

# Teeth and the gastrointestinal tract in mammals: when 1 + 1 = 3



#### Marcus Clauss, Julia Fritz, Jürgen Hummel

Clinic for Zoo Animals, Exotic Pets and Wildlife / AgroVet Strickhof, Vetsuisse Faculty, University of Zurich, Switzerland napfcheck, Planegg, Germany Ruminant Nutrition, Dept. of Animal Science, University of Göttingen, Germany SEB Montpellier 2022









GEORG-AUGUST-UNIVERSITÄT Göttingen

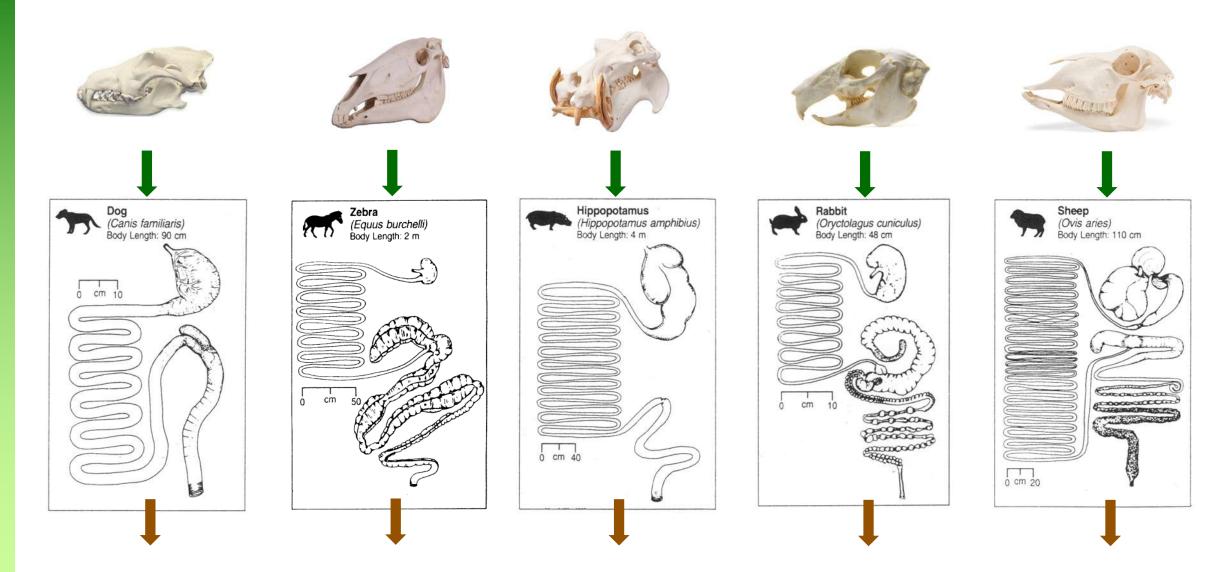




