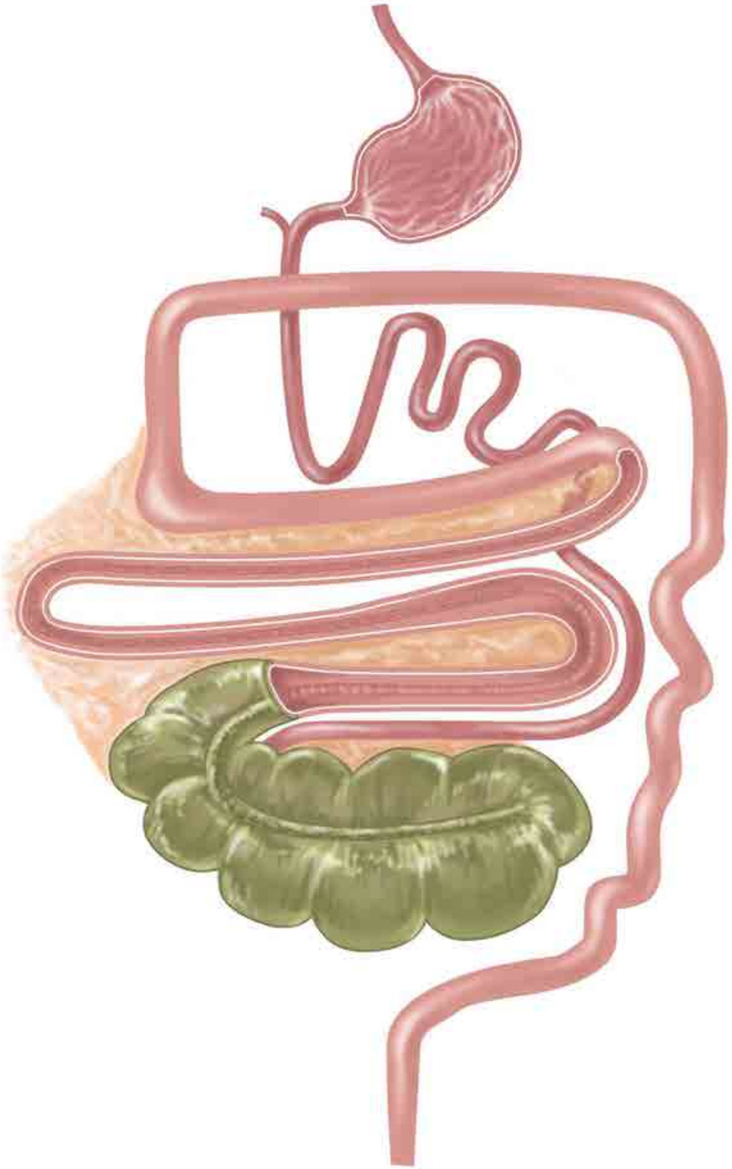


Mucus trap mechanism (Guniea pig, Chinchilla)



from Sakaguchi (2003)

The colonic groove / furrow



from Besselmann (2005)

The colonic groove / furrow

Mara

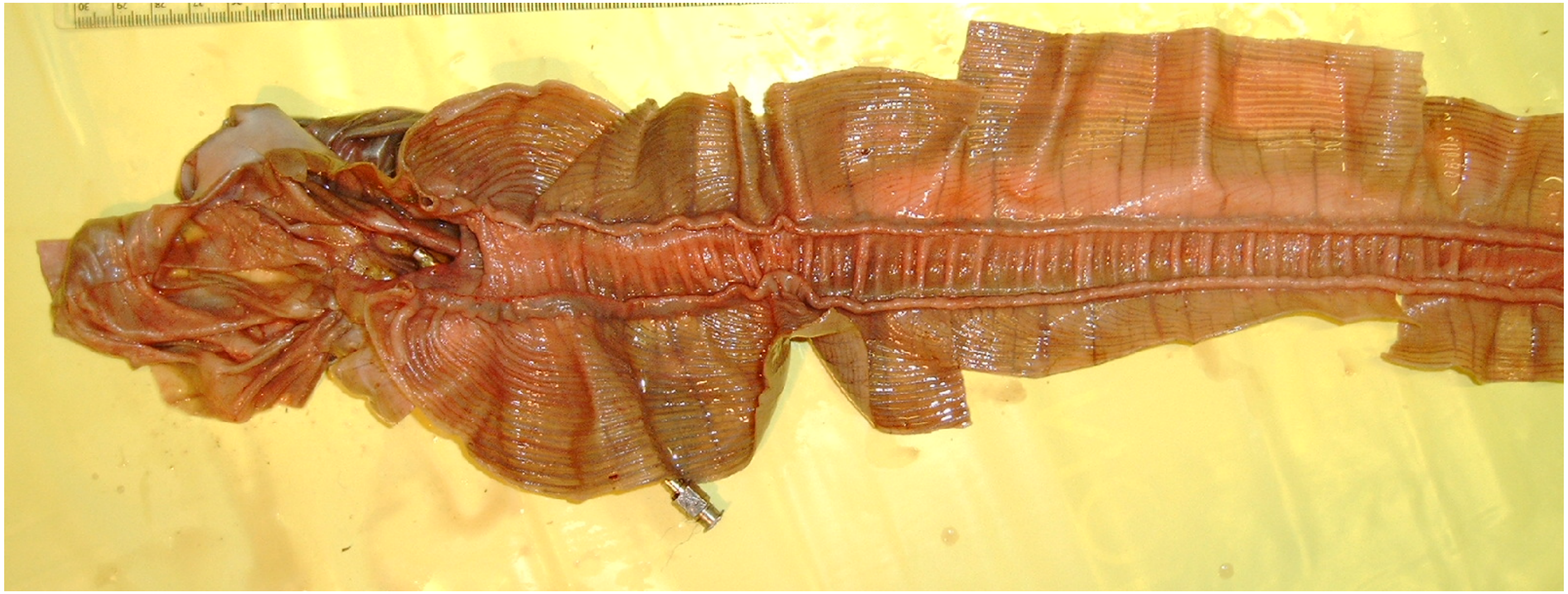


Photo: M. Clauss

Detritivory, coprophagy, and the evolution of digestive mutualisms in Dictyoptera

C.A. Nalepa[1], D.E. Bignell[2] and C. Bandi[3]

Insectes soc. 48 (2001) 194–201

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Insectes soc. 48 (2001) 194–201

ASOCIAL

DETRITIVORY,
GENERAL
COPROPHAGY

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ASOCIAL		GREGARIOUS
DETRITIVORY, GENERAL COPROPHAGY	→	INTRASPECIFIC COPROPHAGY

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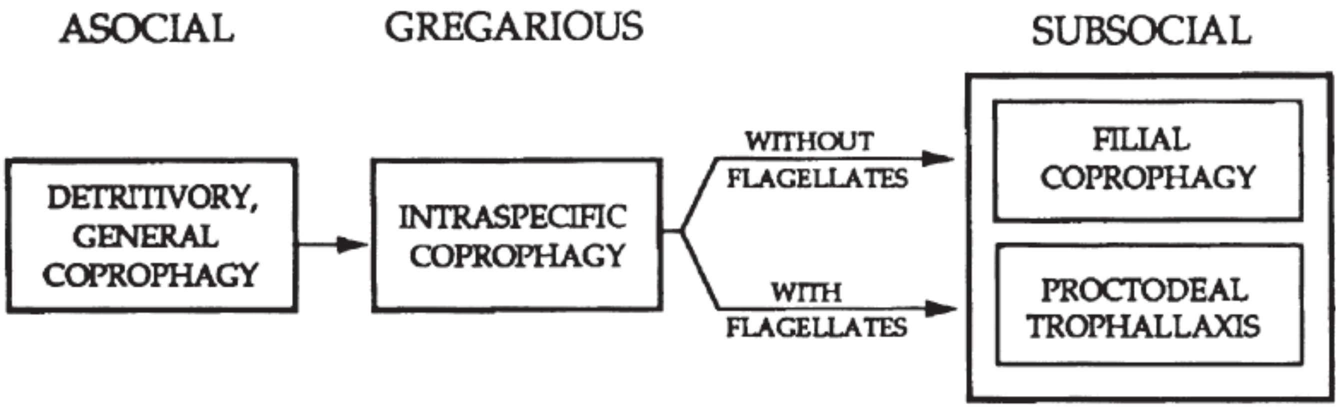



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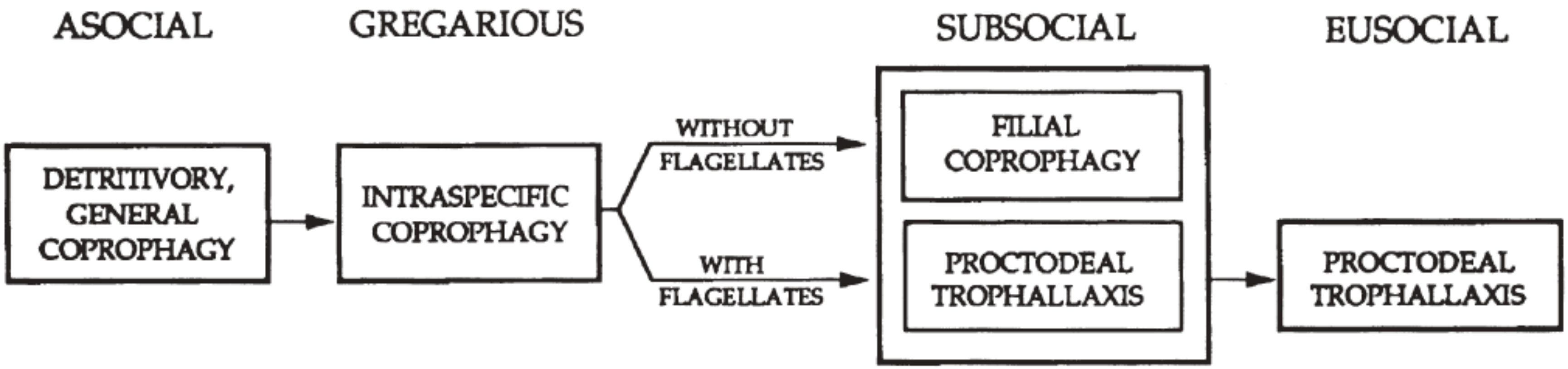


Coprophagy / Trophallaxis








The question is not so much
why such a large variety of hindgut fermenters
practice coprophagy,
but rather
why there is a certain group
of large hindgut fermenters
that does not.



Herbivory

-

diversity concepts

Conceptualizing herbivore diversity

metabolic intensity

Conceptualizing herbivore diversity

metabolic intensity

Conceptualizing herbivore diversity

To achieve a high metabolic intensity, you need

Conceptualizing herbivore diversity

metabolic intensity

To achieve a high metabolic intensity, you need

- *a high food intake*

Conceptualizing herbivore diversity

To achieve a high metabolic intensity, you need

- *a high food intake*
- *a high digestive efficiency*

Conceptualizing herbivore diversity

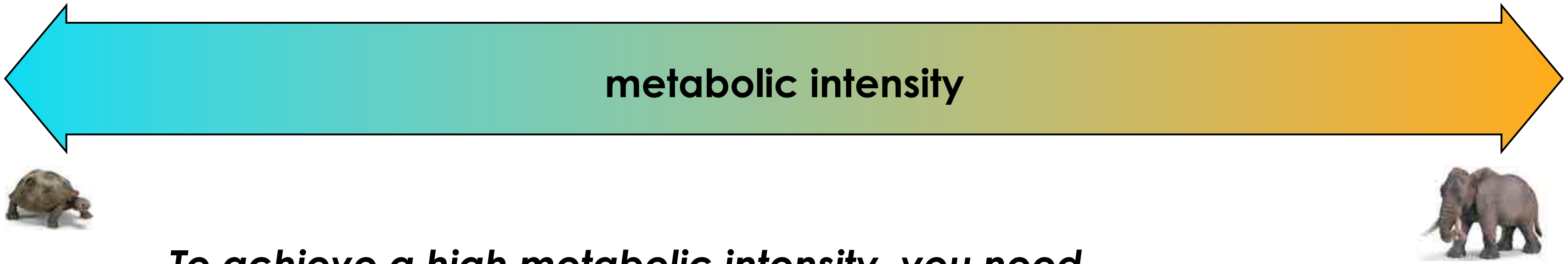
metabolic intensity

To achieve a high metabolic intensity, you need

- *a high food intake*

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

Conceptualizing herbivore diversity



To achieve a high metabolic intensity, you need

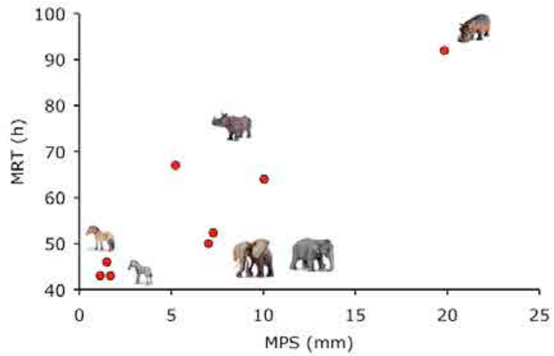
- *a high food intake*

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

Conceptualizing herbivore diversity

metabolic intensity

To achieve a high metabolic intensity, you need



- *a high food intake*

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

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

Conceptualizing herbivore diversity

metabolic intensity

To achieve a high metabolic intensity, you need

- *a high food intake*

?

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

Conceptualizing herbivore diversity

metabolic intensity

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  - *- long retention times*
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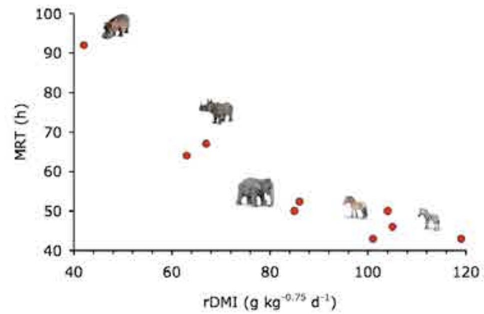


Conceptualizing herbivore diversity

metabolic intensity

To achieve a high metabolic intensity, you need

- *a high food intake*

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

Compensation via gut capacity?

