



# Introduction to herbivore digestive physiology



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*Wildlife Digestive Physiology Vienna 2013*



University of Zurich  
Vetsuisse Faculty



Clinic  
of Zoo Animals, Exotic Pets and Wildlife



# A green world



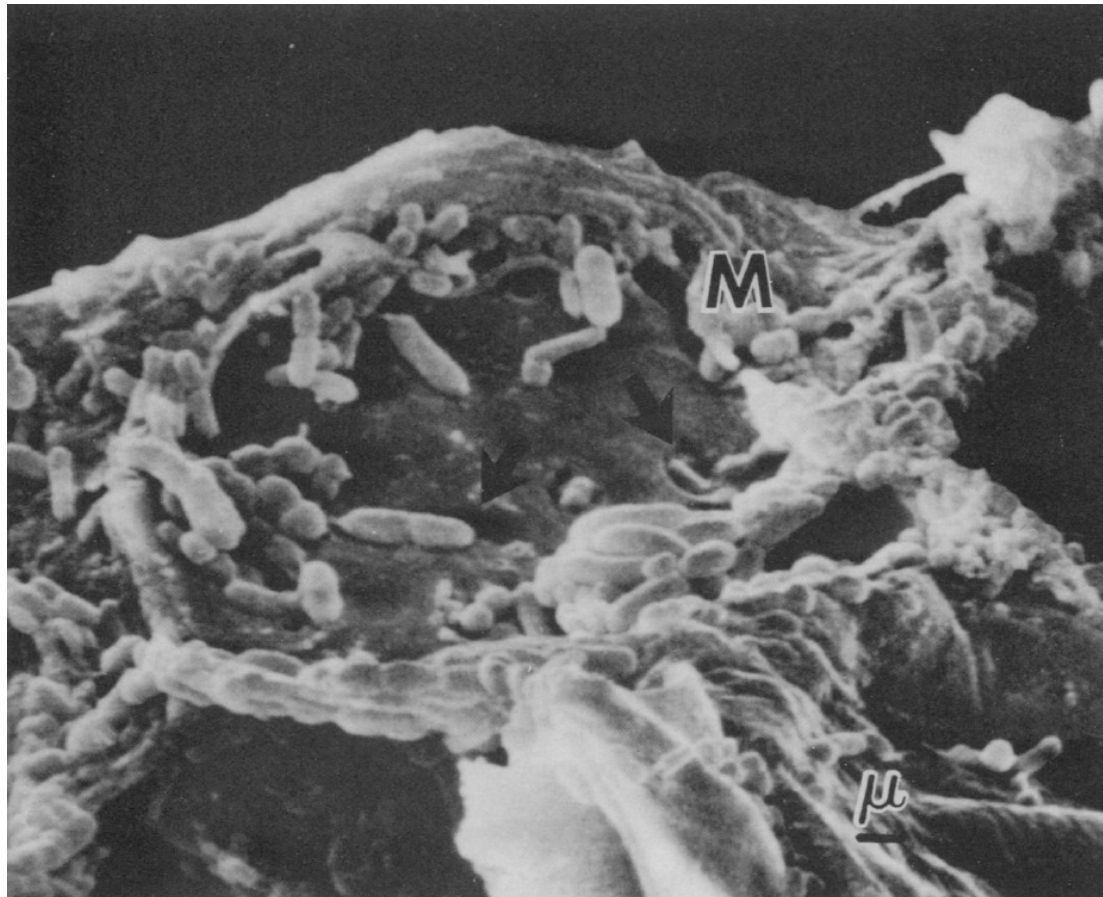


# Primary consumers





# Primary consumers

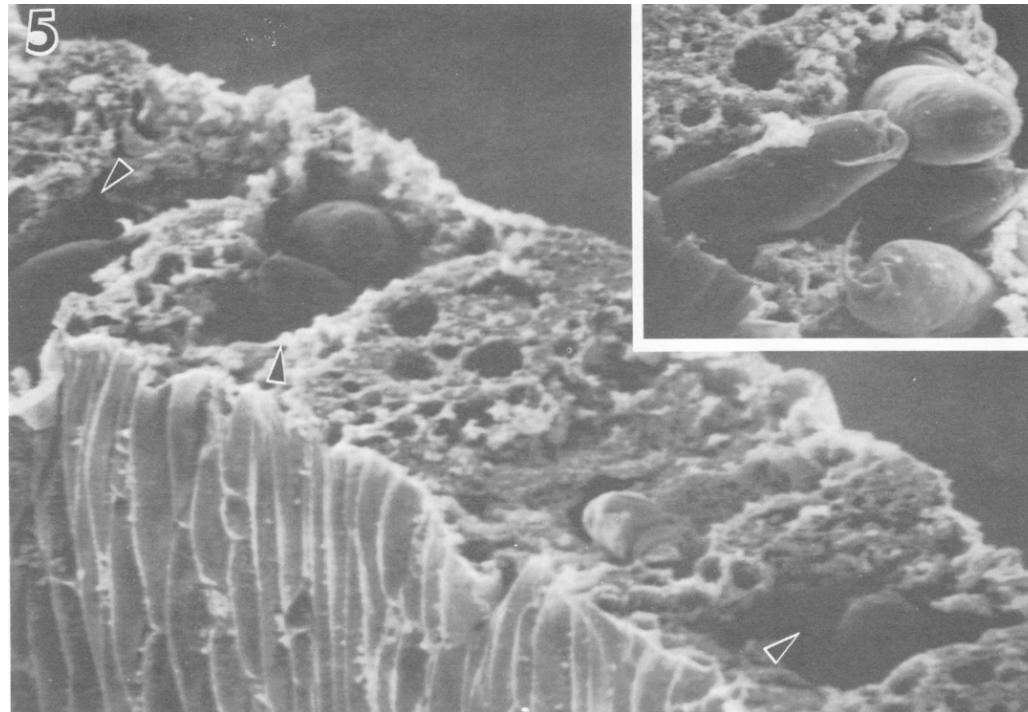


from Akin & Amos (1975)





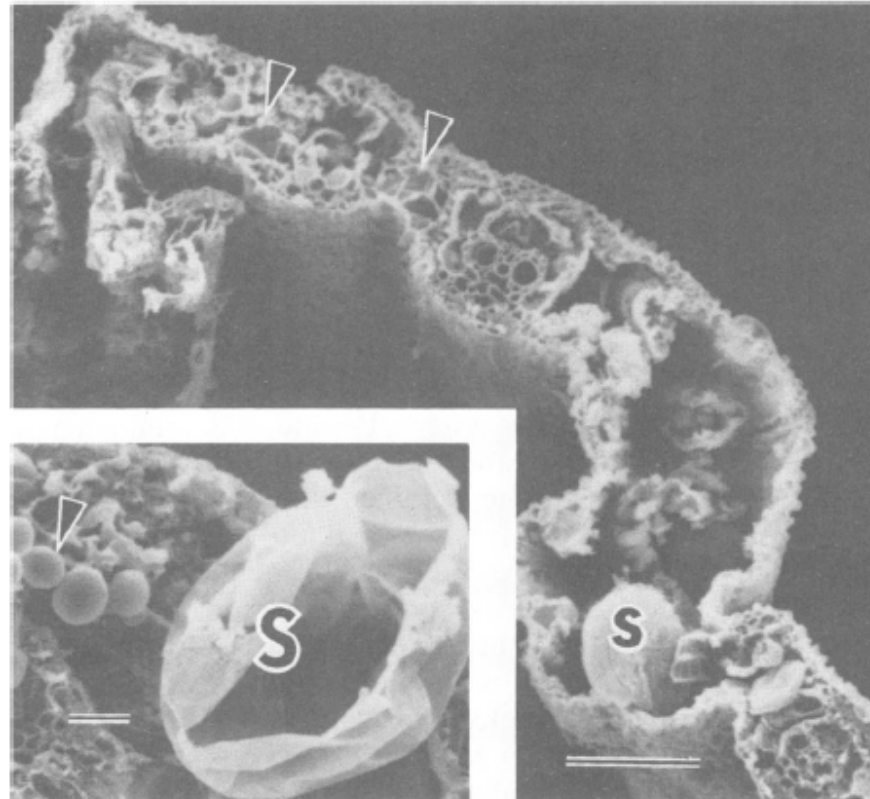
# Primary consumers



from Amos & Akin (1978)



# Primary consumers



from Akin & Benner (1988)



# Primary consumers





# Primary consumers





# Primary consumers







# Primary consumers







# Primary consumers





# Primary consumers







# Primary consumers





# Primary consumers







# Primary consumers







# Primary consumers







# Primary consumers







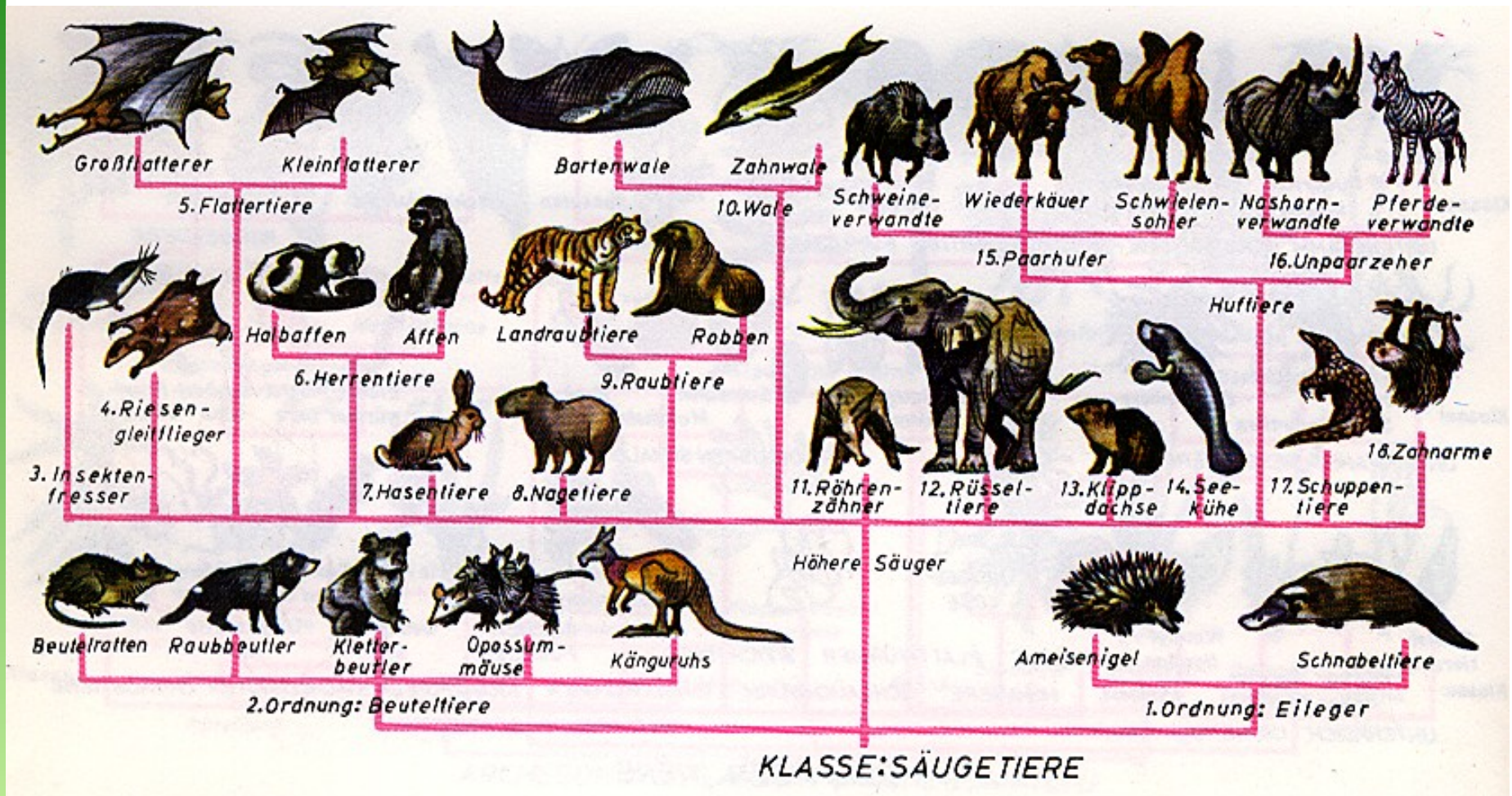
# Primary consumers







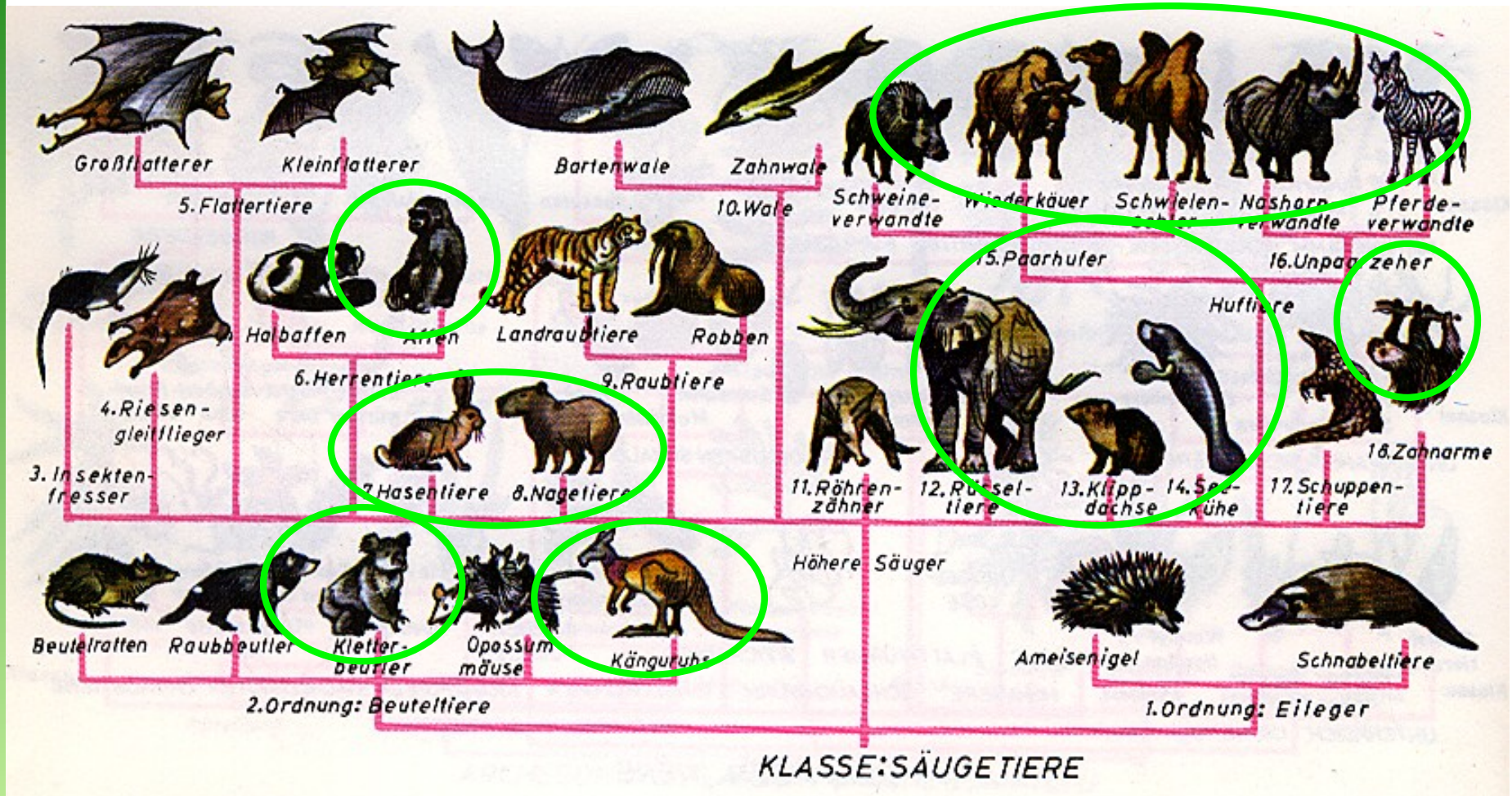
# Herbivory







# Herbivory





# Herbivory

- Vertebrates cannot digest plant fibre by their own enzymes (aut-enzymatically); they have to rely on symbiotic gut microflora (allo-enzymatic digestion).
- Bacterial digestion = ☐ Fermentation ☐
- The host has to supply this microflora with a habitat (so-called ☐ Fermentation chambers ☐).



## Carnivory ...

- ... *is no physiological challenge*
- ... *but a biomechanical and logistical one!*
- ***Digesting prey is easy - catching prey is the hard part!***



## Herbivory ...

- ... *is no logistical challenge*
- ... *but a digestive one!*
- ***Catching plants is easy - digesting plants is the hard part!***



# ***Food chains***

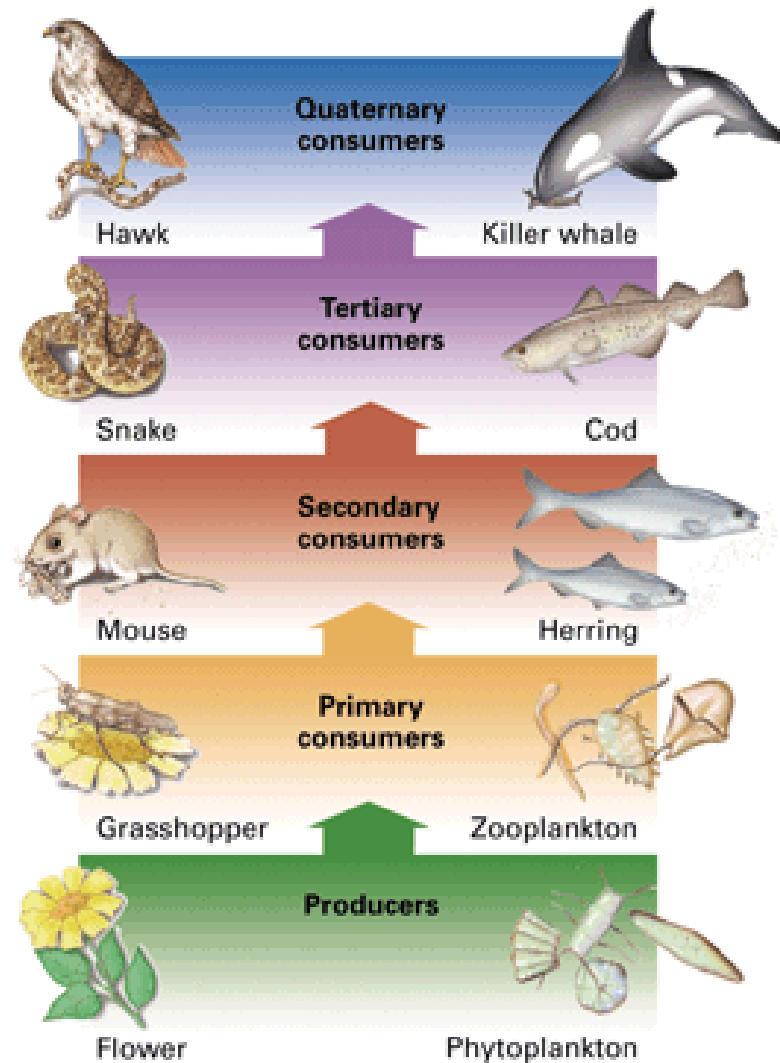




# Food chains

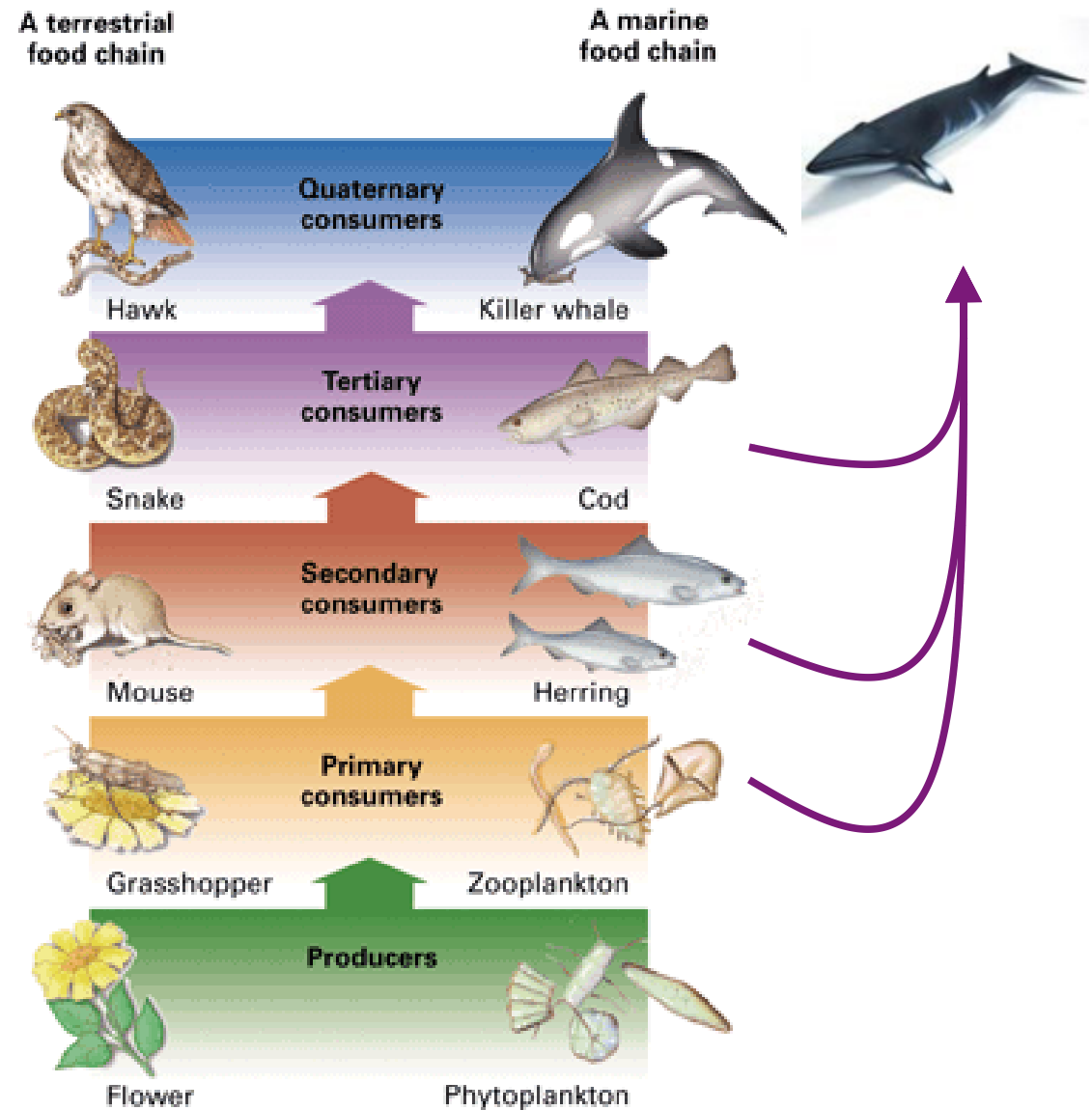
**A terrestrial food chain**

**A marine food chain**



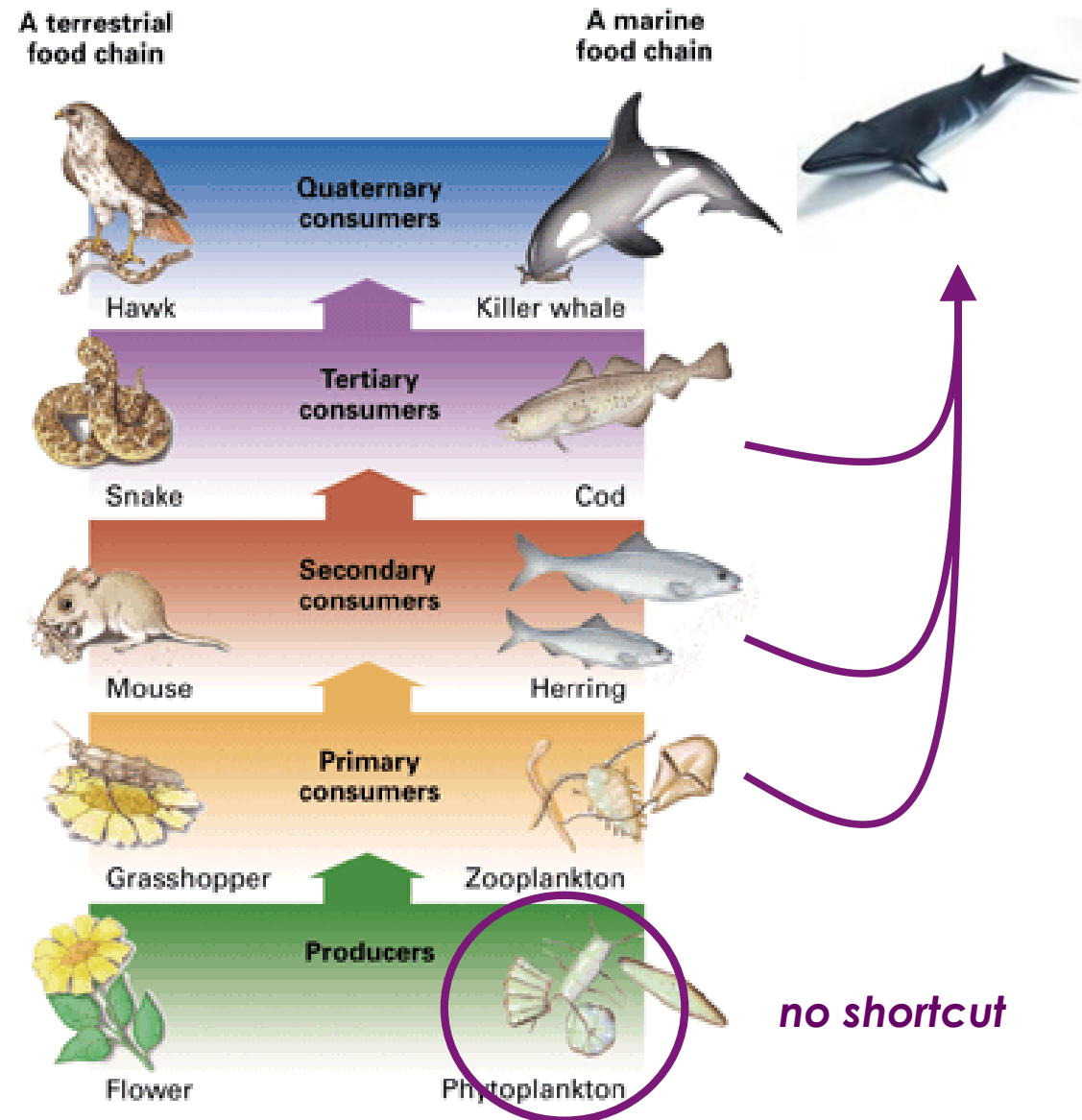


# Food chains - and shortcuts





# Food chains - and shortcuts



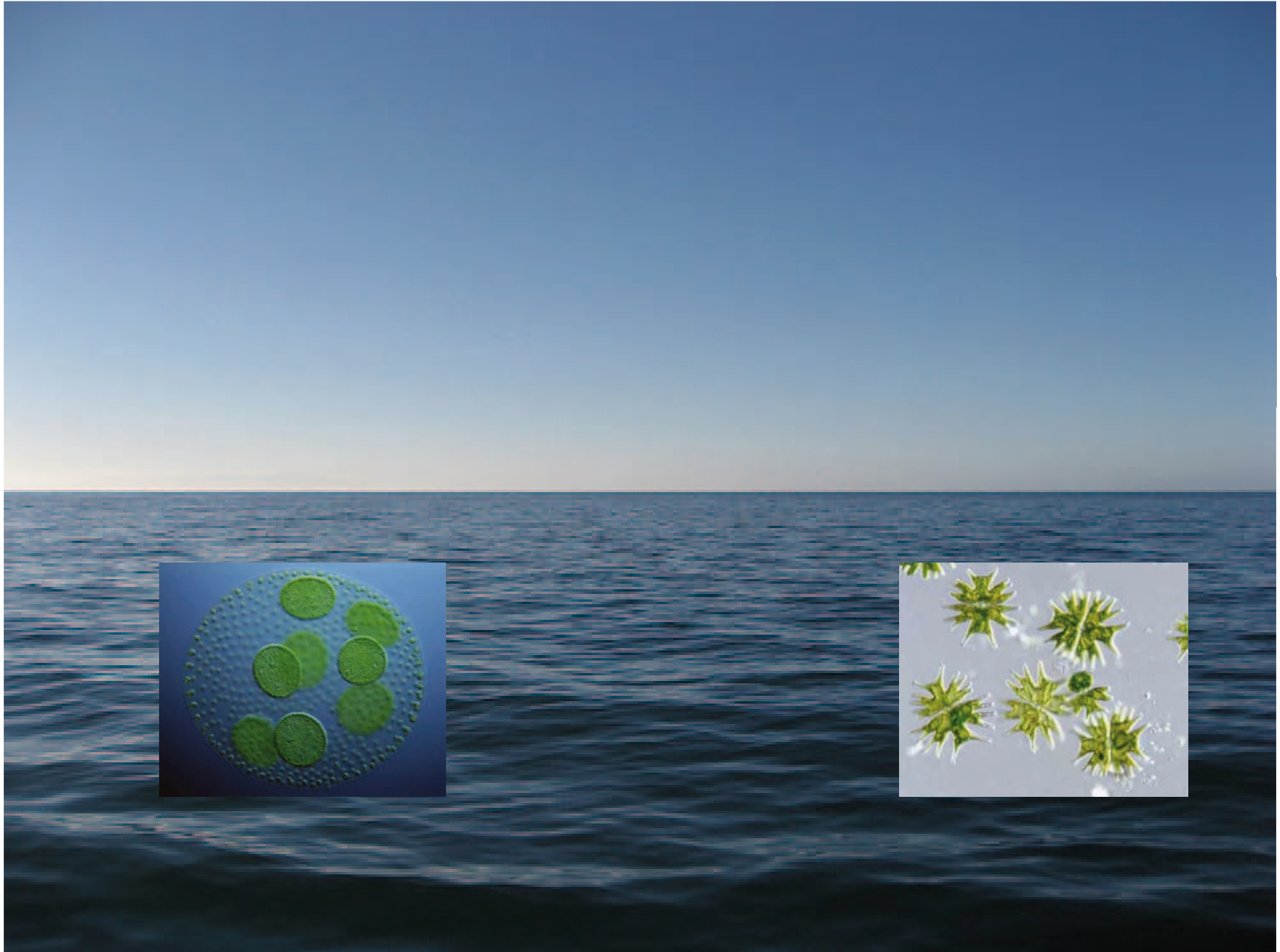


## Productive yet minute packages of plant food in marine systems





# Productive yet minute packages of plant food in marine systems





# Rare large marine herbivores





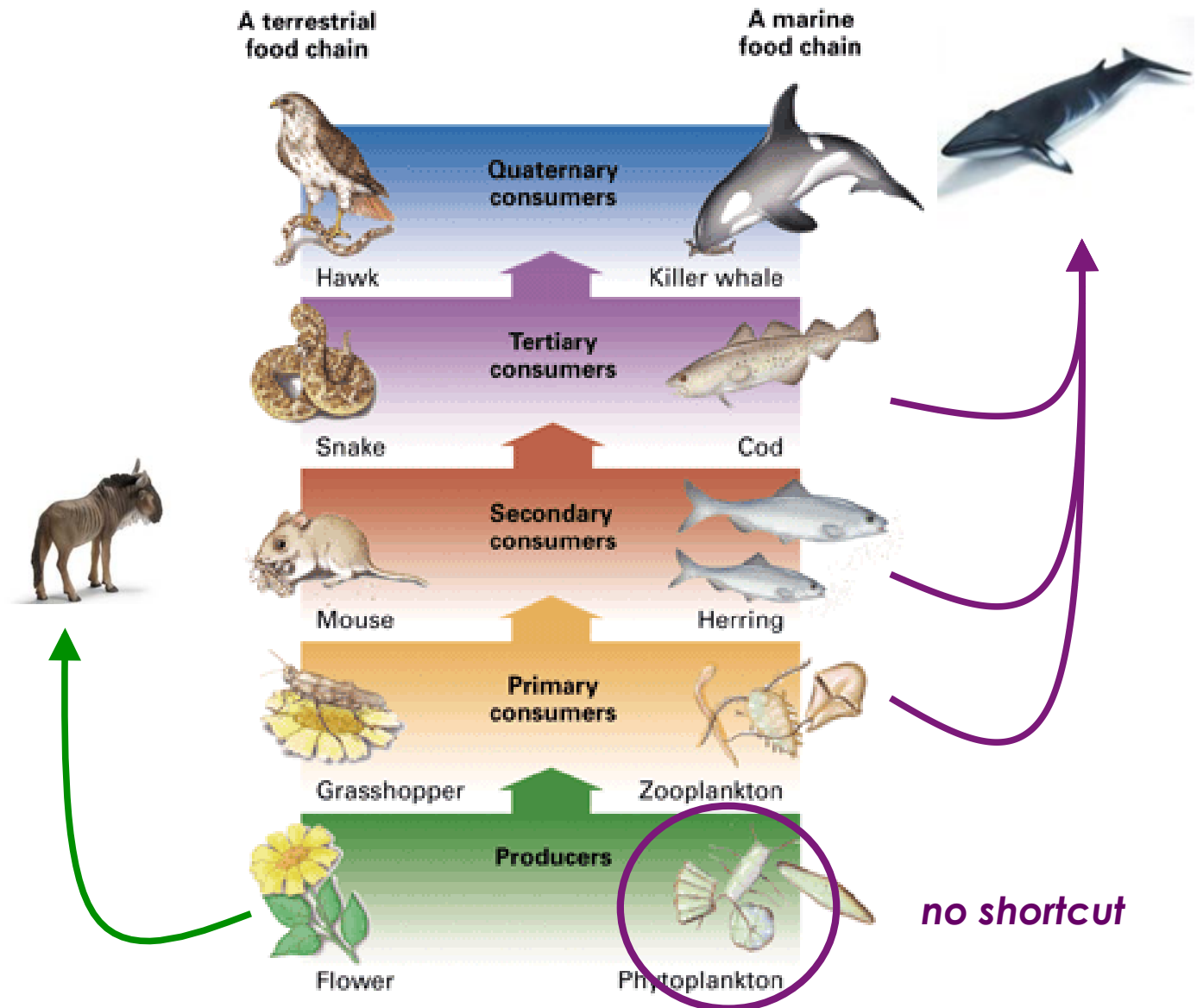


# Rare large marine herbivores





# Food chains - and shortcuts





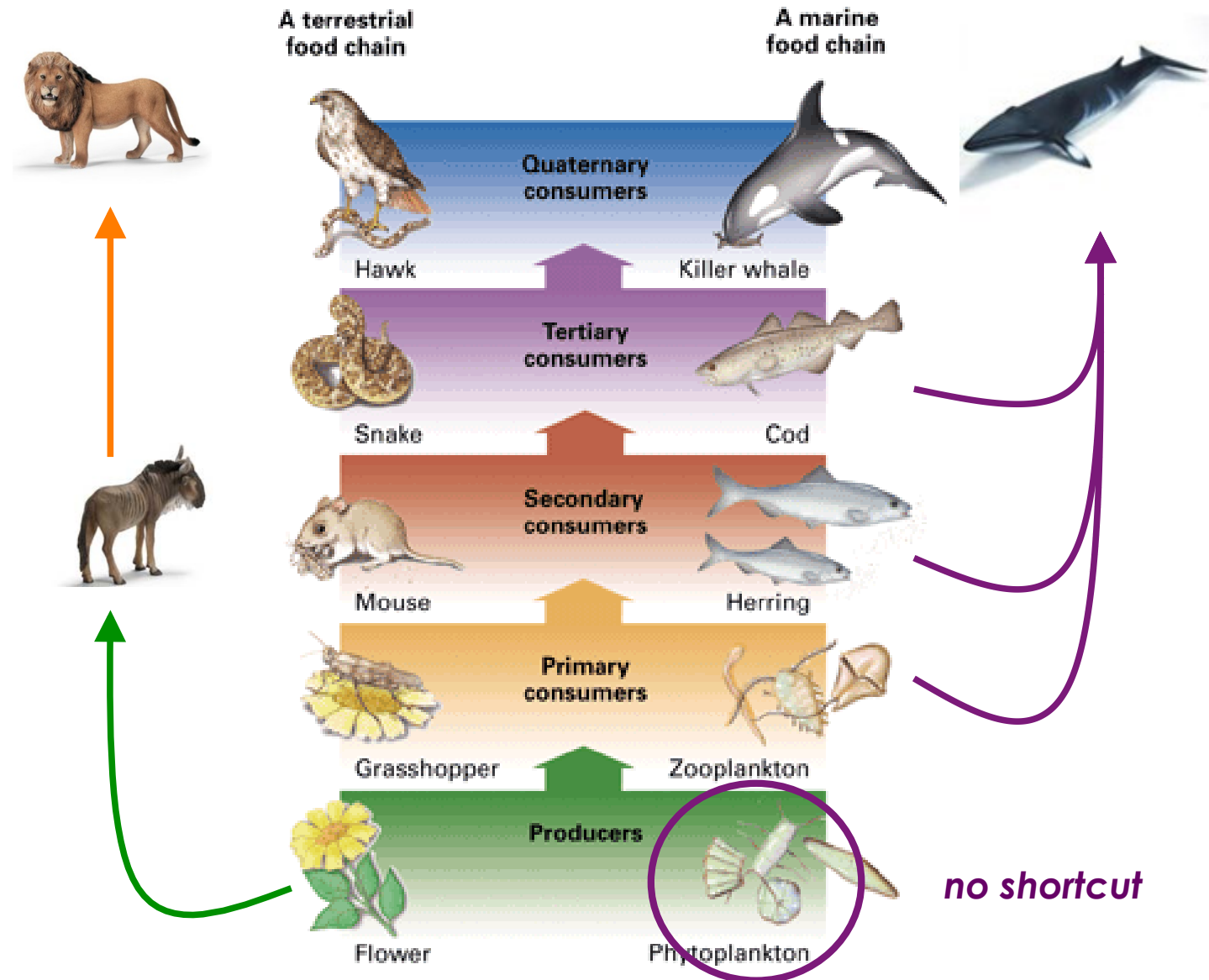
# Ubiquitous dense large packages of plant food in terrestrial systems