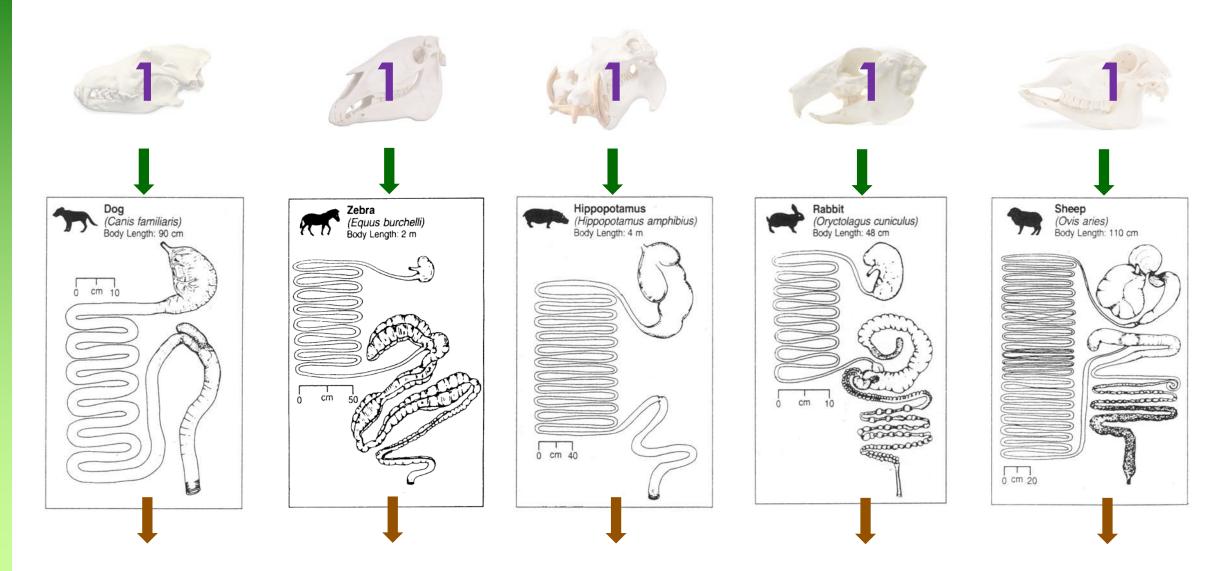
# Sequential processing



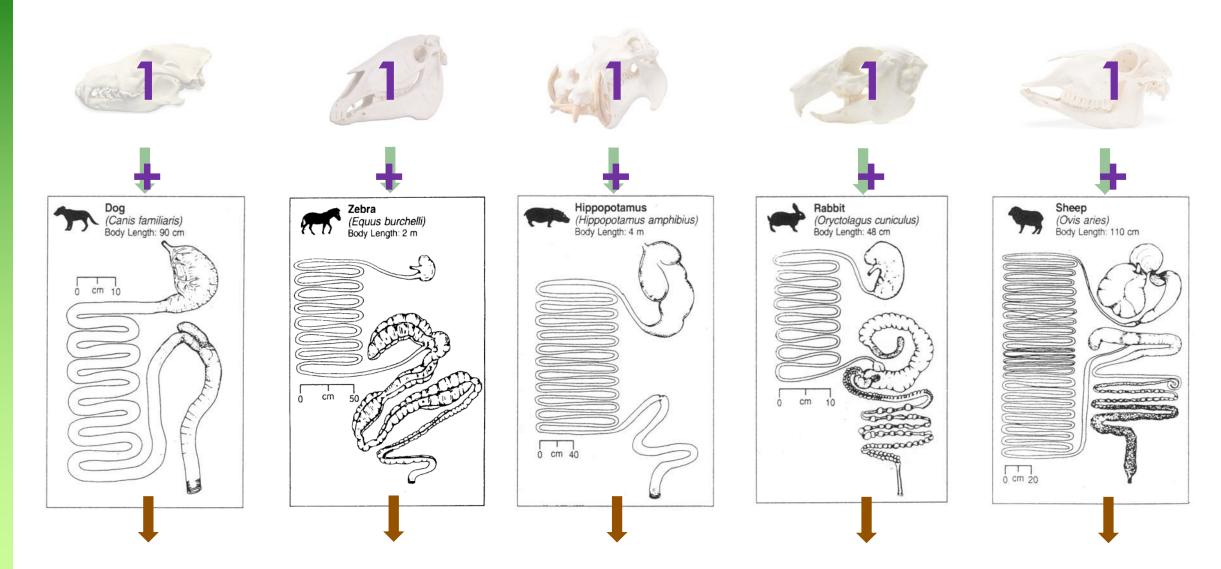
#### A one-way process