Conceptualizing herbivore diversity

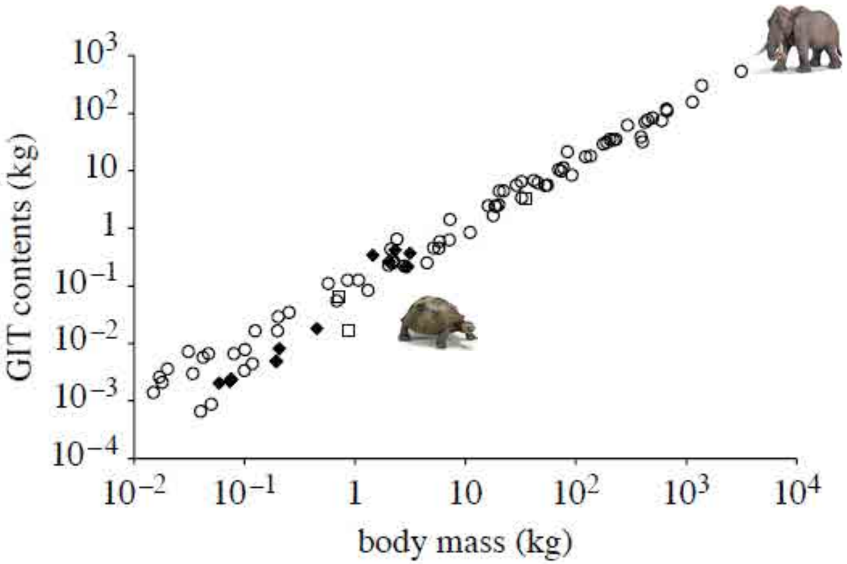
metabolic intensity

Gut capacity is relatively constant across metabolic intensities

Conceptualizing herbivore diversity

metabolic intensity

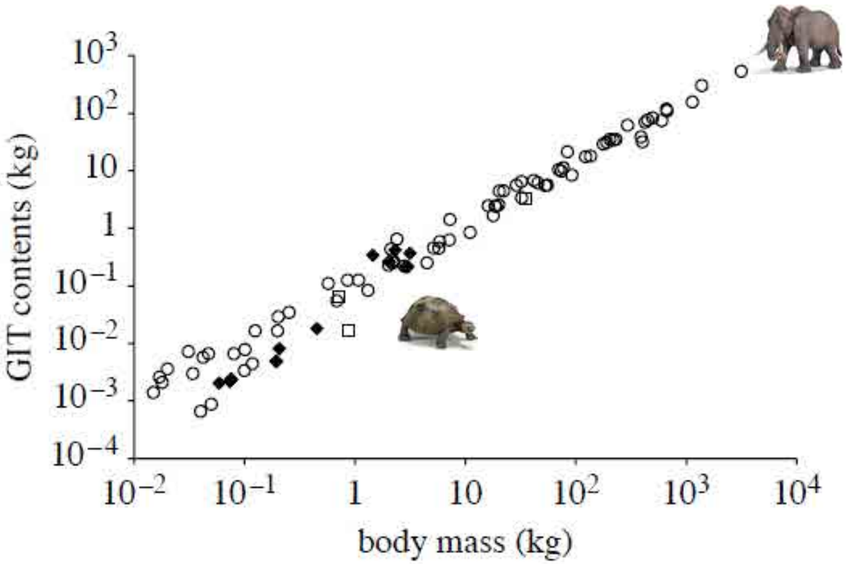
Gut capacity is relatively constant across metabolic intensities

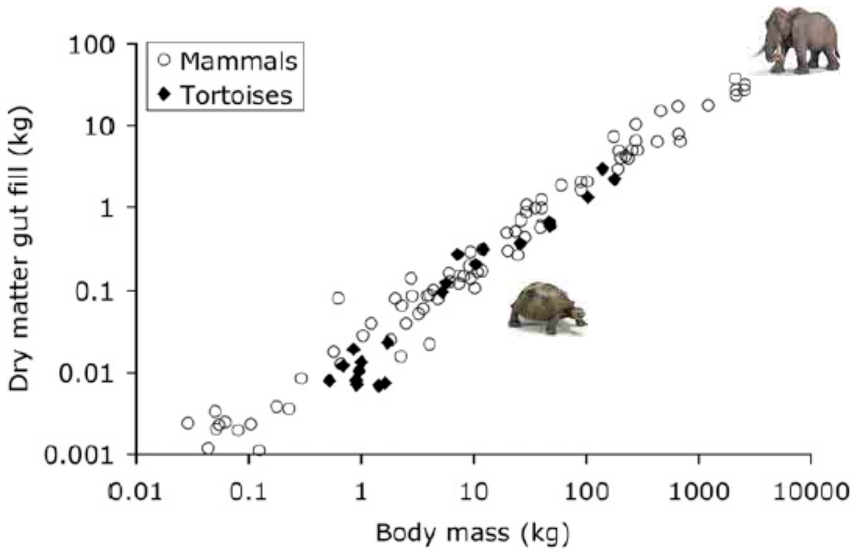


from Franz et al. (2009)

Conceptualizing herbivore diversity

Gut capacity is relatively constant across metabolic intensities

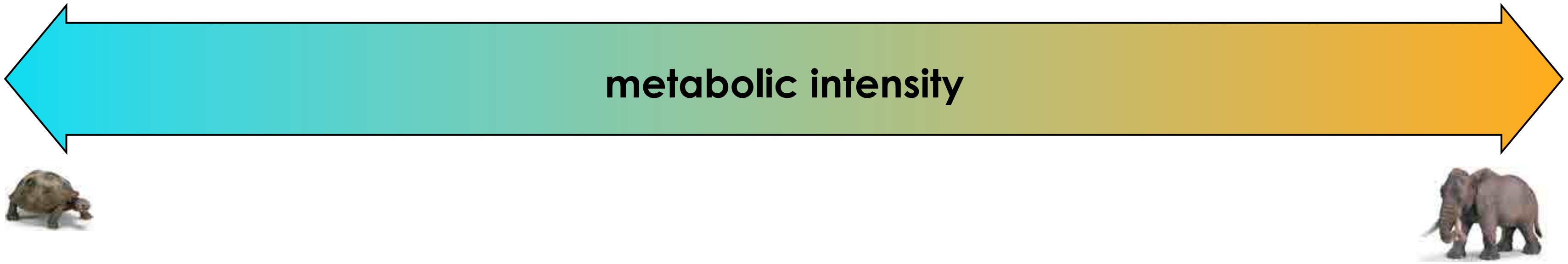


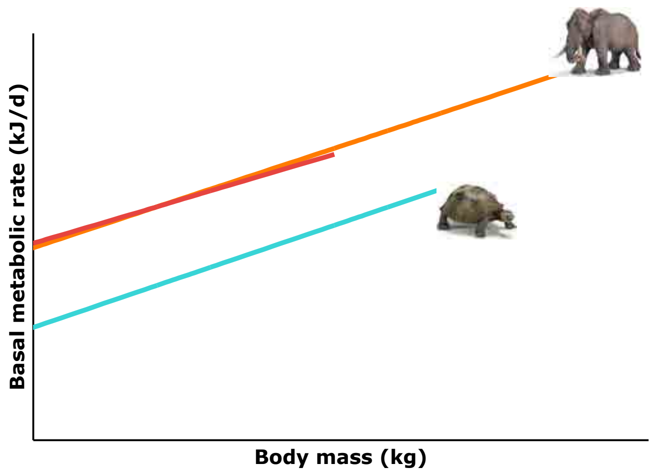


from Franz et al. (2009)

from Franz et al. (2011)

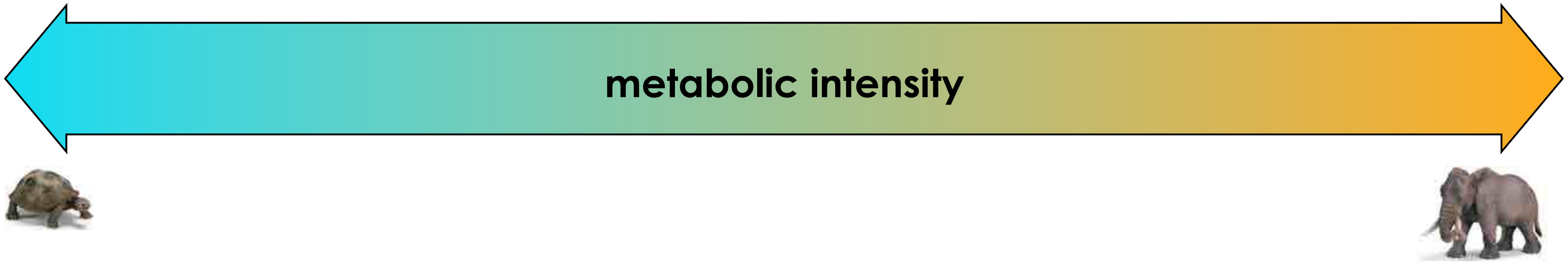
Conceptualizing herbivore diversity

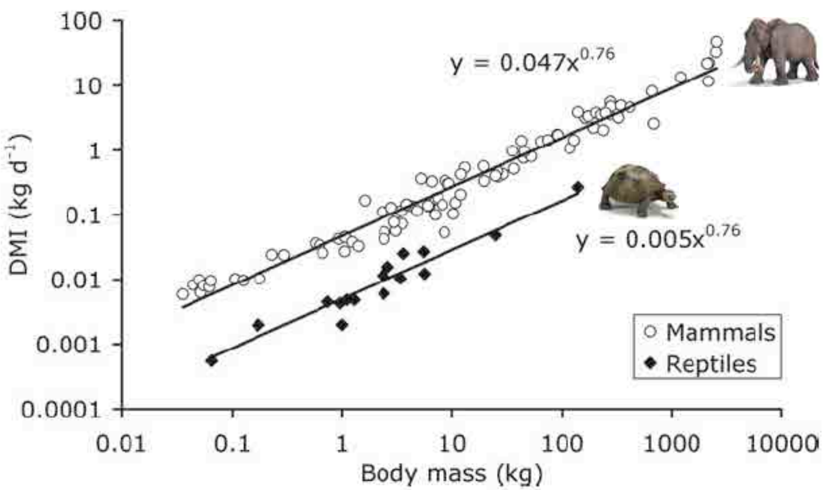


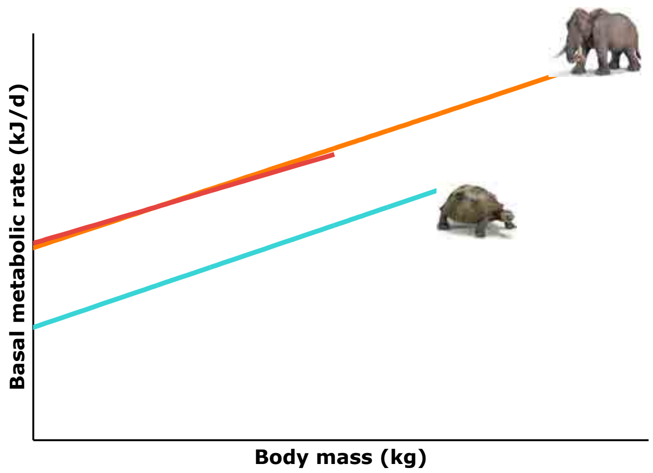


after Kirkwood (1996)

Conceptualizing herbivore diversity







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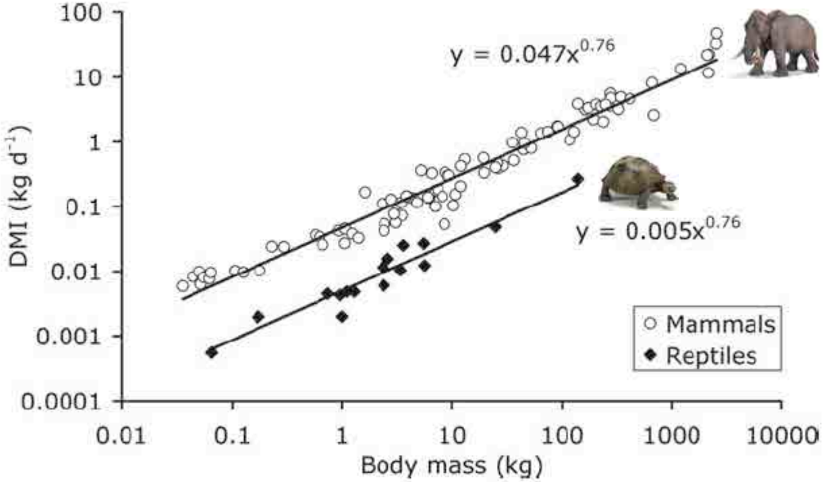
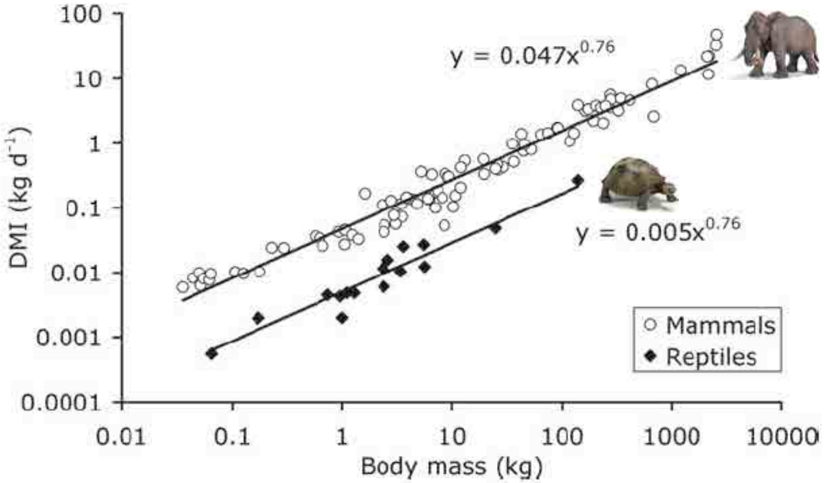
Conceptualizing herbivore diversity

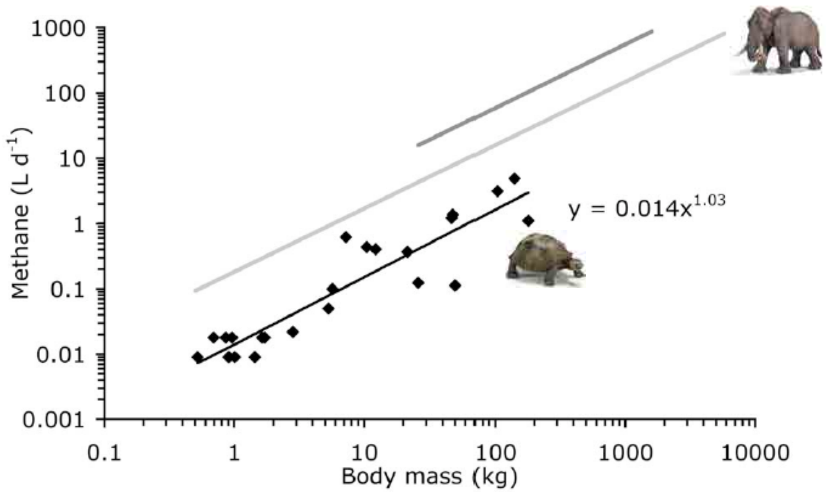


from Franz et al. (2011)