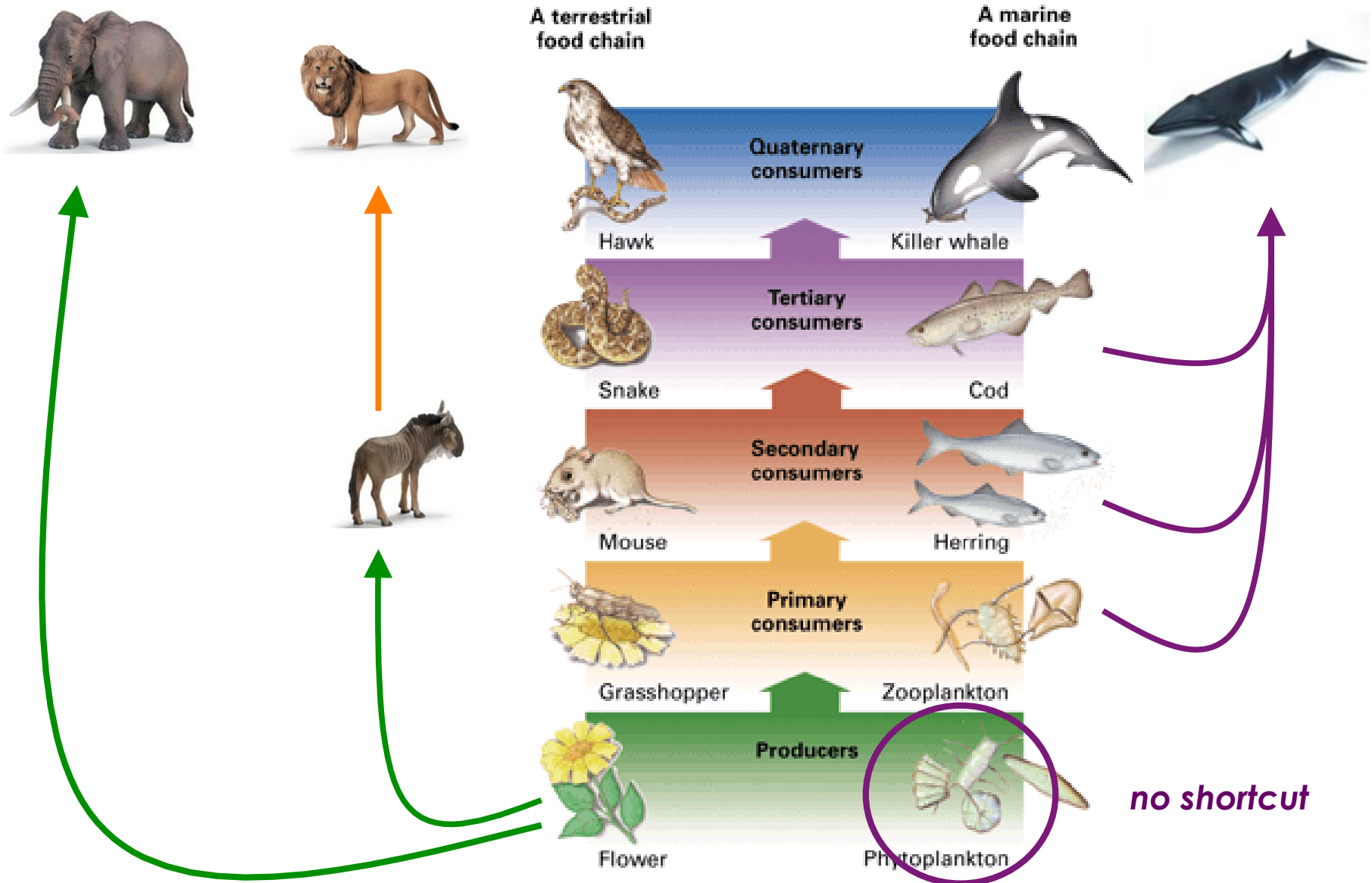


# Food chains - and shortcuts





# Food chains - and shortcuts





# *Herbivory*

-

## *Principles* *(fibre digestion)*



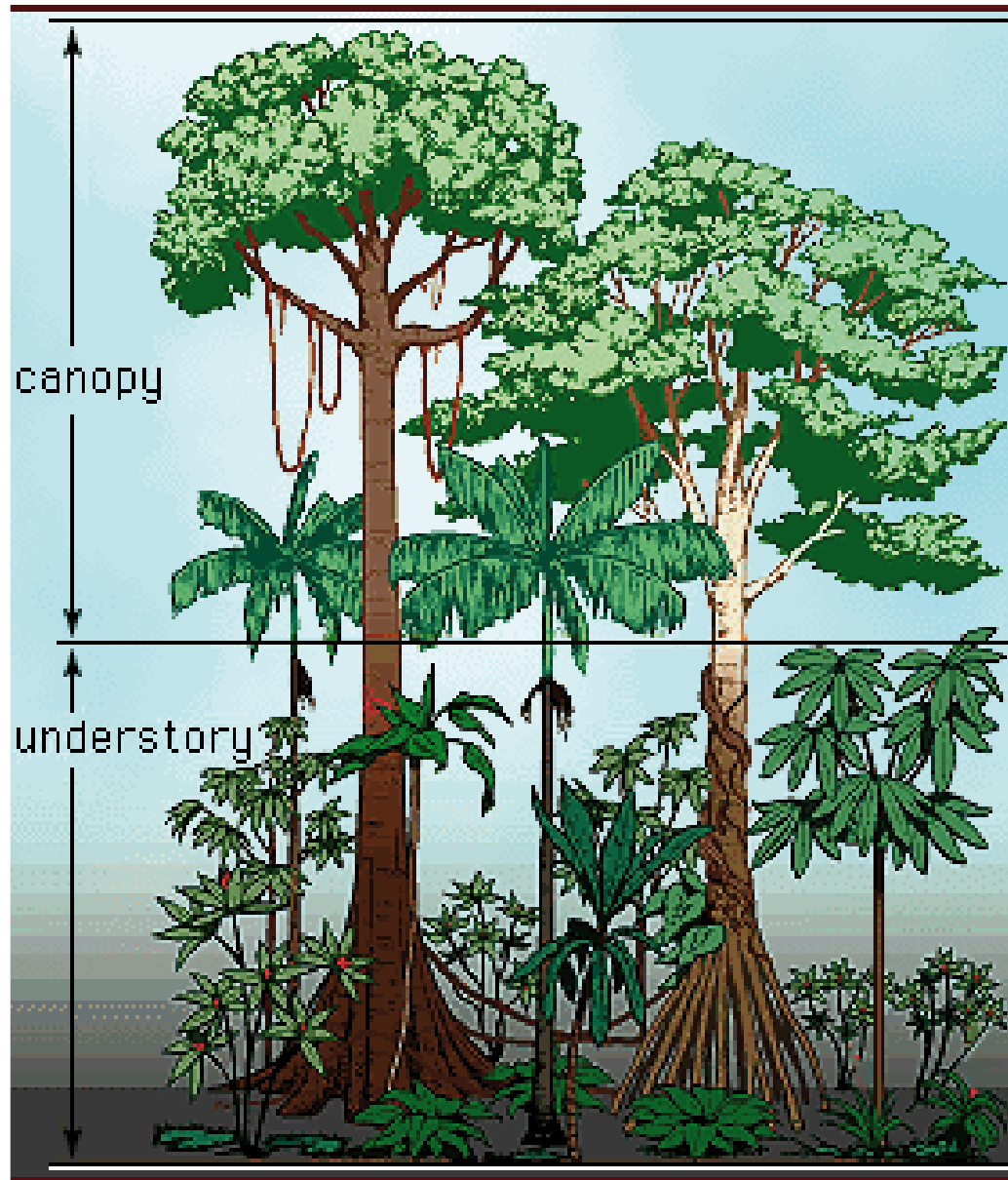


# Competition for light ...



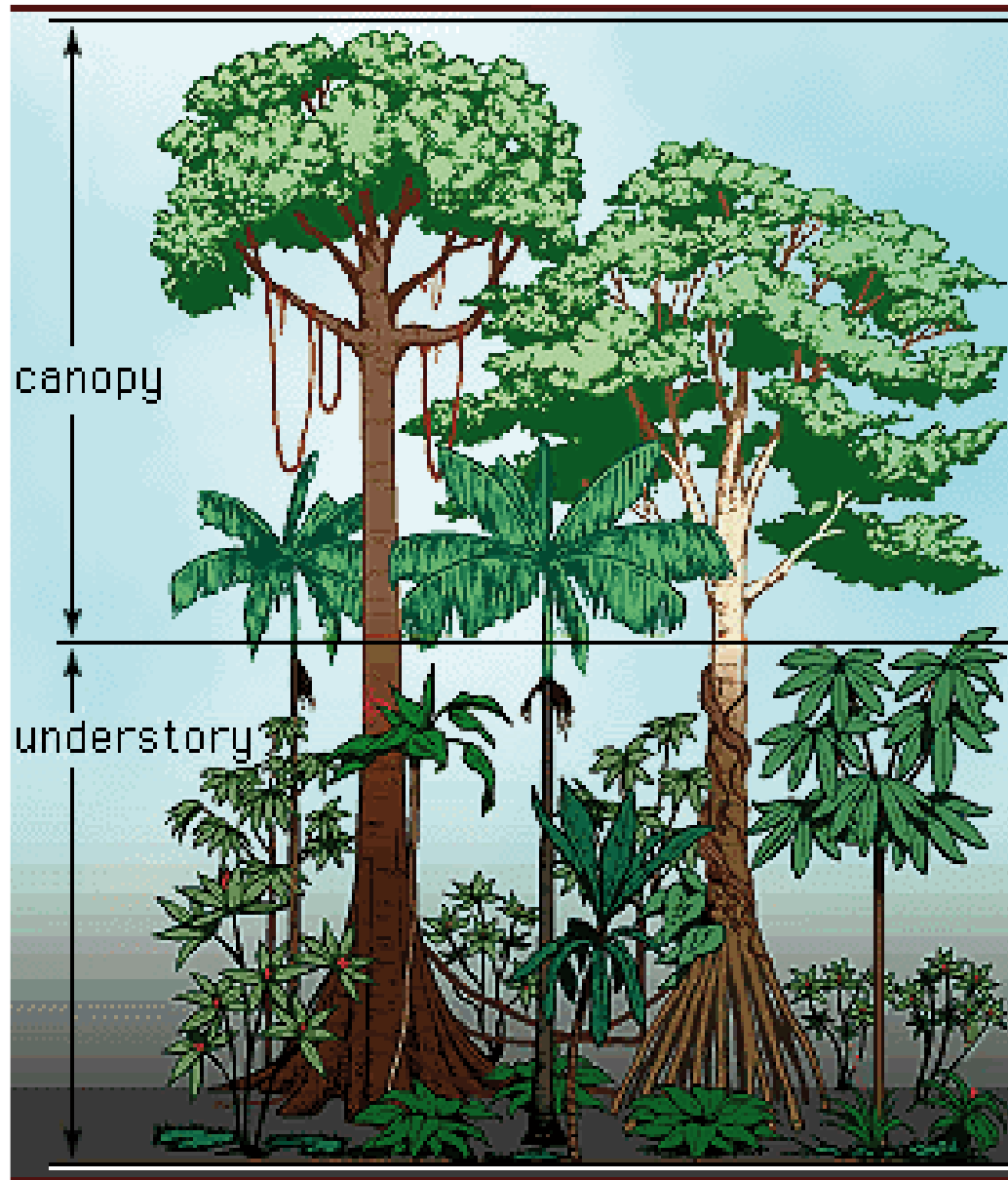


# Competition for light ...





# Competition for light ...

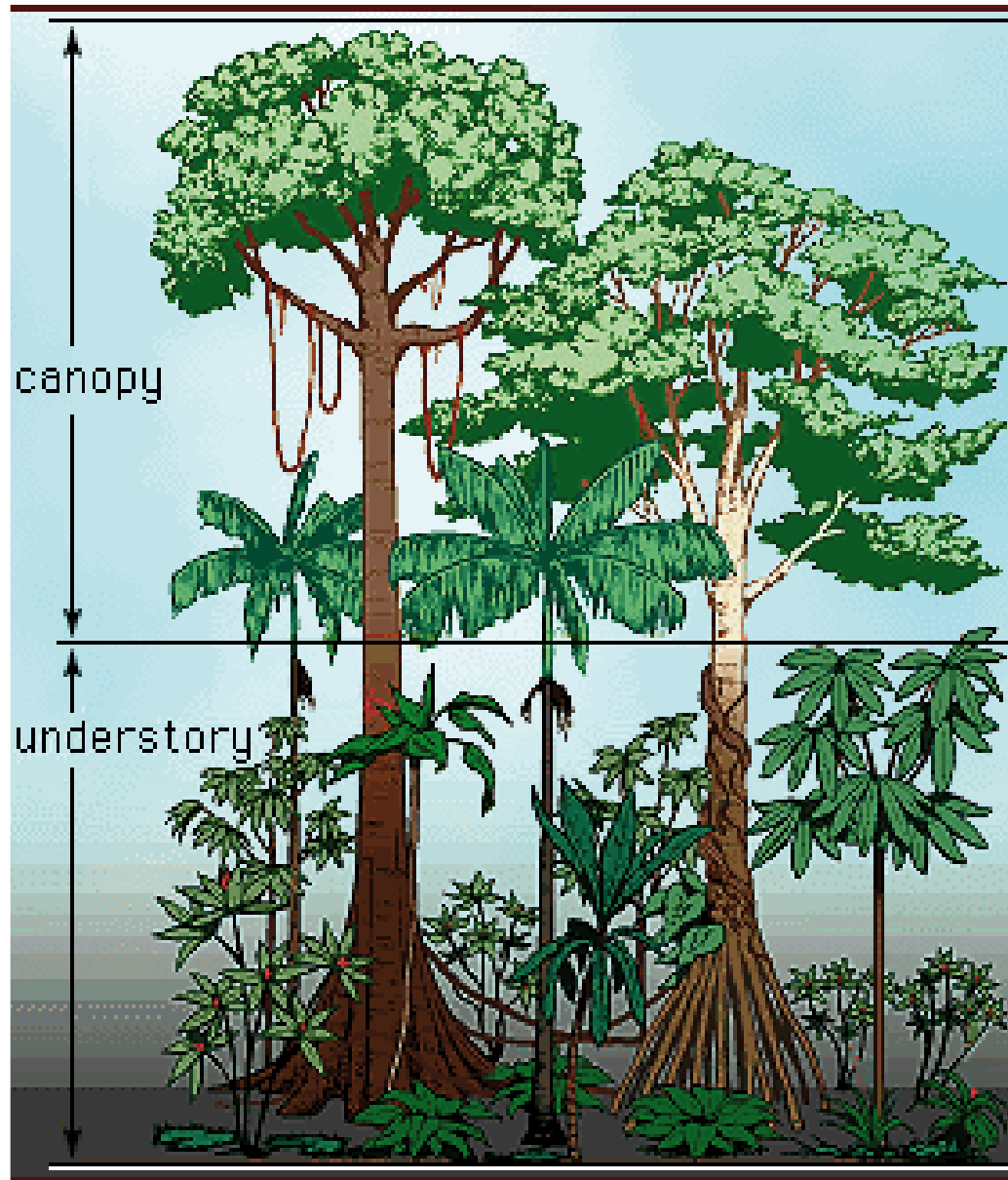


... results in a  
struggle against  
gravity in  
terrestrial  
systems:





# Competition for light ...

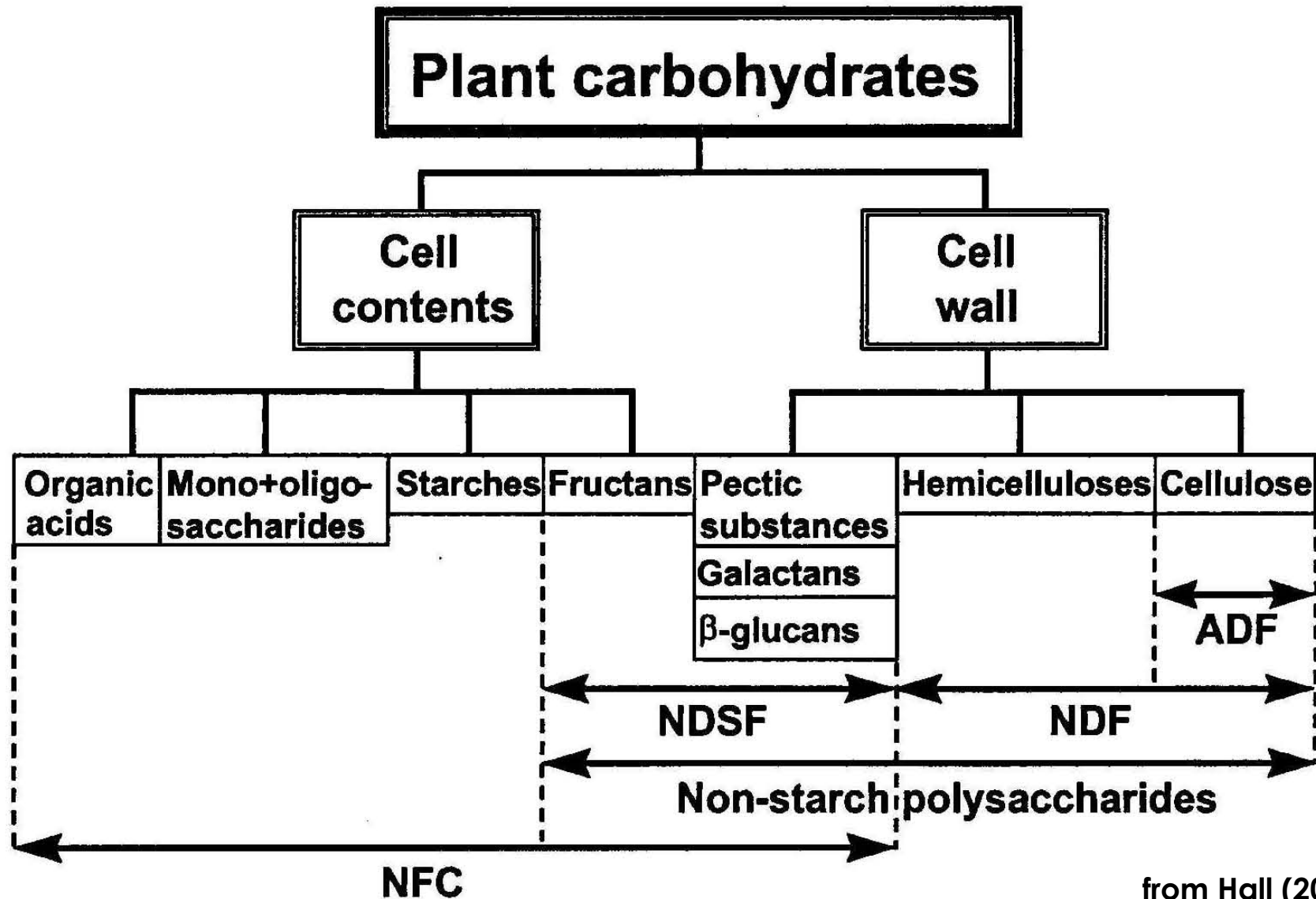


... results in a  
struggle against  
gravity in  
terrestrial  
systems:

the evolution of  
'fibre'



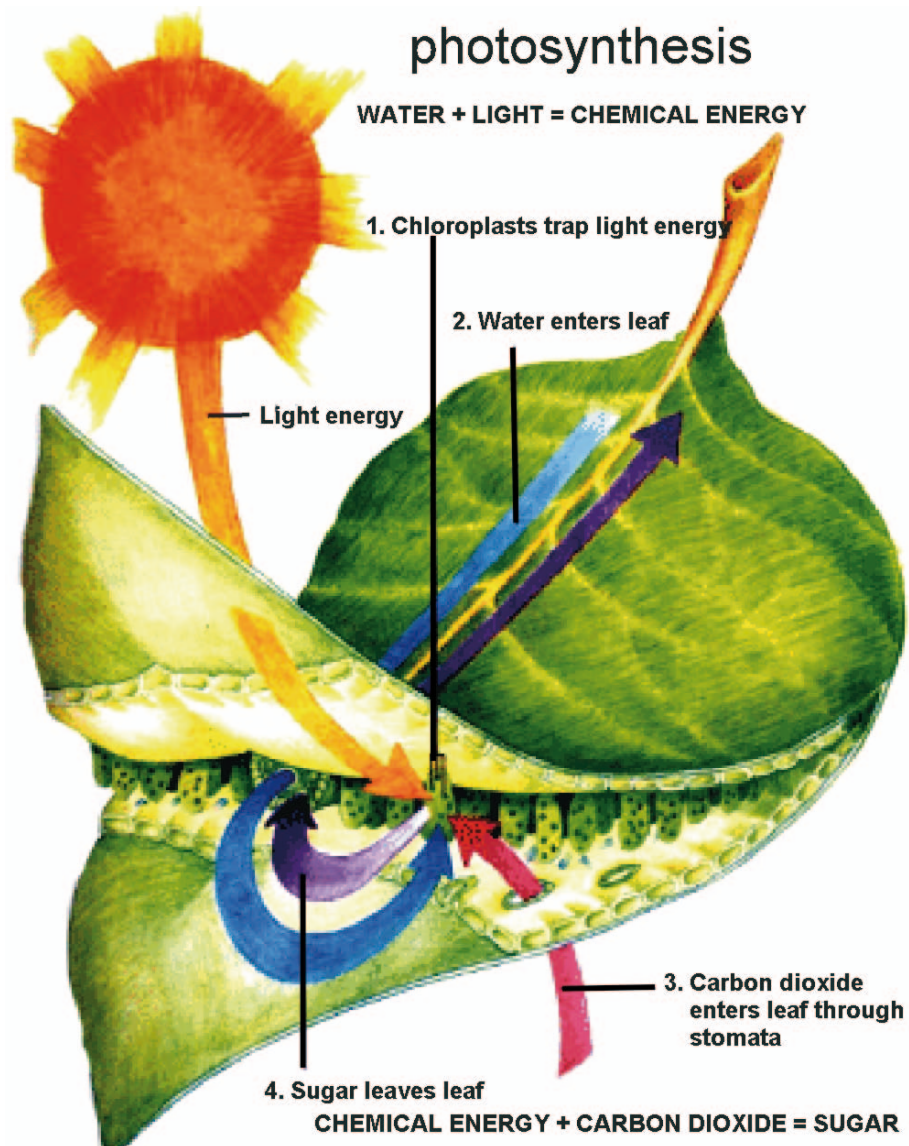
# Fibre analysis



from Hall (2003)

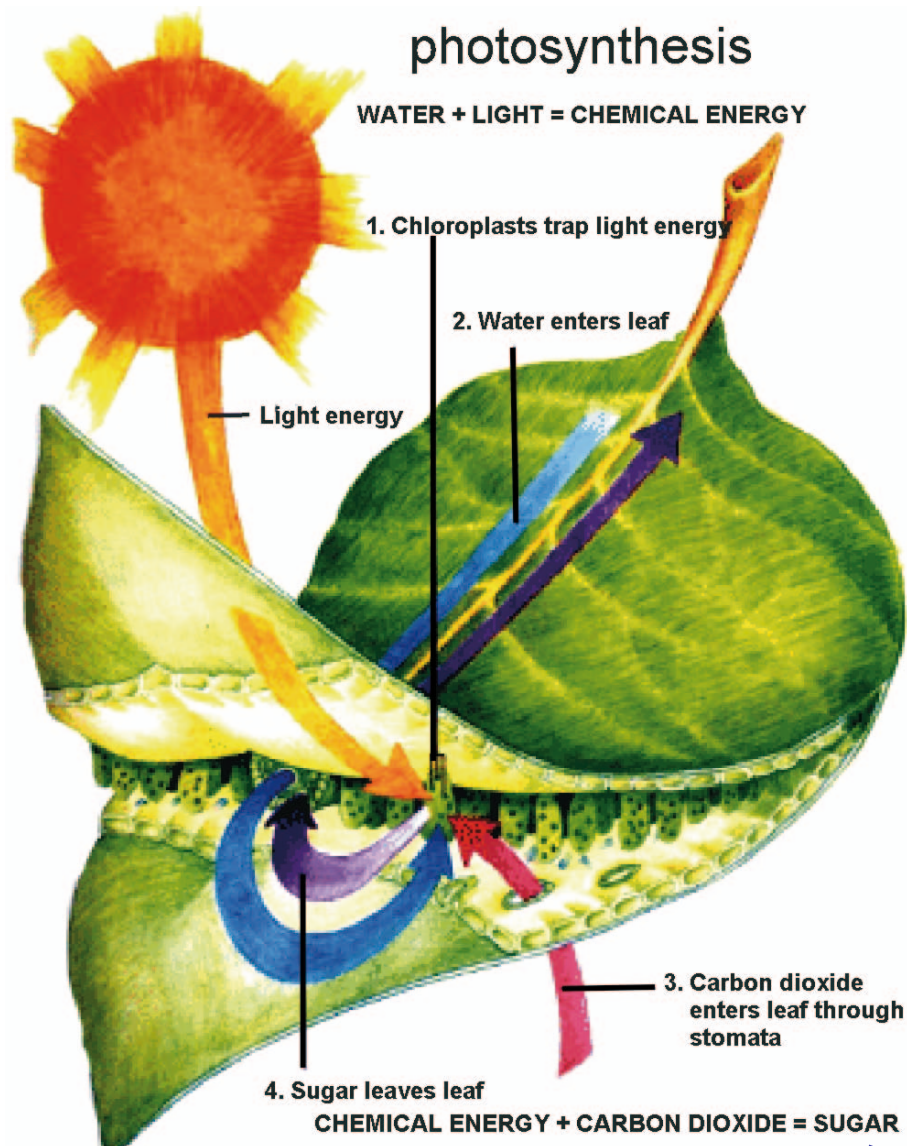


# Photosynthesis





# Photosynthesis



**O<sub>2</sub>**





# First fundamental question

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



# First fundamental question

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# First fundamental question

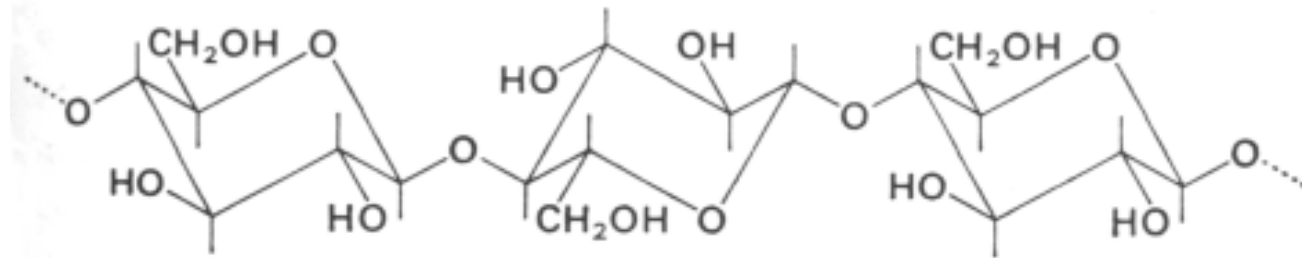
**Do you want to use plant fibre or only the plant cell contents?**





# Fibre digestion

**Organic polymers**  
(cellulose, hemicellulose)



from Karasov & Martinez del Rio (2007)





# Fibre digestion

**Organic polymers**  
(cellulose, hemicellulose)



**Hydrolysis**  
(soluble sugars)



# Fibre digestion

**Organic polymers**  
(cellulose, hemicellulose)



**Hydrolysis**  
(soluble sugars)



**Primary fermentation**  
(lactate, succinate)



# Fibre digestion

**Organic polymers**  
(cellulose, hemicellulose)



**Hydrolysis**  
(soluble sugars)



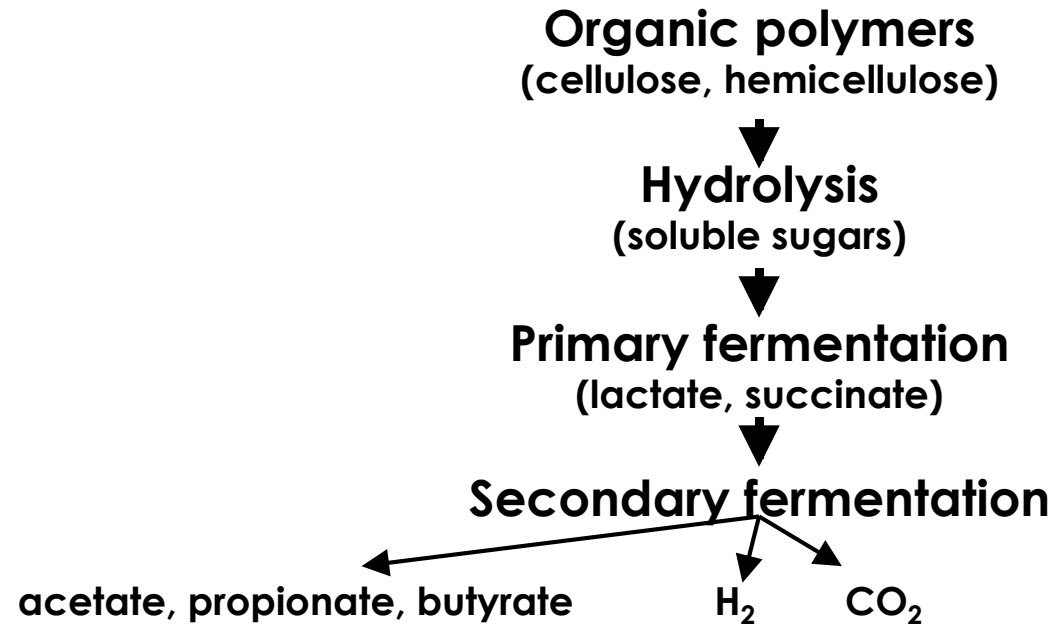
**Primary fermentation**  
(lactate, succinate)