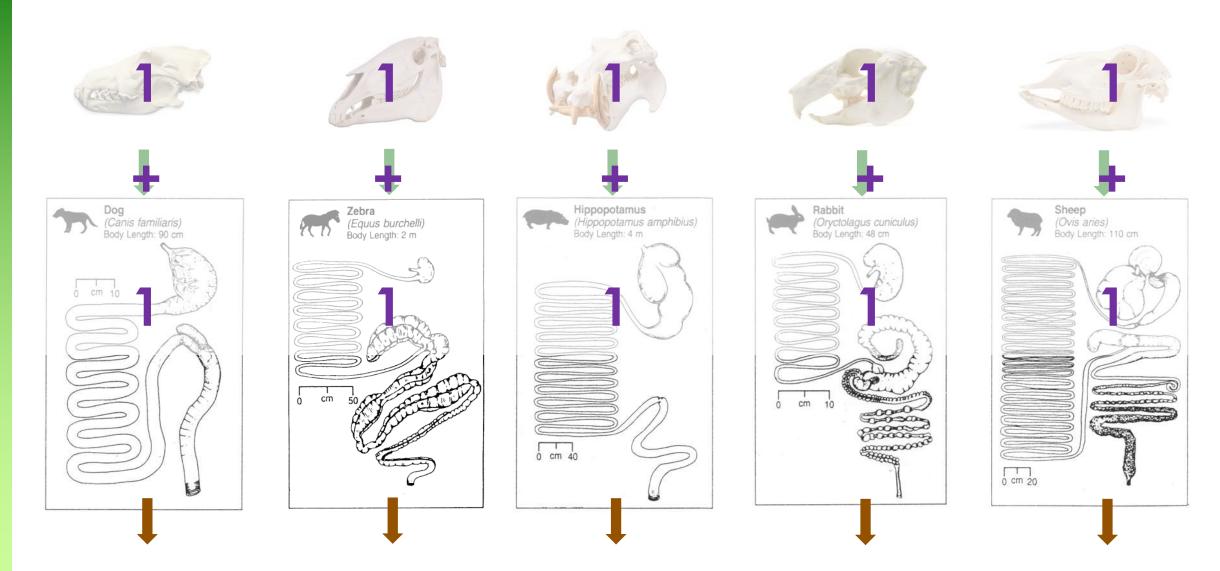




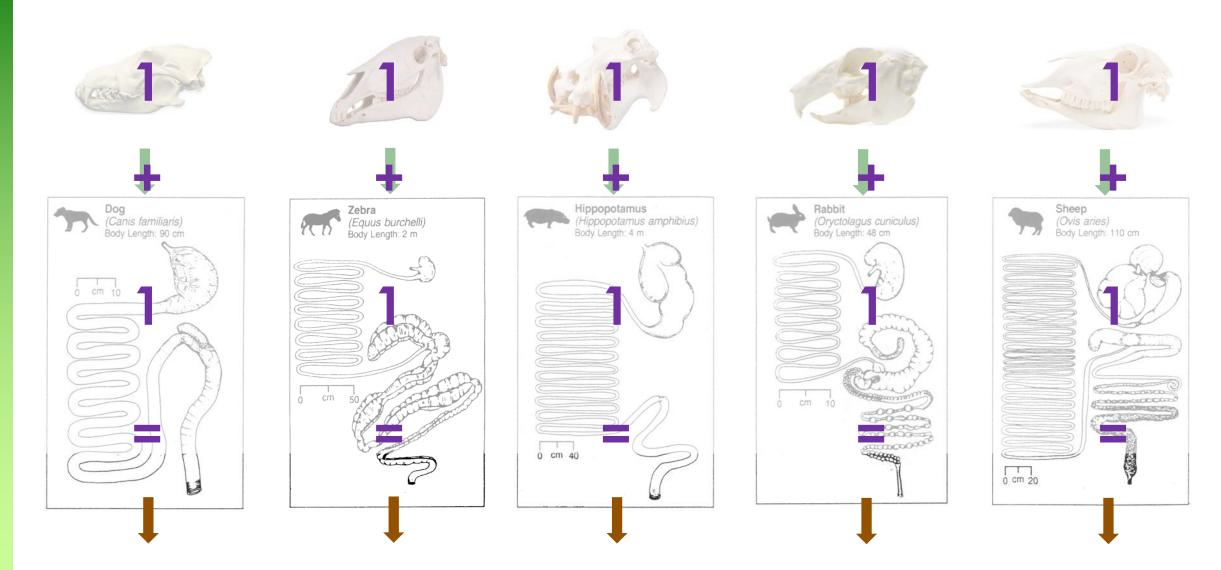




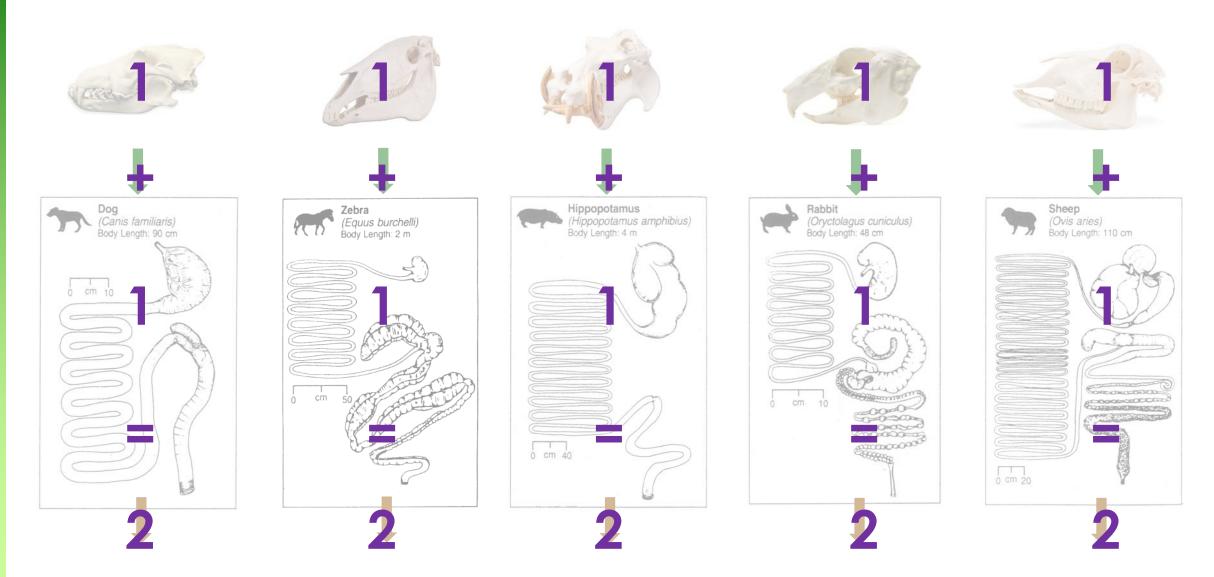