Conceptualizing herbivore diversity

metabolic intensity

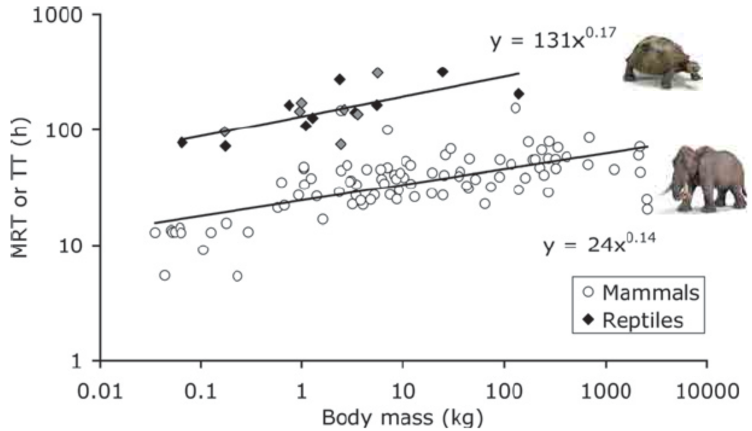




from Franz et al. (2011a)

from Franz et al. (2011b)

Conceptualizing herbivore diversity



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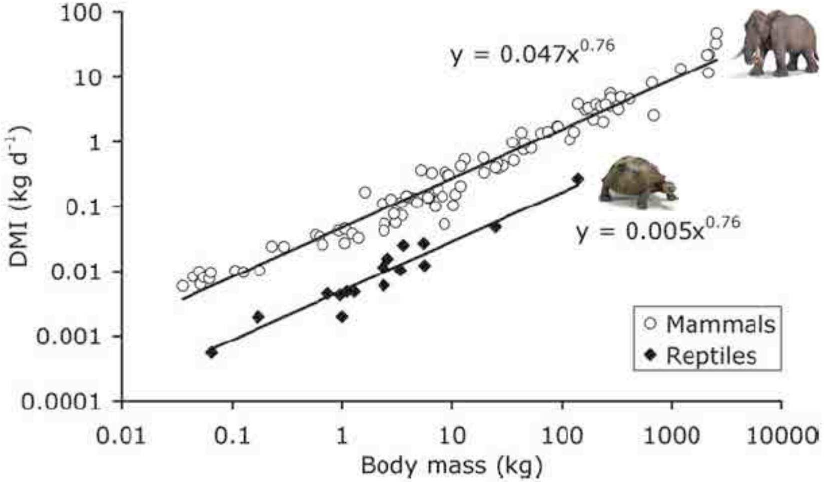

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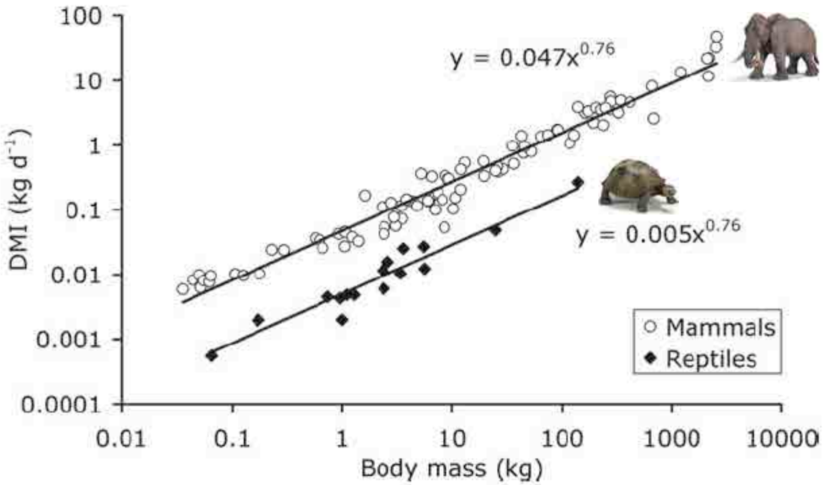
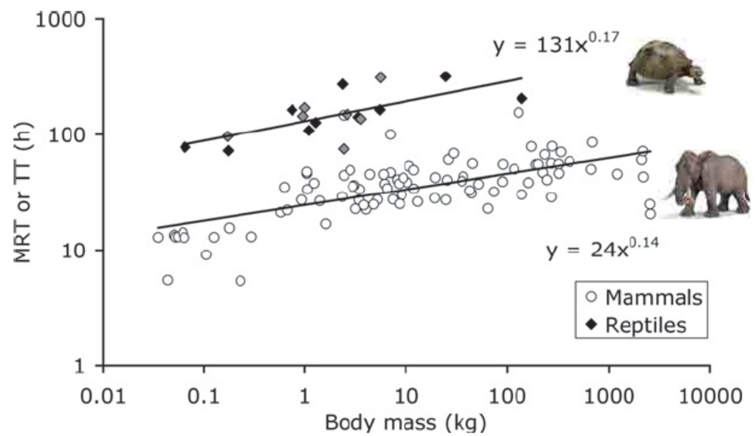
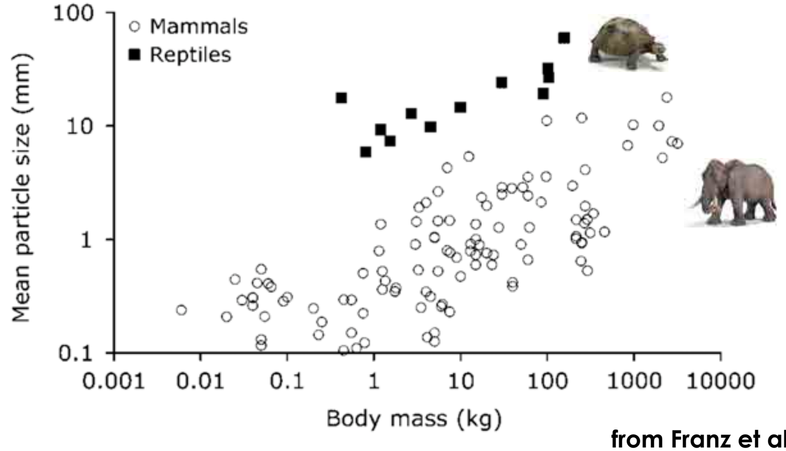
Conceptualizing herbivore diversity



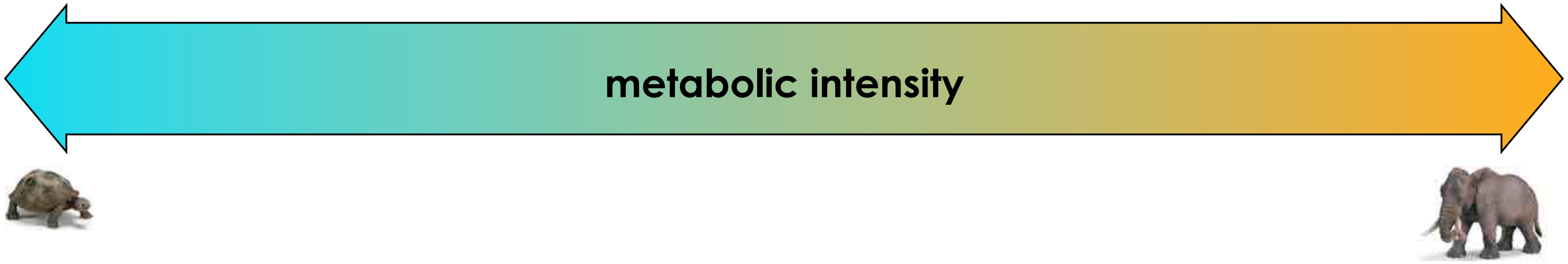




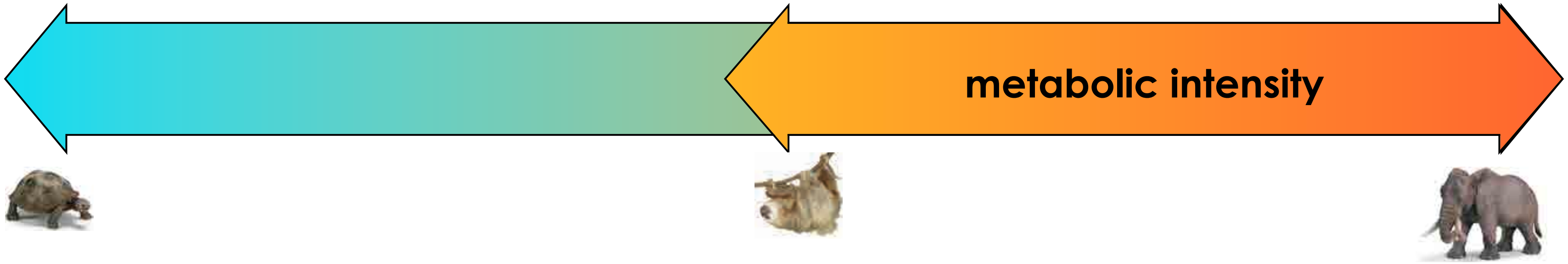
from Franz et al. (2011)

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

Conceptualizing herbivore diversity

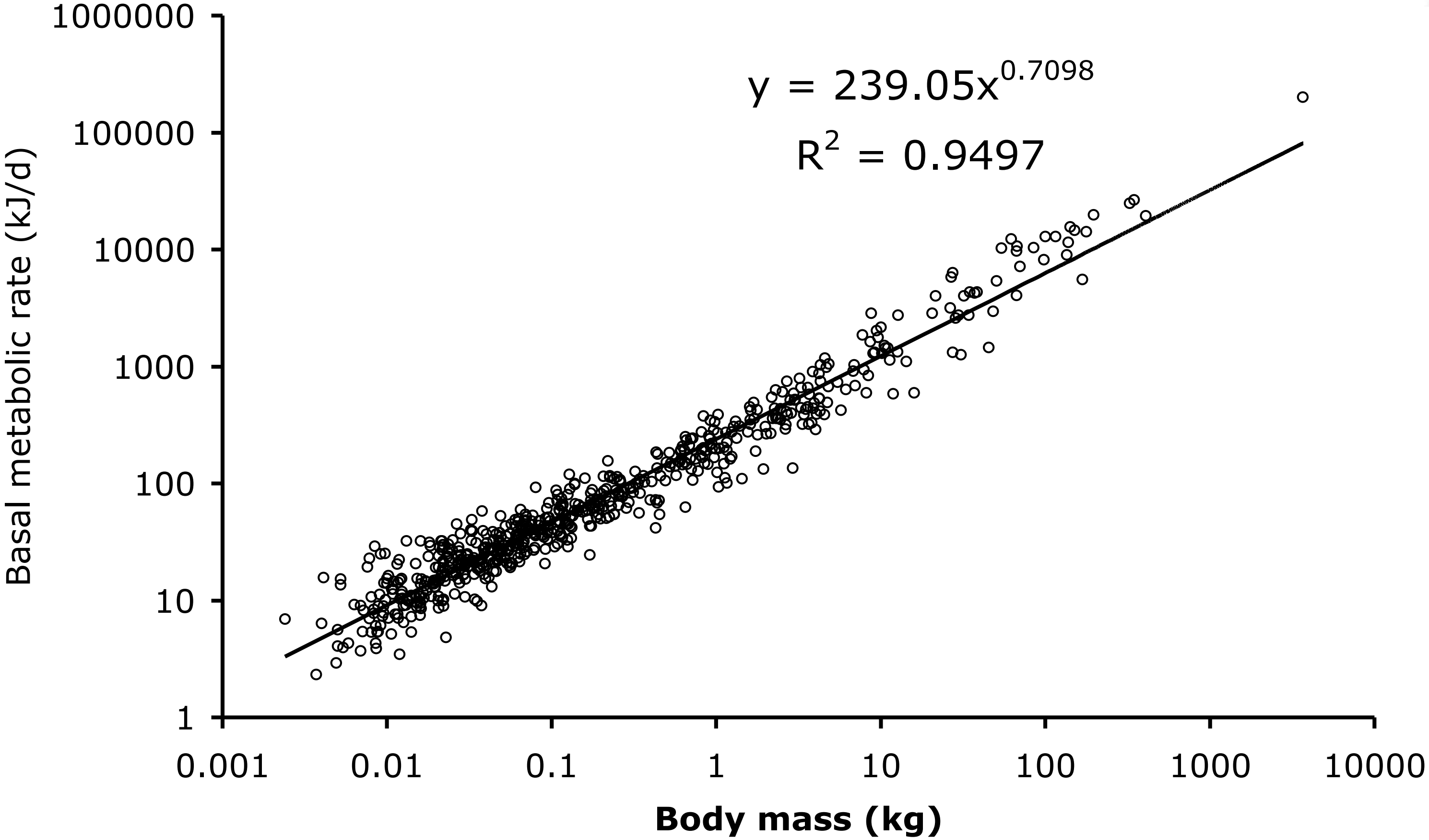


Conceptualizing herbivore diversity



Conceptualizing herbivore diversity

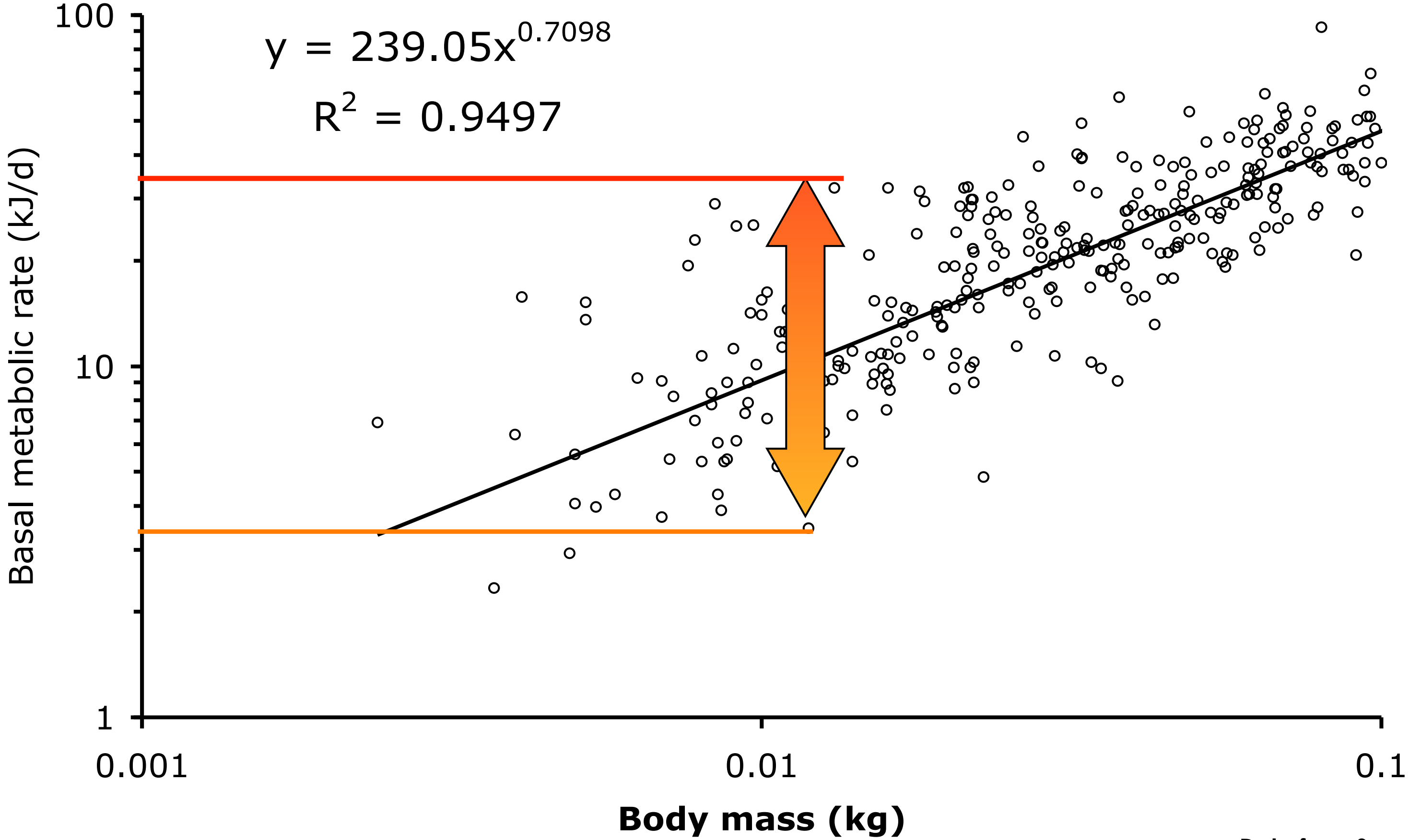
metabolic intensity



Data from Savage et al. (2004)