**Secondary fermentation**



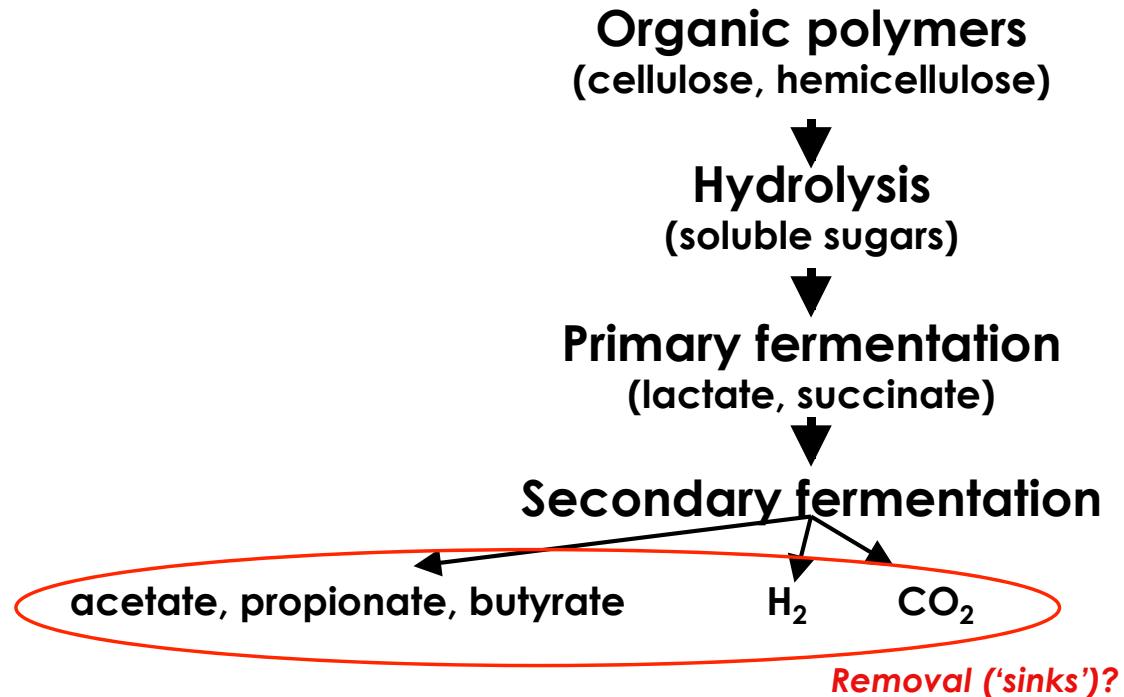
# Fibre digestion





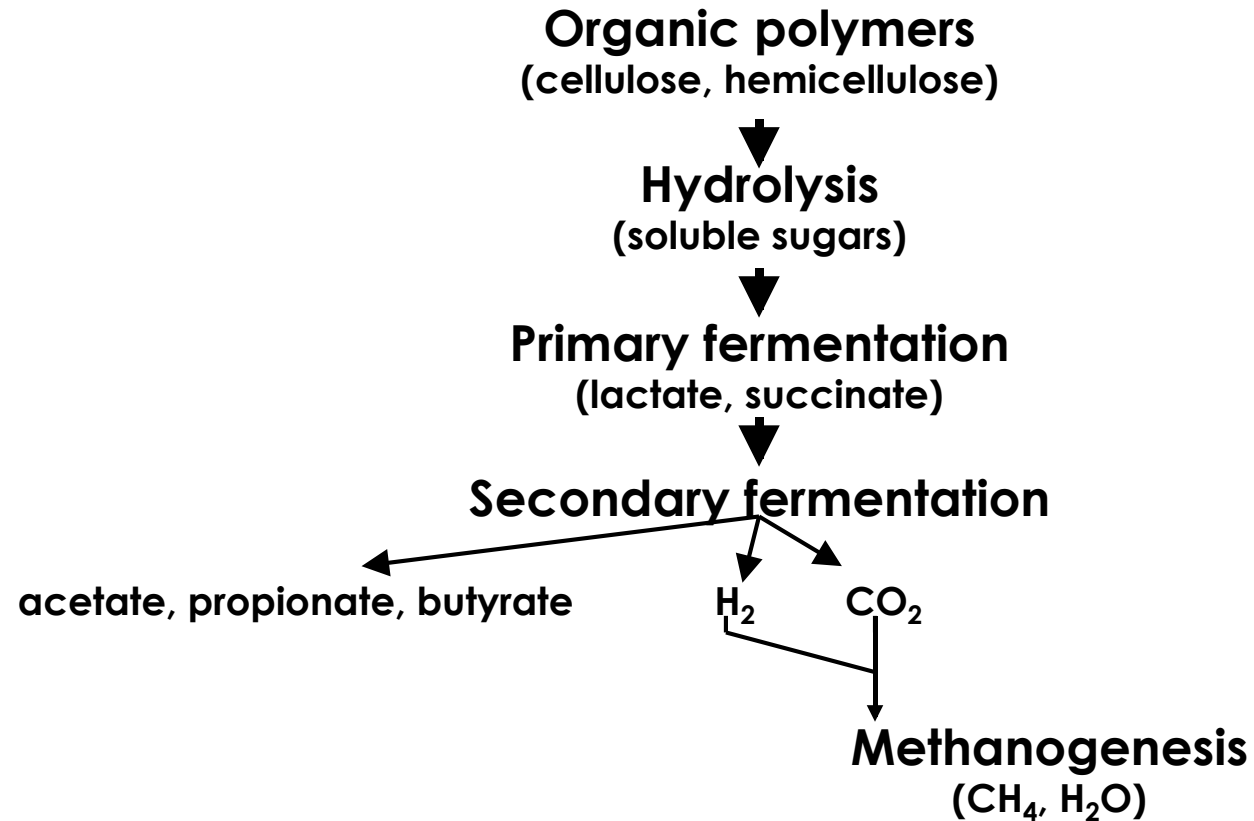


# Fibre digestion



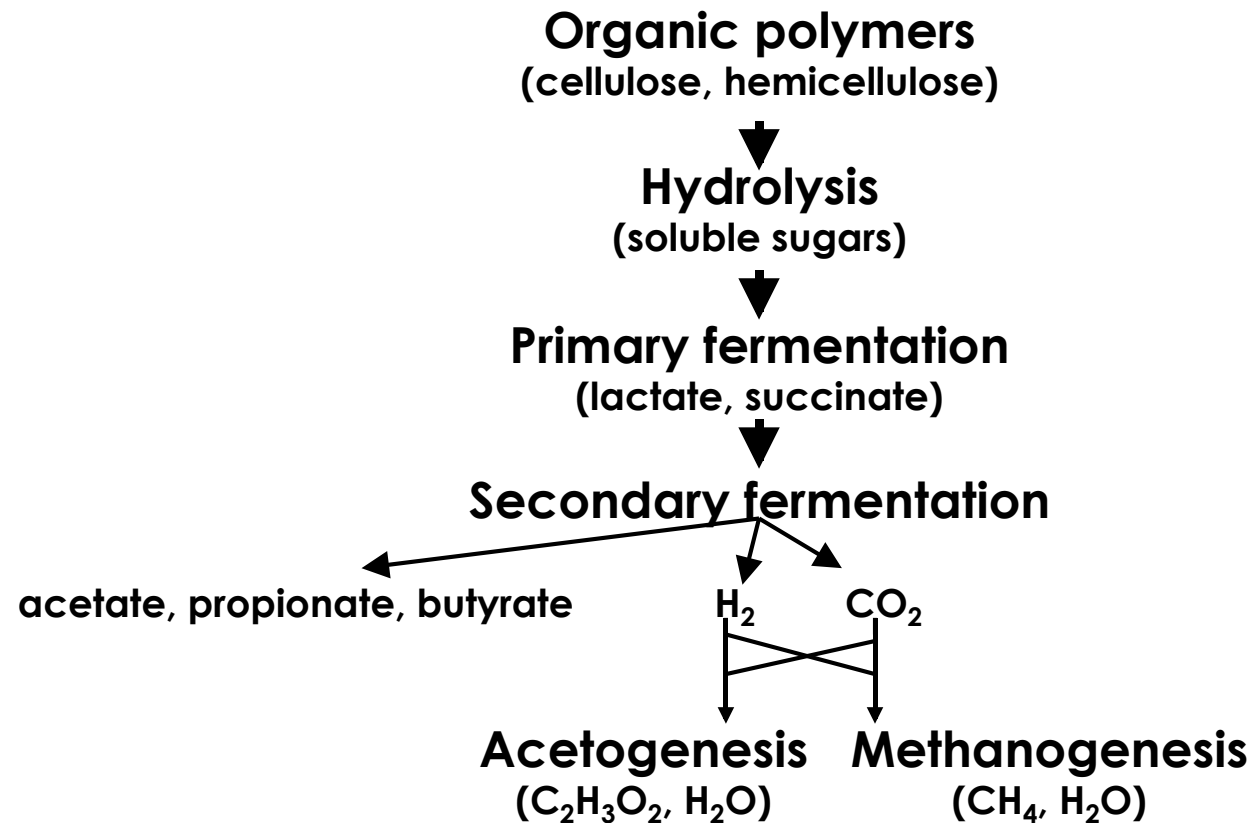


# Fibre digestion



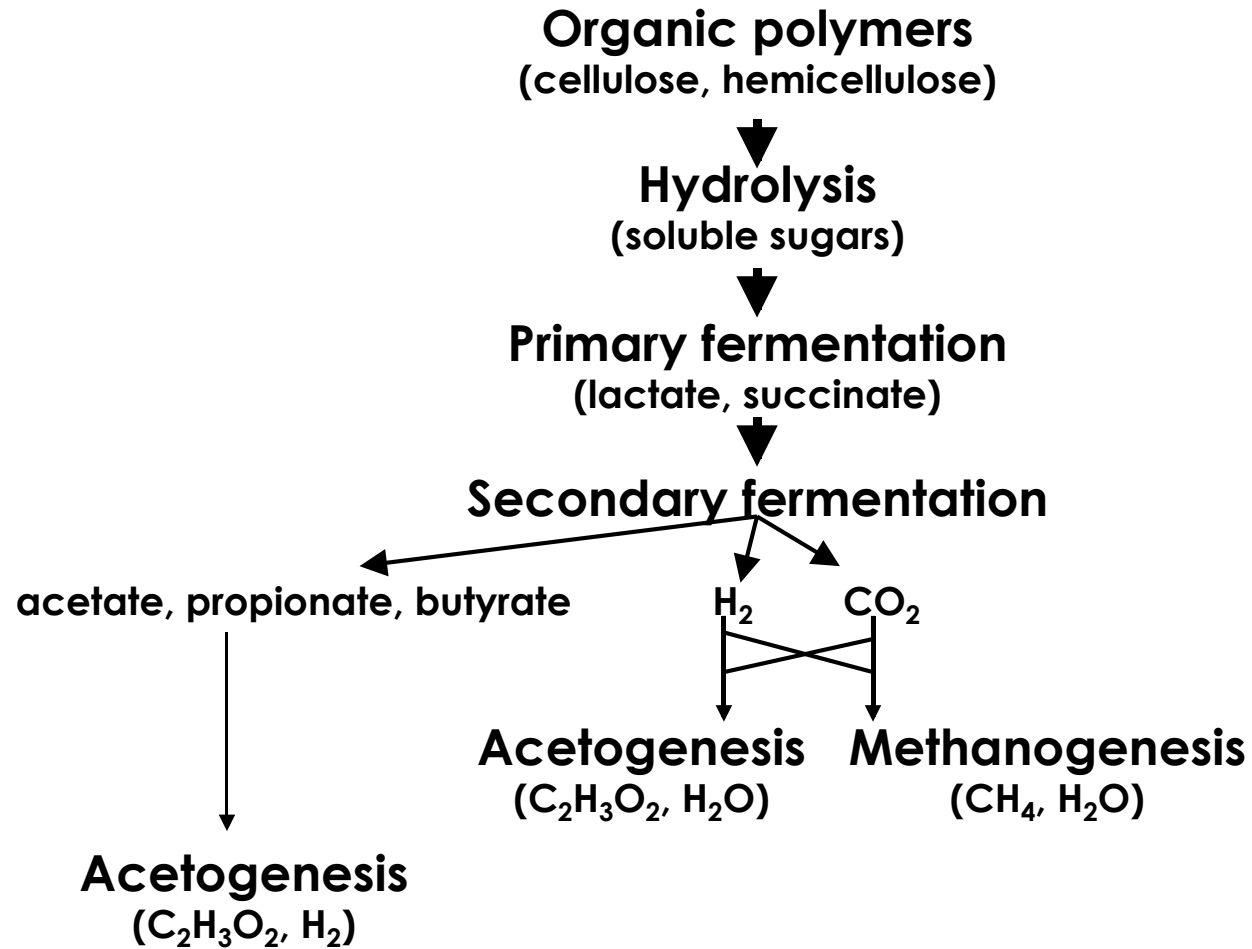


# Fibre digestion





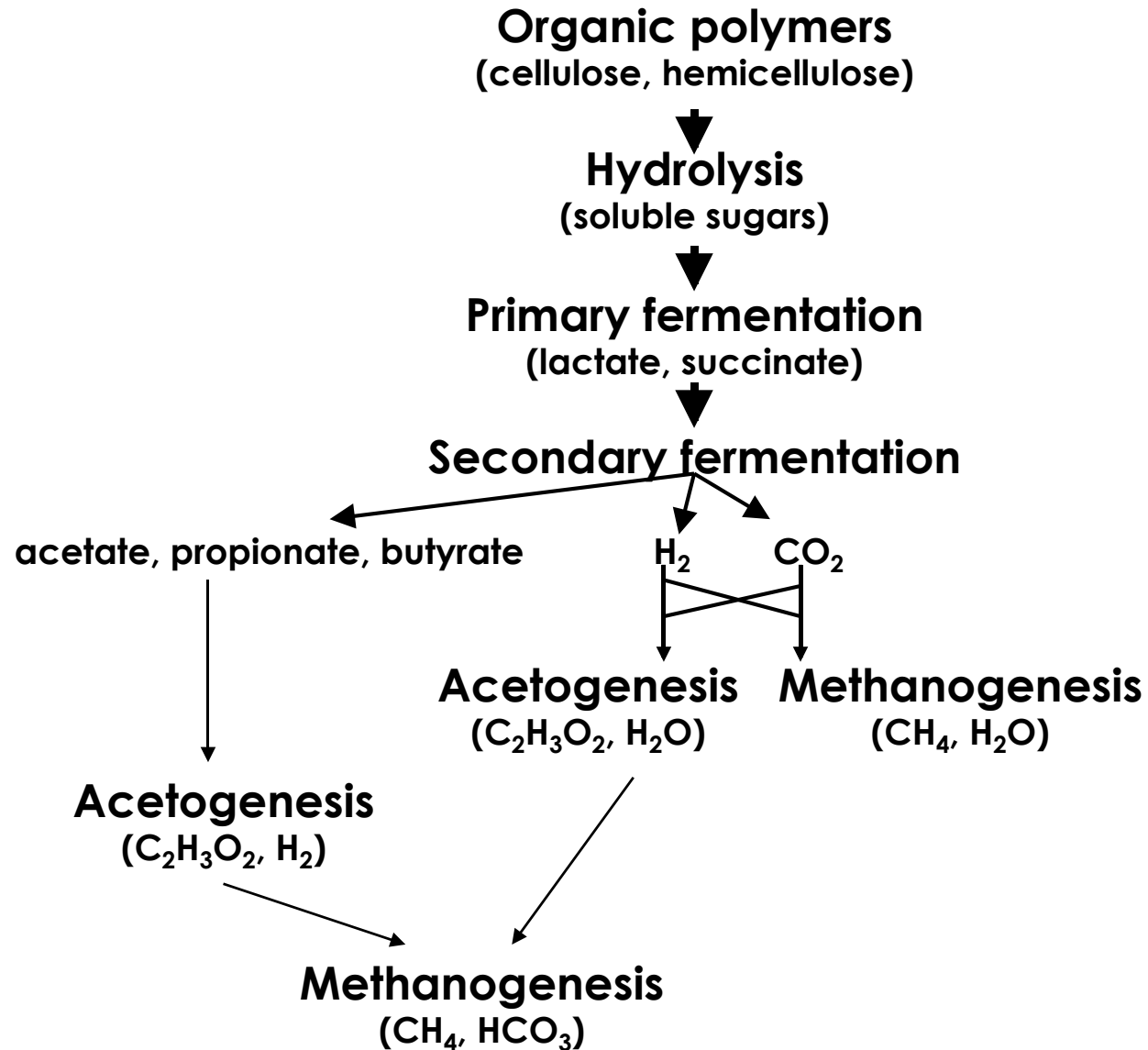
# Fibre digestion





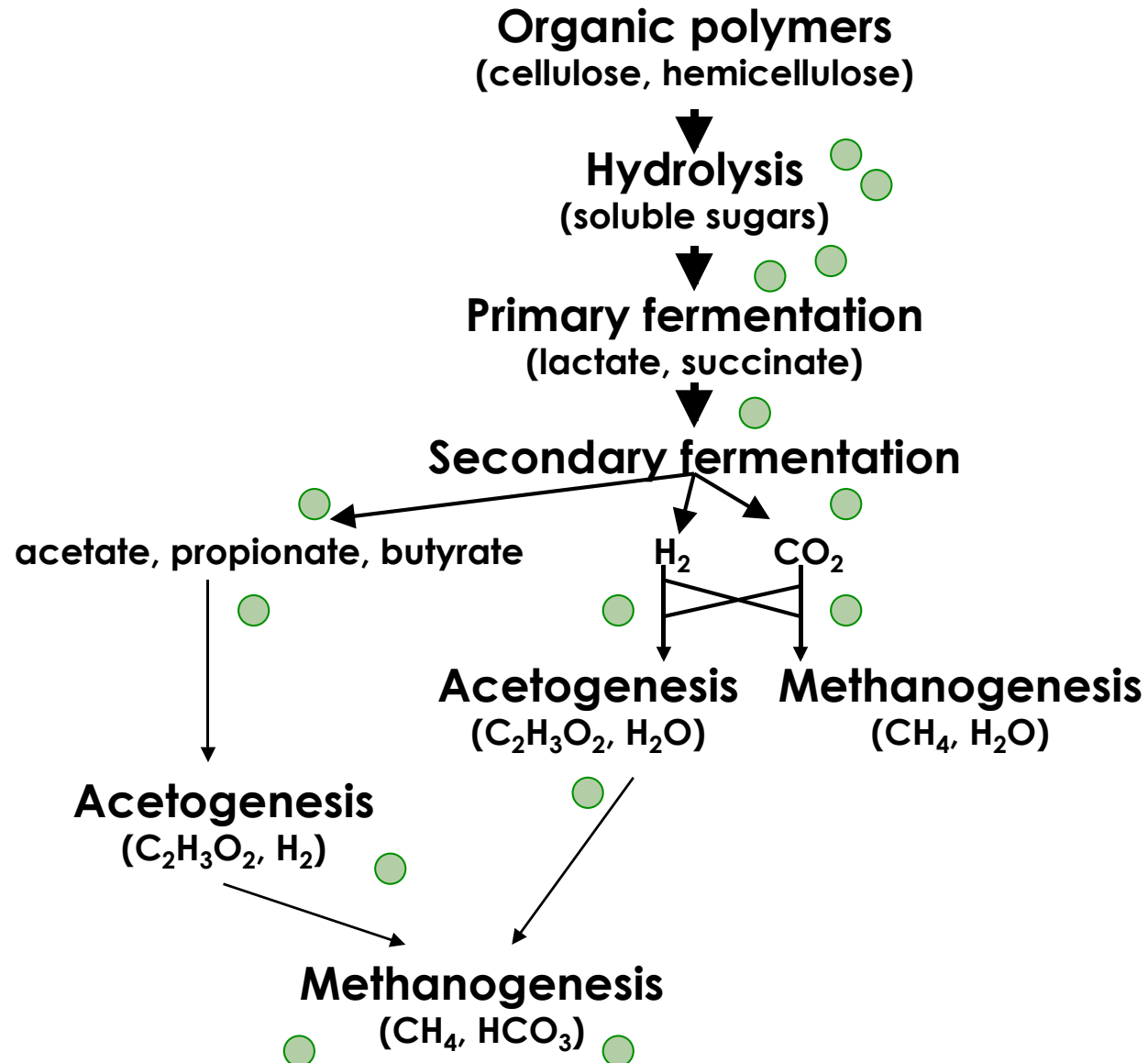
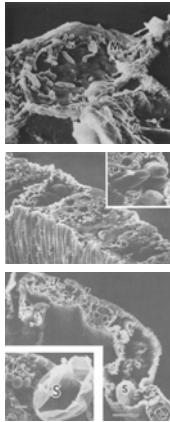


# Fibre digestion



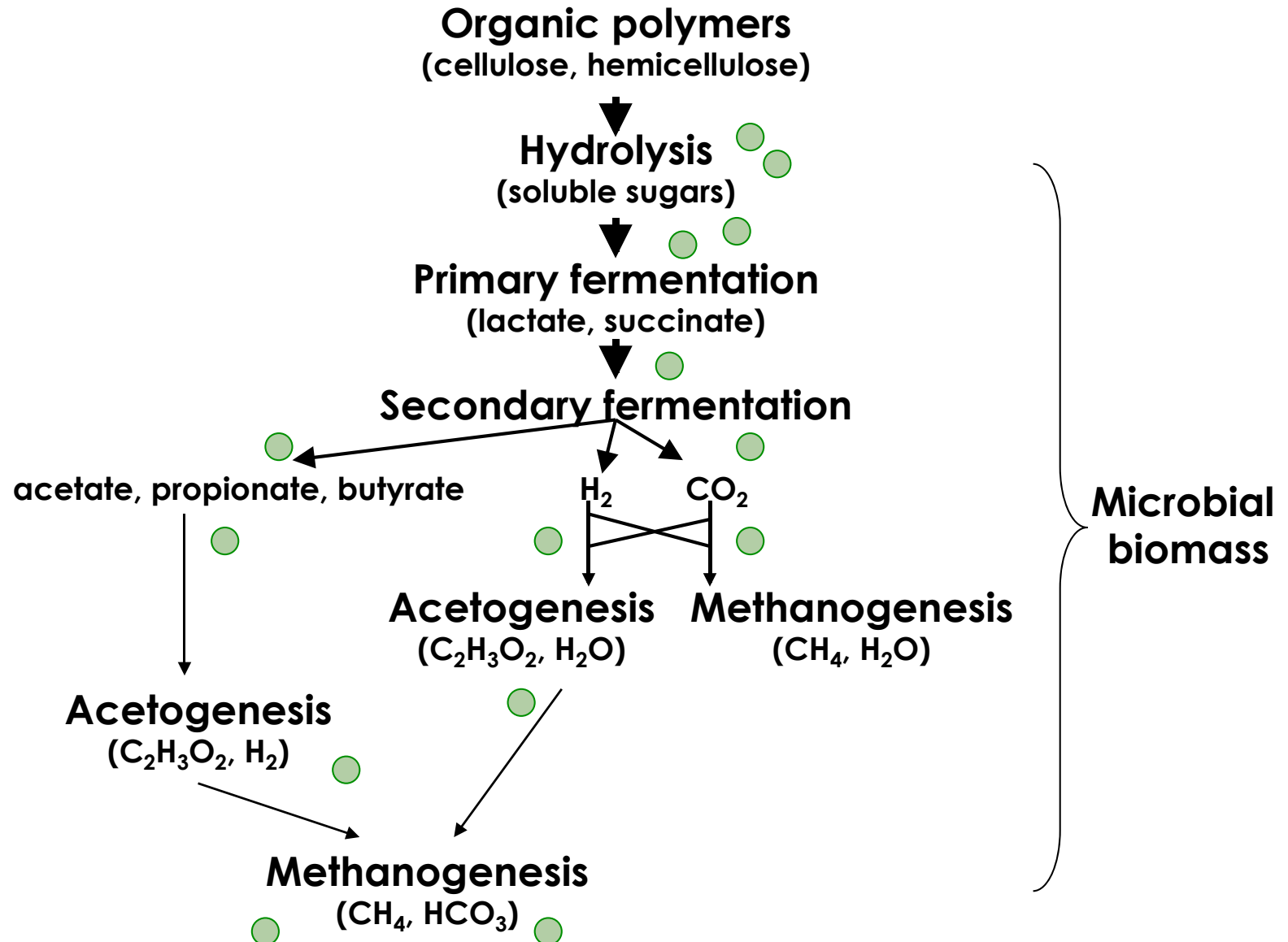
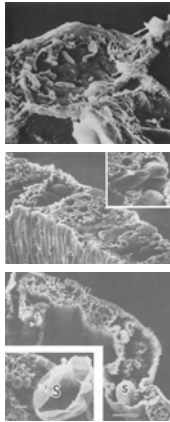