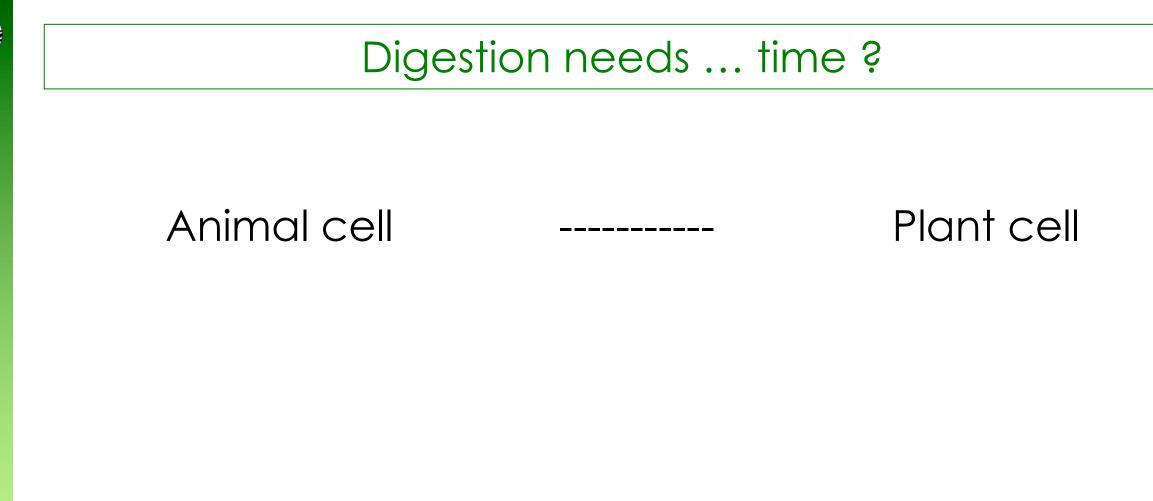




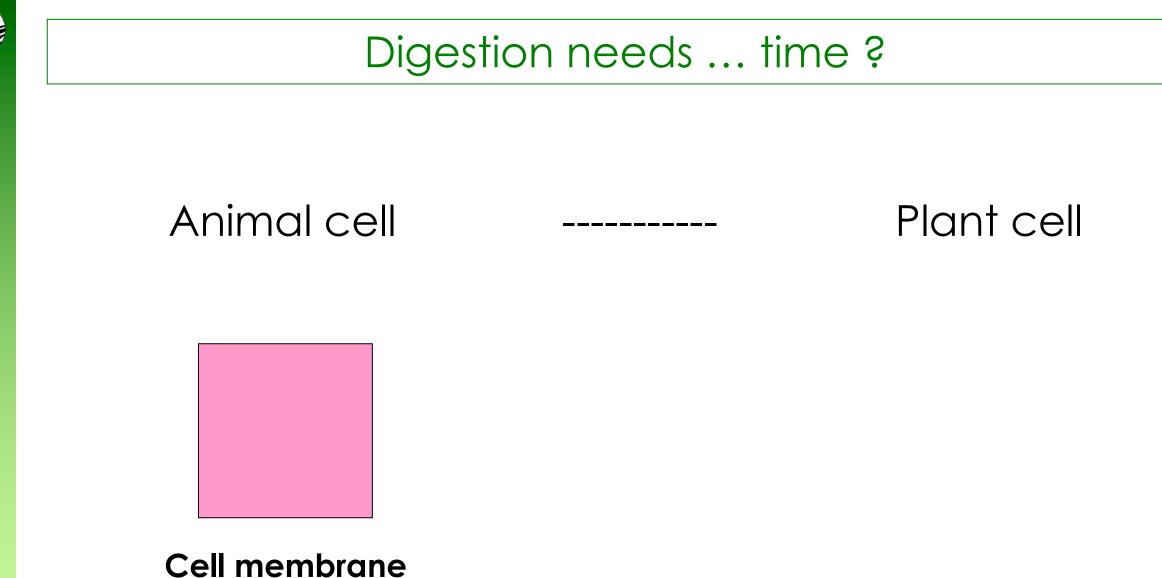


# The sequence of chewing and digestion: teeth are essential for endothermy