Conceptualizing herbivore diversity

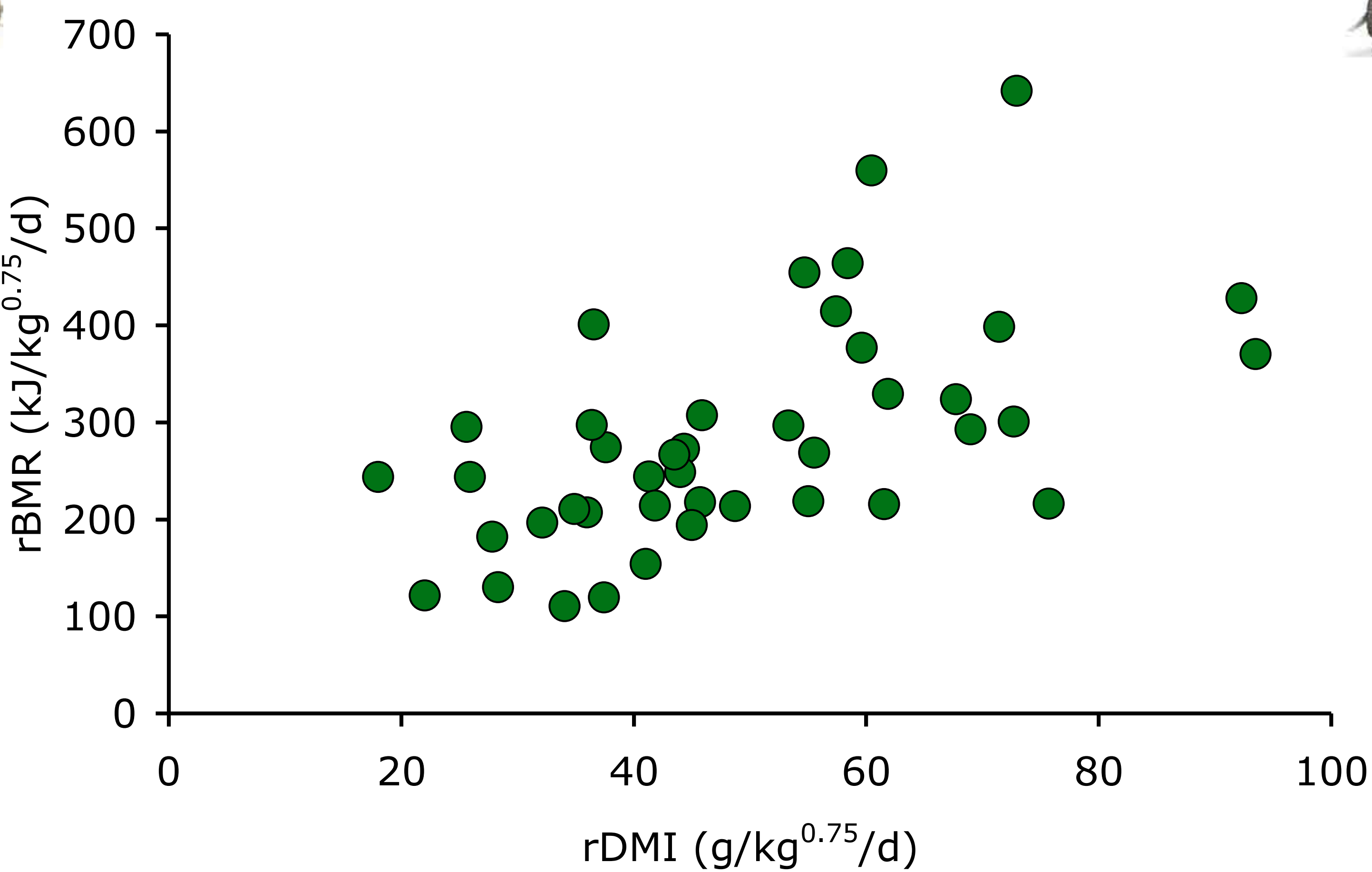
metabolic intensity



Data from Savage et al. (2004)

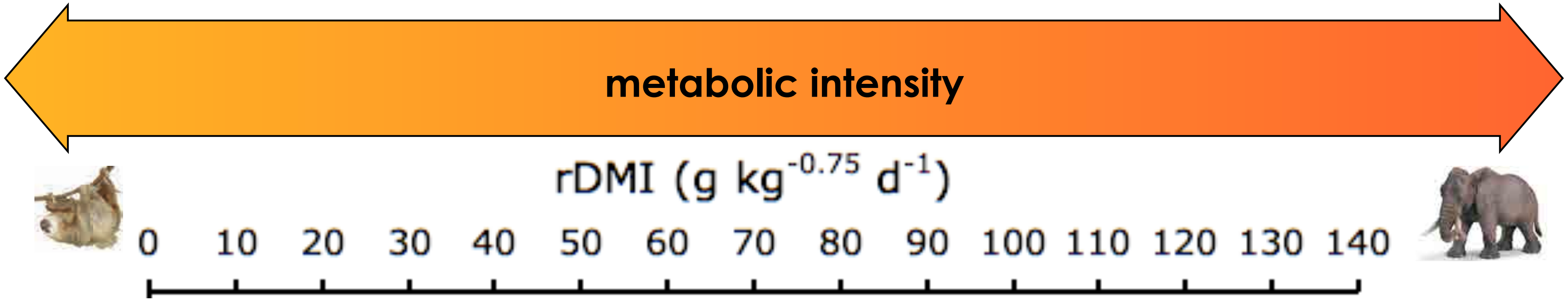
Conceptualizing herbivore diversity

metabolic intensity



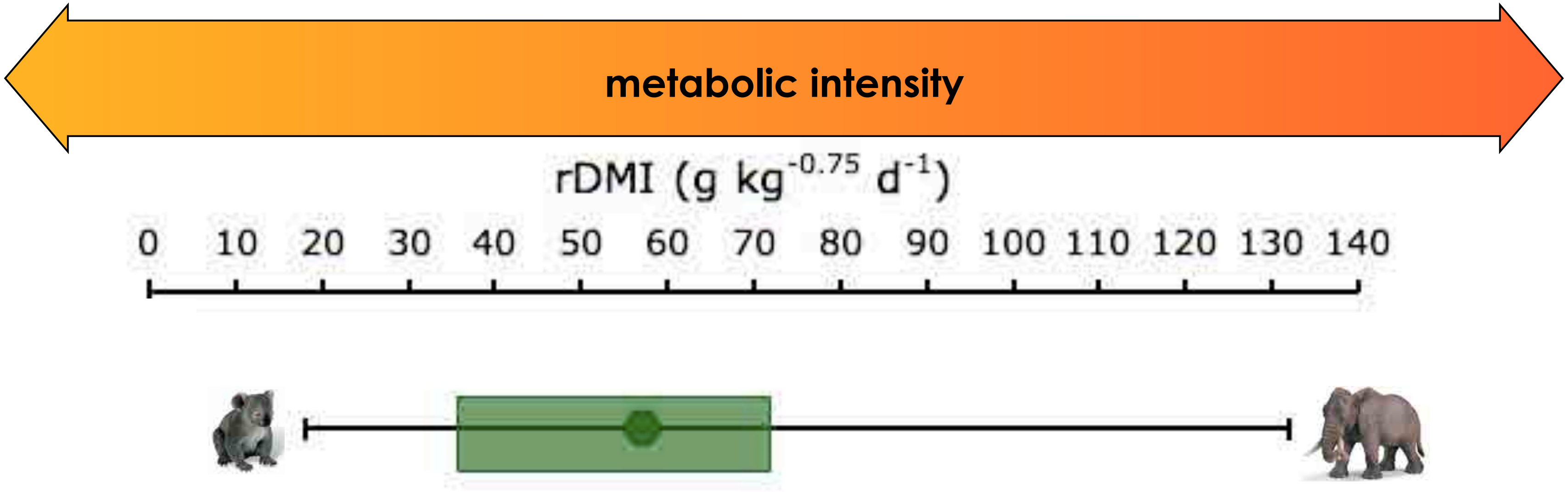
Data overlap from Savage et al. (2004) and Clauss et al. (2007)

Conceptualizing herbivore diversity



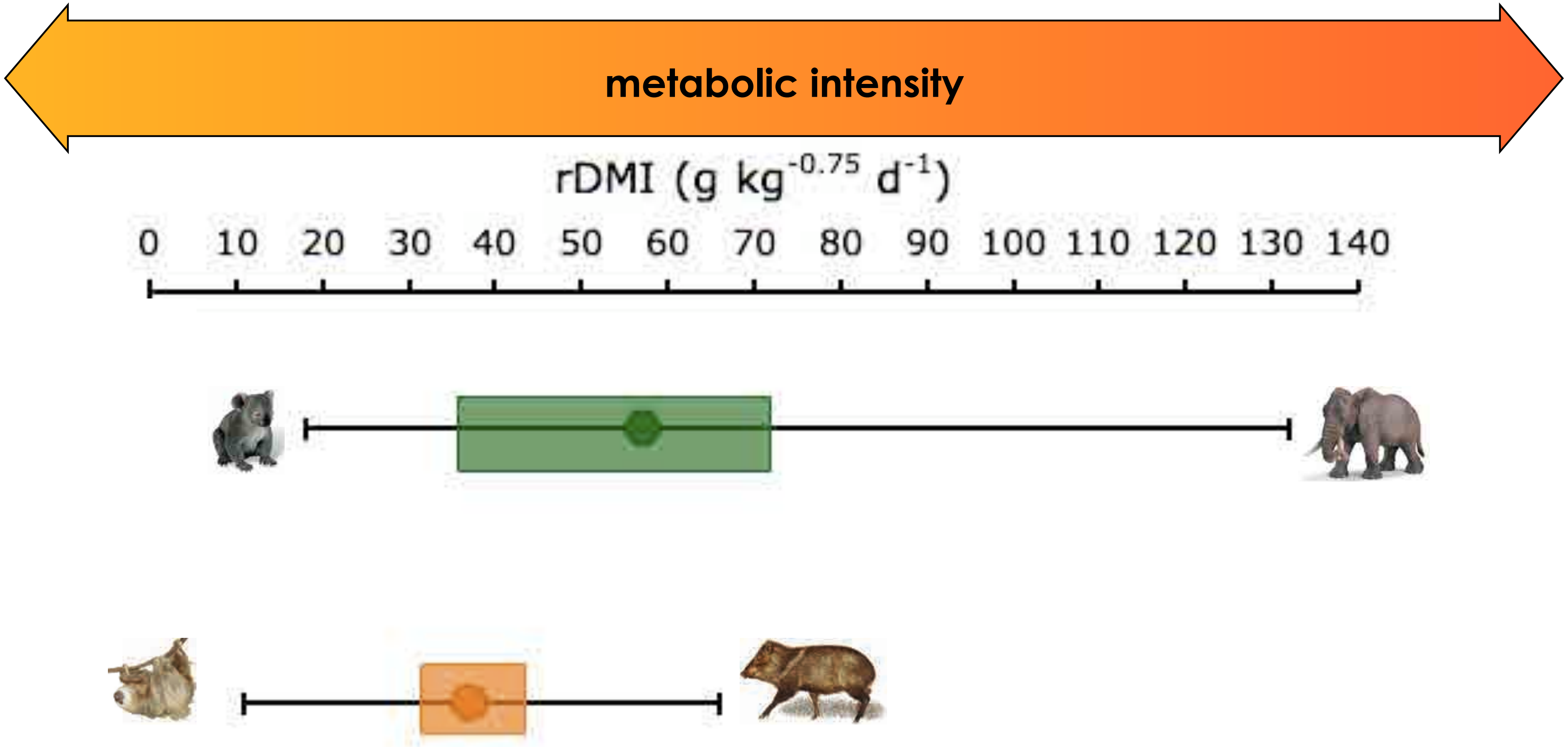
from Clauss et al. (2010)

Conceptualizing herbivore diversity



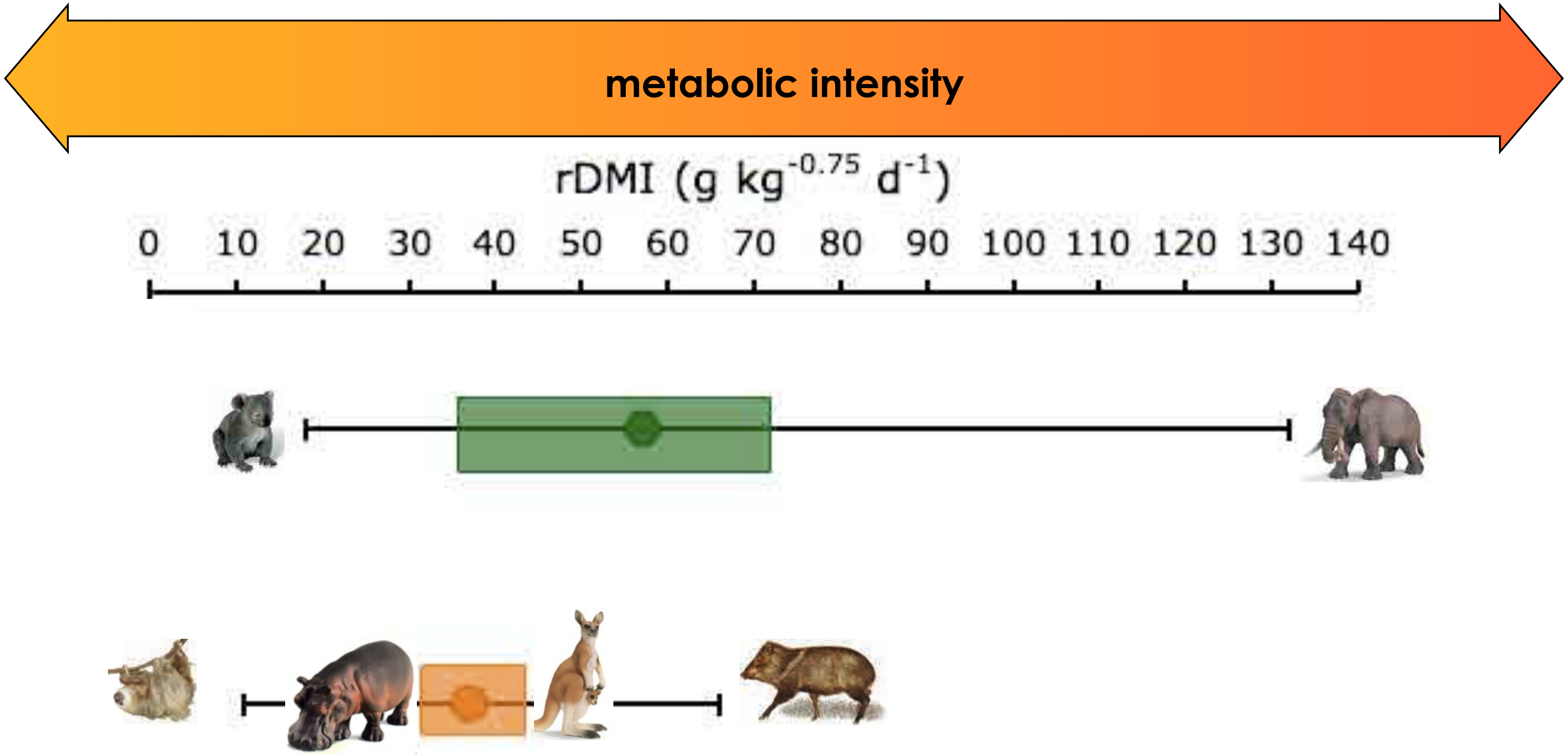
from Clauss et al. (2010)