# Fibre digestion



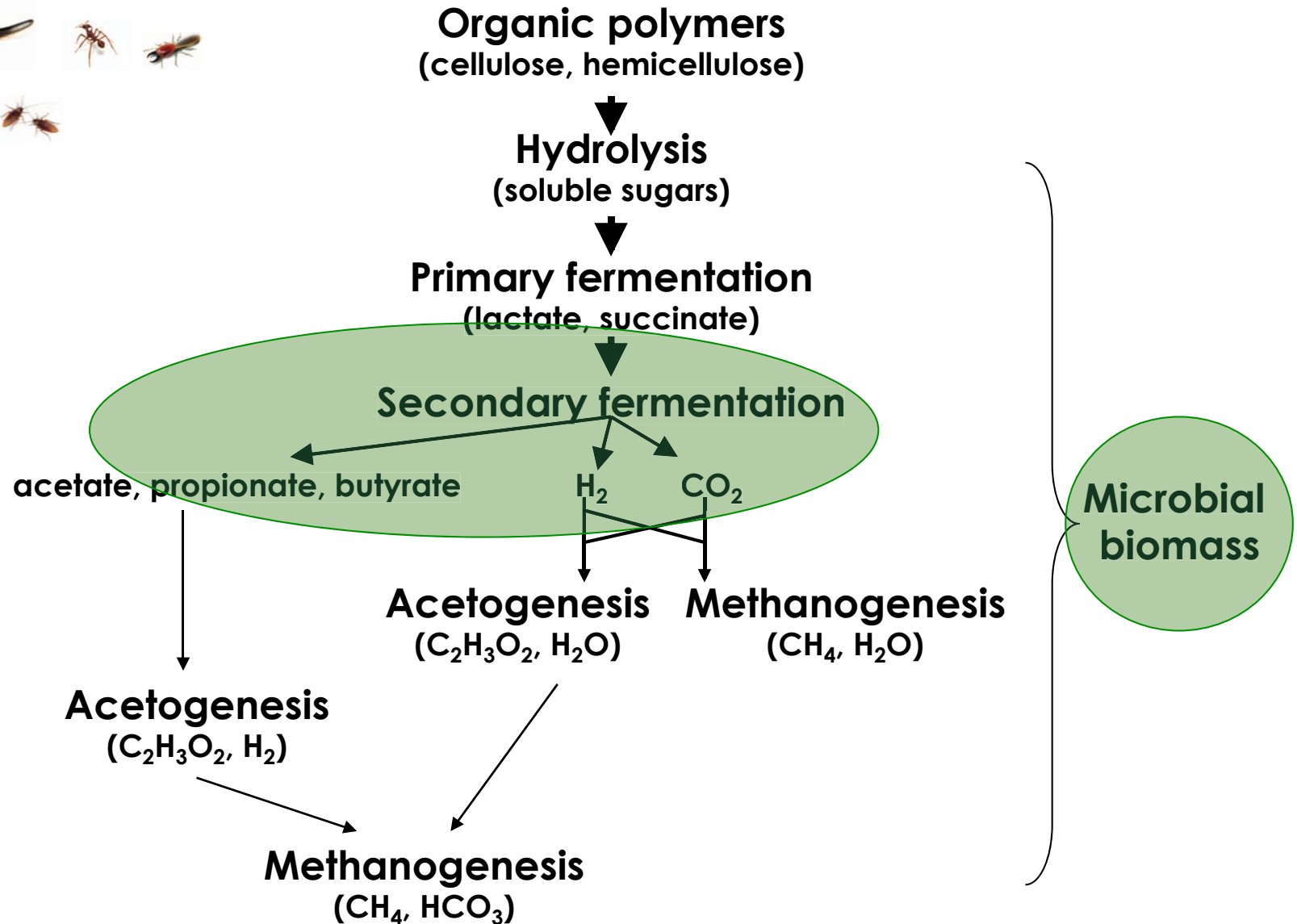


# Fibre digestion





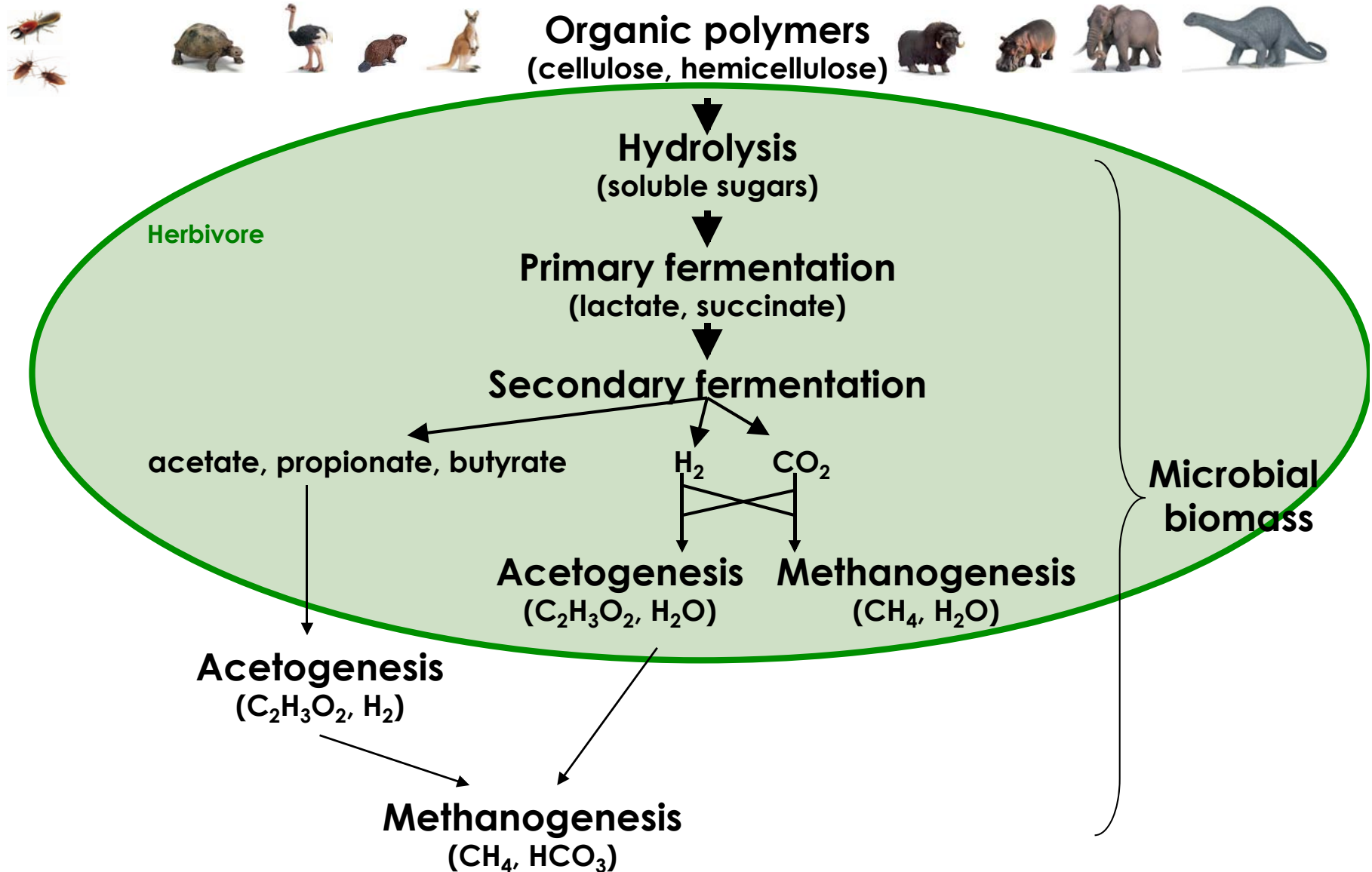
# Fibre digestion





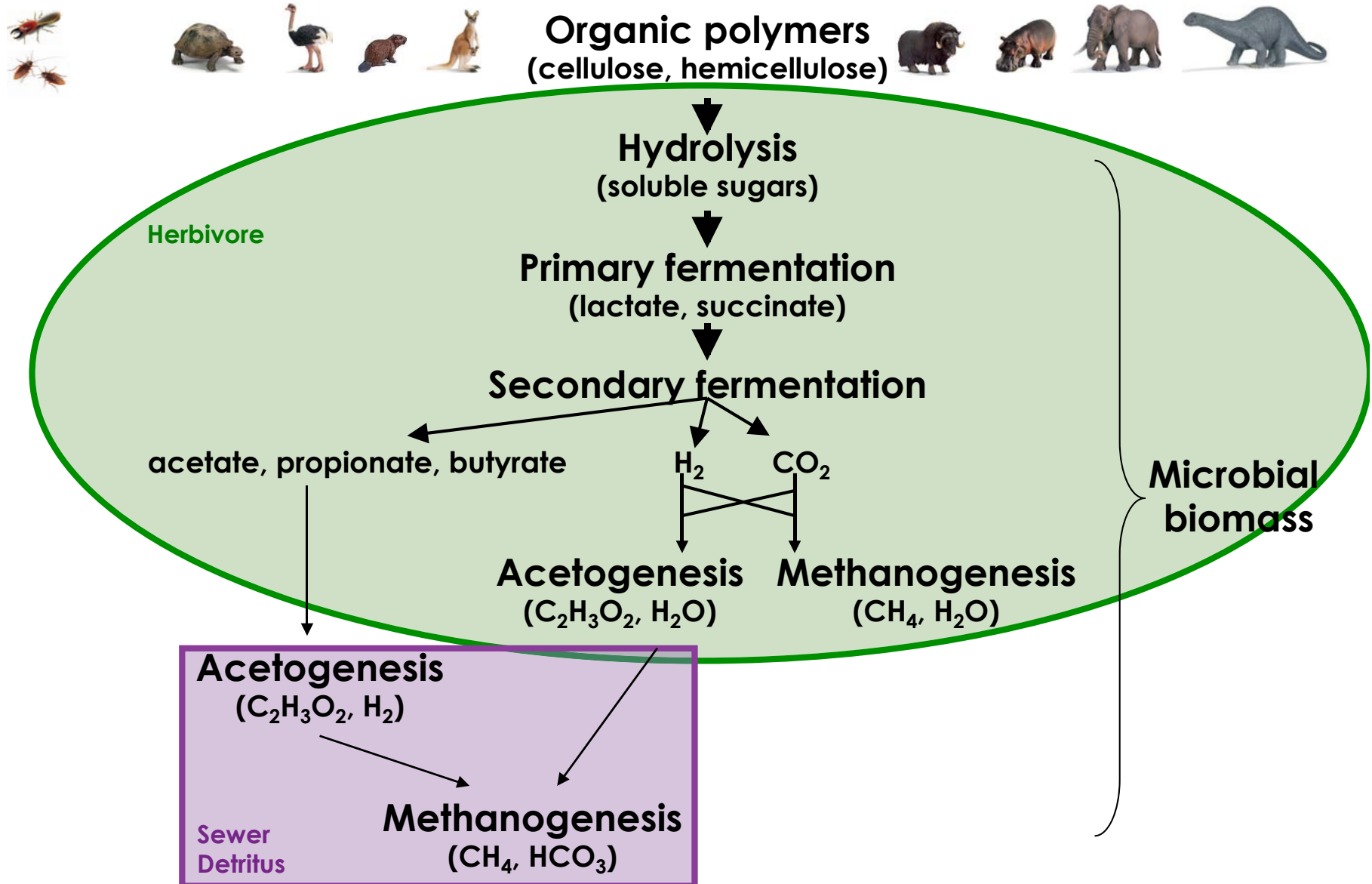


# Fibre digestion



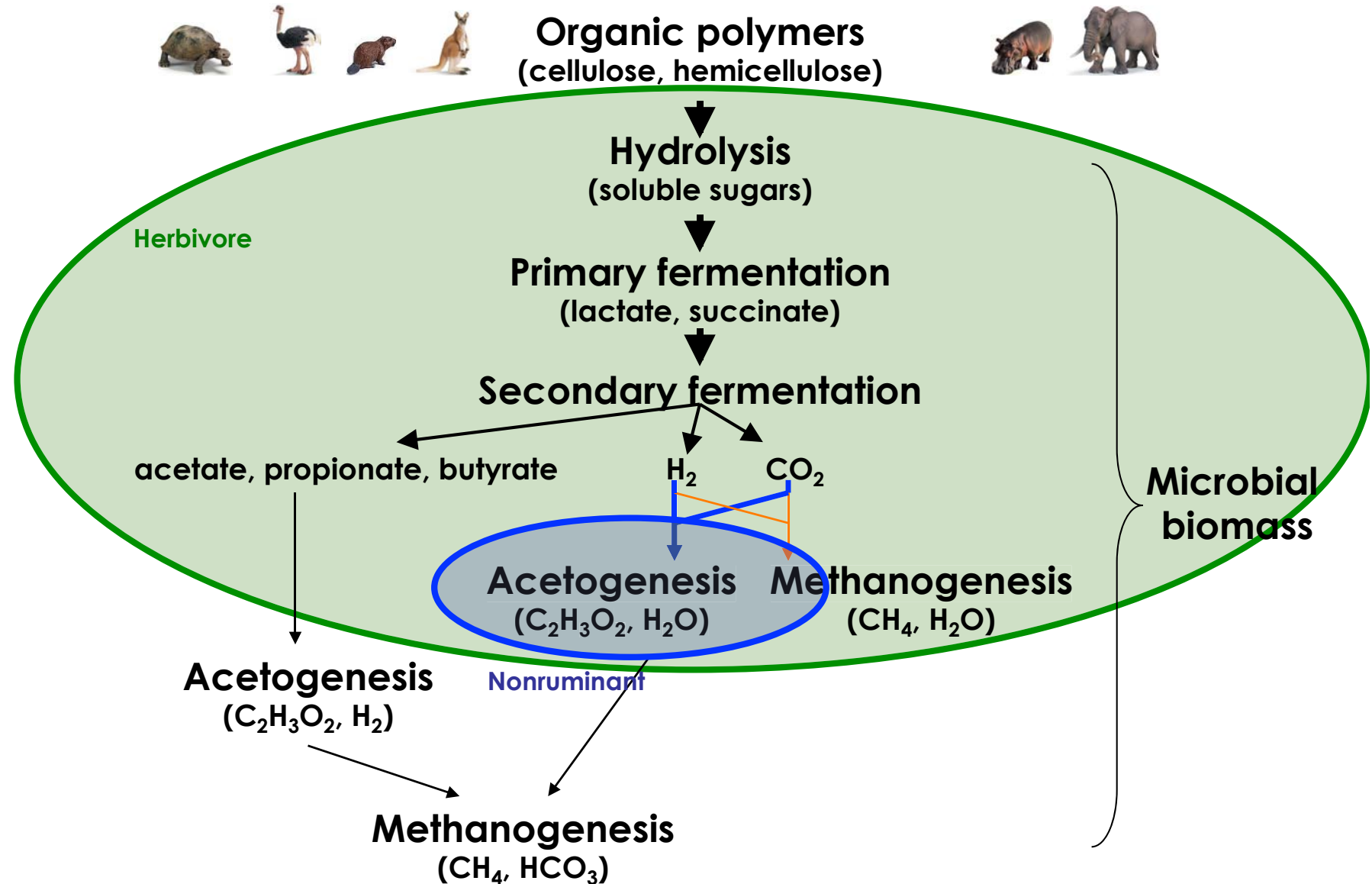


# Fibre digestion



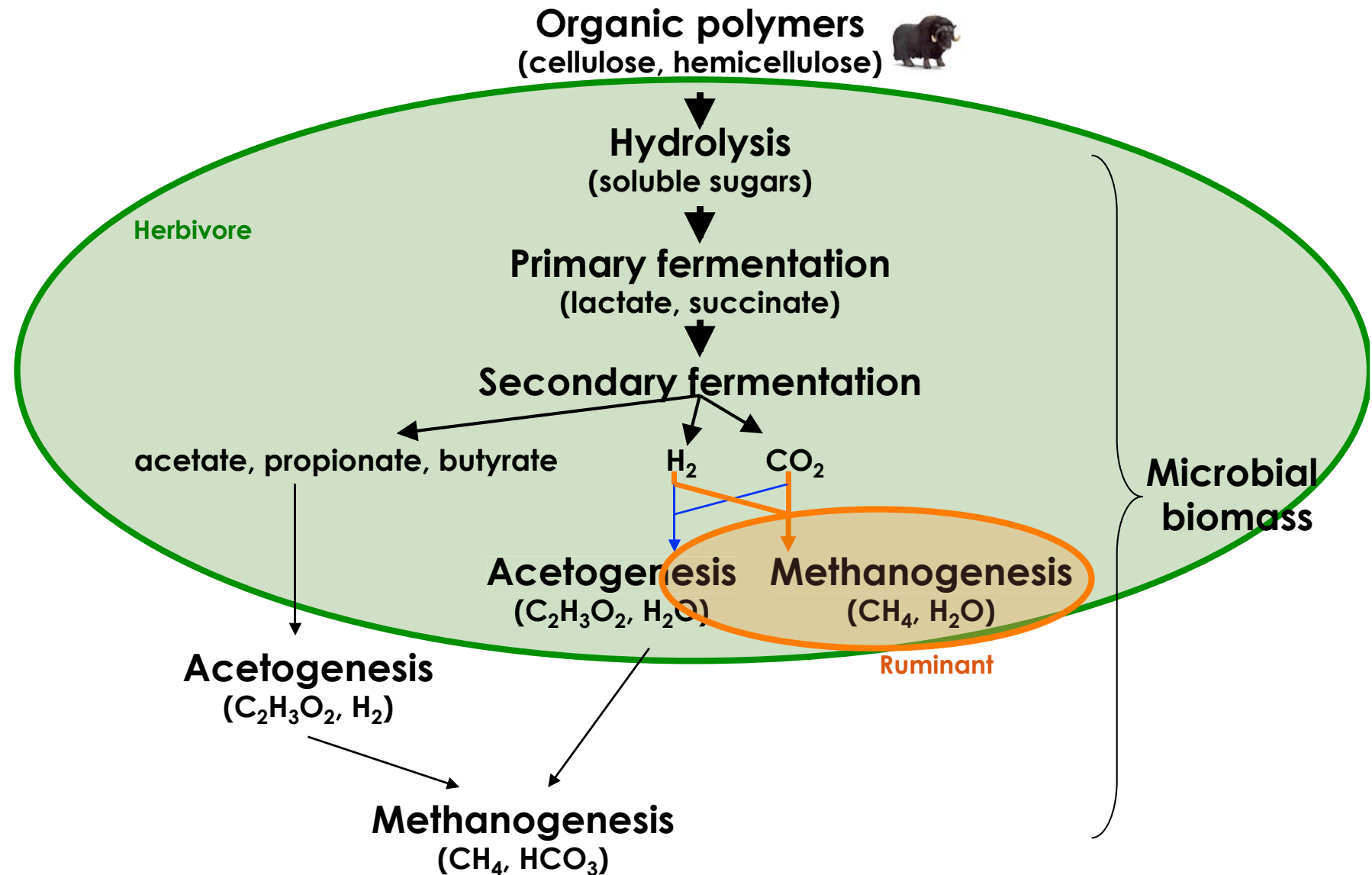


# Fibre digestion



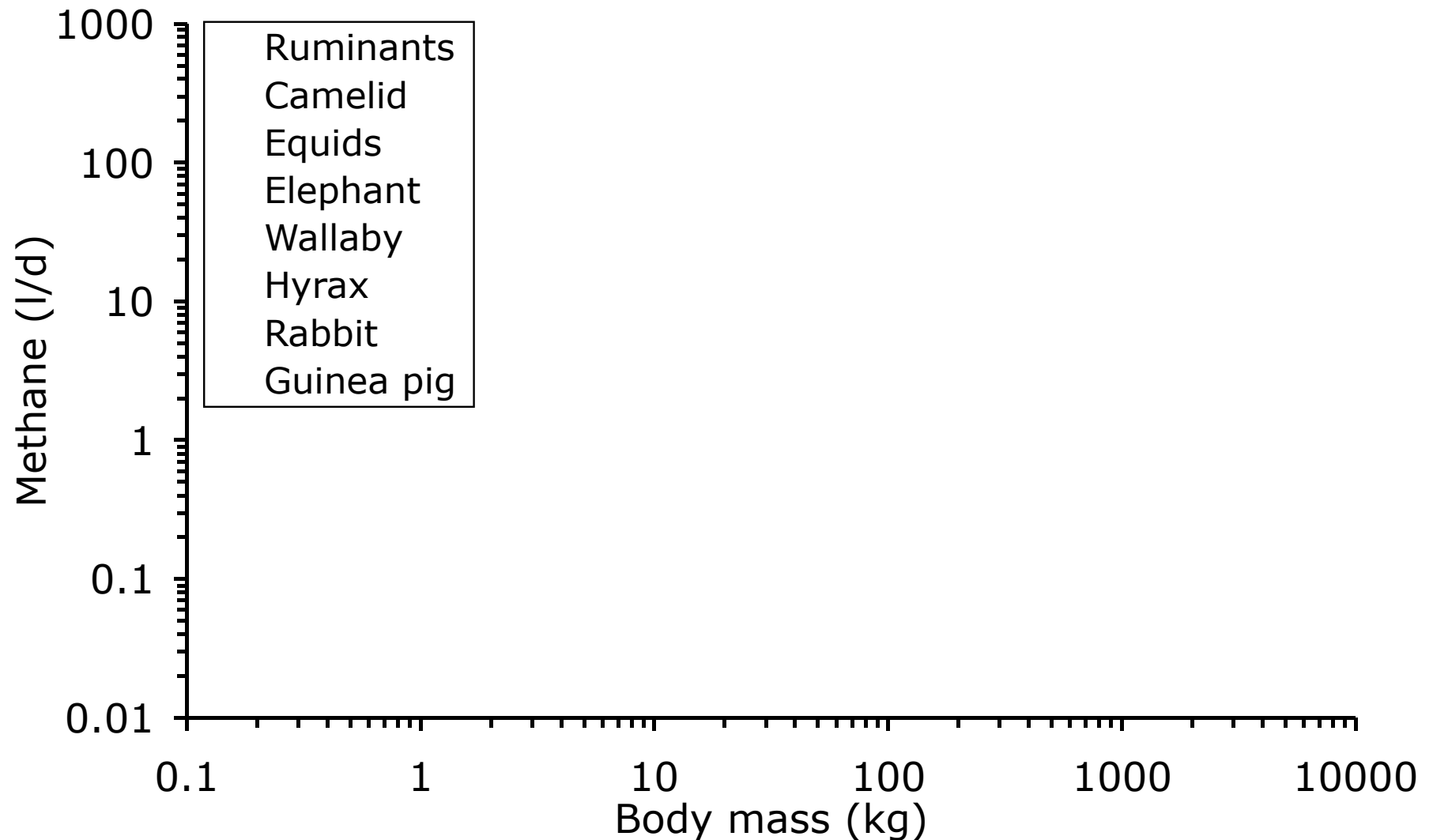


# Fibre digestion





# Methane allometry in herbivores

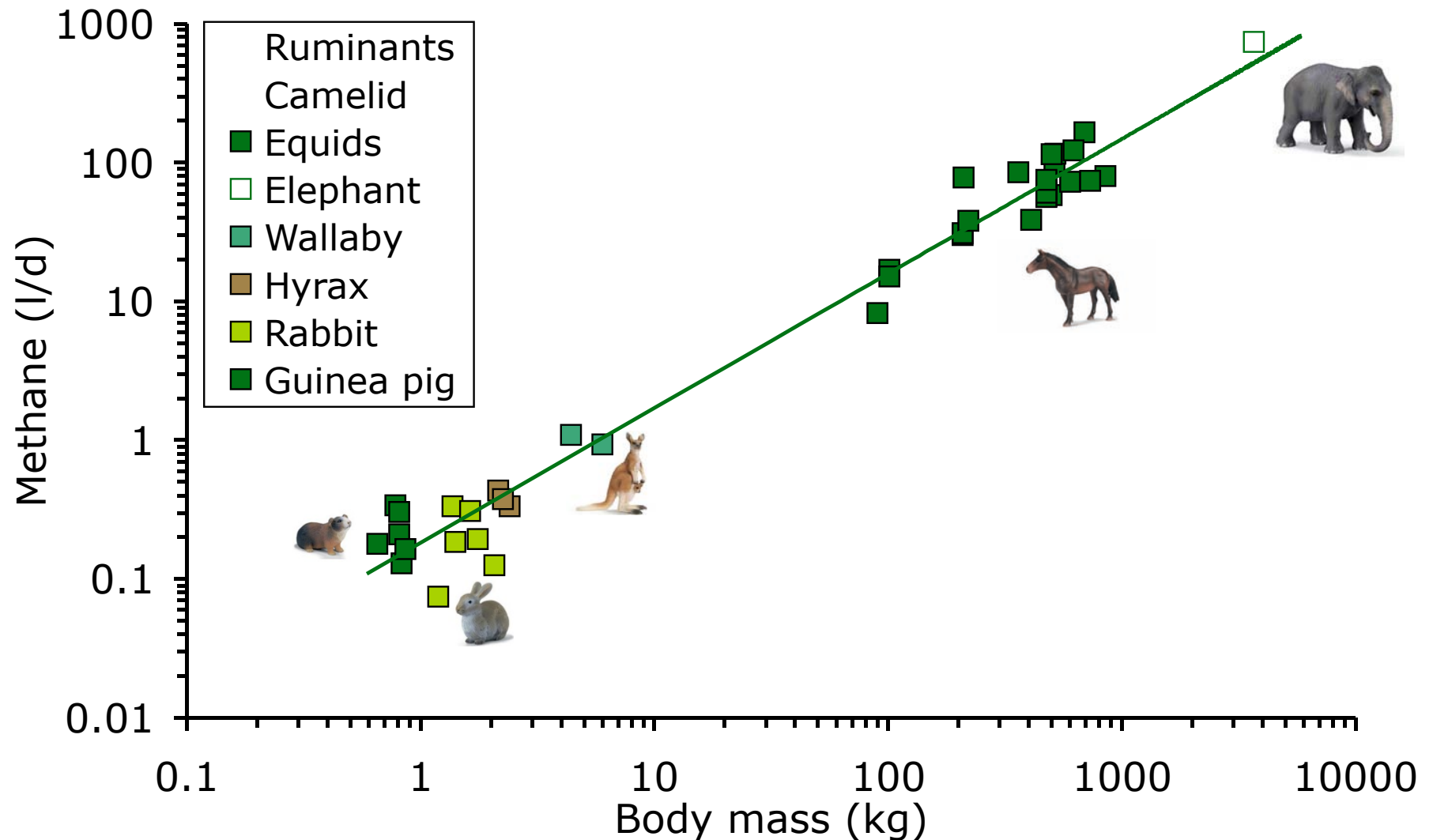


from Franz et al. (2011)





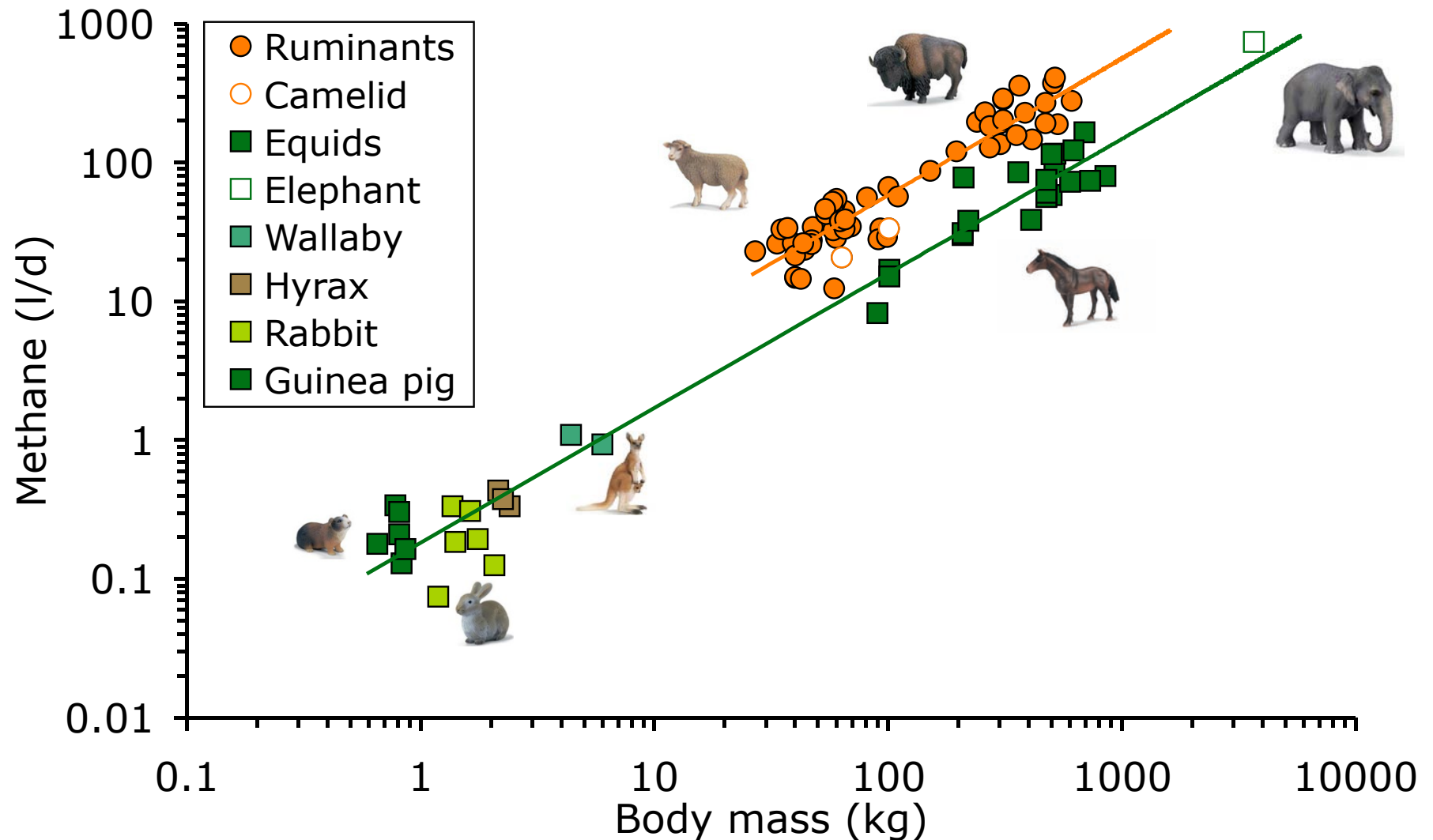
# Methane allometry in herbivores



from Franz et al. (2011)



# Methane allometry in herbivores



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<sup>1</sup>, D. E. Bignell<sup>2</sup> and C. Bandi<sup>3</sup>**

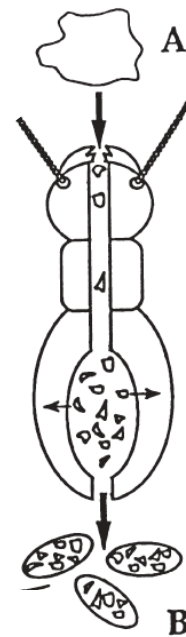
*Insectes soc.* 48 (2001) 194–201



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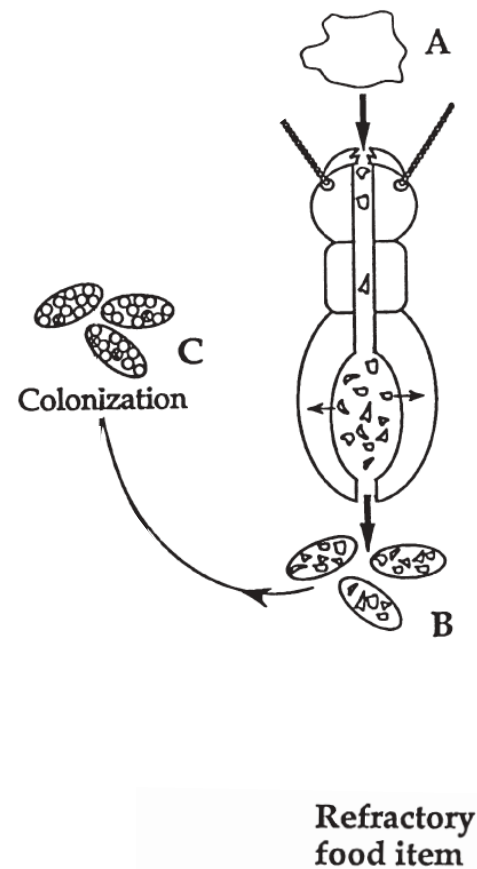
Refractory  
food item



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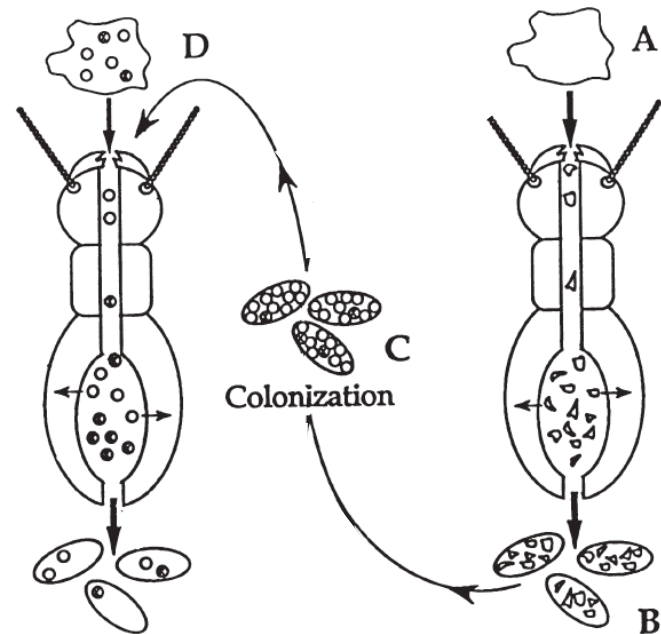




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## Microbes

- transient or digested
- gut fauna

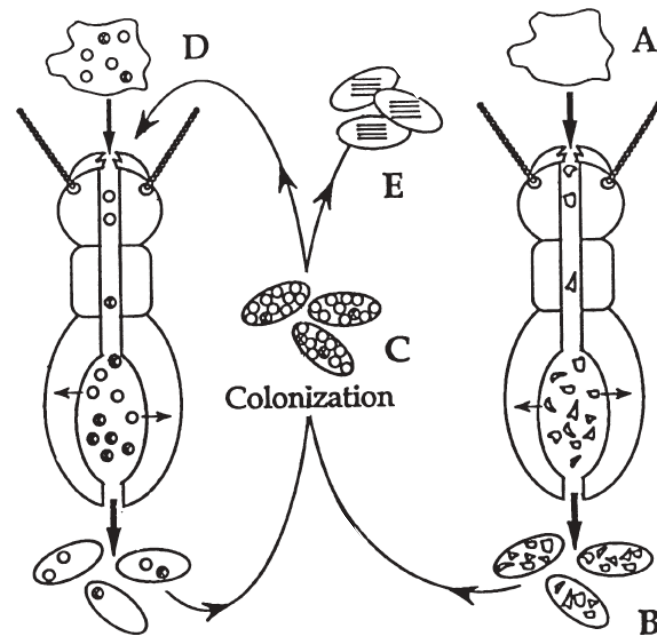
## Refractory food item



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## Microbes

- transient or digested
- gut fauna

## Refractory food item

## Metabolites, exoenzymes

- ≡ of free living microbes

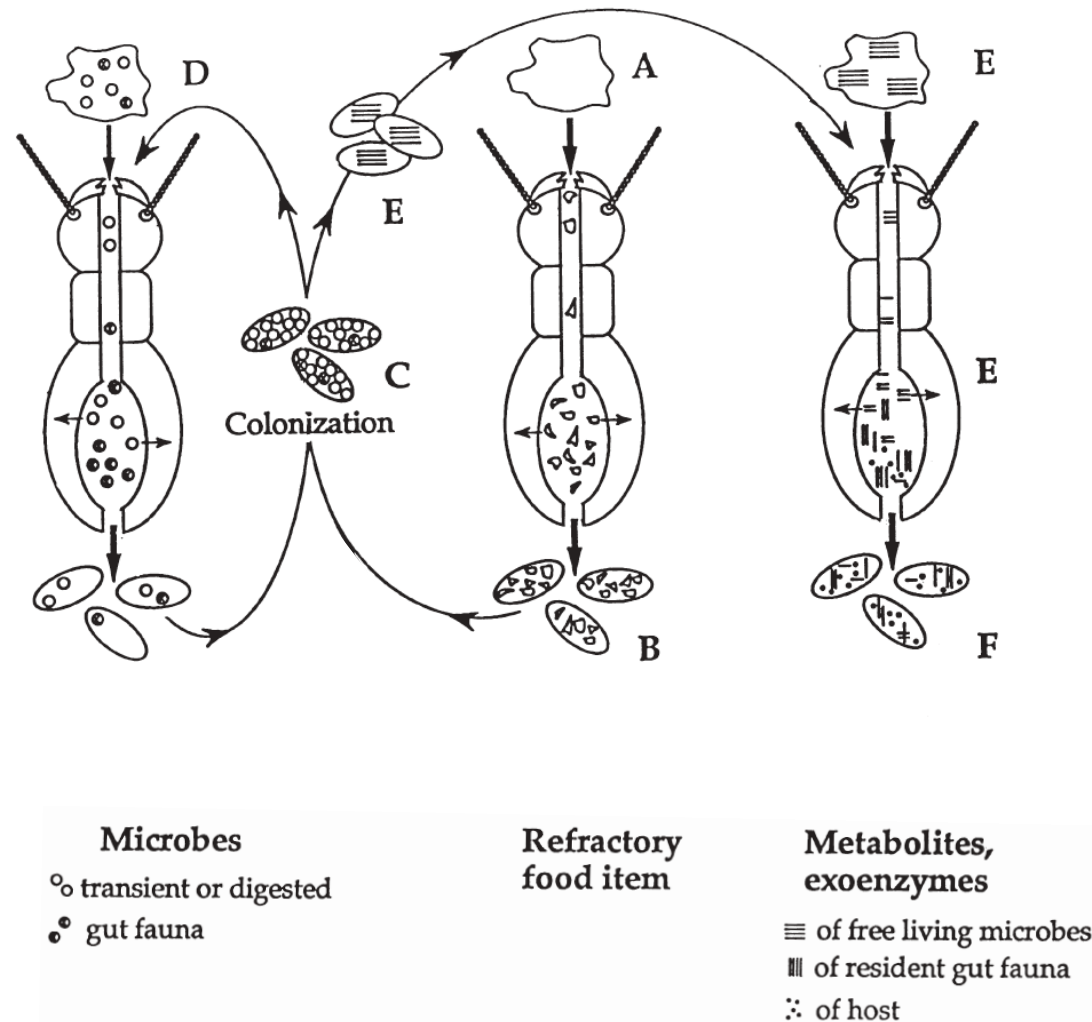




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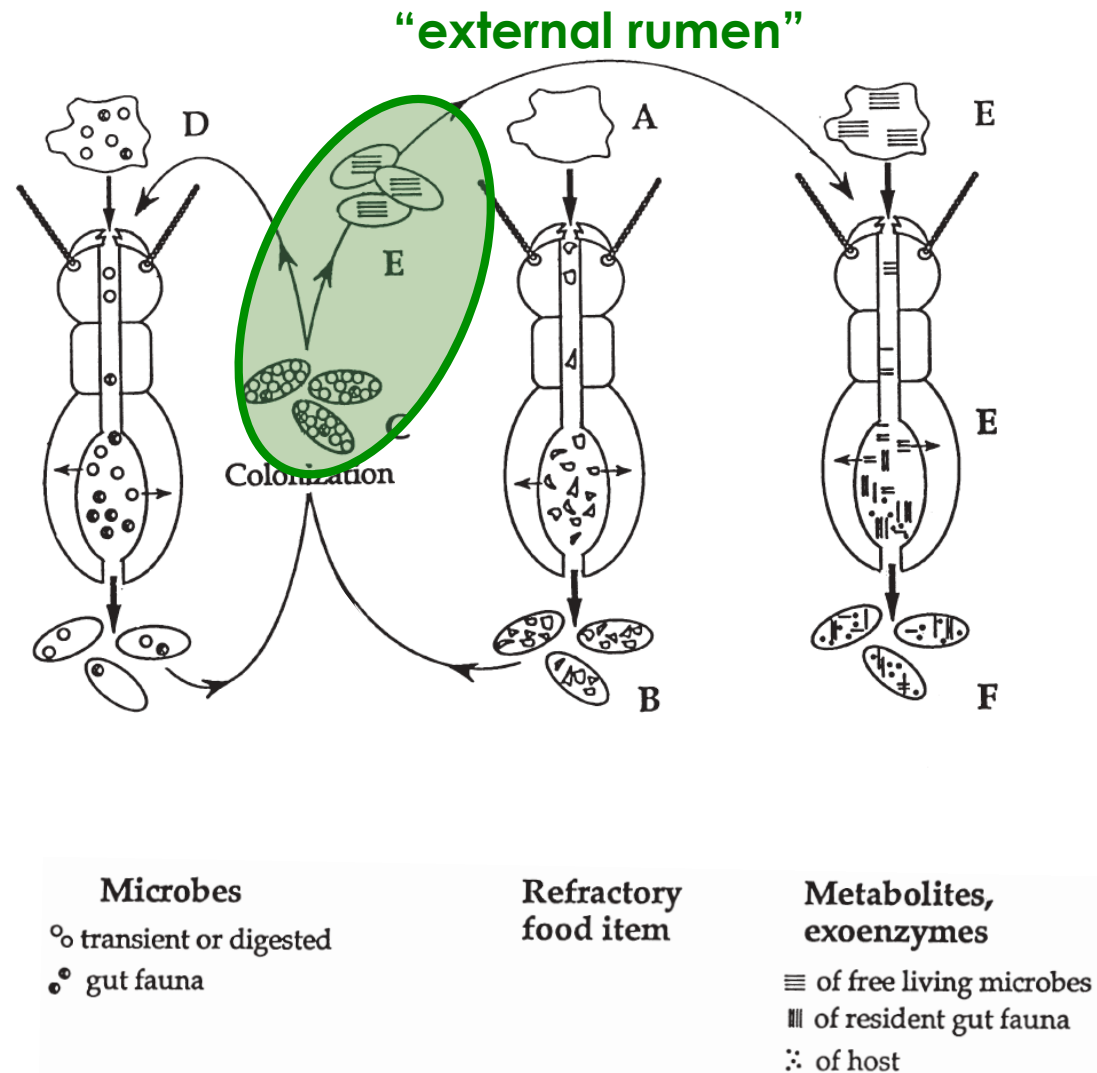




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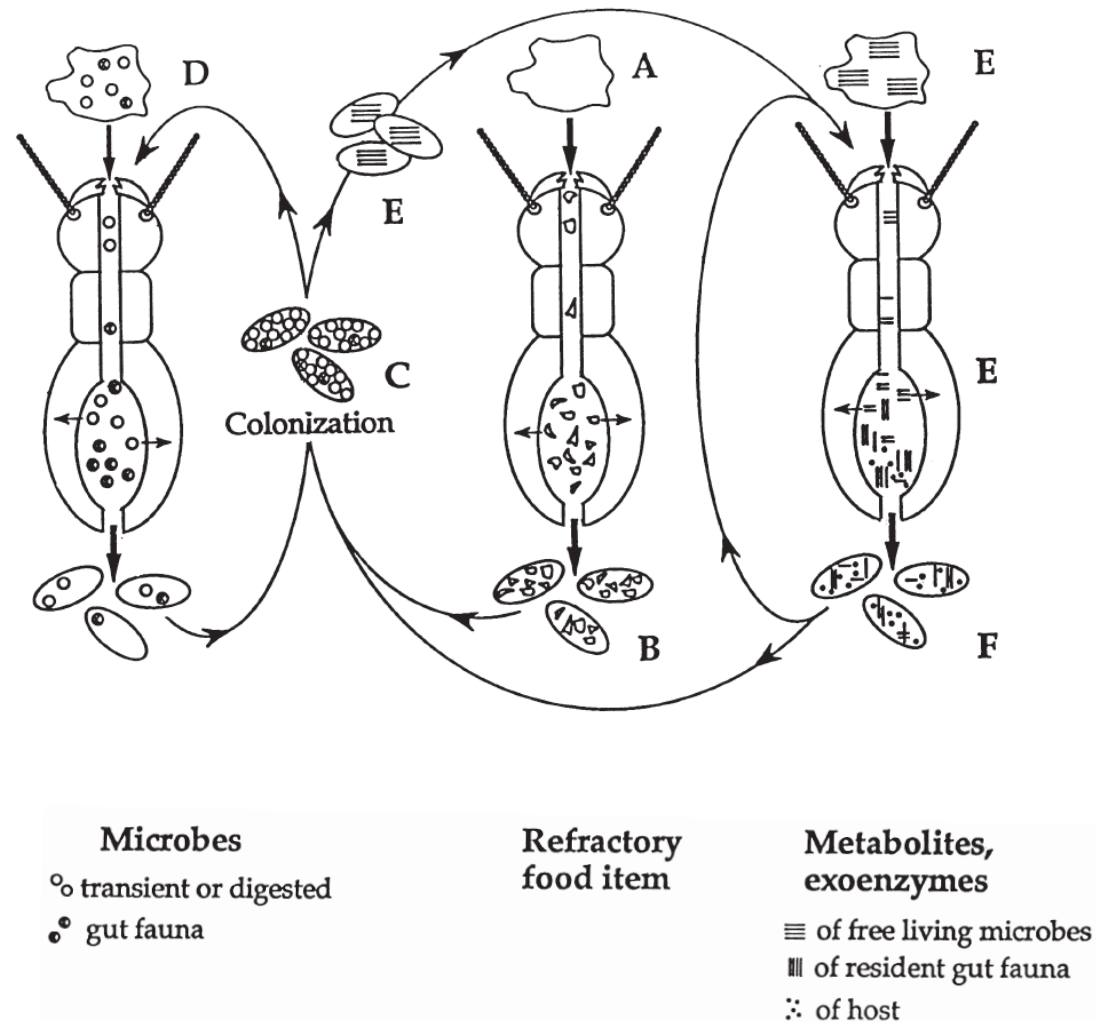




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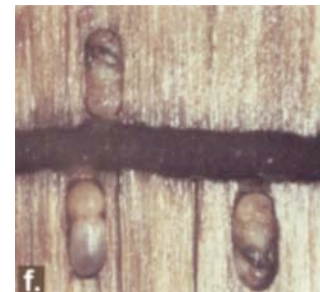
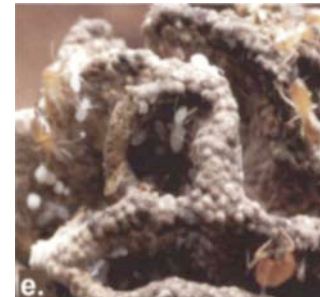
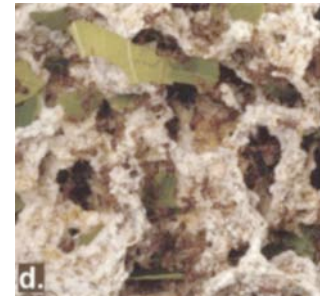
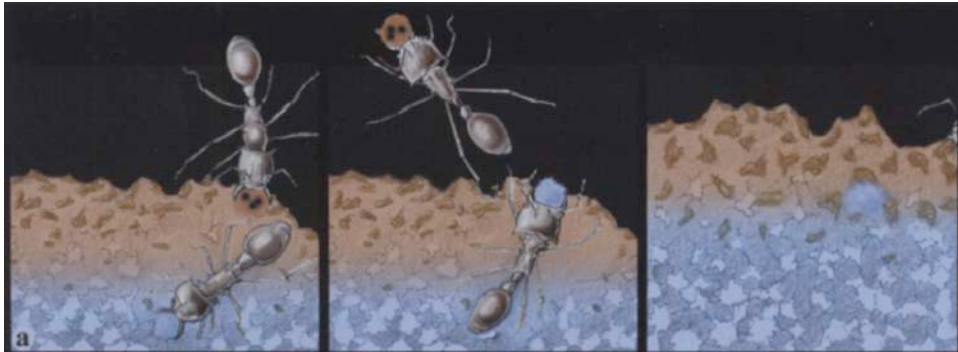




# THE EVOLUTION OF AGRICULTURE IN INSECTS

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

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





# Body size

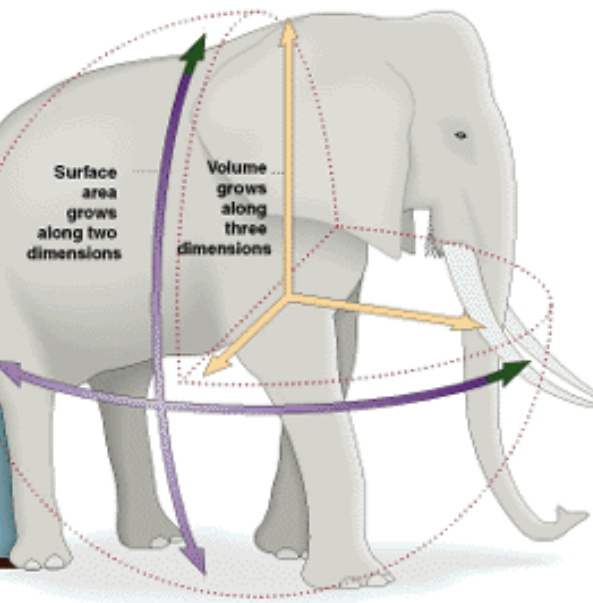
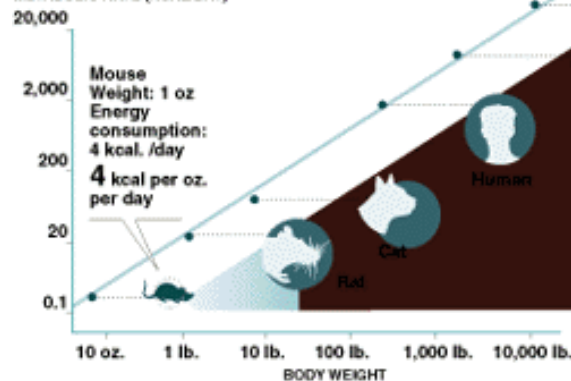
Most biologists consider body mass the most important characteristic of an organism. It is also (mostly) easy to measure.