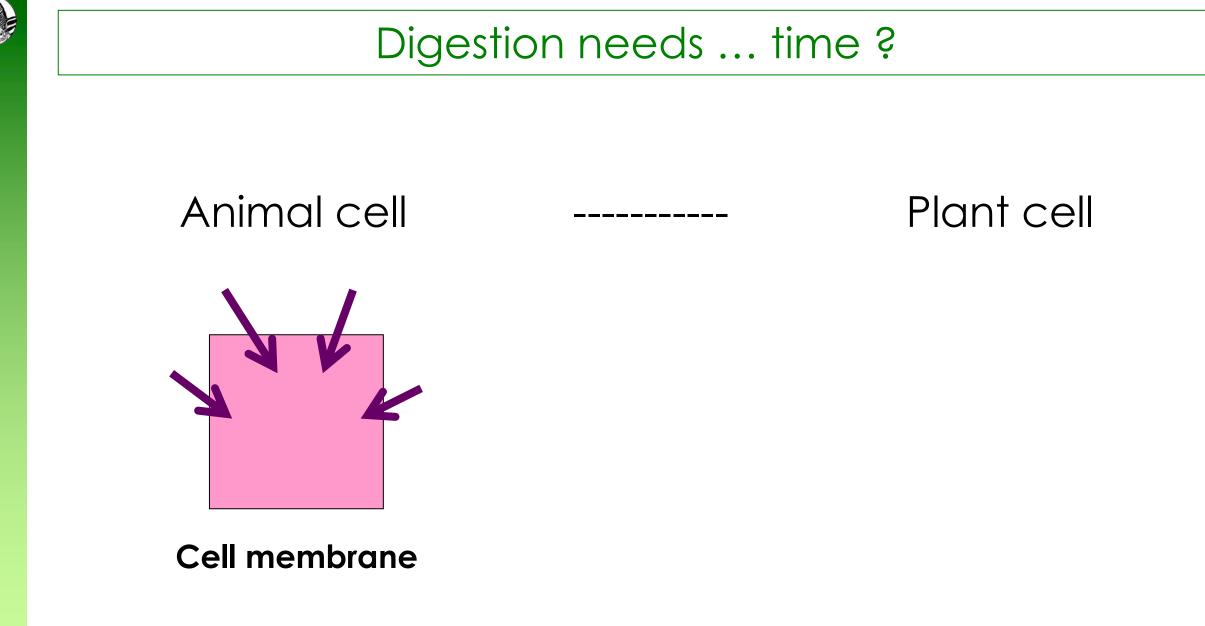






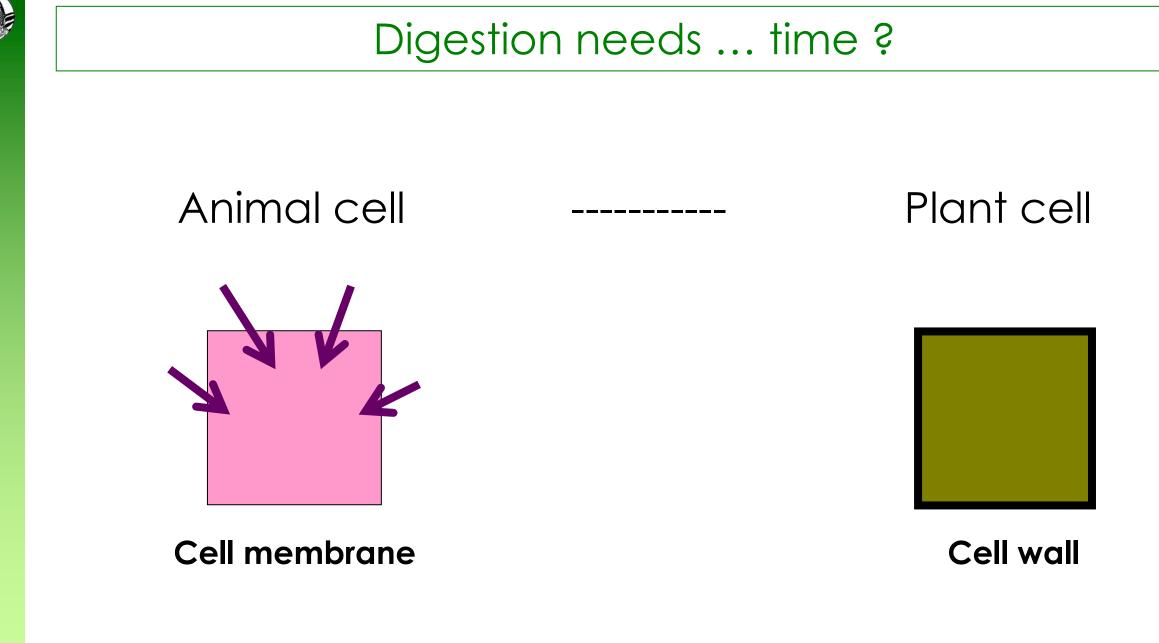




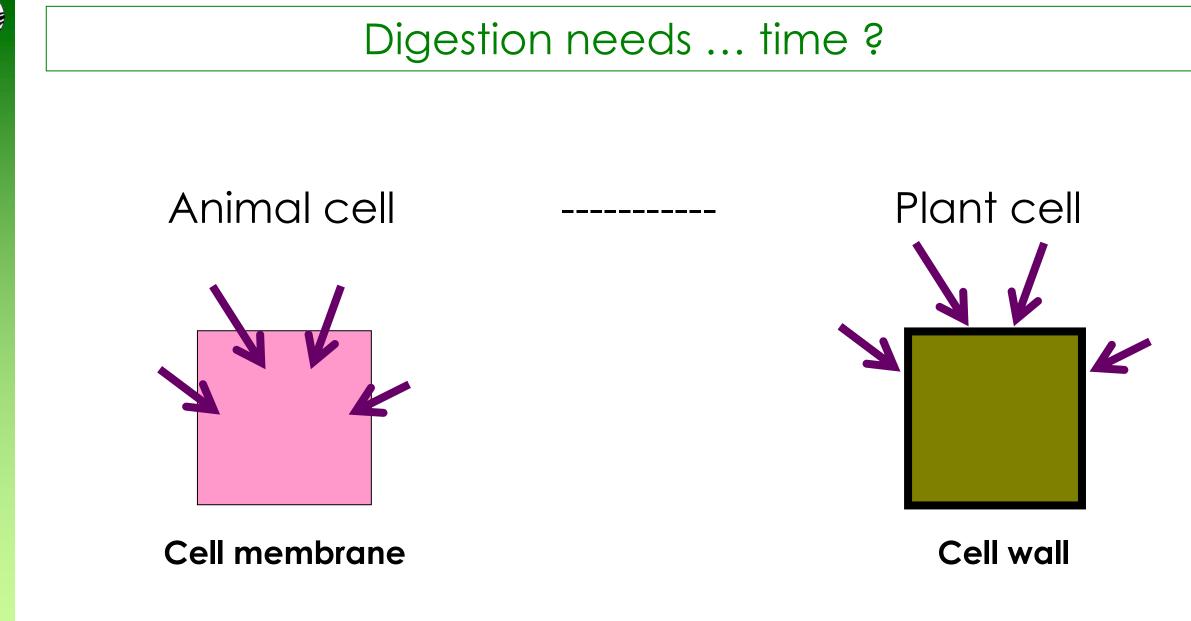


Hummel et al. (2020)