Conceptualizing herbivore diversity



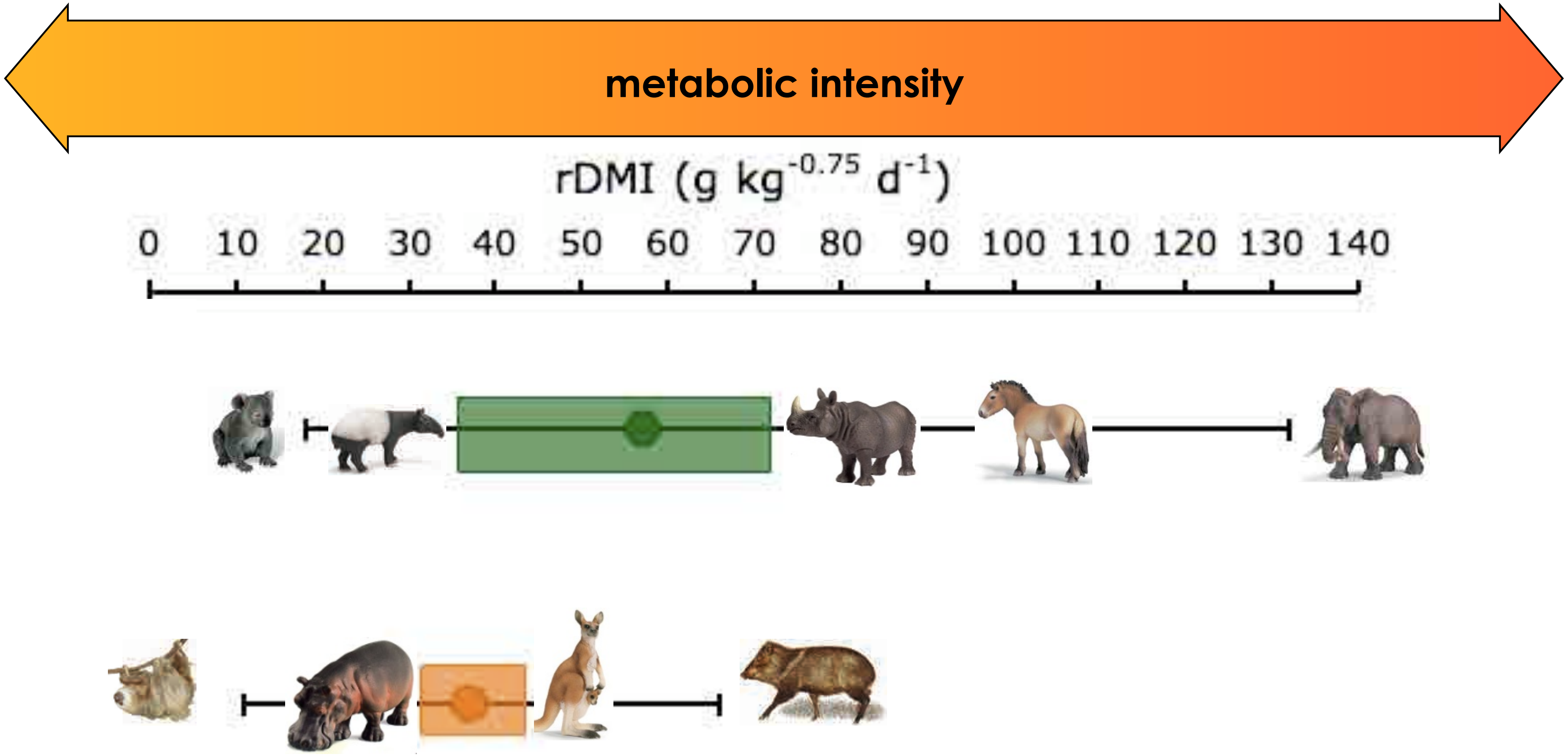
from Clauss et al. (2010)

Conceptualizing herbivore diversity



from Clauss et al. (2010)

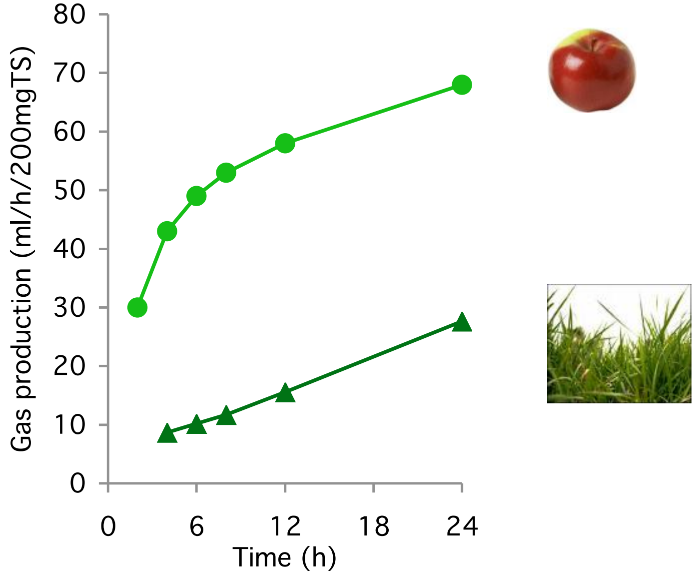
Conceptualizing herbivore diversity



from Clauss et al. (2010)

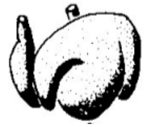
Two Preconditions

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



from Hummel et al. (2006ab)

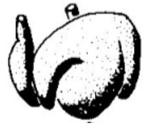
Digestive Strategies

		
Low intake **⇒ long passage**		
High intake **⇒ short passage**		

Digestive Strategies

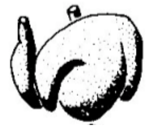
Low intake **⇒ long passage**	**Autoenzymatic digestion followed by thorough fermentative digestion** ✓	
High intake **⇒ short passage**		

Digestive Strategies



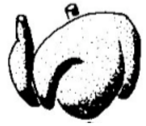
Low intake **⇒ long passage**	**Autoenzymatic digestion followed by thorough fermentative digestion** ✓	
High intake **⇒ short passage**	**Autoenzymatic digestion followed by cursory fermentative digestion** ✓	

Digestive Strategies

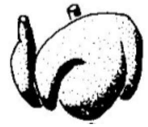
Low intake **⇒ long passage**	**Autoenzymatic digestion followed by thorough fermentative digestion ✓**	**Fermentative digestion followed by autoenzymatic digestion of products (and remains) ✓**
High intake **⇒ short passage**	**Autoenzymatic digestion followed by cursory fermentative digestion ✓**	

Digestive Strategies



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

Digestive Strategies

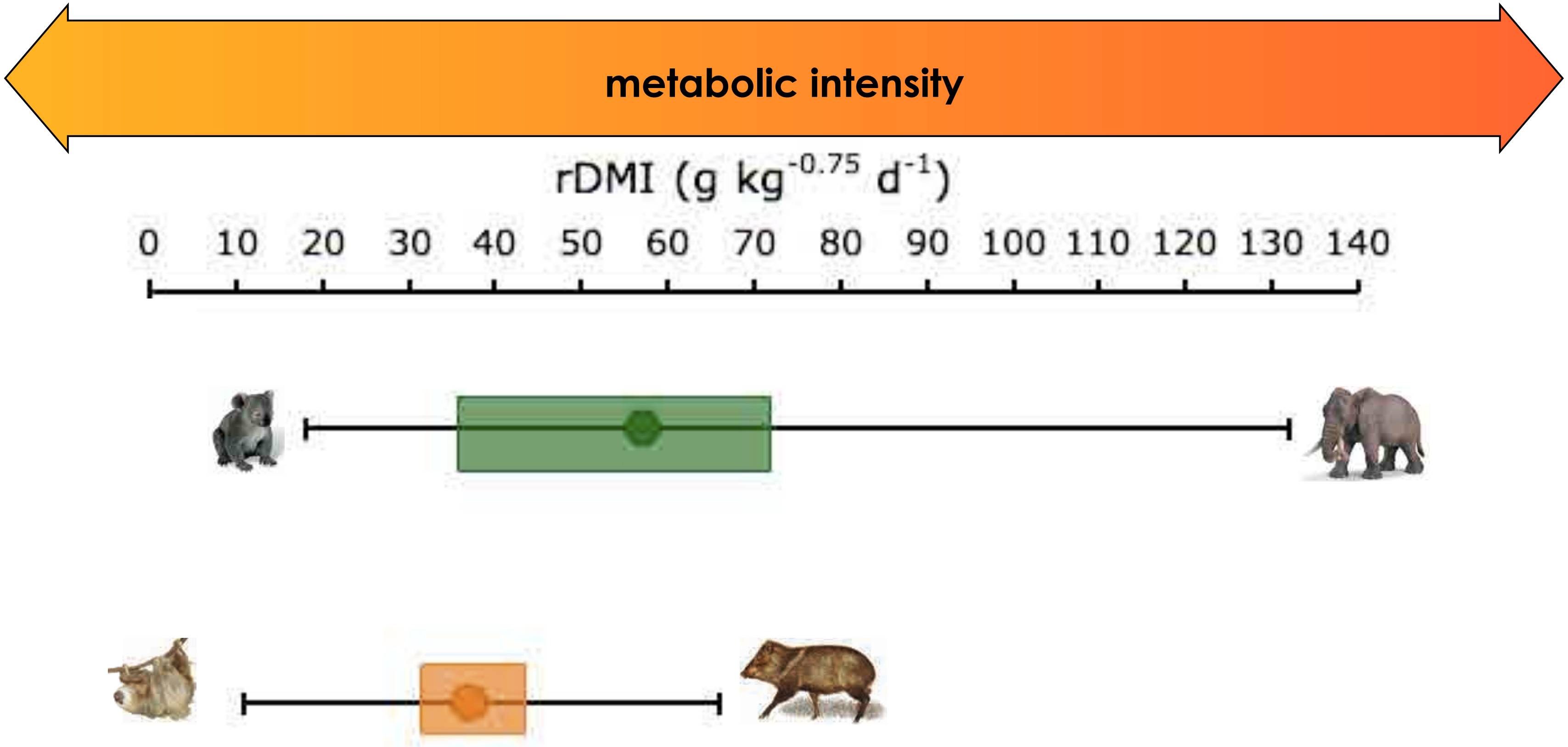
		
Low intake ⇒ long passage	**Autoenzymatic digestion followed by thorough fermentative digestion** ✓	**Fermentative digestion followed by autoenzymatic digestion of products (and remains)** ✓
High intake ⇒ short passage	**Autoenzymatic digestion followed by cursory fermentative digestion** ✓	~~*Cursory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

From Digestive to Metabolic Strategies

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

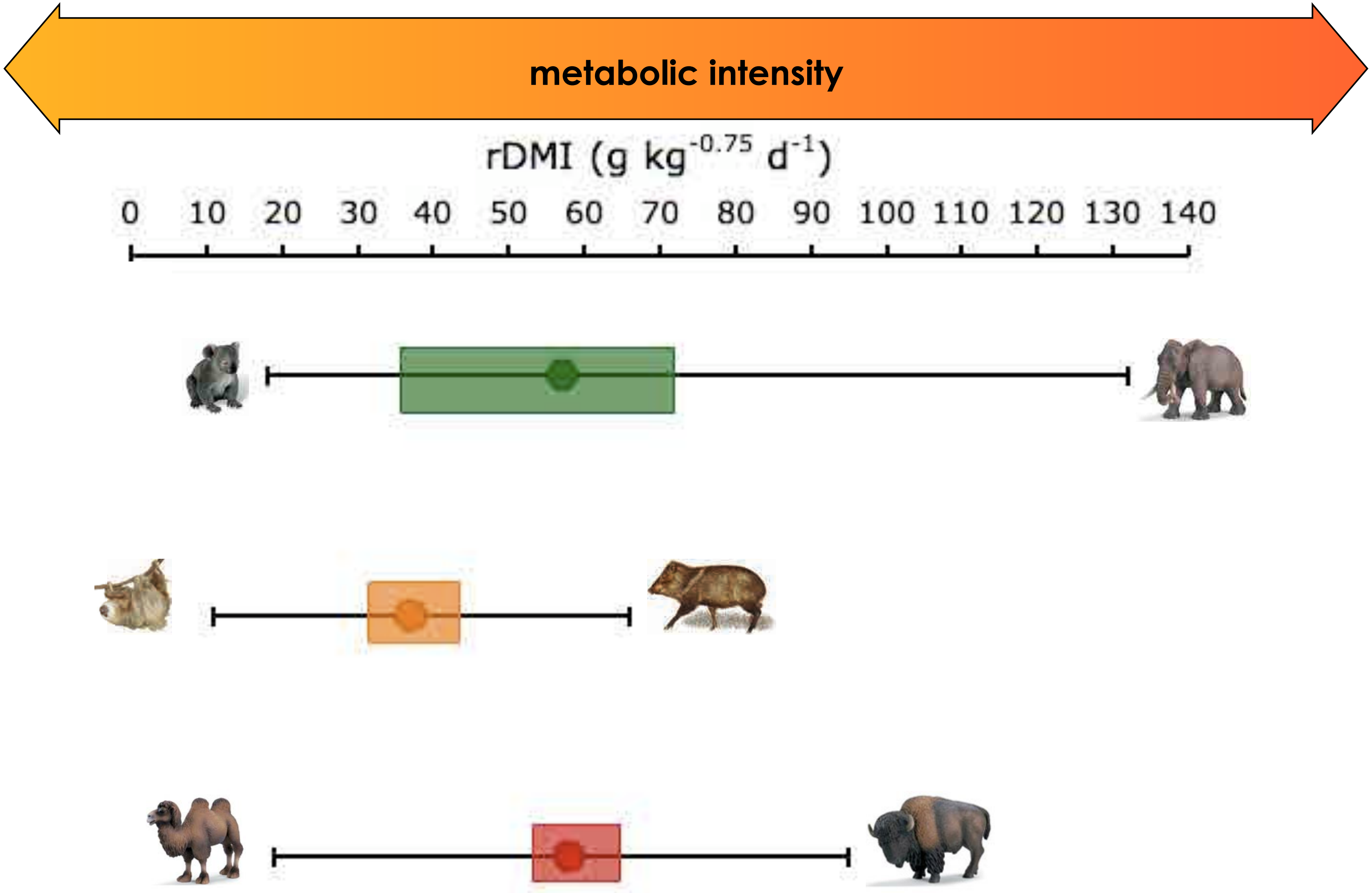
Herbivory
-
the ruminant revolution

Conceptualizing herbivore diversity



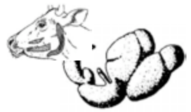
from Clauss et al. (2010)