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*

An Example of Scaling:  
Metabolic Rate

METABOLIC RATE (KCAL/DAY)







# Two fundamental questions

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

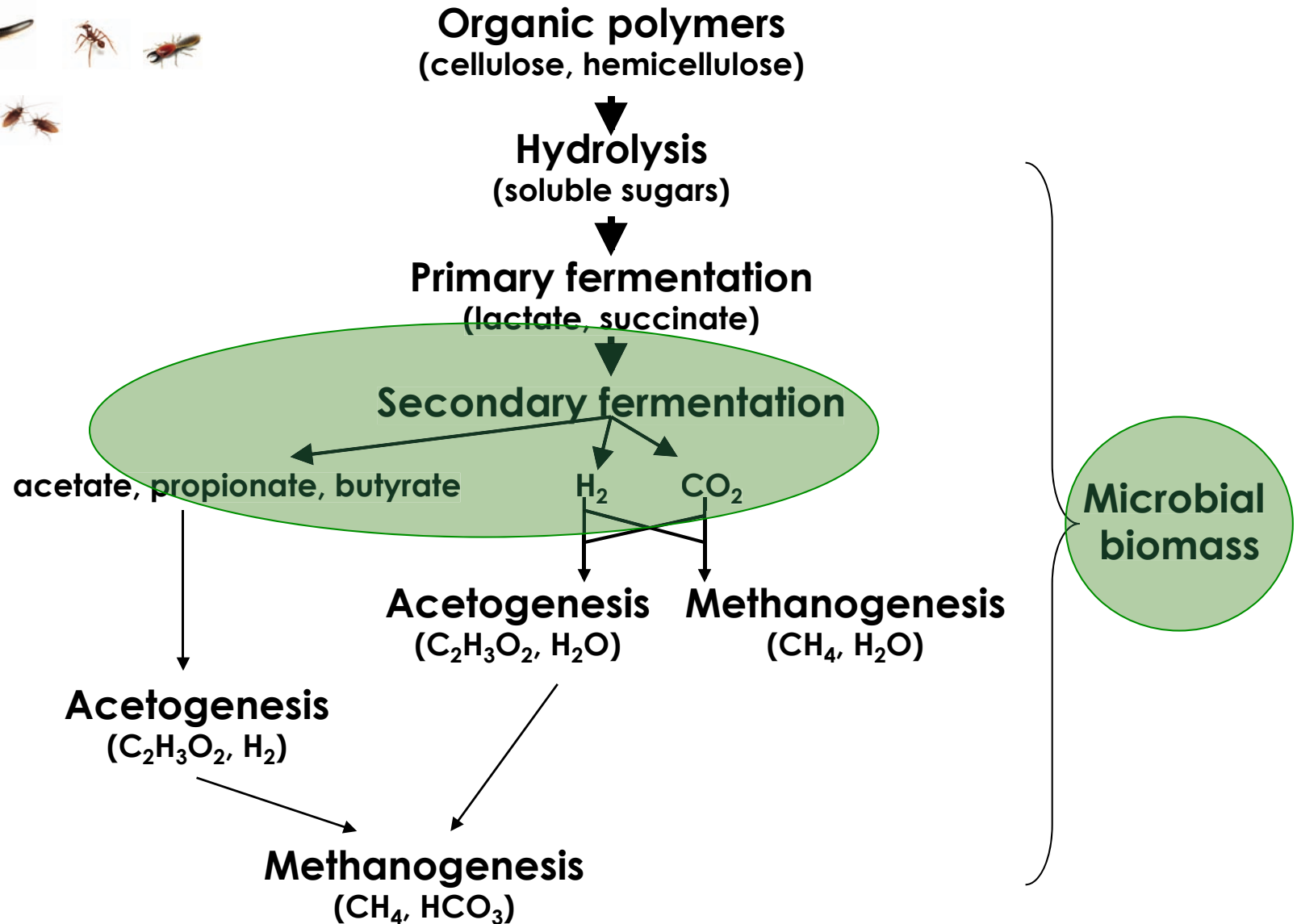
*In-house fibre digestion necessitates anatomical and physiological adaptations that might be costly in some circumstances.*

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)*

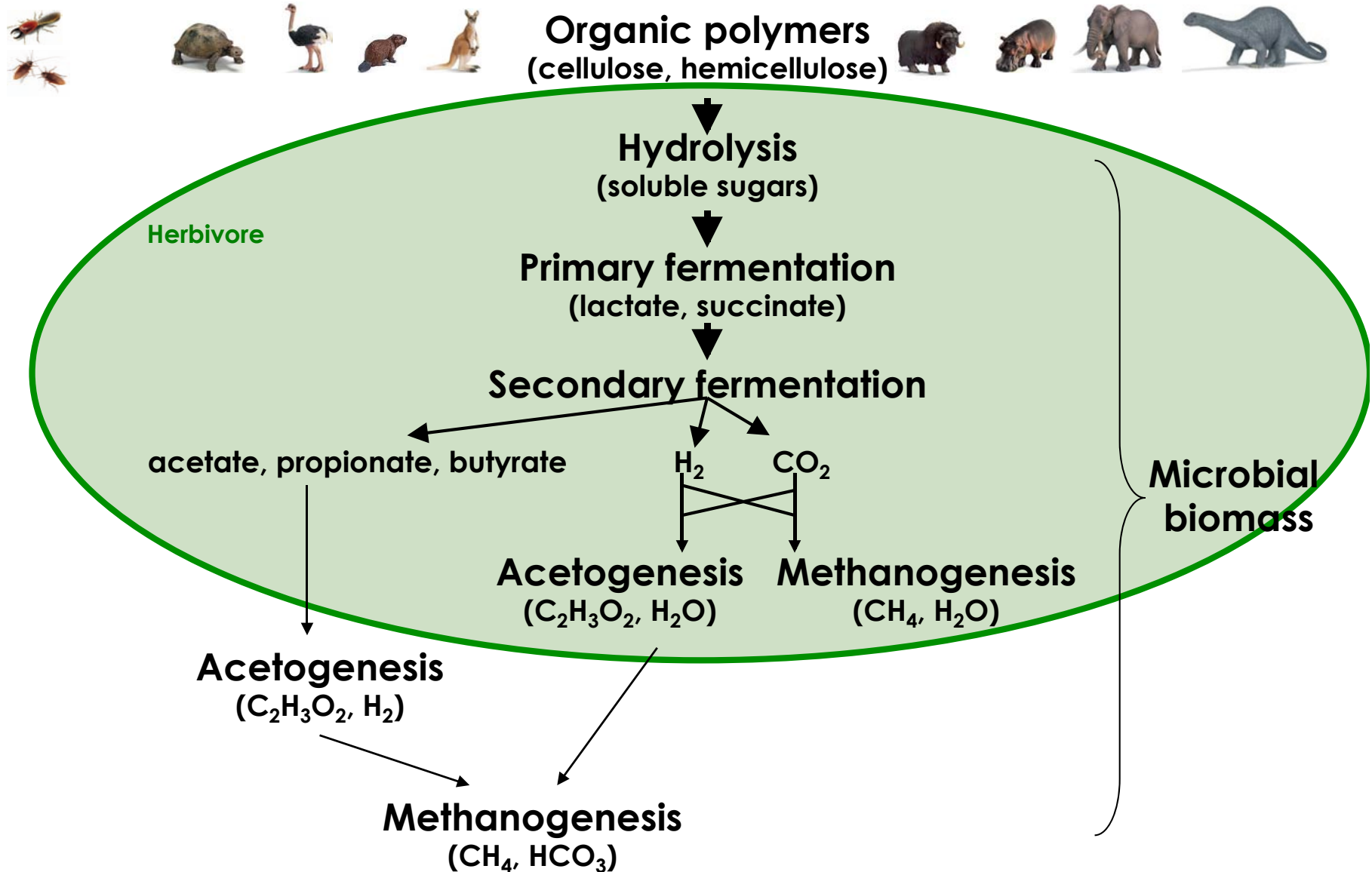


# Fibre digestion



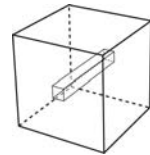


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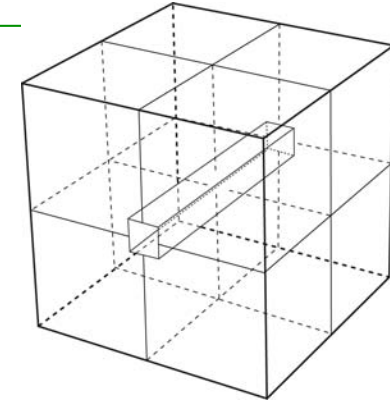




# Surface/volume geometry



**6:1**



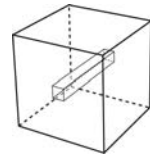
**24:8=3:1**

*... affects all surface-related processes*

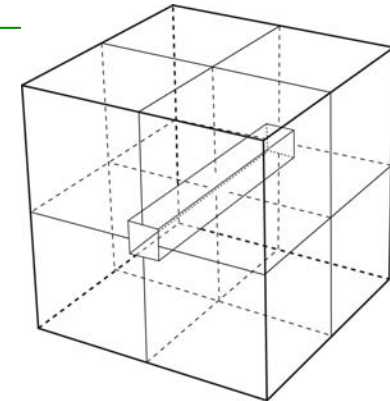
**heat loss**   **----->**   **energy requirements**   **----->**   **food intake**



# Surface/volume geometry

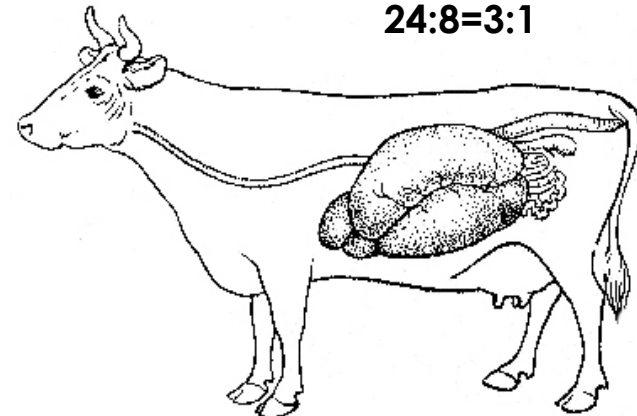
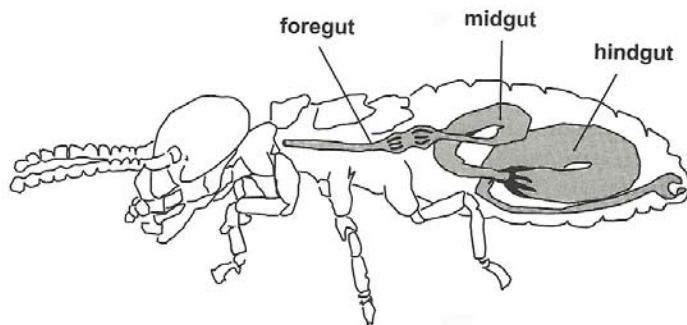


**6:1**



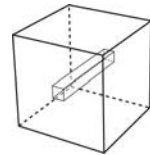
**24:8=3:1**

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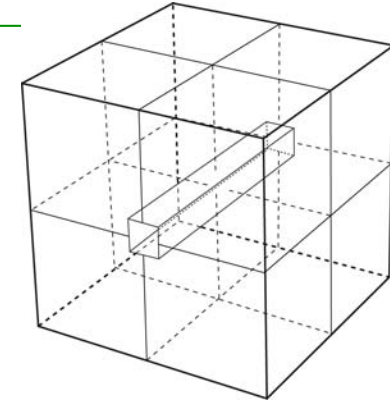




# Surface/volume geometry

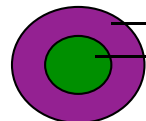
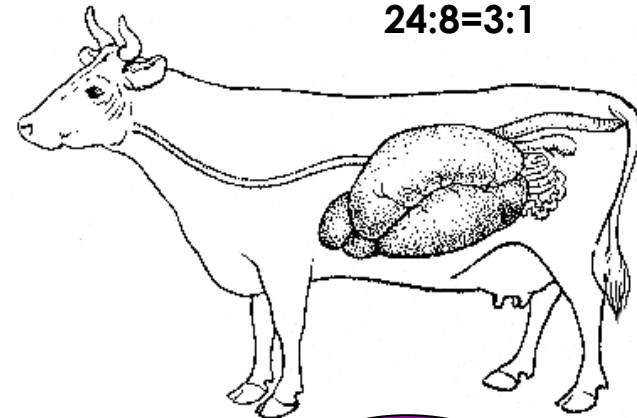
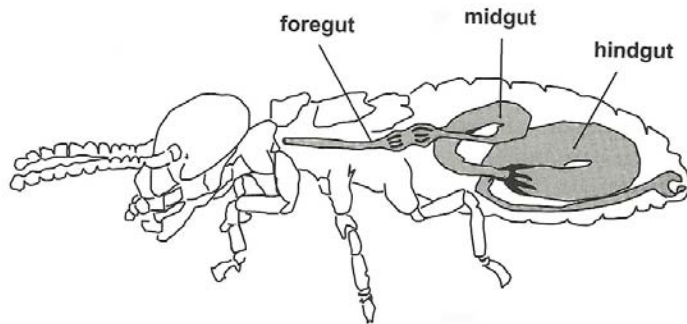


6:1



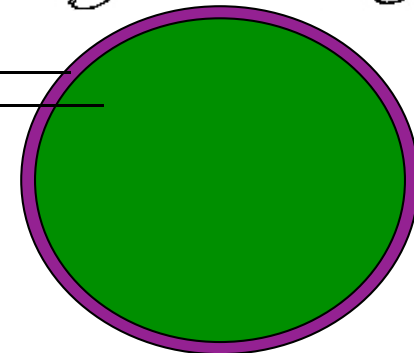
24:8=3:1

... affects all surface-related processes



oxic  
anoxic

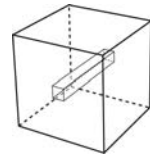
gut contents



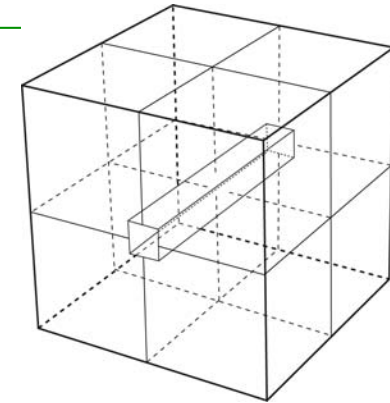




# Surface/volume geometry

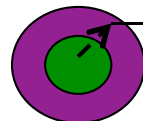
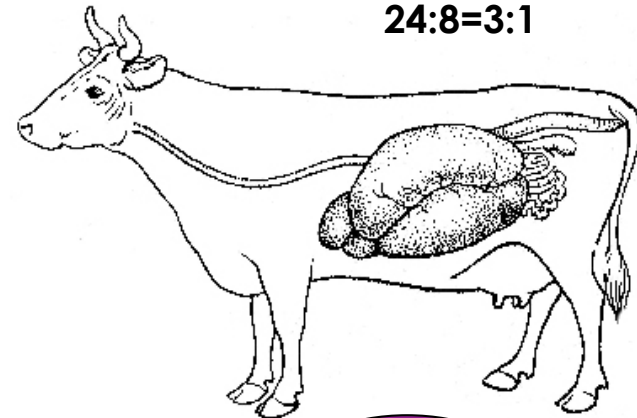
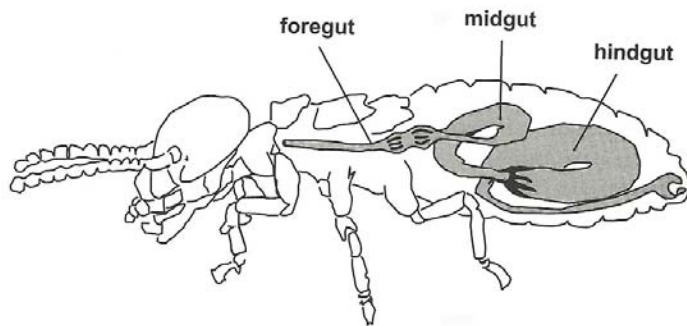


6:1



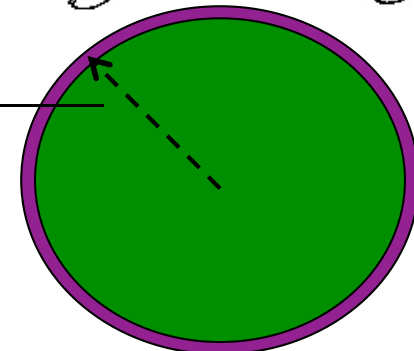
24:8=3:1

... affects all surface-related processes



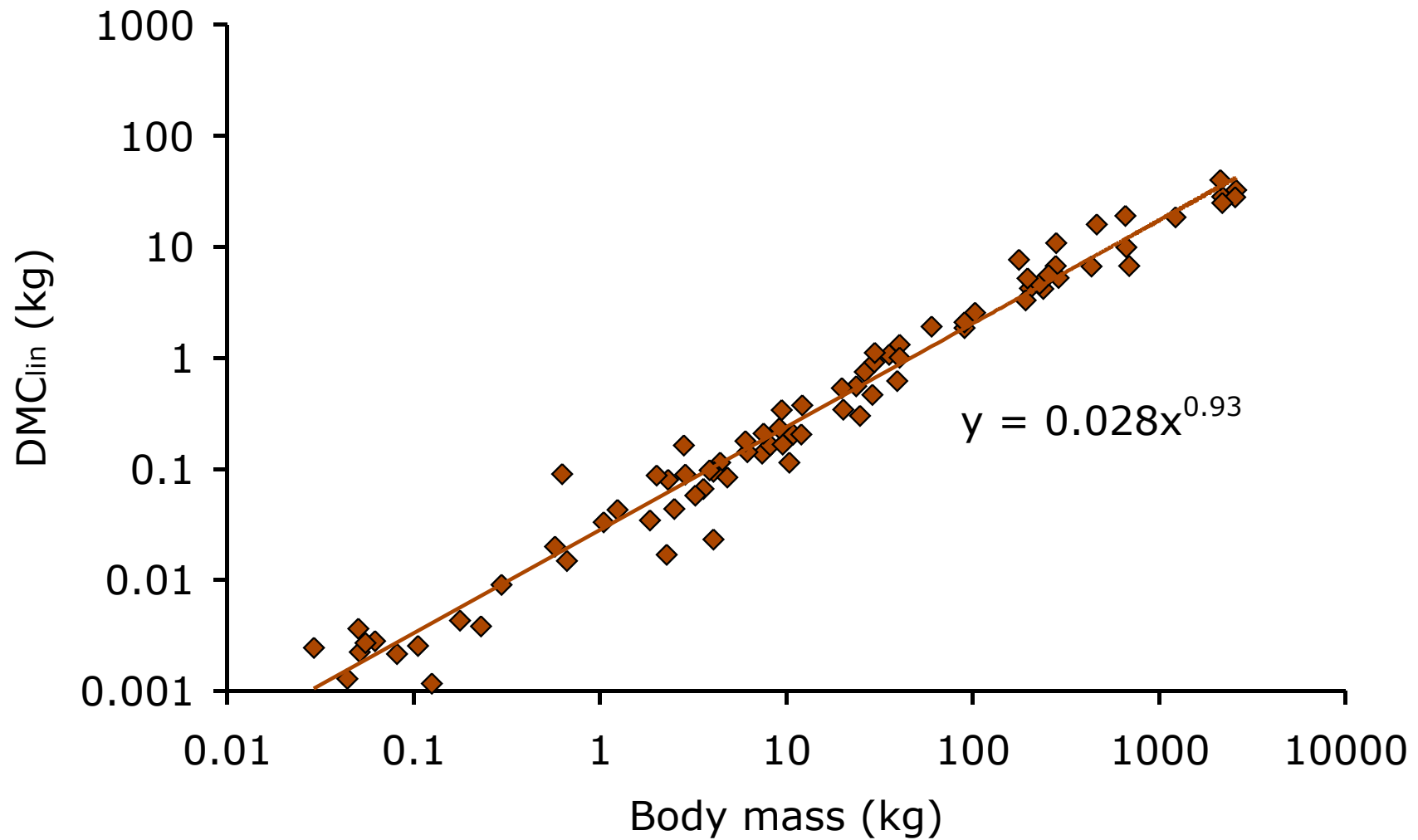
short  
long

diffusion ways



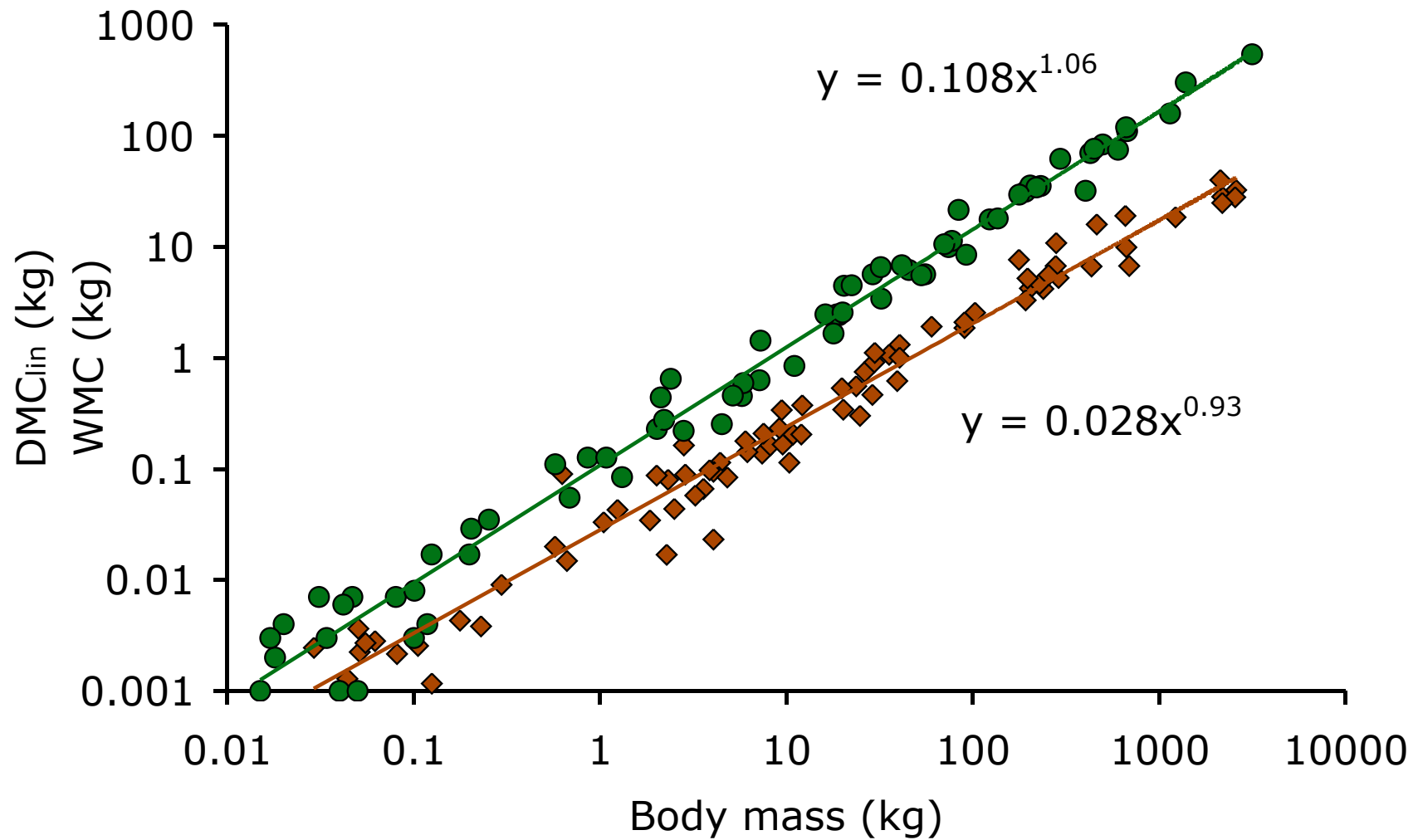


# Gut moisture content



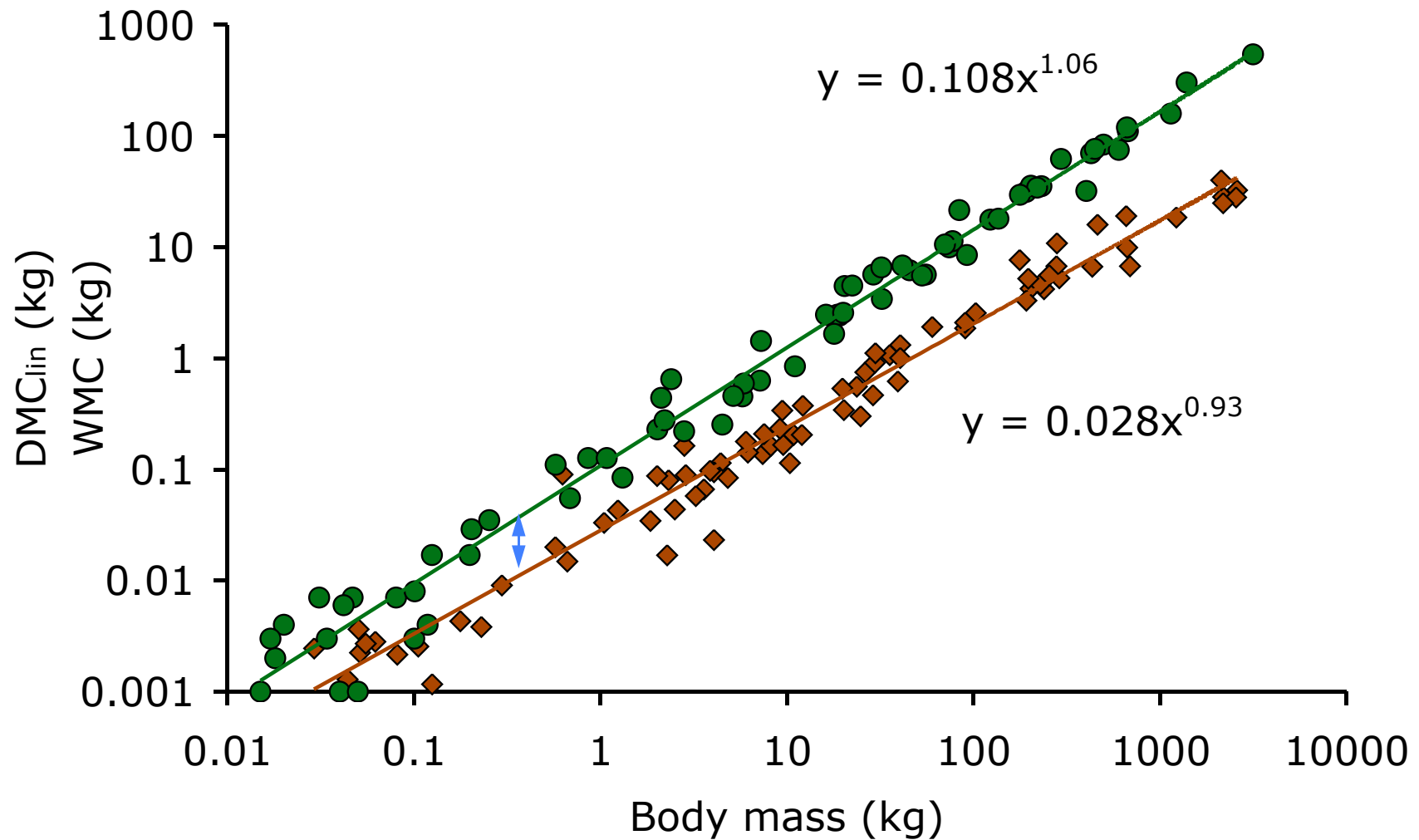


# Gut moisture content



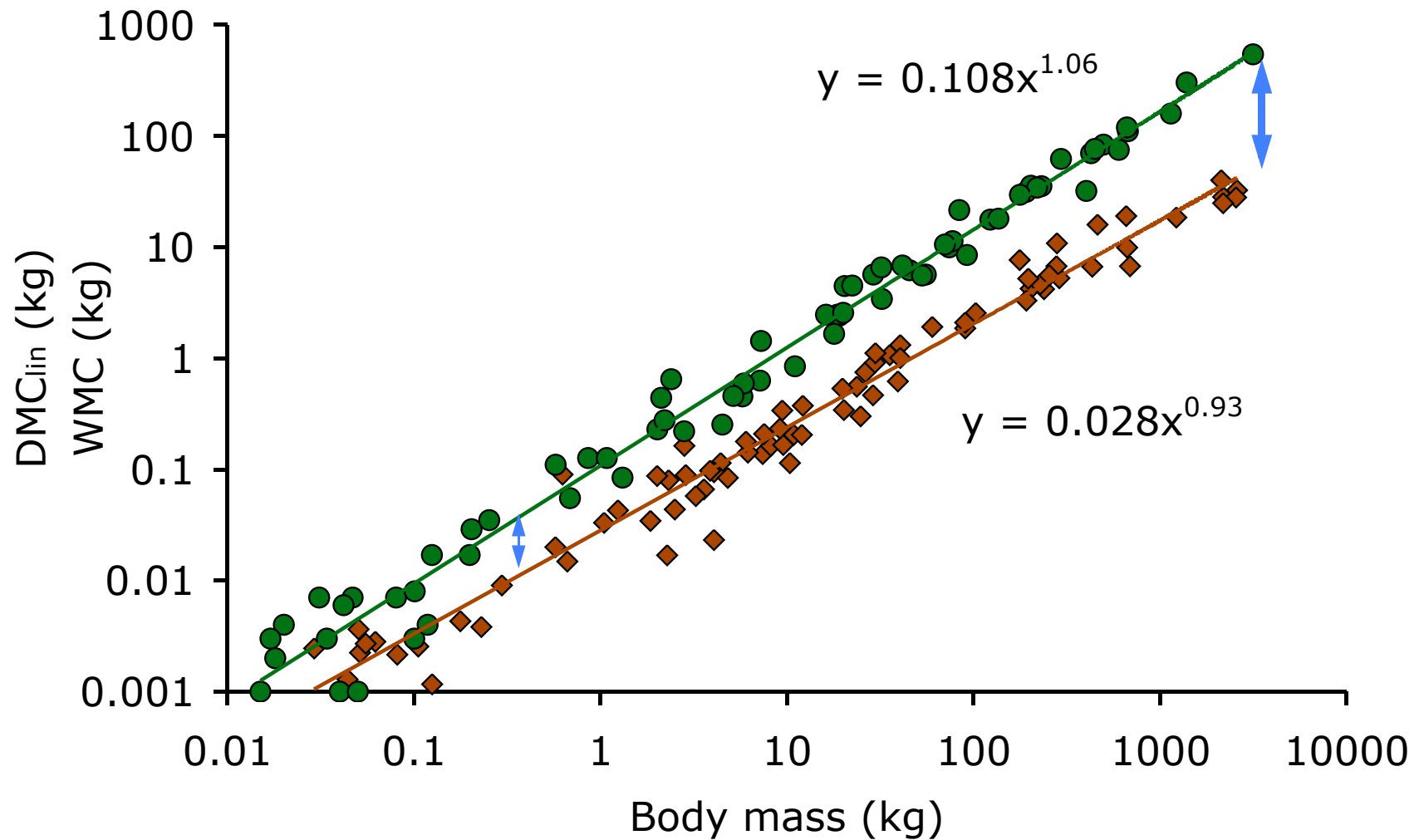


# Gut moisture content



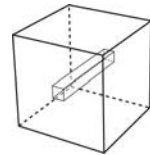


# Gut moisture content

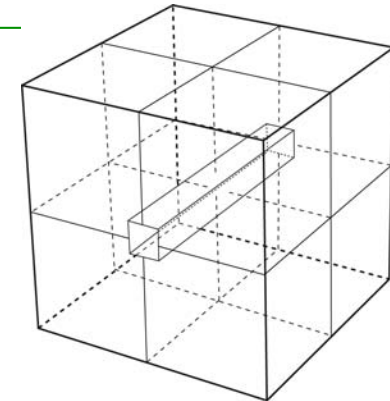




# Surface/volume geometry

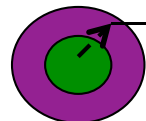
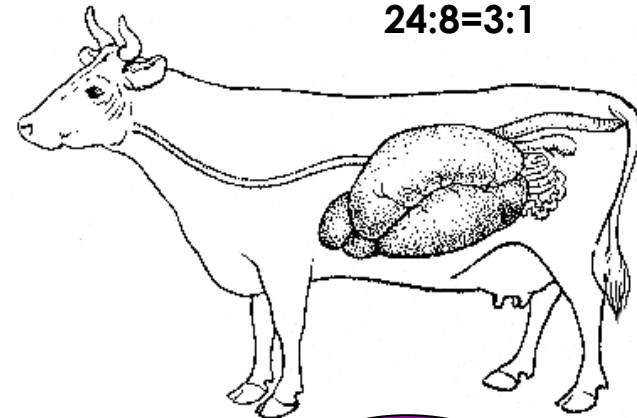
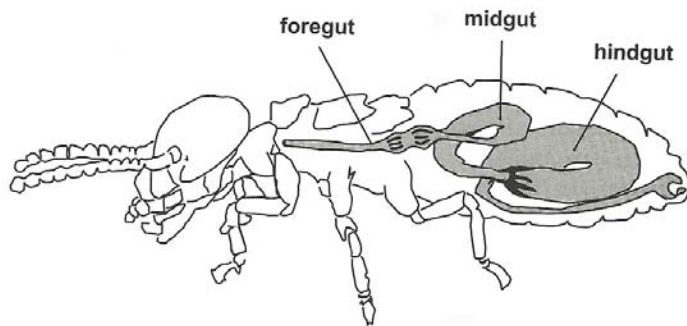


6:1



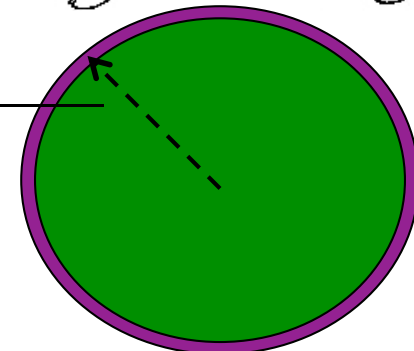
24:8=3:1

... affects all surface-related processes



short  
long

diffusion ways







# *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*

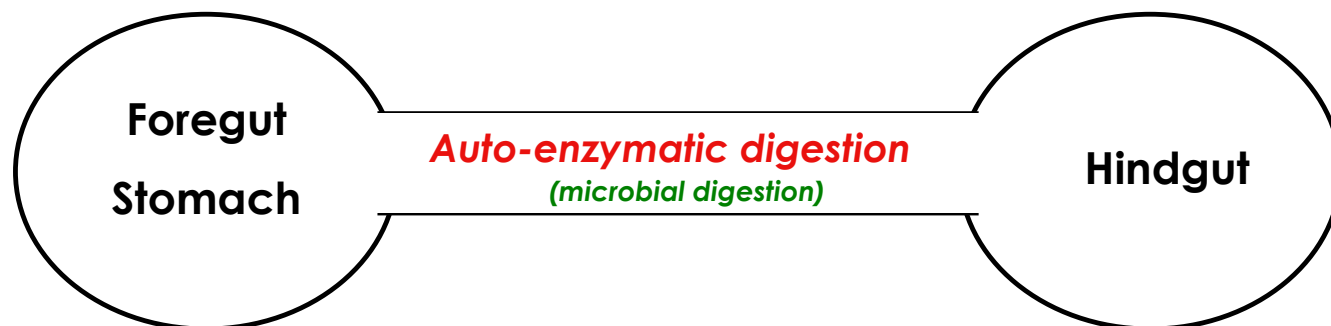




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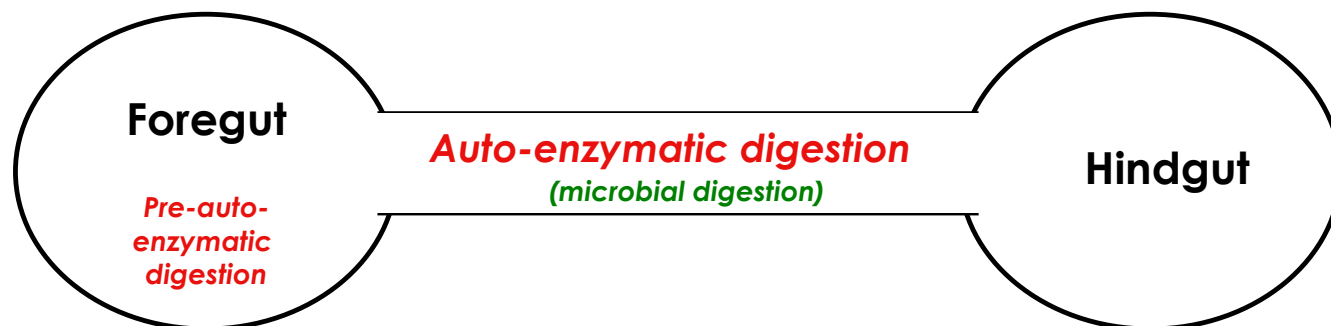




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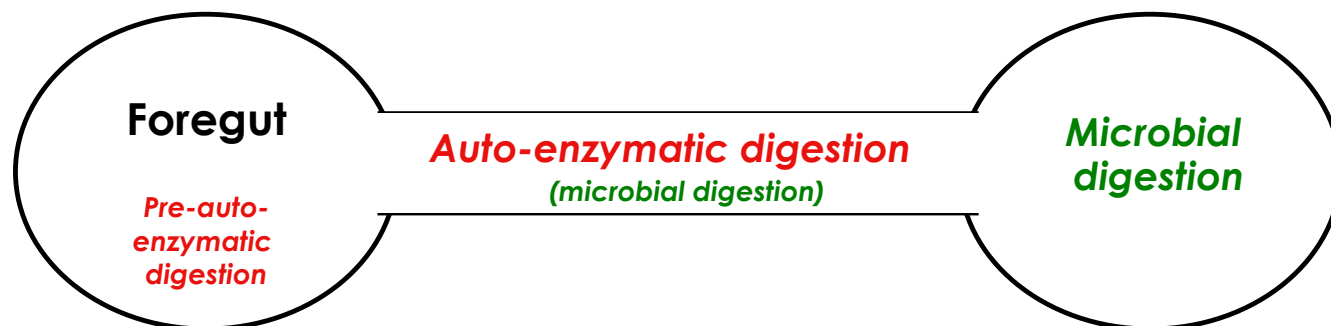