Conceptualizing herbivore diversity

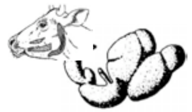


from Clauss et al. (2010)

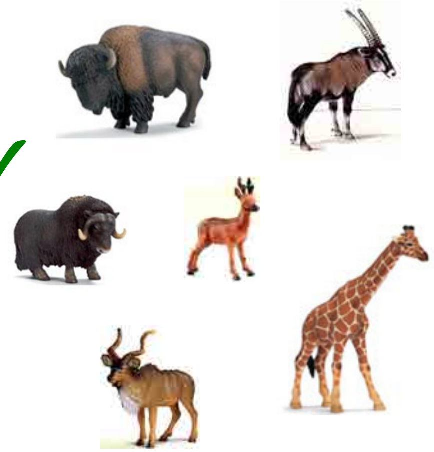
Digestive and Metabolic Strategies

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

Digestive and Metabolic Strategies

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

Digestive and Metabolic Strategies

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

Conceptualizing herbivore diversity

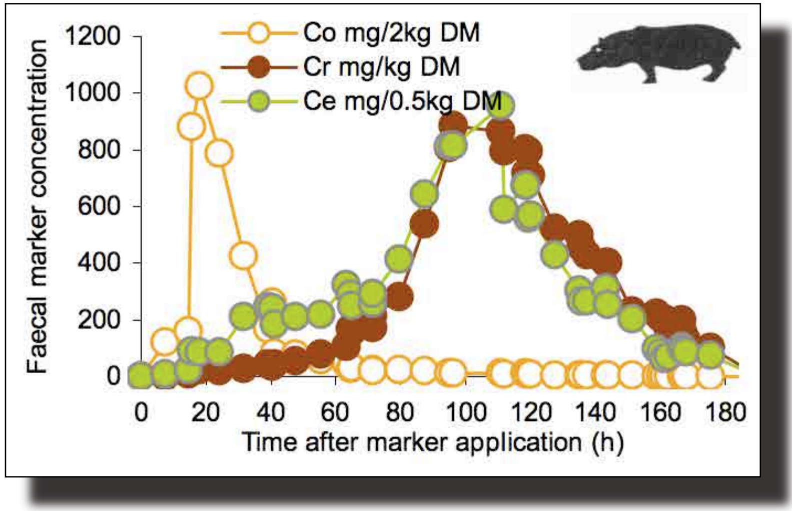
To achieve a high metabolic intensity, you need

- *a high food intake*

Sorting!

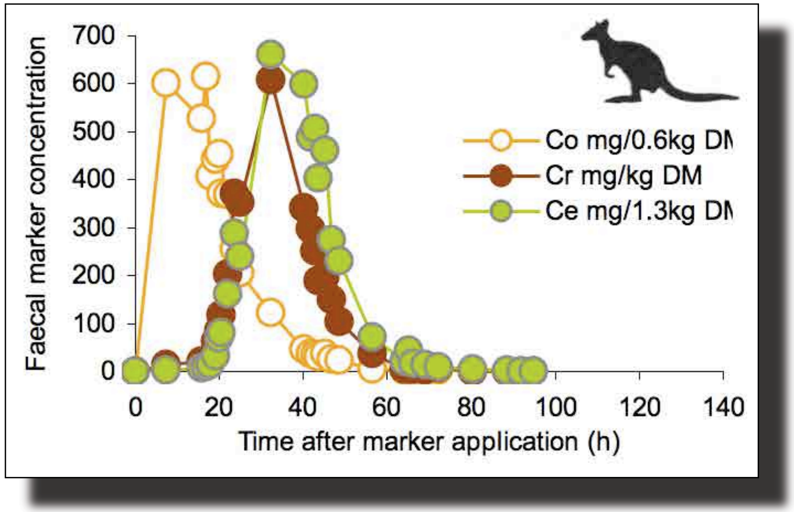
- *a high digestive efficiency*
  - *- long retention times*
  - *- intensive particle size reduction*
  - *- (high feeding selectivity)*

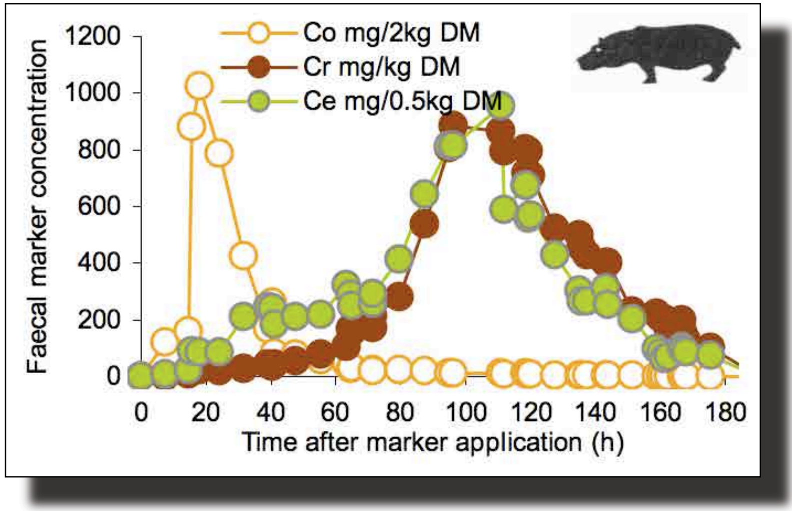
Ruminant vs. Nonruminant Foregut Fermentation



Schwarm et al. (2008)

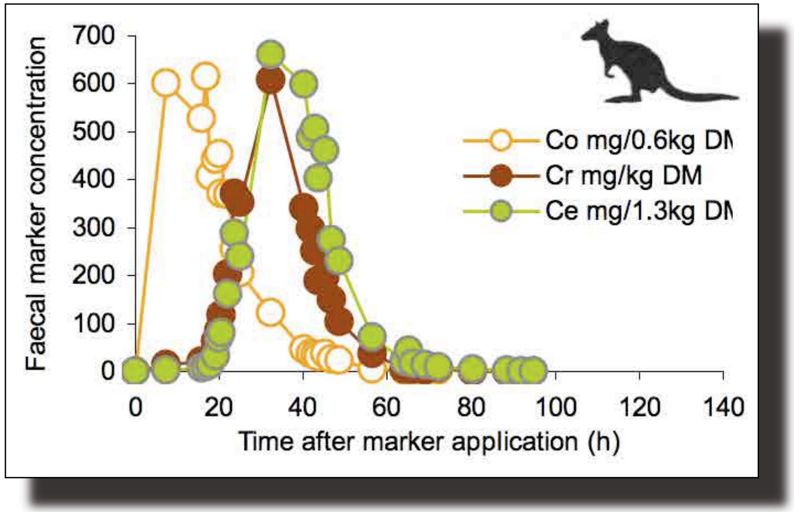
Ruminant vs. Nonruminant Foregut Fermentation

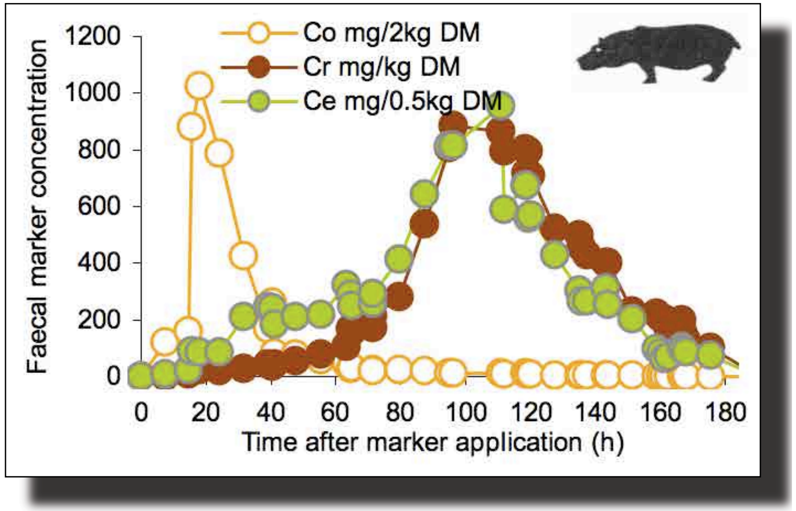




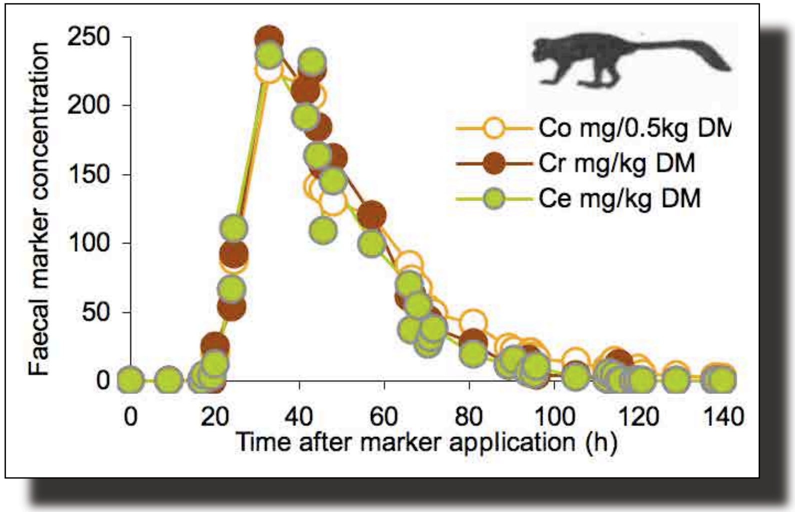
Schwarm et al. (2008,2009)

Ruminant vs. Nonruminant Foregut Fermentation

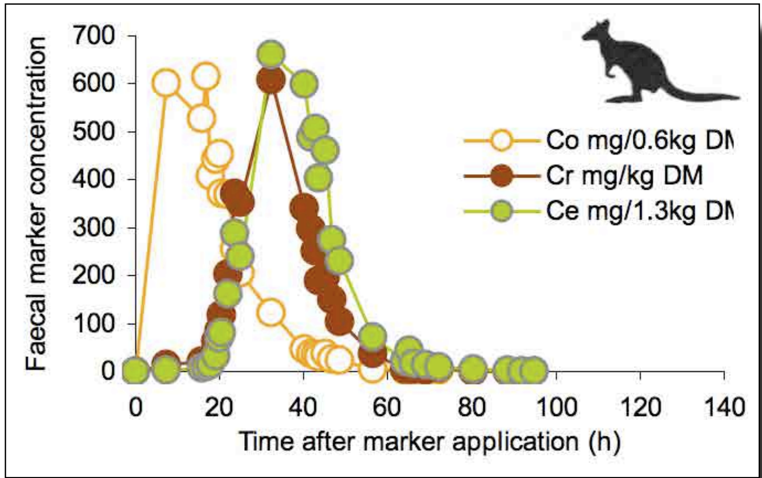


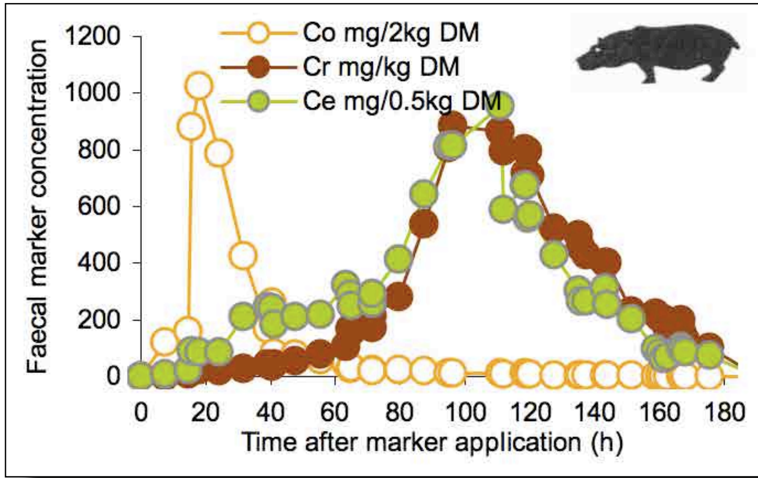


Schwarm et al. (2008,2009)

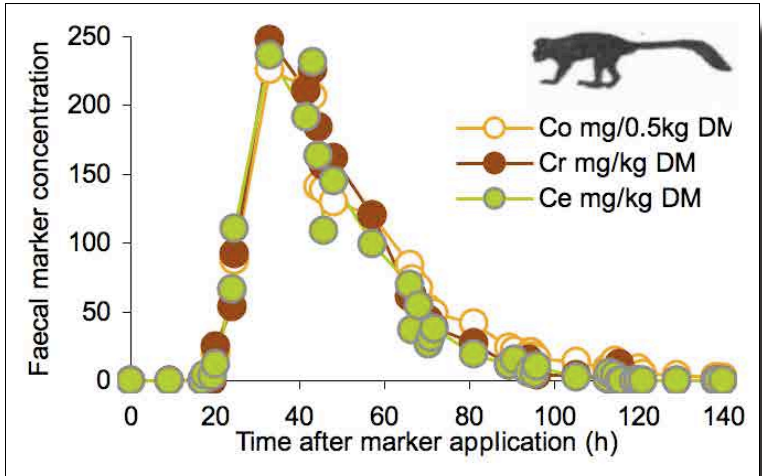


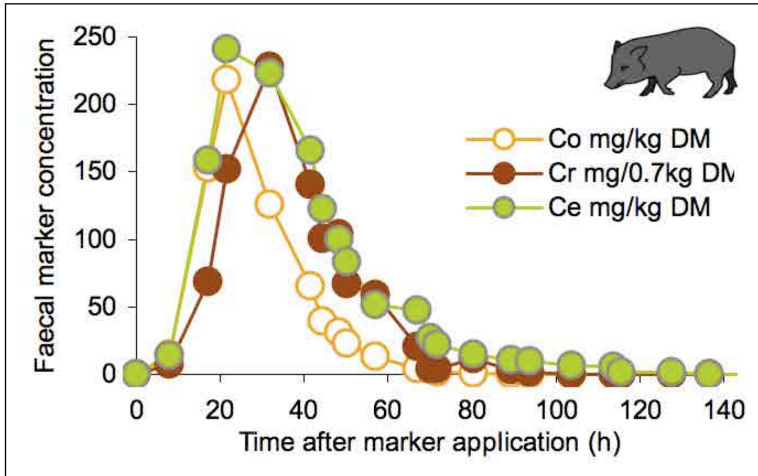
Ruminant vs. Nonruminant Foregut Fermentation



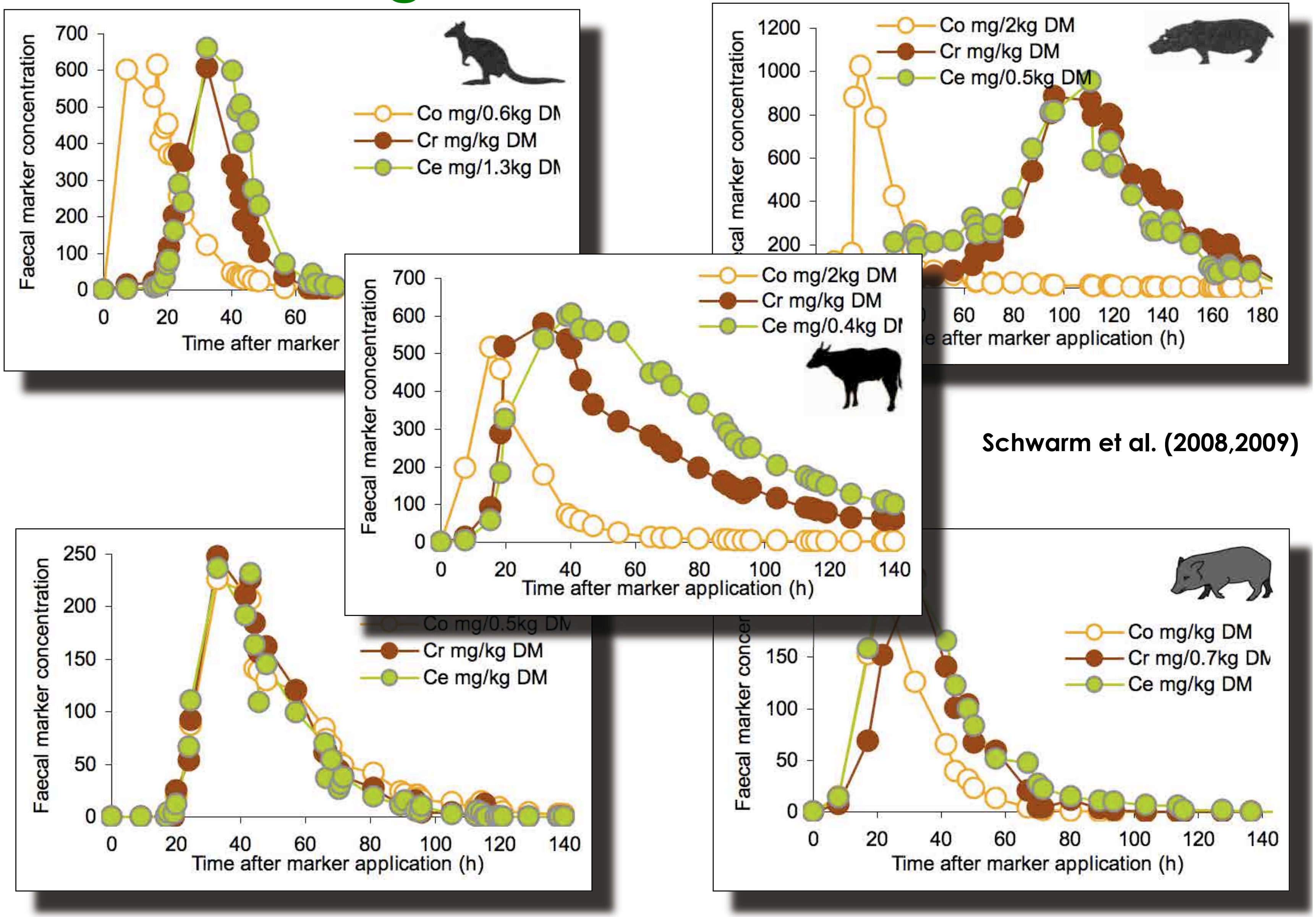


Schwarm et al. (2008,2009)



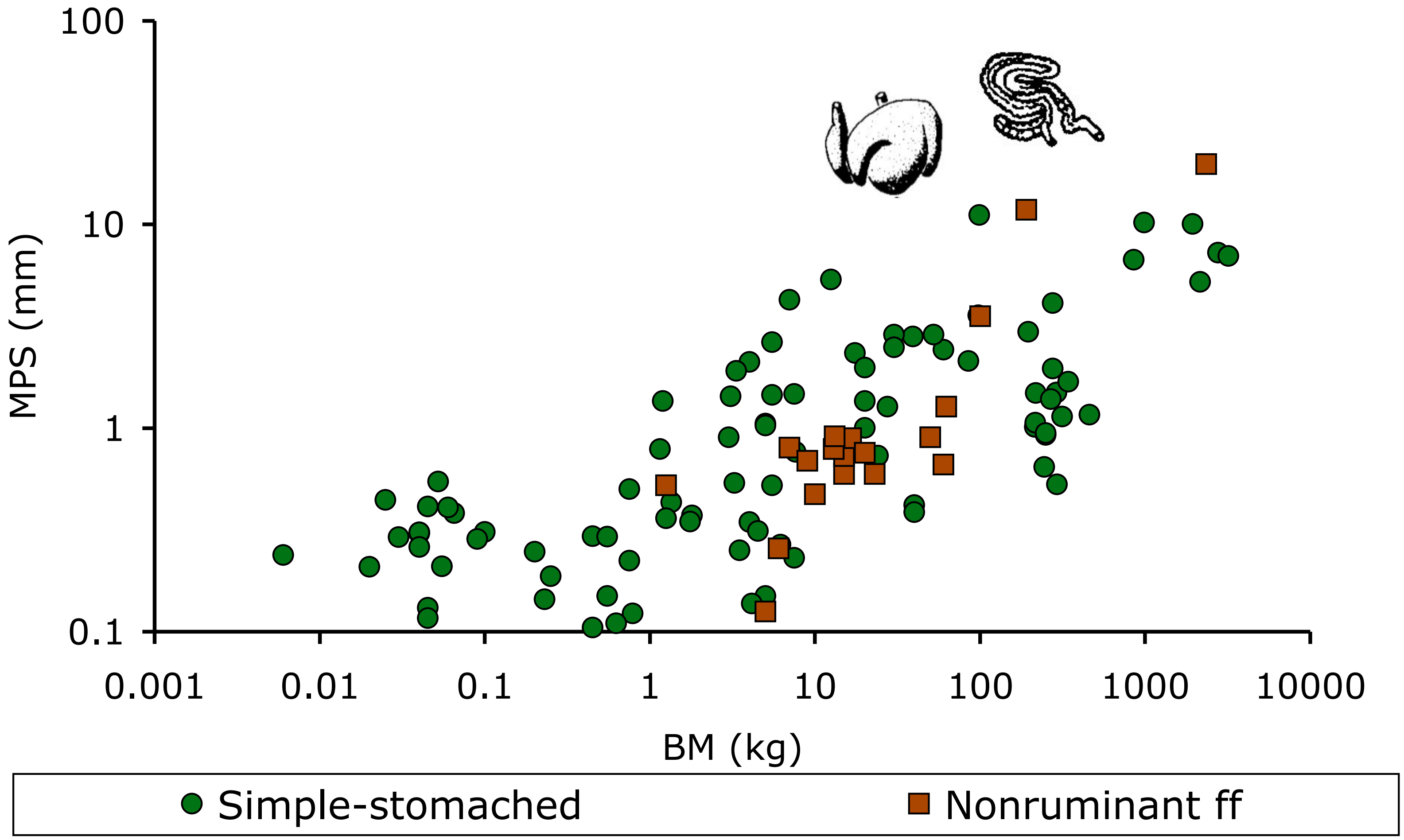


Ruminant vs. Nonruminant Foregut Fermentation



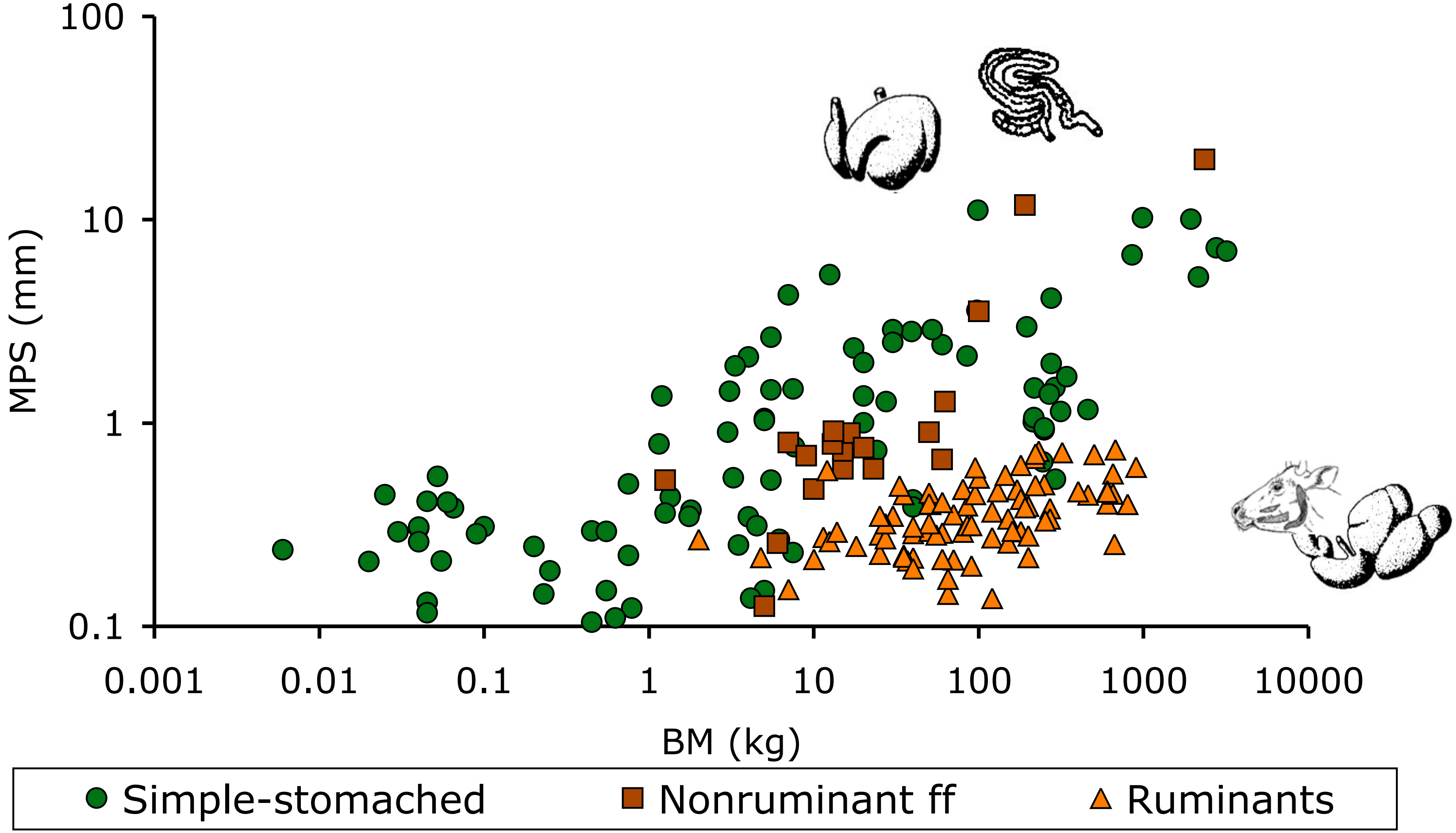
Schwarm et al. (2008,2009)

Ingesta particle size (chewing efficiency)



from Fritz et al. (2009)

Ingesta particle size (chewing efficiency)