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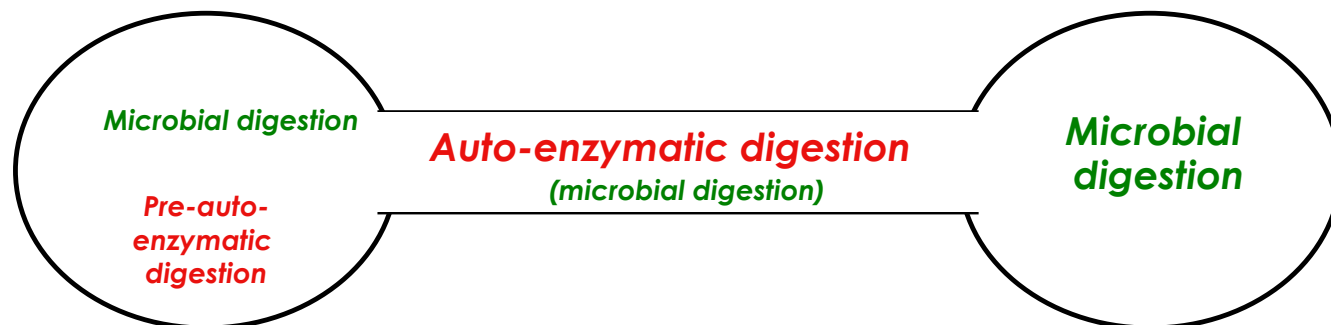




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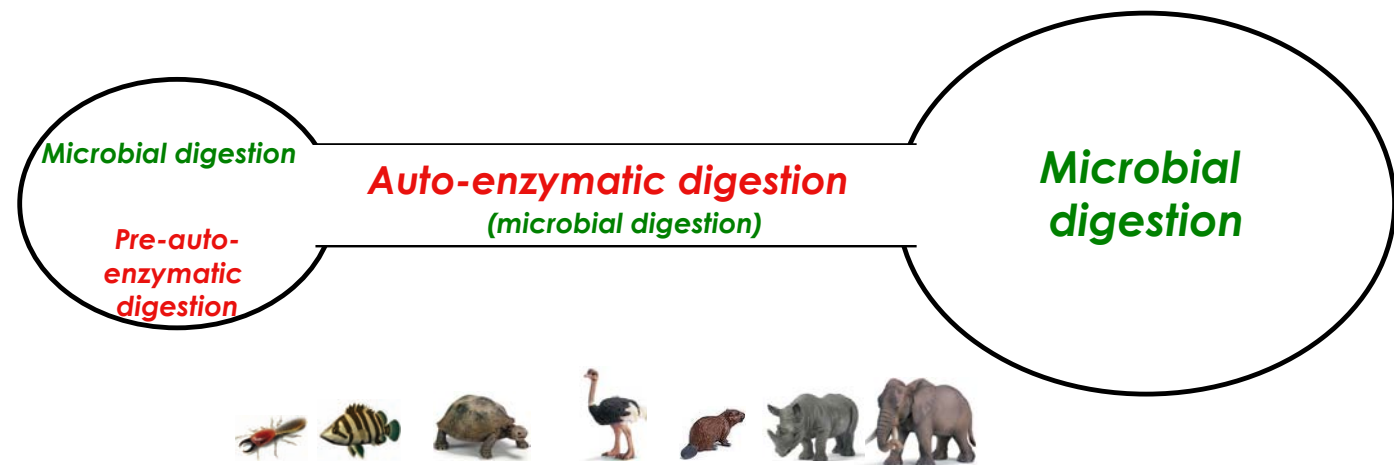




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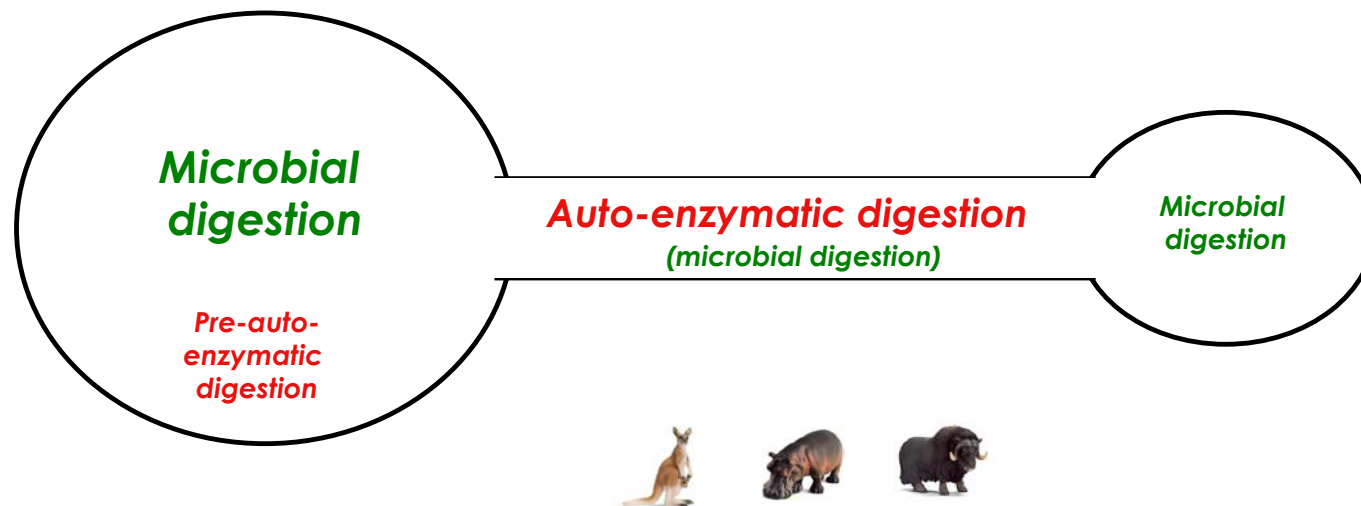




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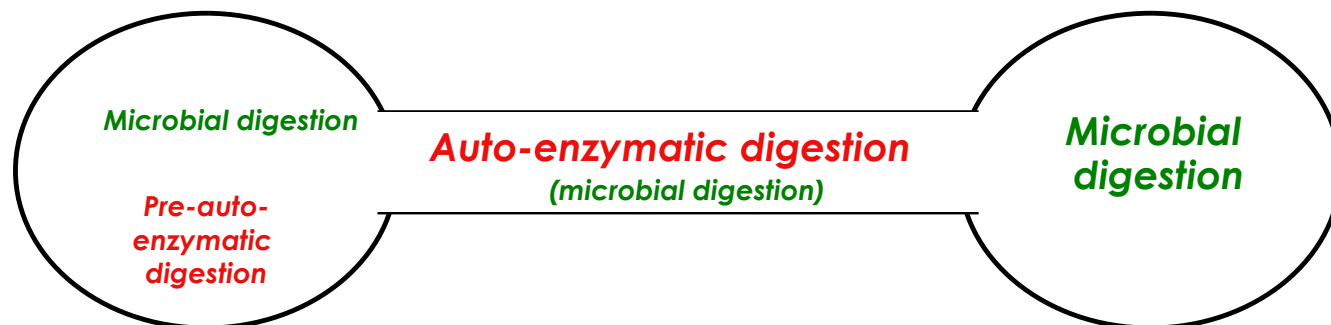




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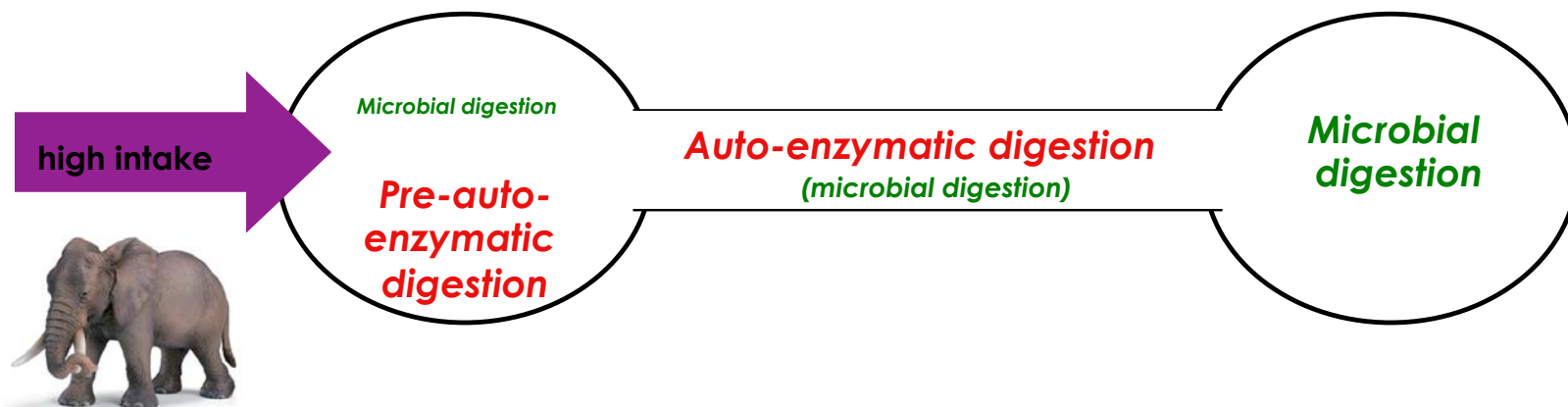




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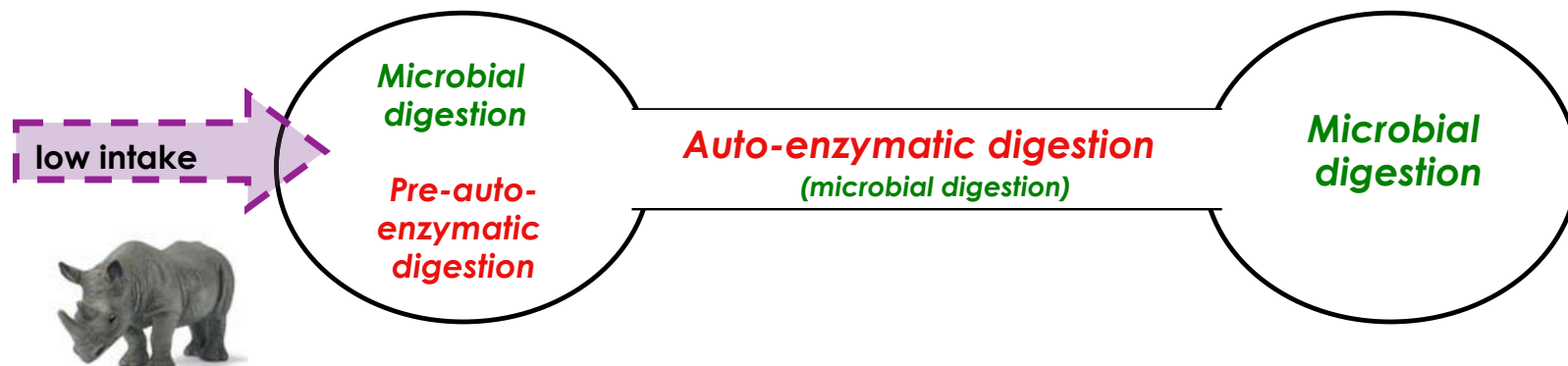




# Two fundamental questions

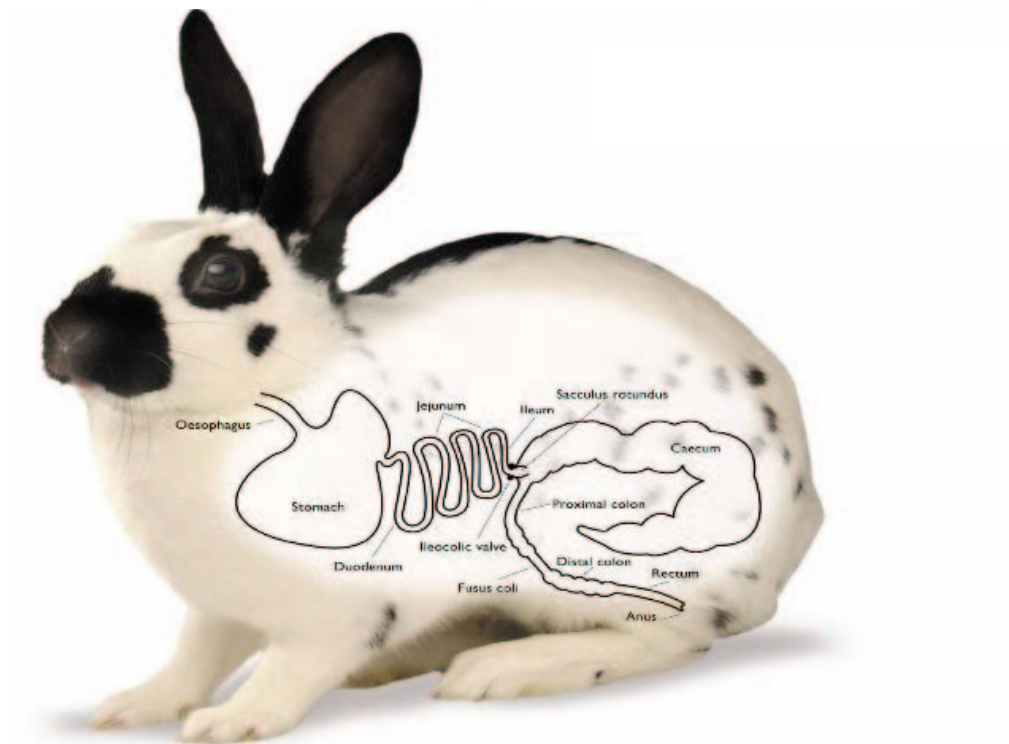
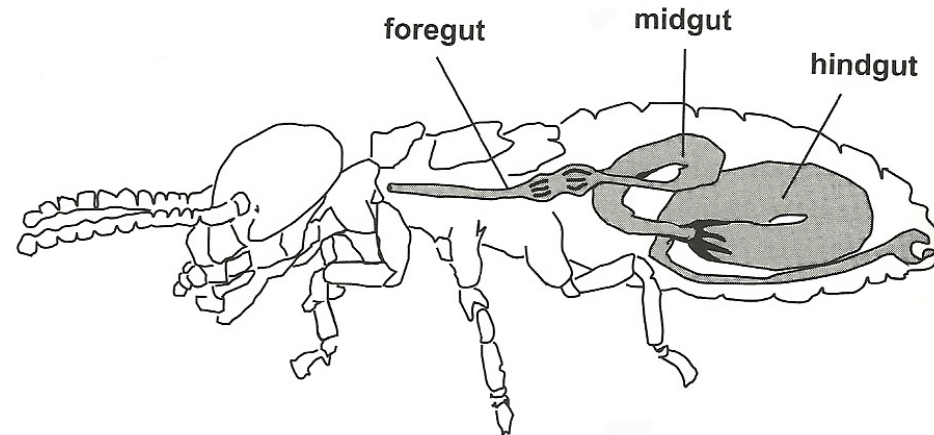
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# Hindgut fermentation - 'the conventional approach'



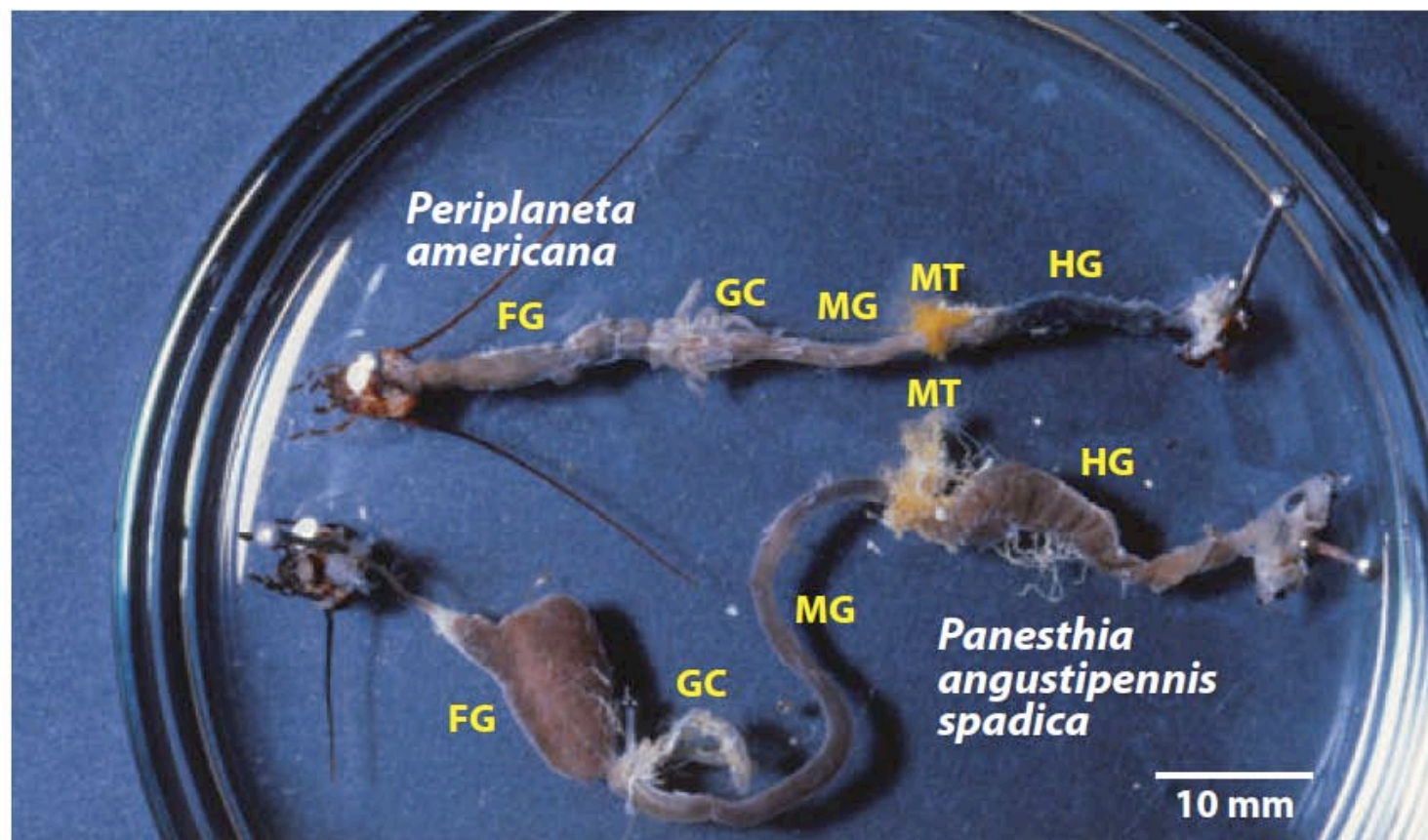




# Cellulolytic Systems in Insects

Hirofumi Watanabe<sup>1</sup> and Gaku Tokuda<sup>2</sup>

Annu. Rev. Entomol. 2010. 55:609–32

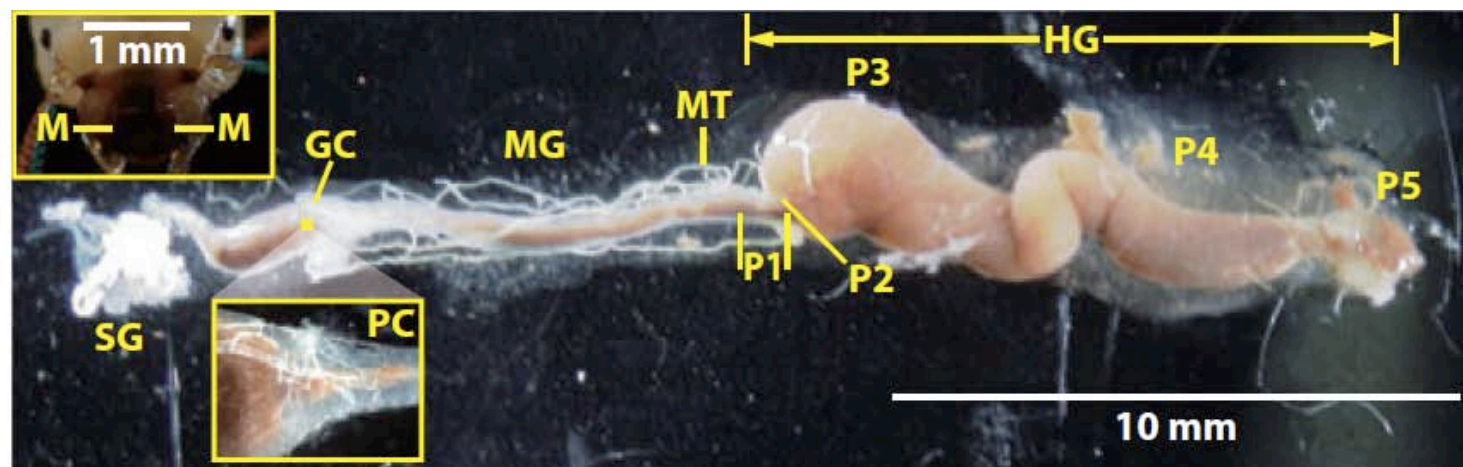
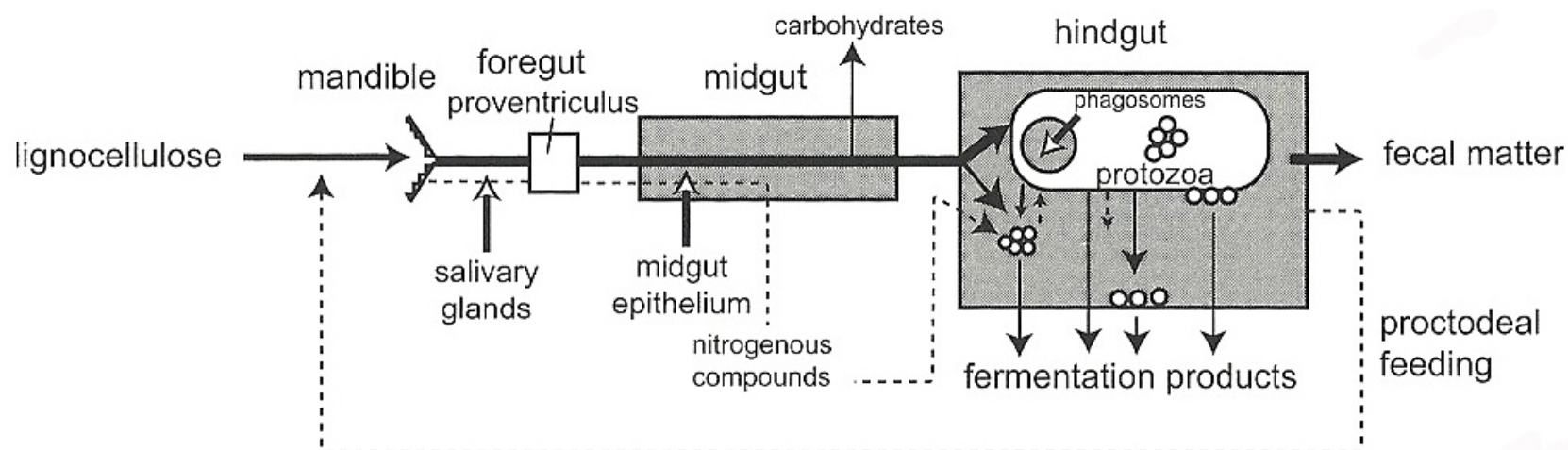




# Cellulolytic Systems in Insects

Hirofumi Watanabe<sup>1</sup> and Gaku Tokuda<sup>2</sup>

Annu. Rev. Entomol. 2010. 55:609–32



scheme from Karasov & Martinez del Rio (2007)





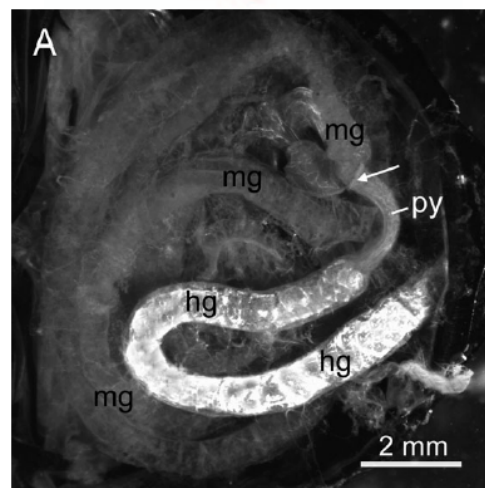
# Elongated Hindguts in Desert-Living Dung Beetles (Scarabaeidae: Scarabaeinae) Feeding on Dry Dung Pellets or Plant Litter

Peter Holter<sup>1\*</sup> and Clarke H. Scholtz<sup>2</sup>

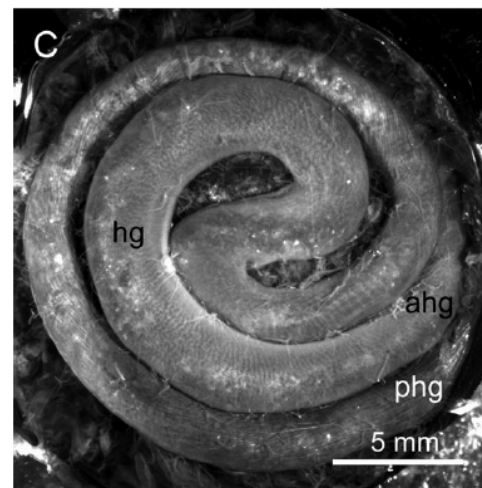
JOURNAL OF MORPHOLOGY 274:657–662 (2013)



*Scarabaeus* spp.  
(fresh dung)



*Pachysoma* spp.  
(plant litter)

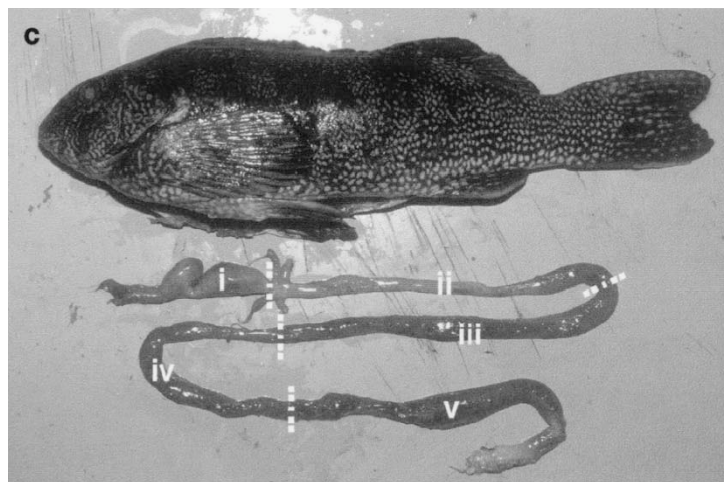
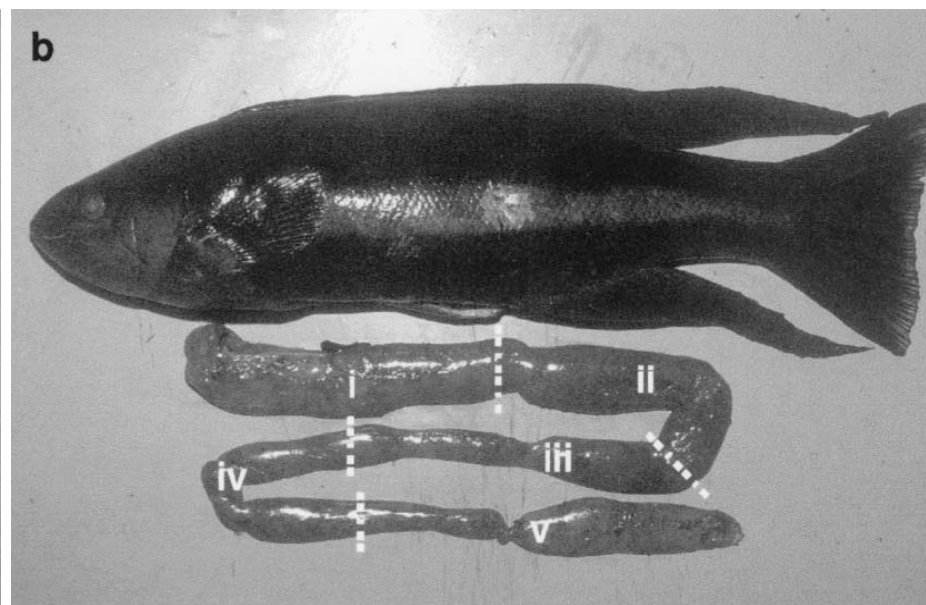
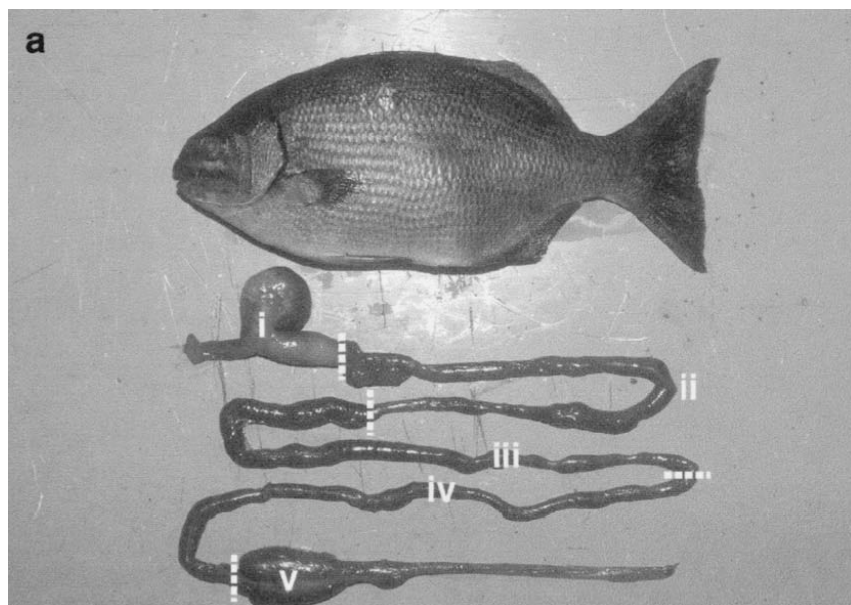




# Hindgut Fermentation in Three Species of Marine Herbivorous Fish

Douglas O. Mountfort,<sup>1\*</sup> Jane Campbell,<sup>2</sup> and Kendall D. Clements<sup>2</sup>

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





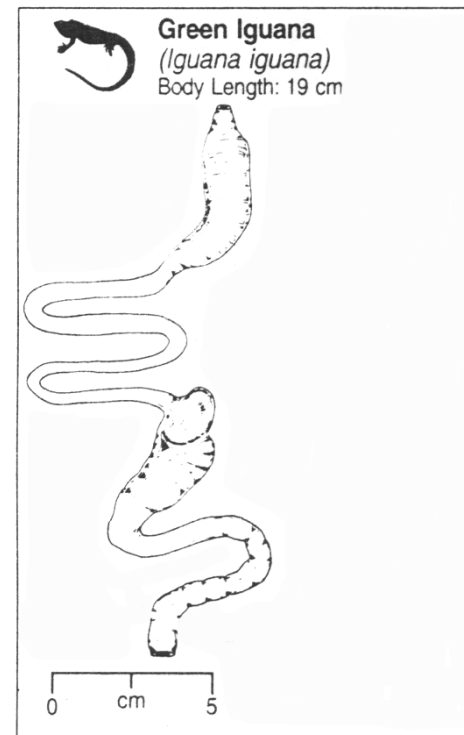
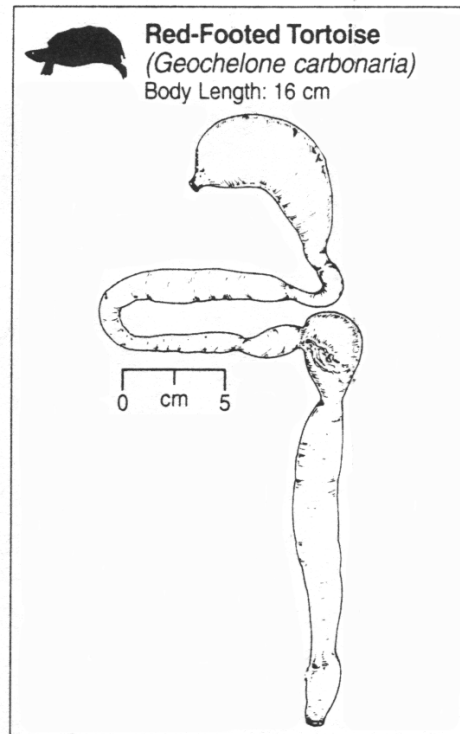


# Herbivorous fish





# Hindgut Fermentation - Reptiles

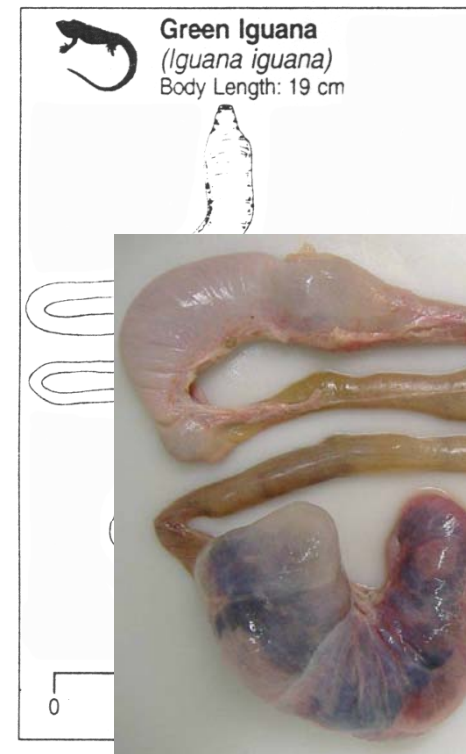
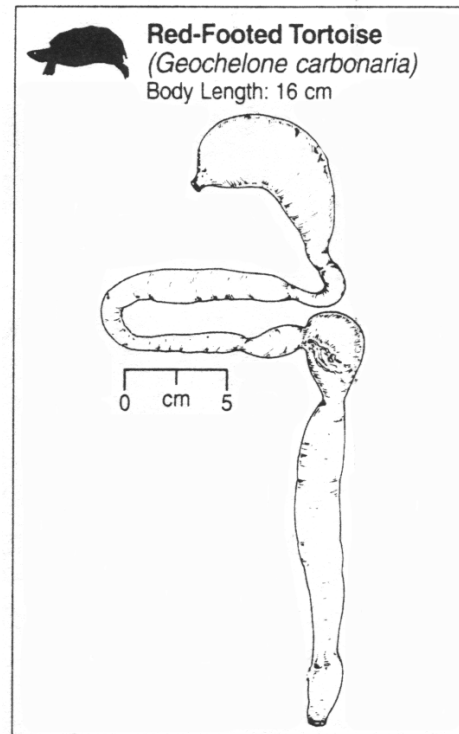


from Stevens & Hume (1995)