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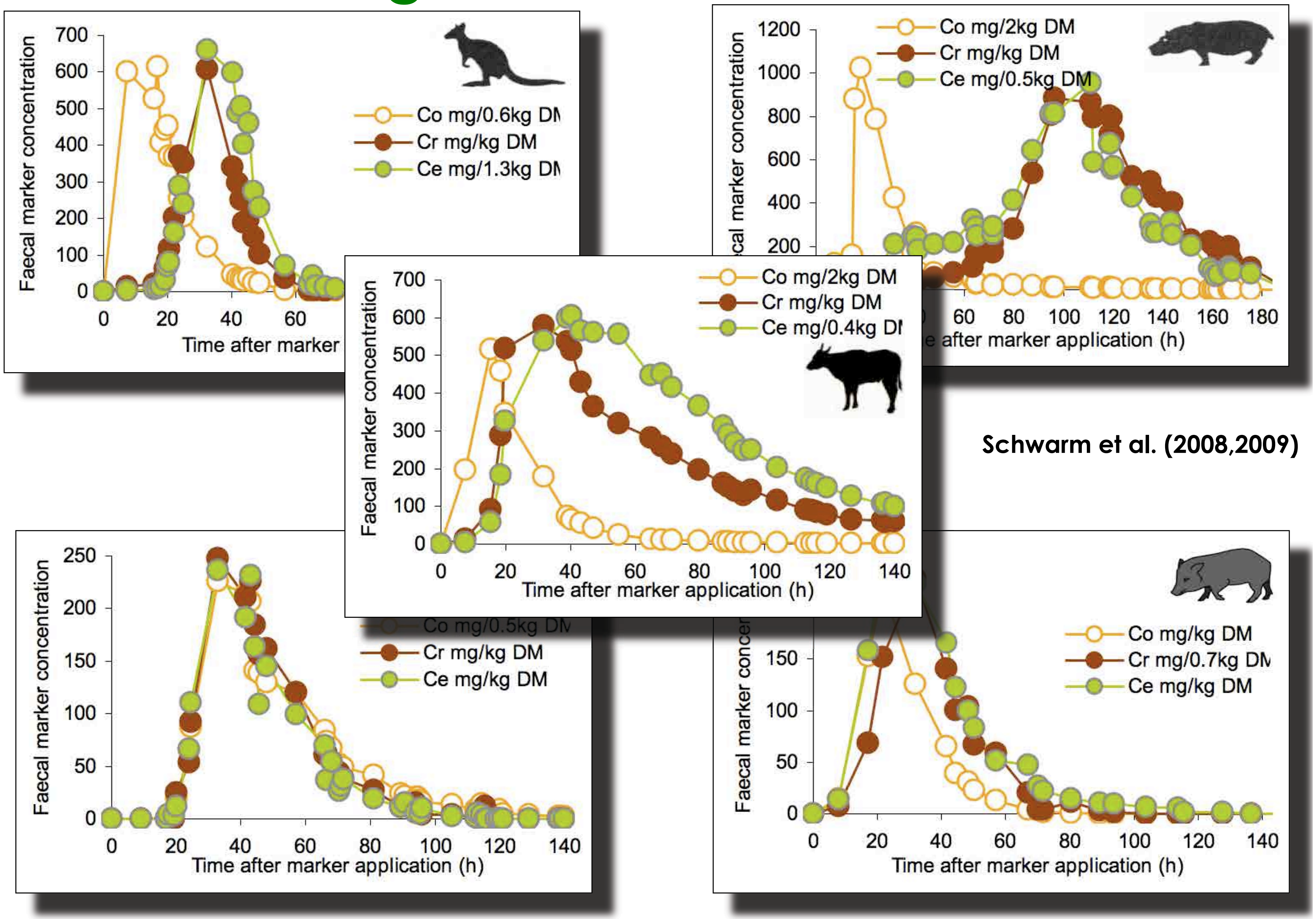
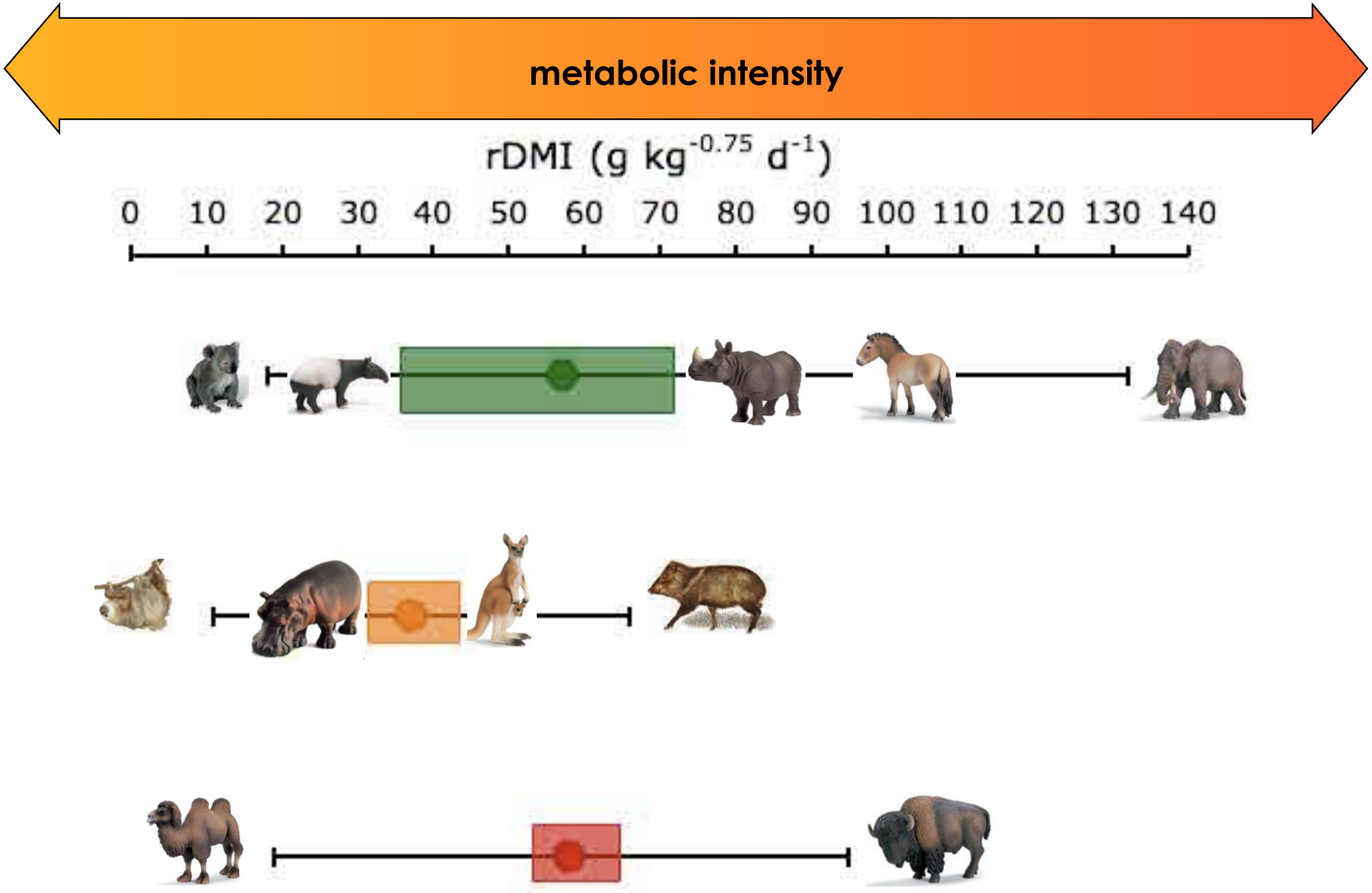
Ruminant vs. Nonruminant Foregut Fermentation



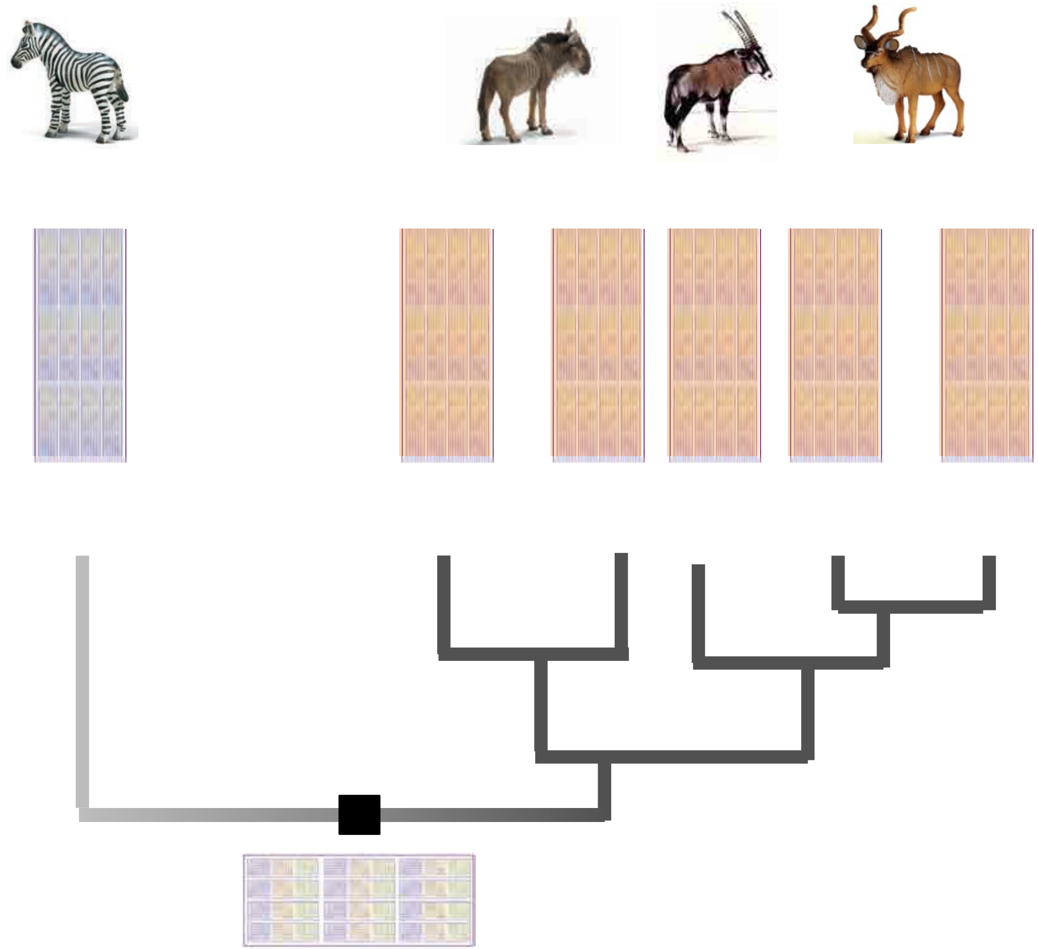
Schwarm et al. (2008,2009)

Conceptualizing herbivore diversity

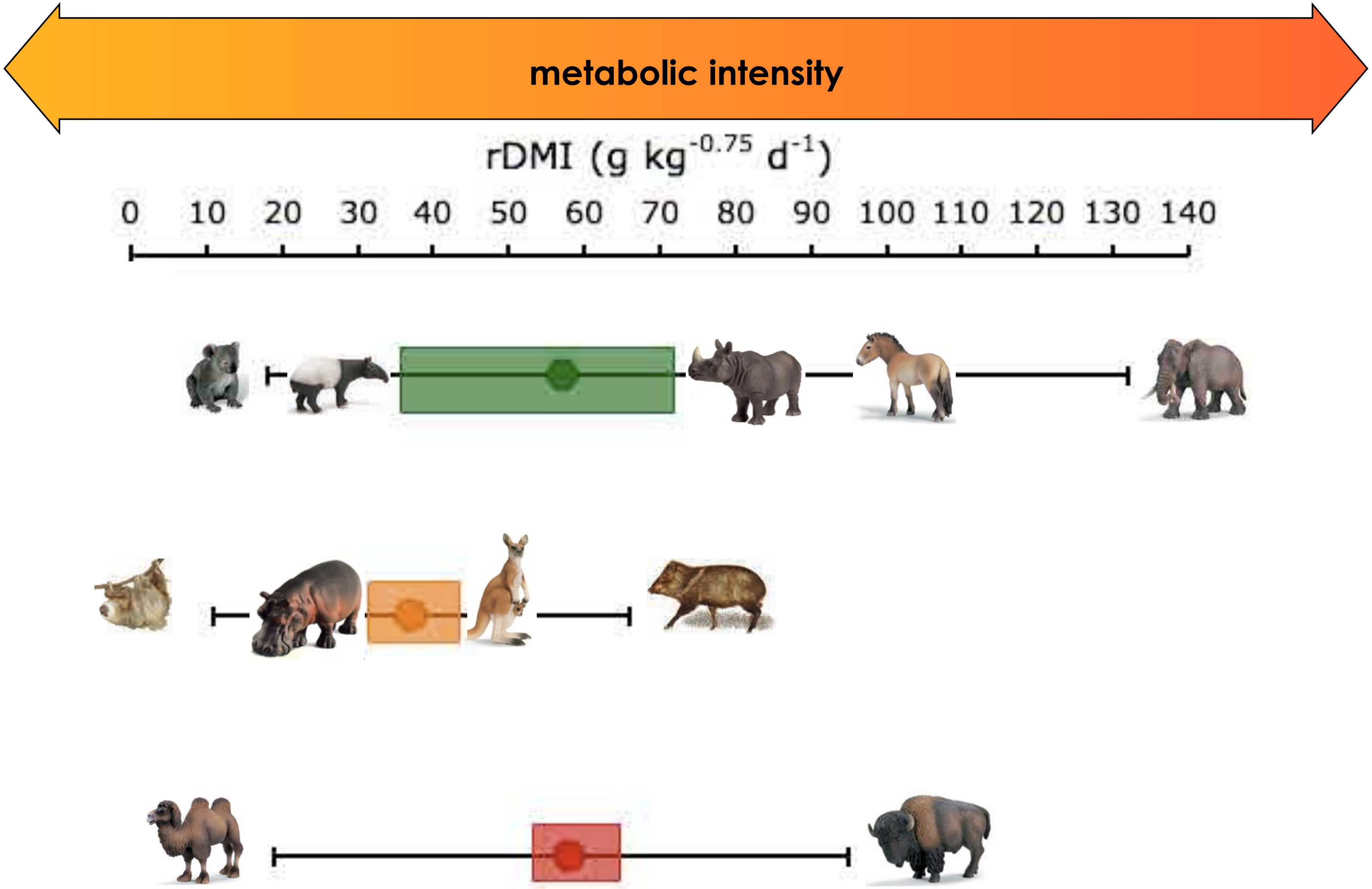


from Clauss et al. (2010)

Detailed function: solutions of different efficiency



Conceptualizing herbivore diversity



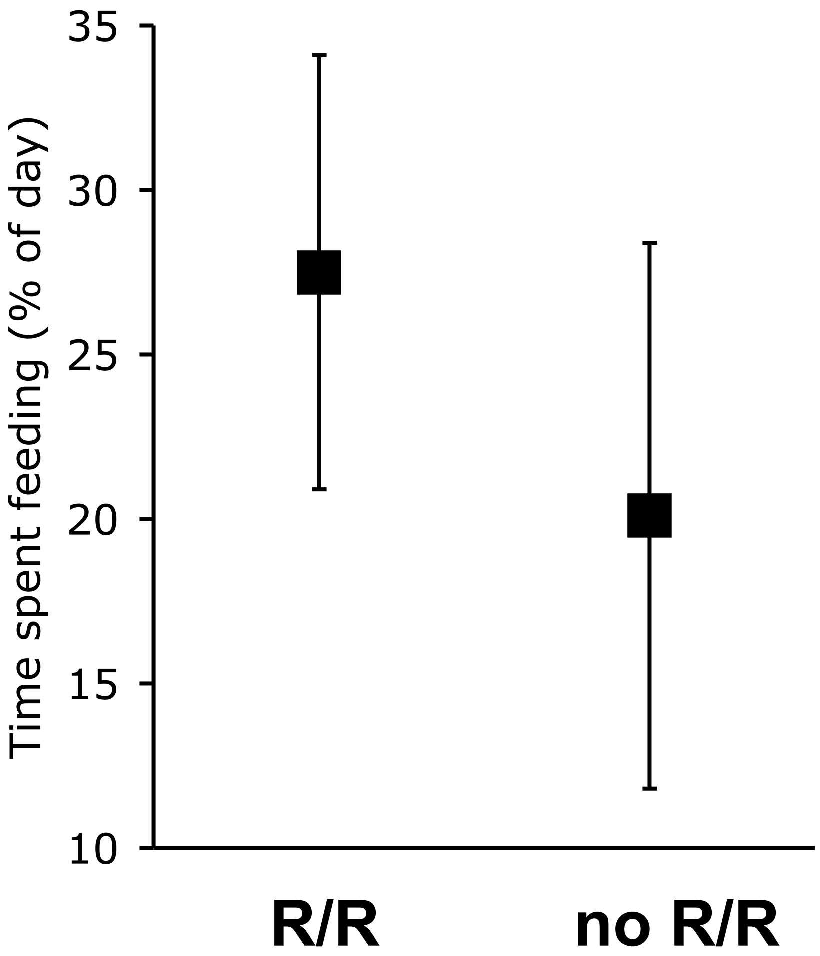
from Clauss et al. (2010)

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)

Summary I

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

Summary II

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

***thank you
for your attention***