# Hindgut Fermentation - Reptiles

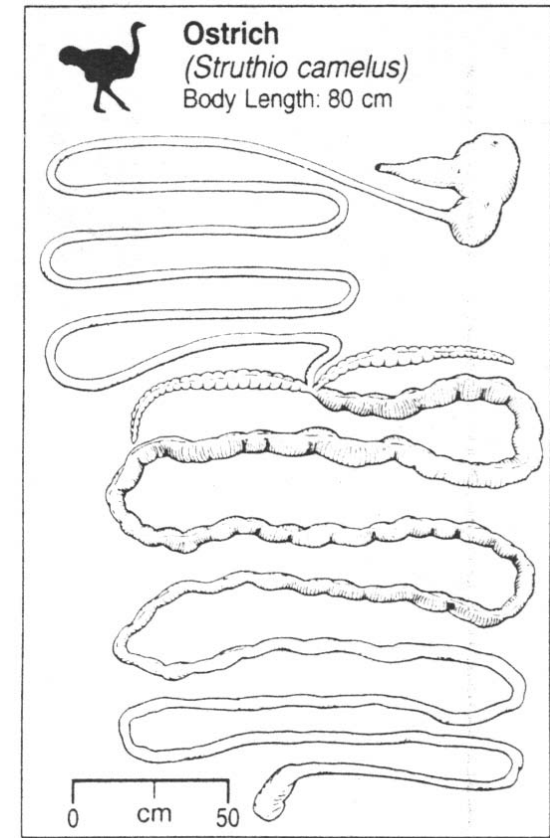
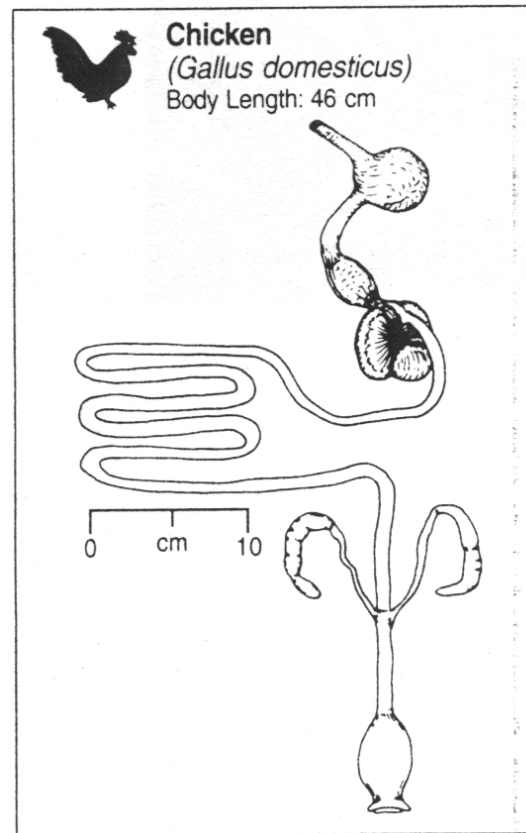
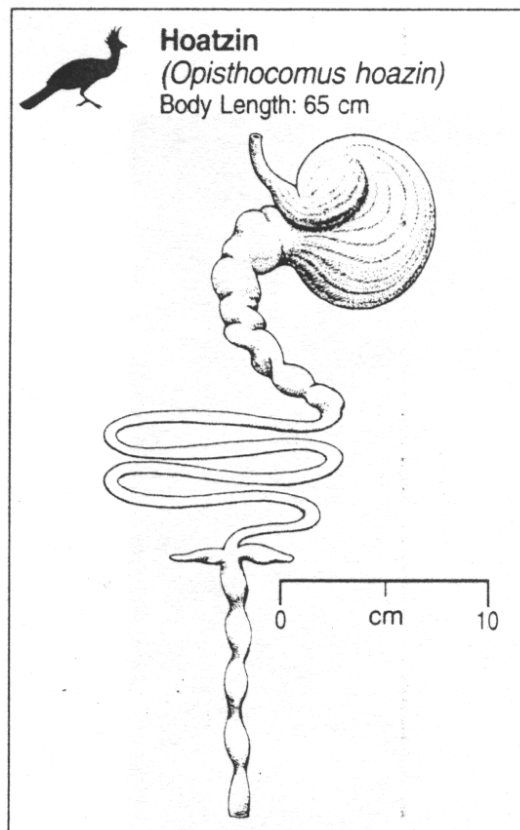


from Stevens & Hume (1995)

Photo: J. Fritz



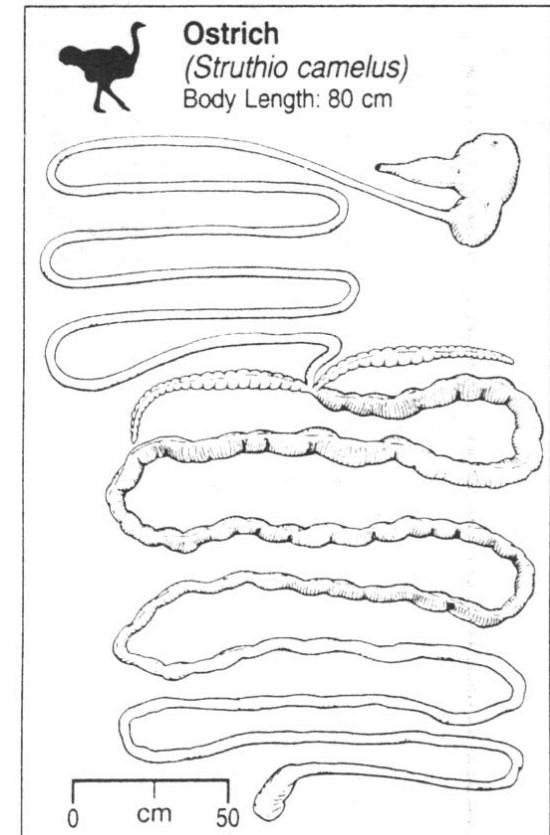
# Herbivores - Birds



from Stevens und Hume (1995)



# Herbivores - Birds



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





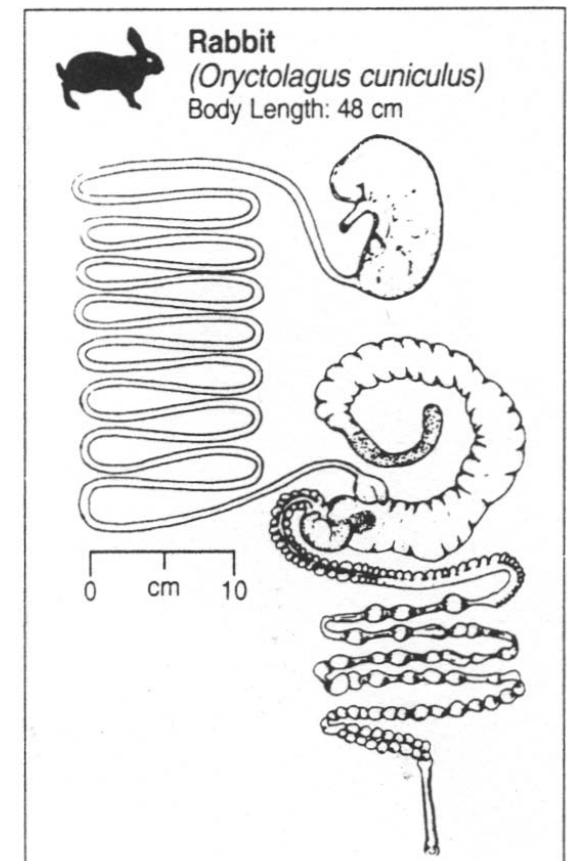
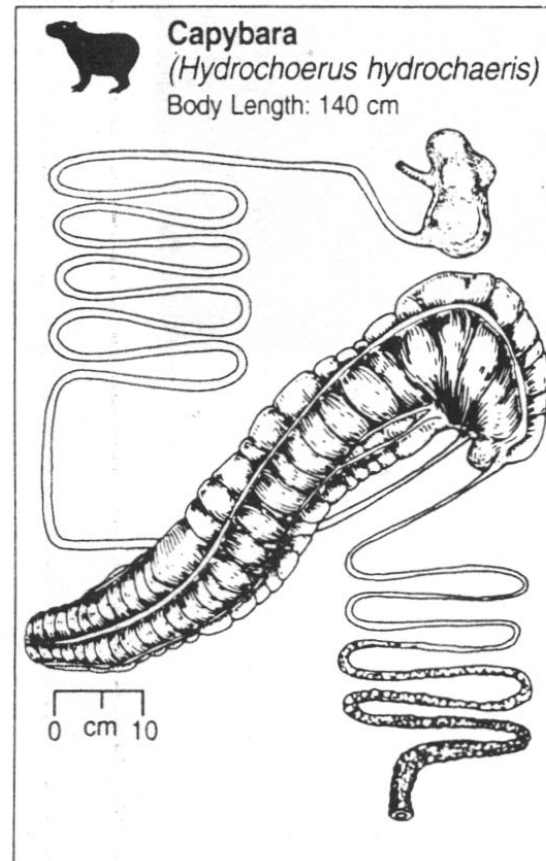
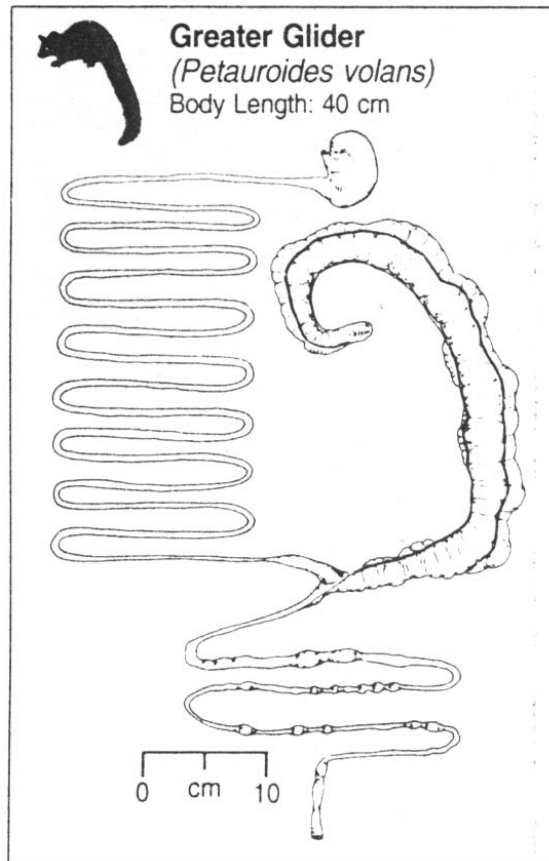
# Herbivores - Birds



Photos: J. Fritz



# Hindgut Fermentation - Caecum

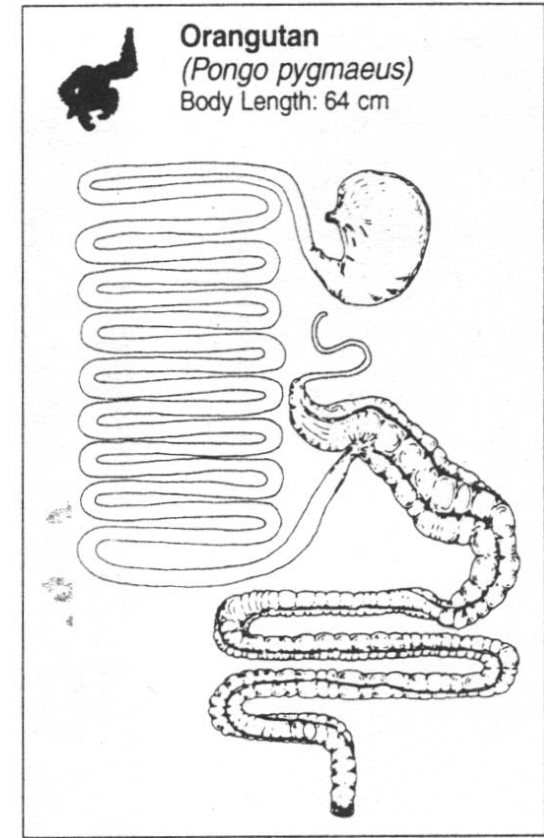
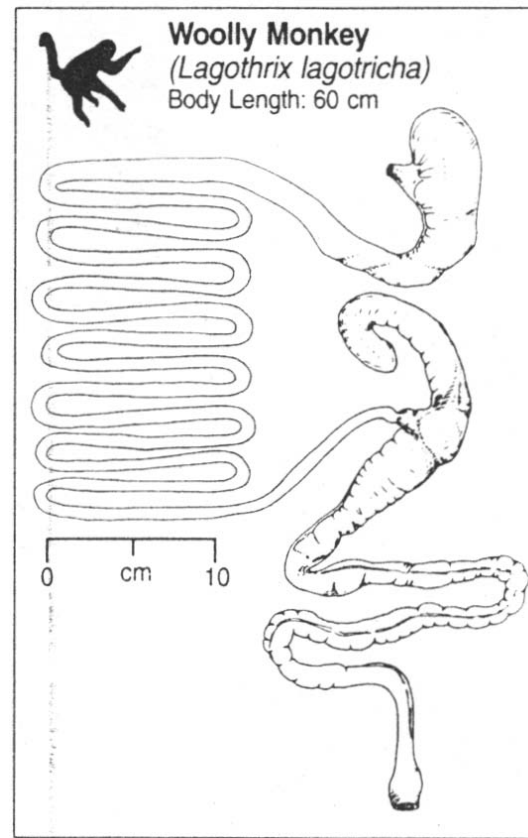
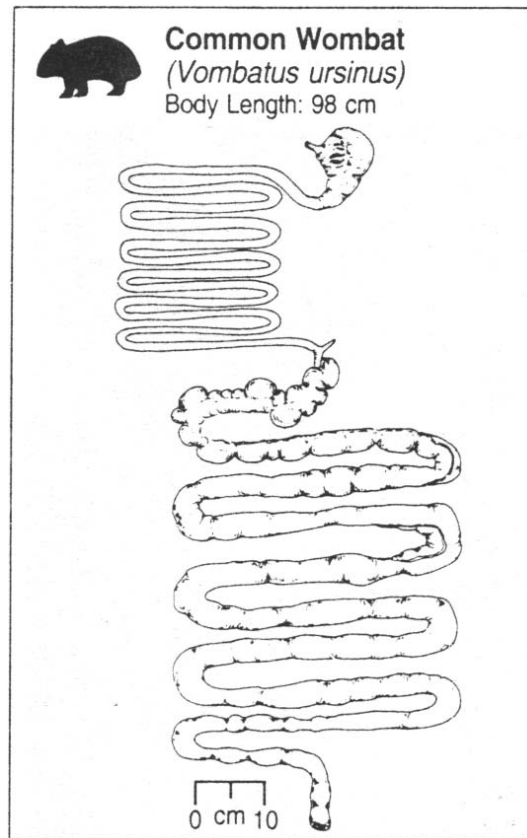


from Stevens & Hume (1995)





# Herbivores - Colon fermenters

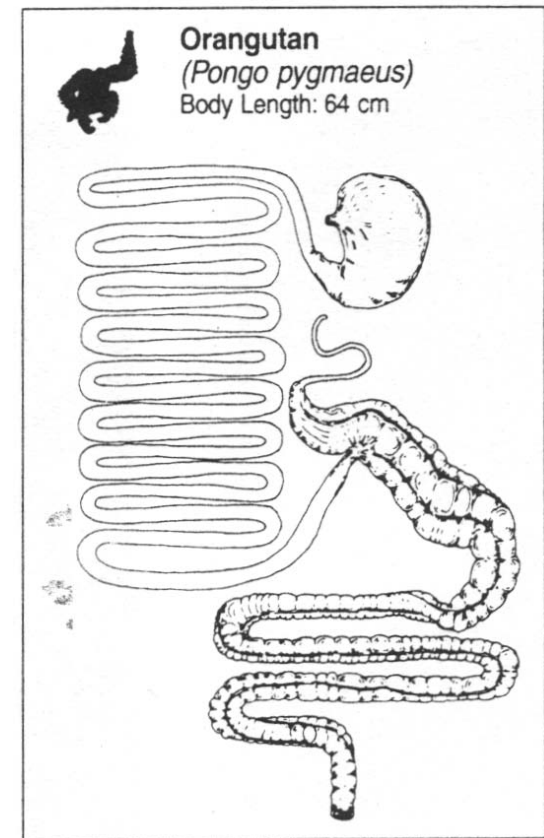
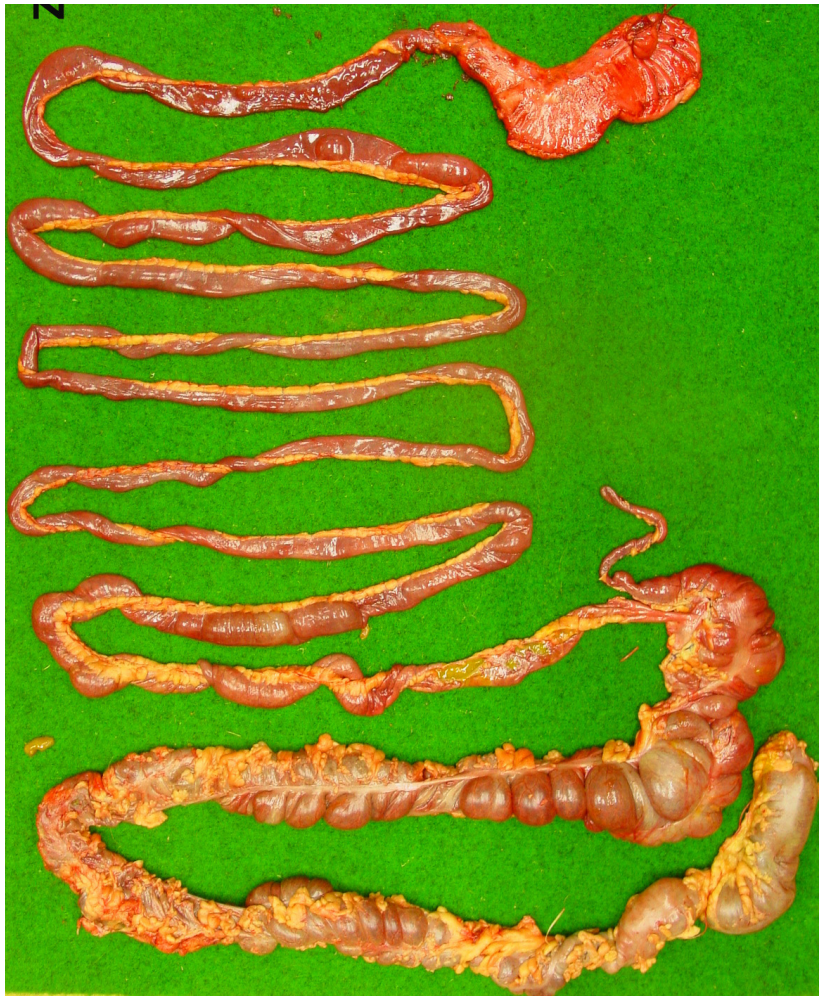


from Stevens und Hume (1995)





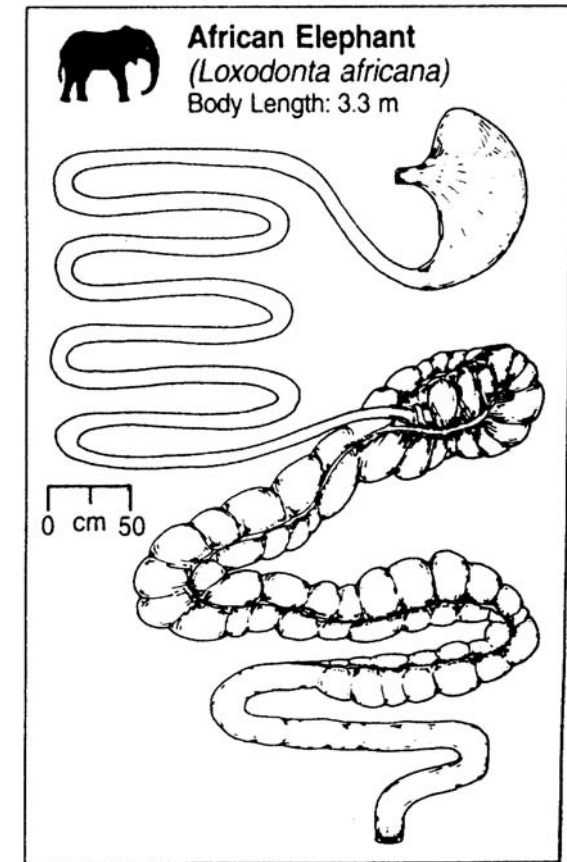
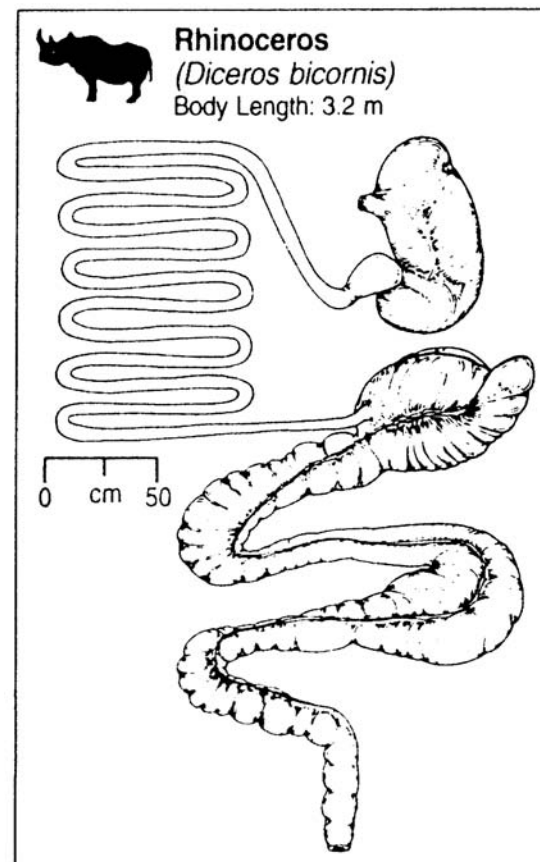
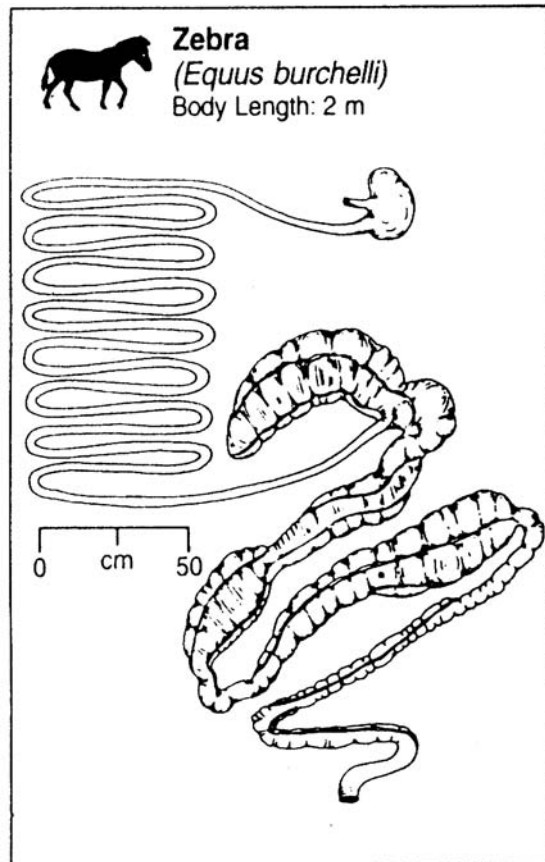
# Herbivores - Colon fermenters



from Stevens und Hume (1995)  
Photo: M. Clauss



# Hindgut Fermentation - Colon

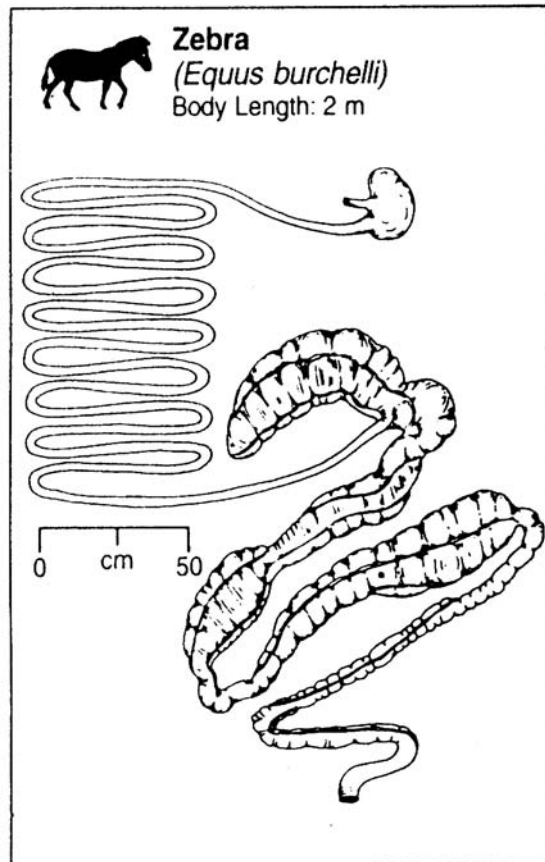


from Stevens & Hume (1995)





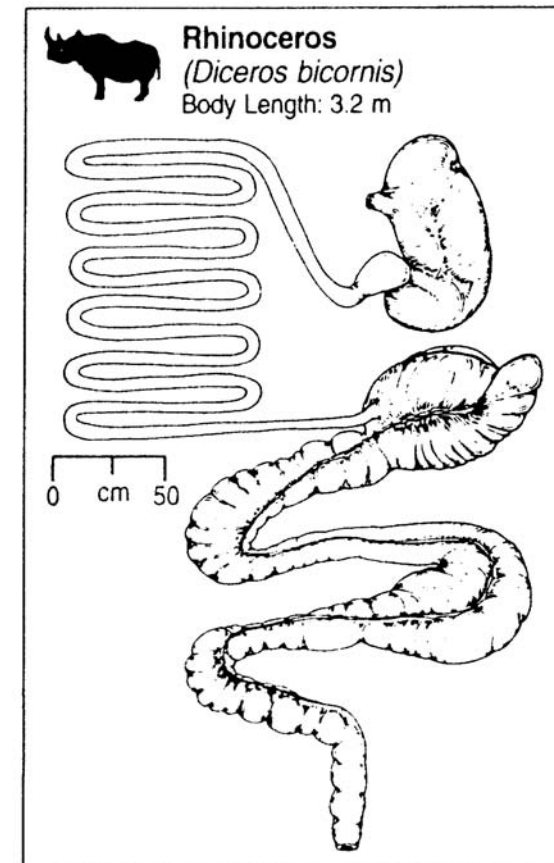
# Hindgut Fermentation - Colon



from Stevens & Hume (1995)



# Hindgut Fermentation - Colon

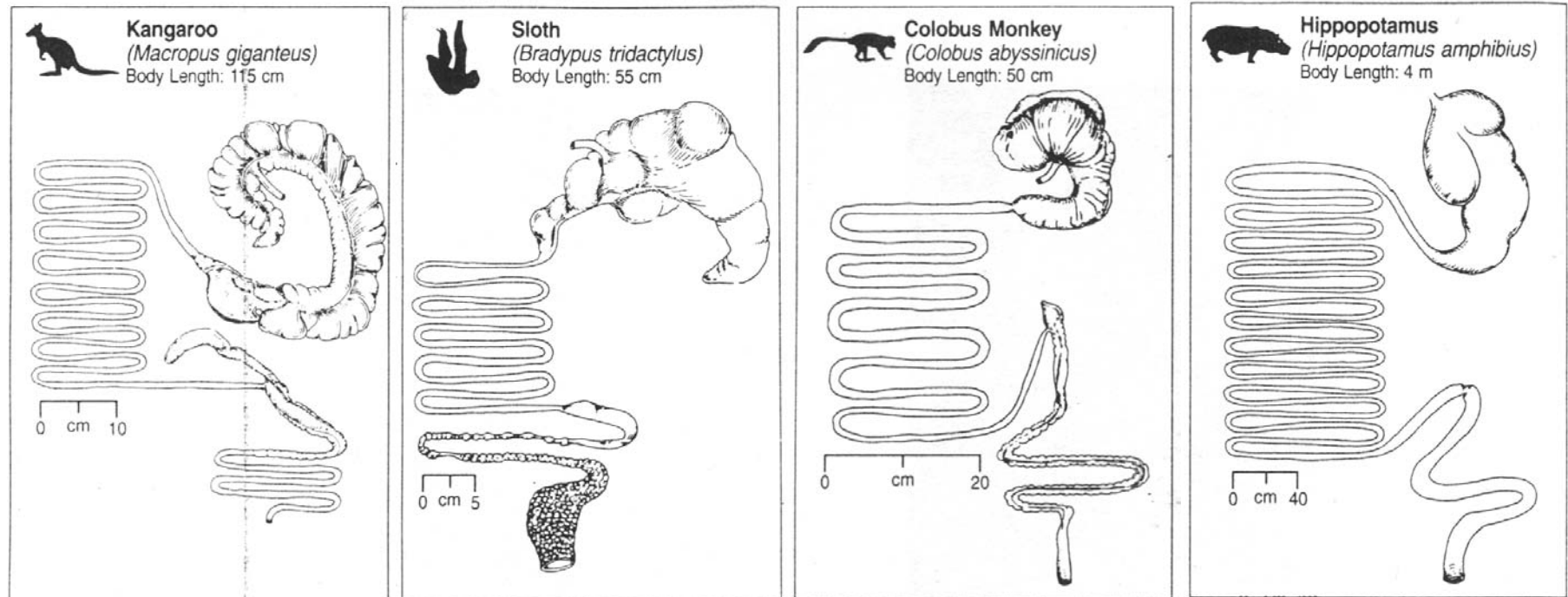


from Stevens & Hume (1995)  
White rhino photo: D. Müller





# Foregut Fermentation



from Stevens & Hume (1995)



# Foregut Fermentation



Photos A. Schwarm/  
M. Clauss





# Foregut Fermentation

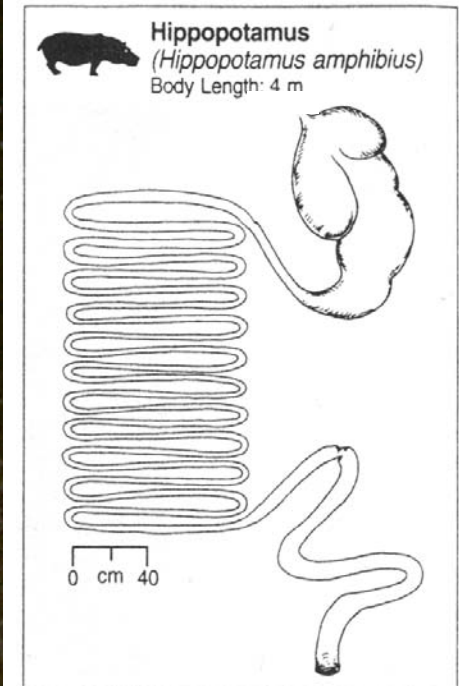


Photo M. Clauss



# Foregut Fermentation

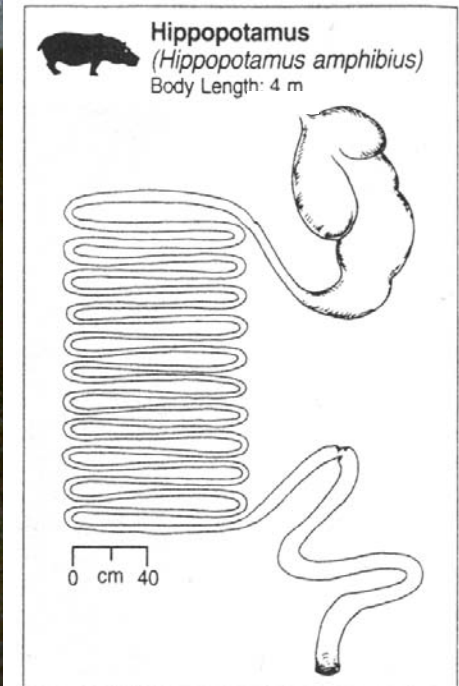
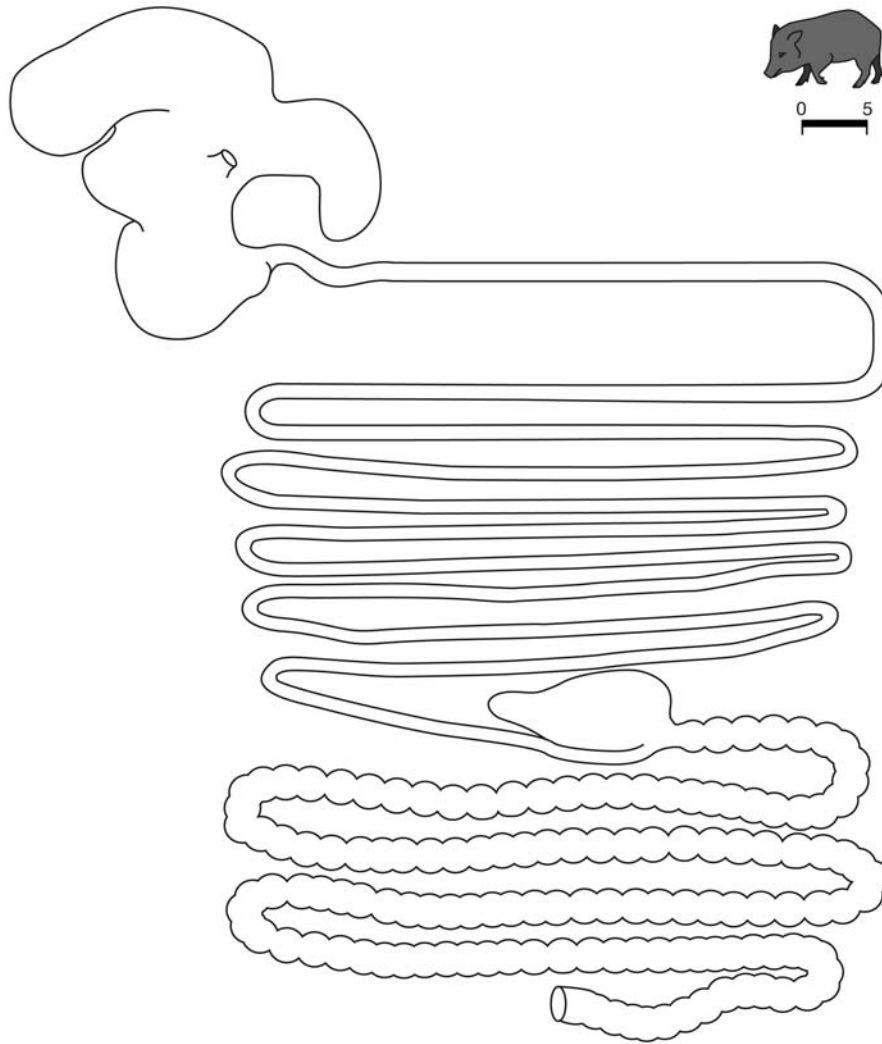


Photo M. Clauss





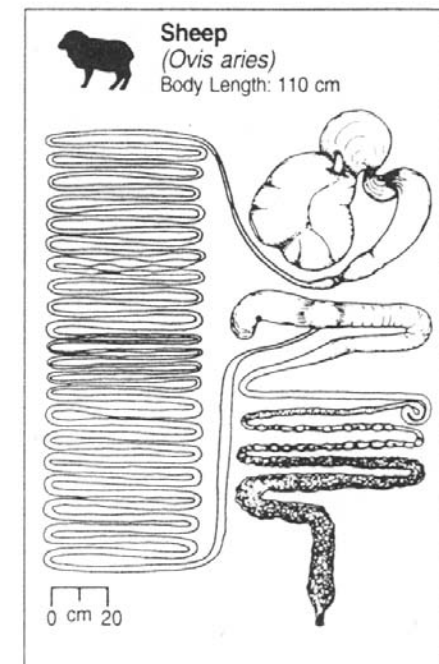
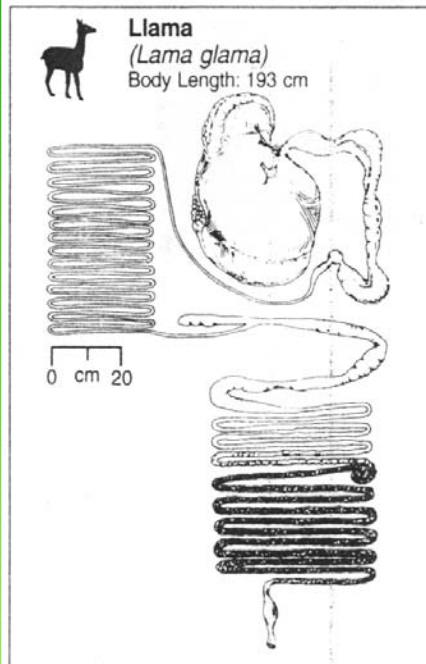
# Herbivores - Foregut fermenters



from Schwarm et al. (in prep.)  
Photo: A. Schwarm



# Foregut Fermentation - Ruminant



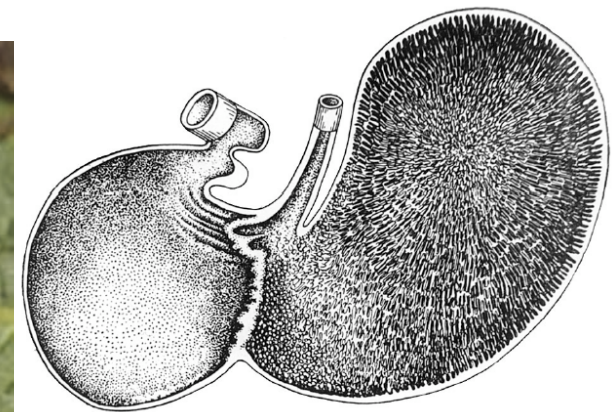
aus Stevens & Hume (1995)  
Photo Llama: A. Riek





# 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)

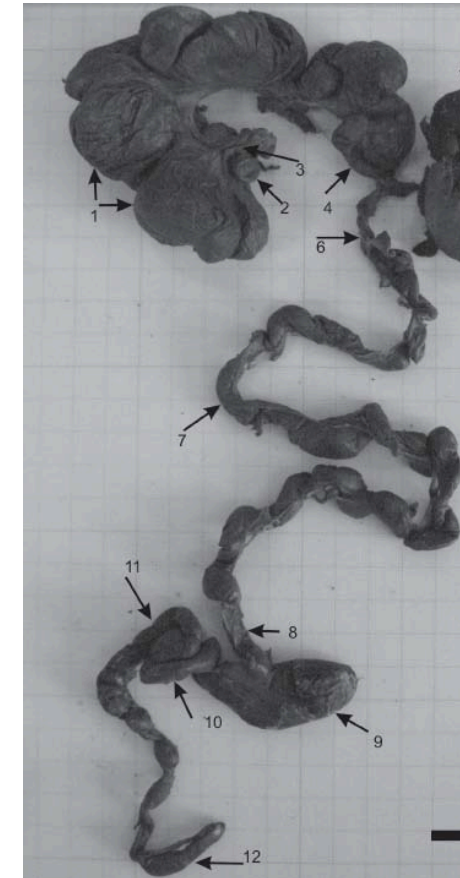


# Foregut/Hindgut Fermenters

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



Laotian rock rat  
(*Laonastes aenigmamus*)  
kangaroo-like forestomach



from Scopin et al. (2011)



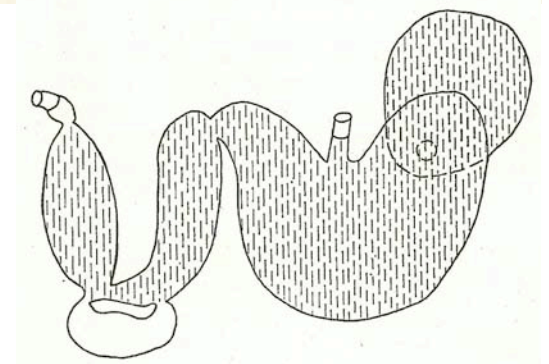
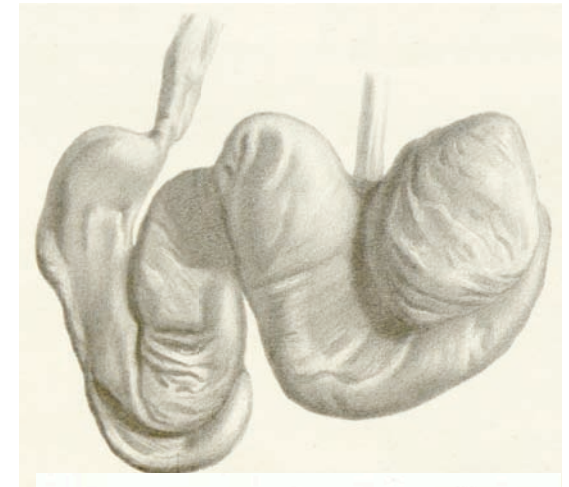


# Foregut/Hindgut Fermenters

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



Maned (crested) rat  
(*Lophiomys imhausi*)  
complex forestomach

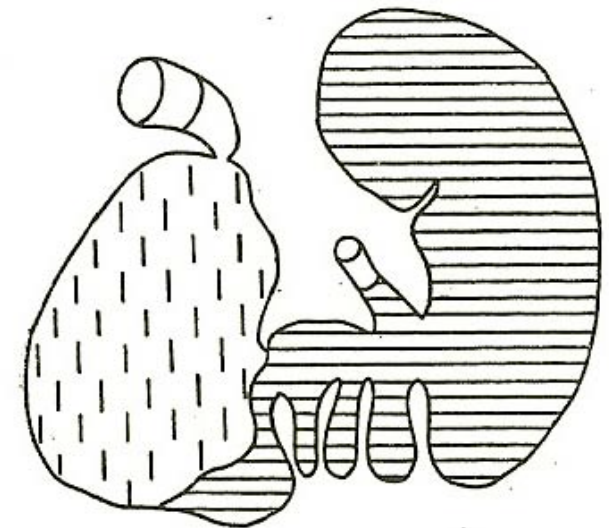


from Vrontsov (1967)



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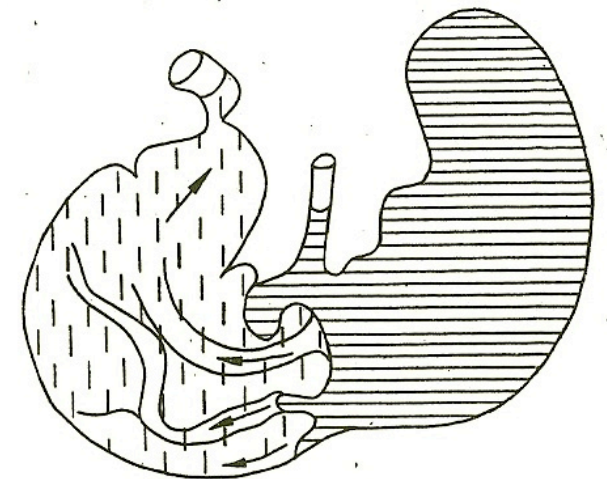
White-tailed ant ( *Brachytarsomys albicauda* )  
complex forestomach

from Vrontsov (1967)



# 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.

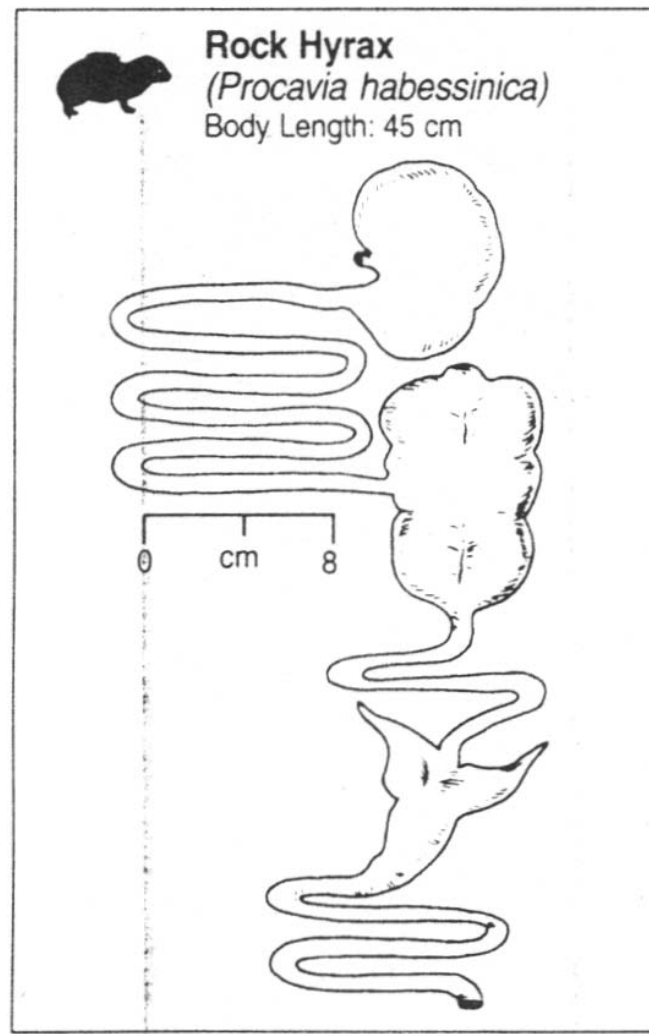


Malagas giant rat  
(*Hypogeomys antimena*)  
complex forestomach

from Vrontsov (1967)



# Herbivores - Hyrax

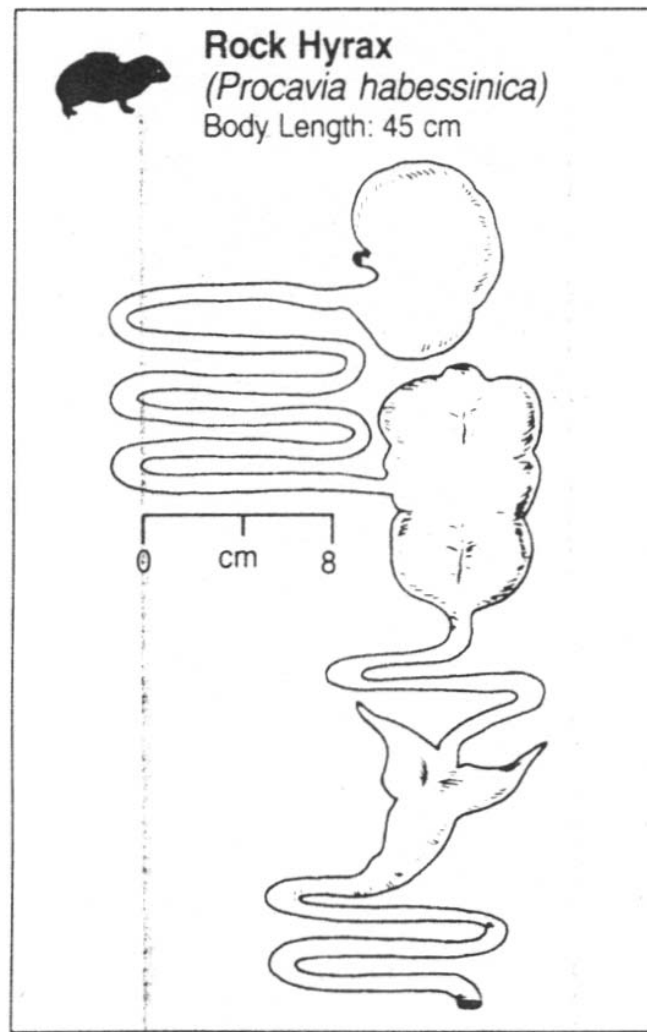


from Stevens und Hume (1995)





# Herbivores - Hyrax



from Stevens und Hume (1995)





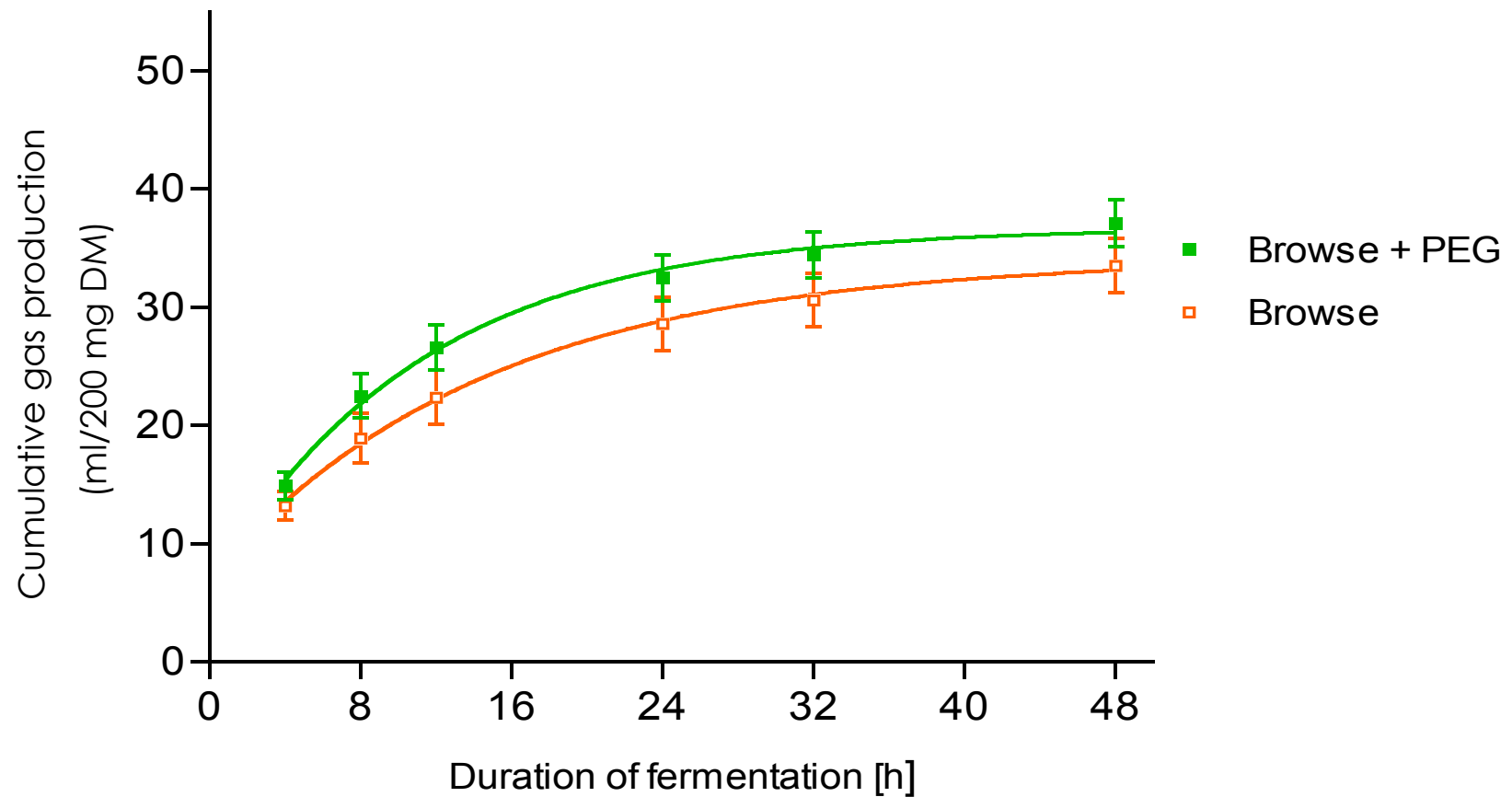
# Analysing for energy in plant material

## ***in vitro* fermentation (gas production)**

- May give a more ☐biological☐estimation (compared to bomb calorimetry) of digestibility of energy - but higher variability
- Based on the use of enzymes (in vitro digestion) or gut microbes (in vitro fermentation), or a combination of both
- In vitro fermentation can be used to simulate foregut fermentation or other sections of the GIT with fermentative capacity



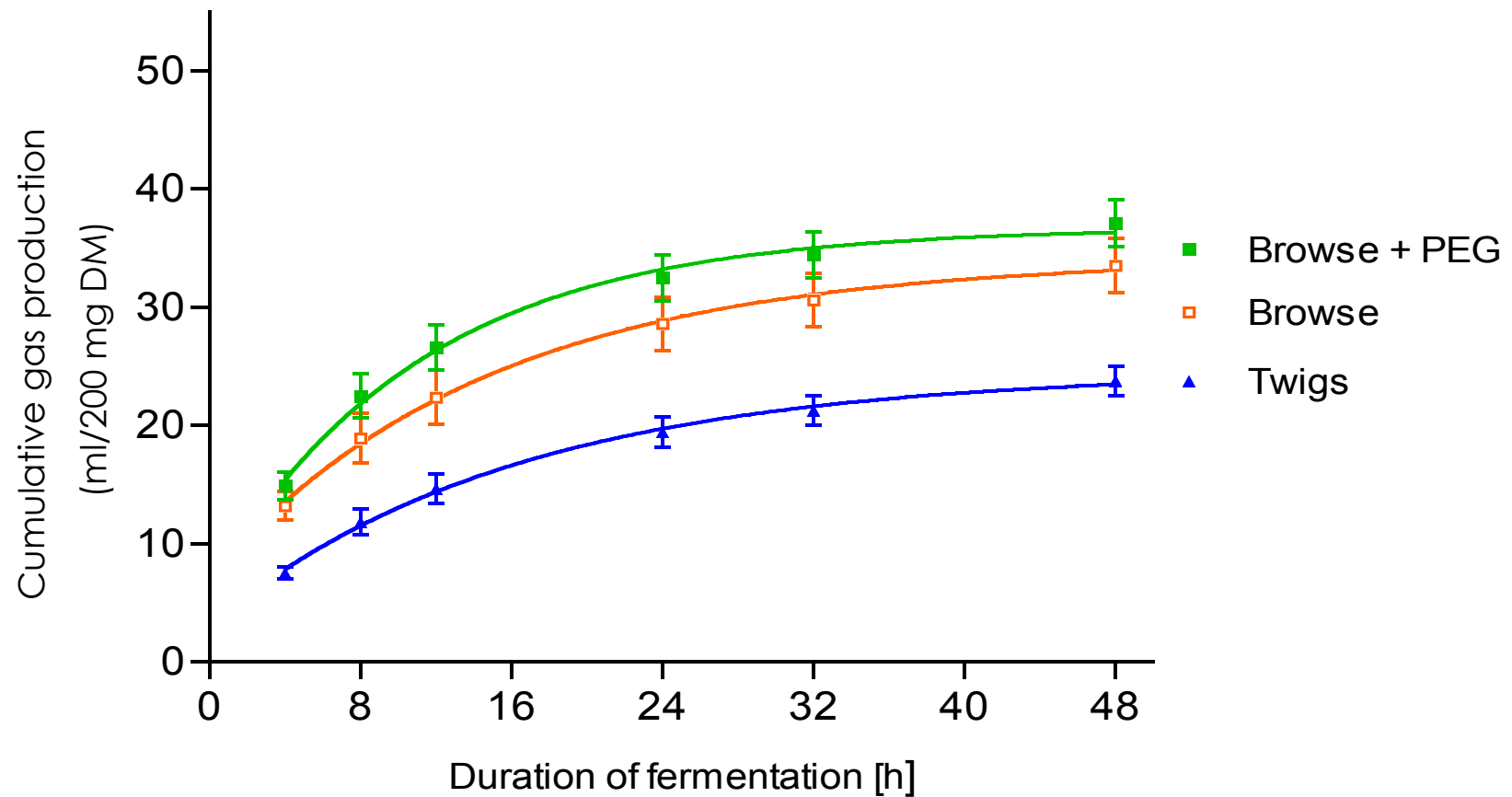
# Forage fermentation patterns



from Hummel et al. (2006)



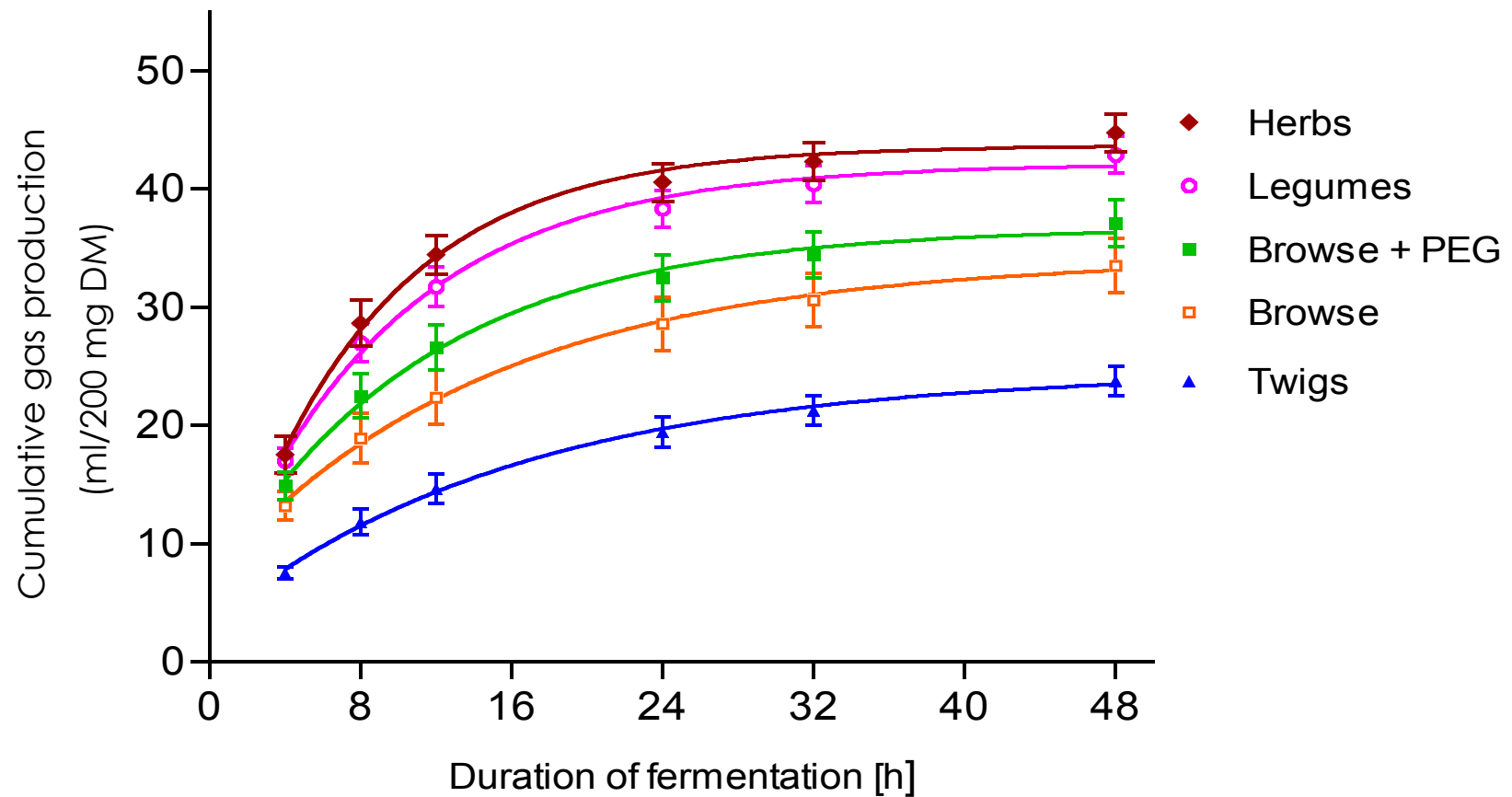
# Forage fermentation patterns



from Hummel et al. (2006)



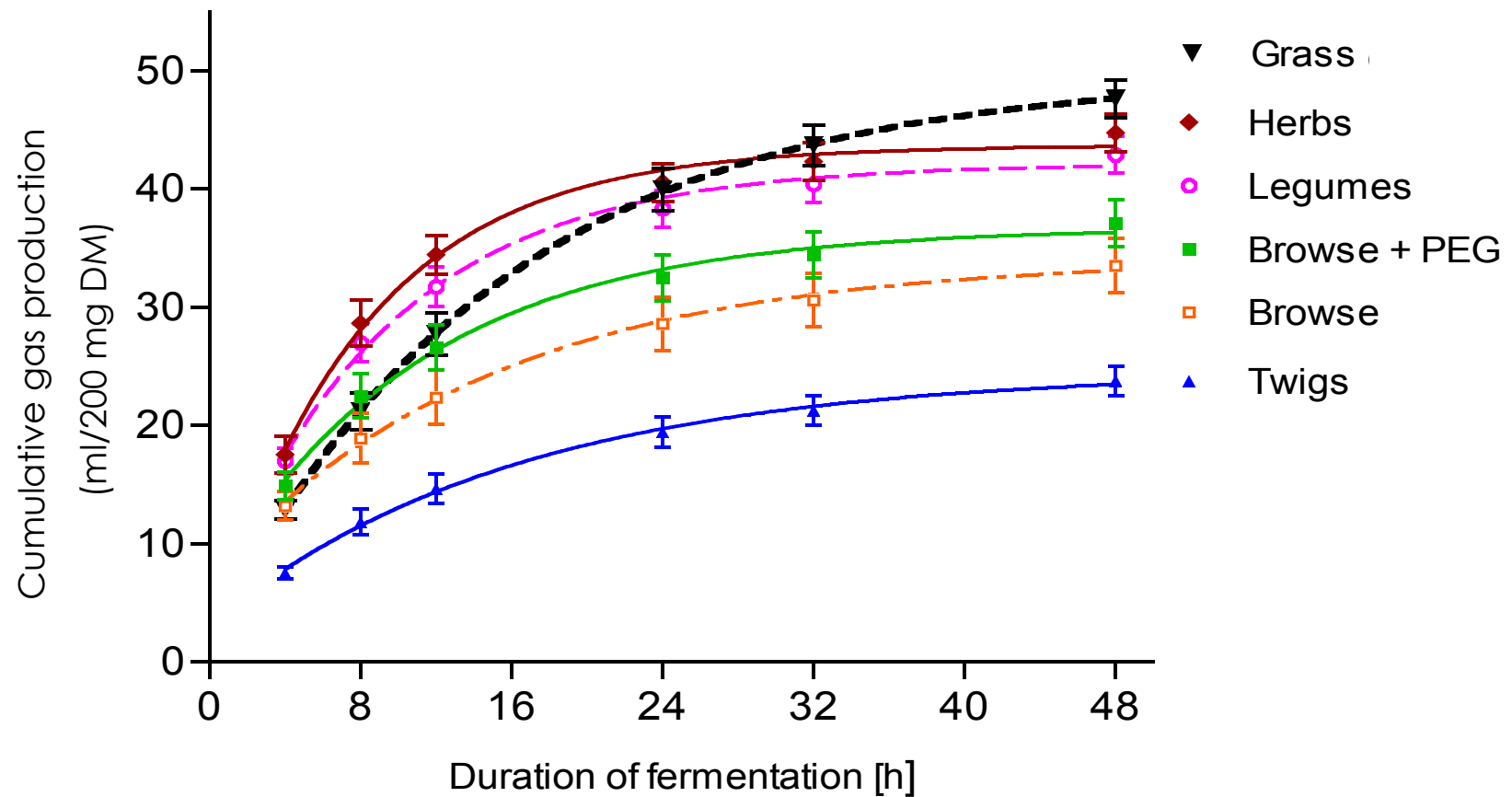
# Forage fermentation patterns



from Hummel et al. (2006)



# Forage fermentation patterns

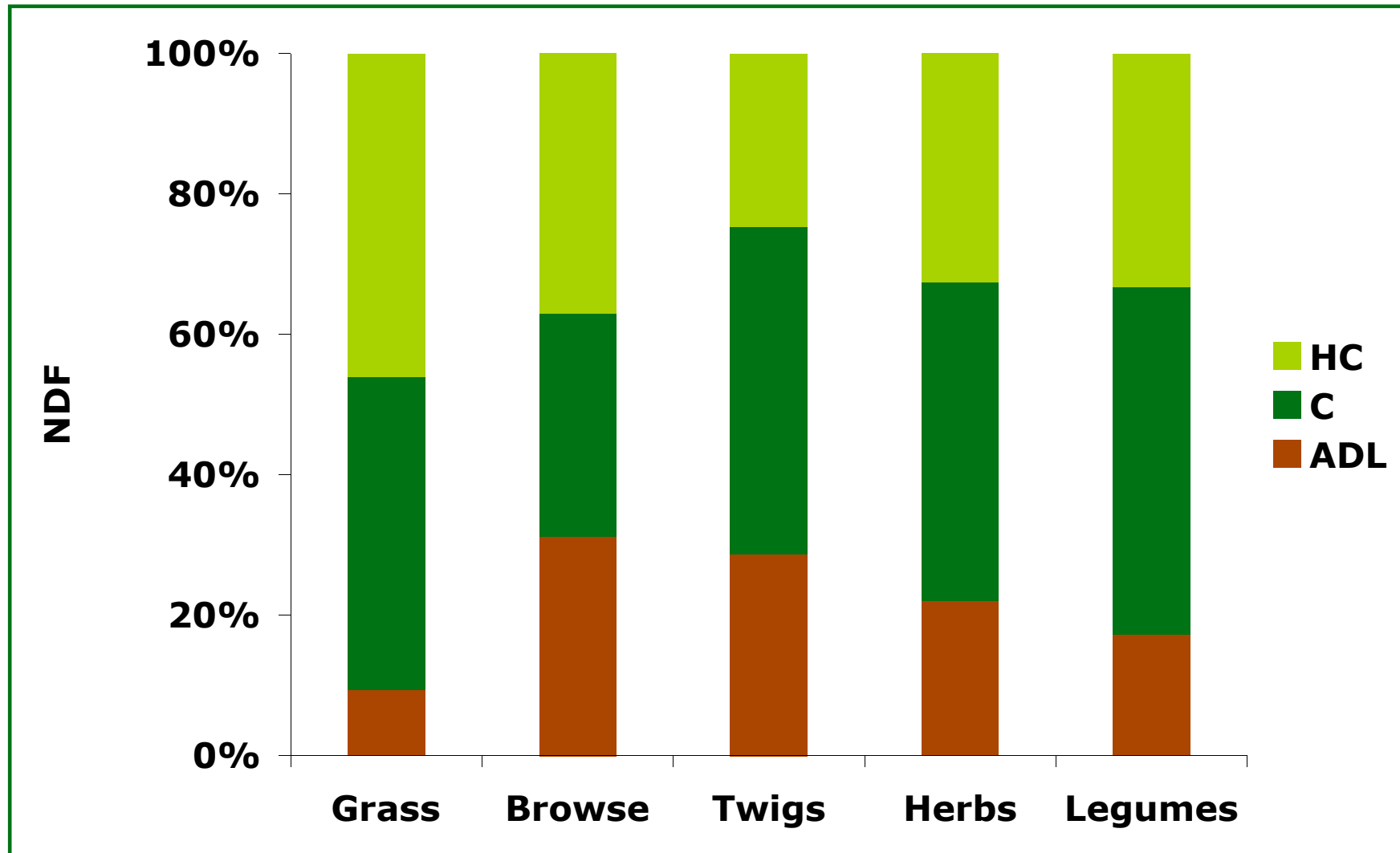


from Hummel et al. (2006)





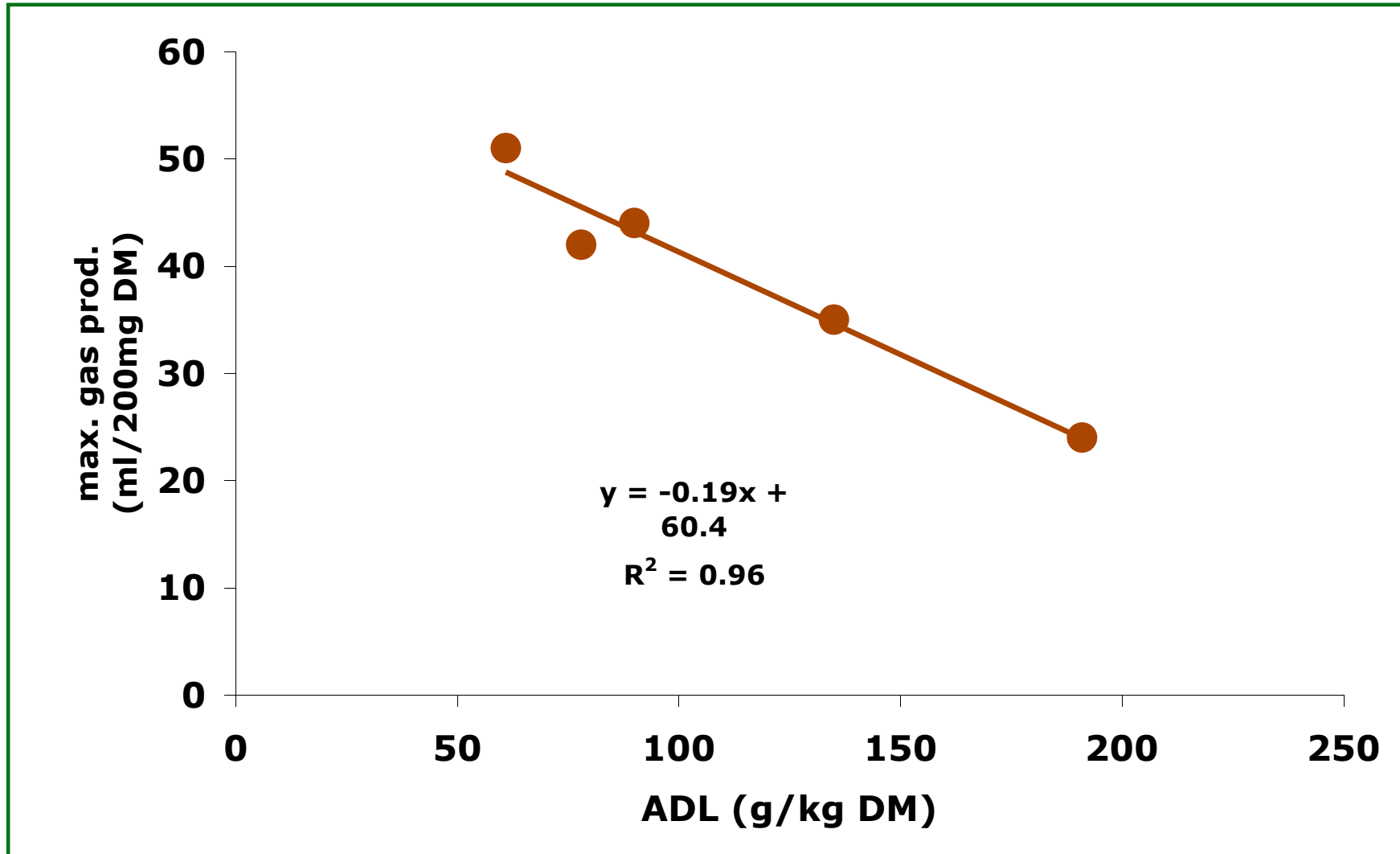
# Fibre composition of forages



from Hummel et al. (2006)



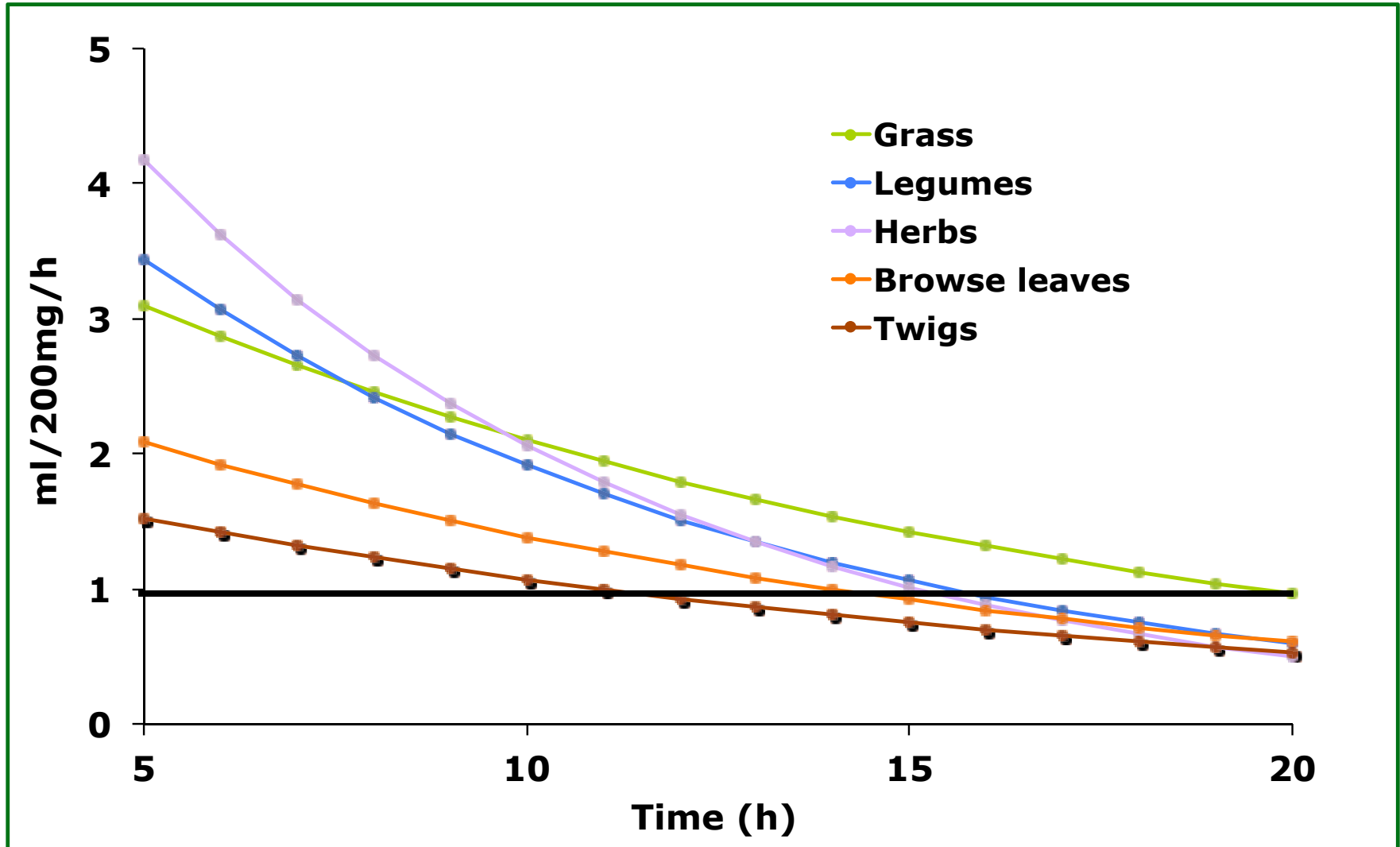
# Lignin is a major constraint on digestibility



from Hummel et al. (2006)



# Forage fermentation patterns



from Hummel et al. (2006)



*thank you  
for your attention*