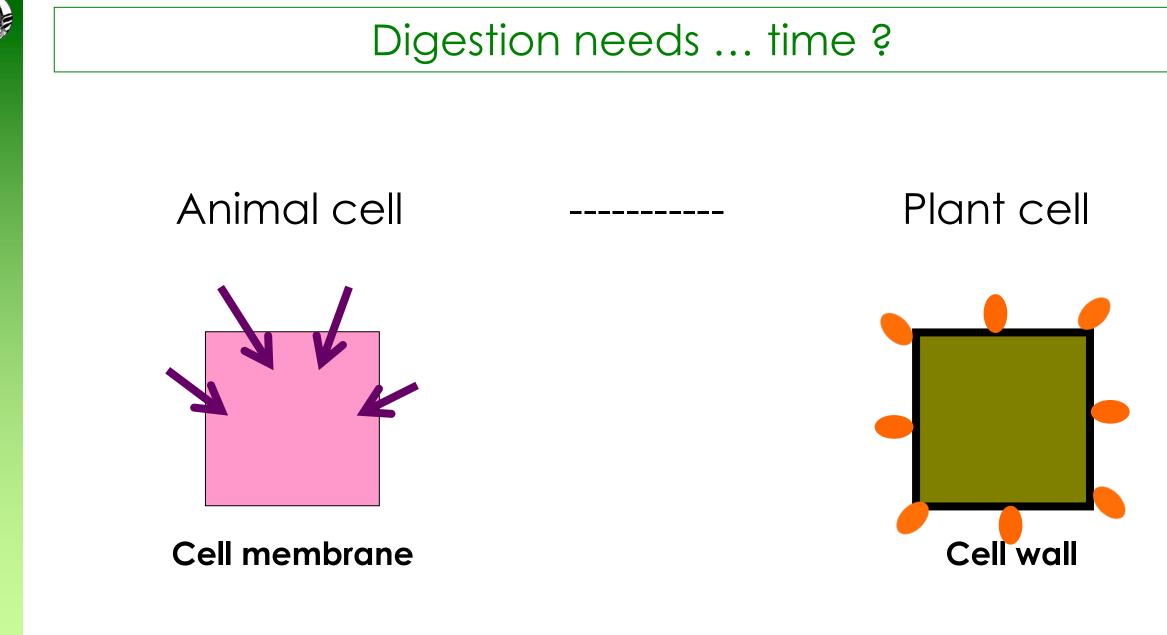




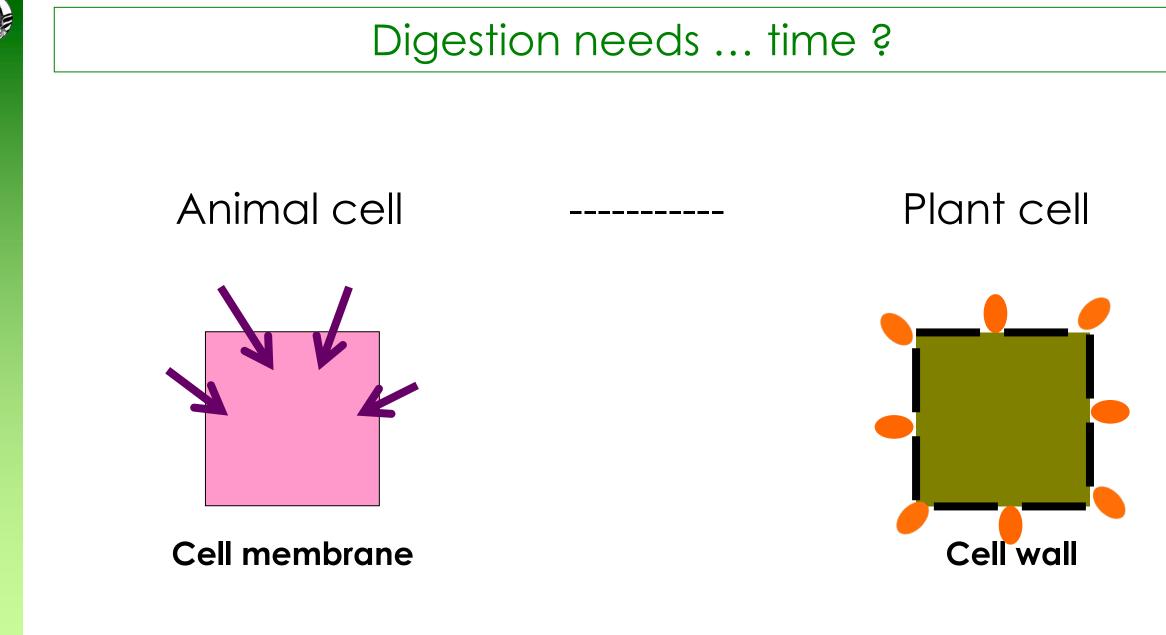




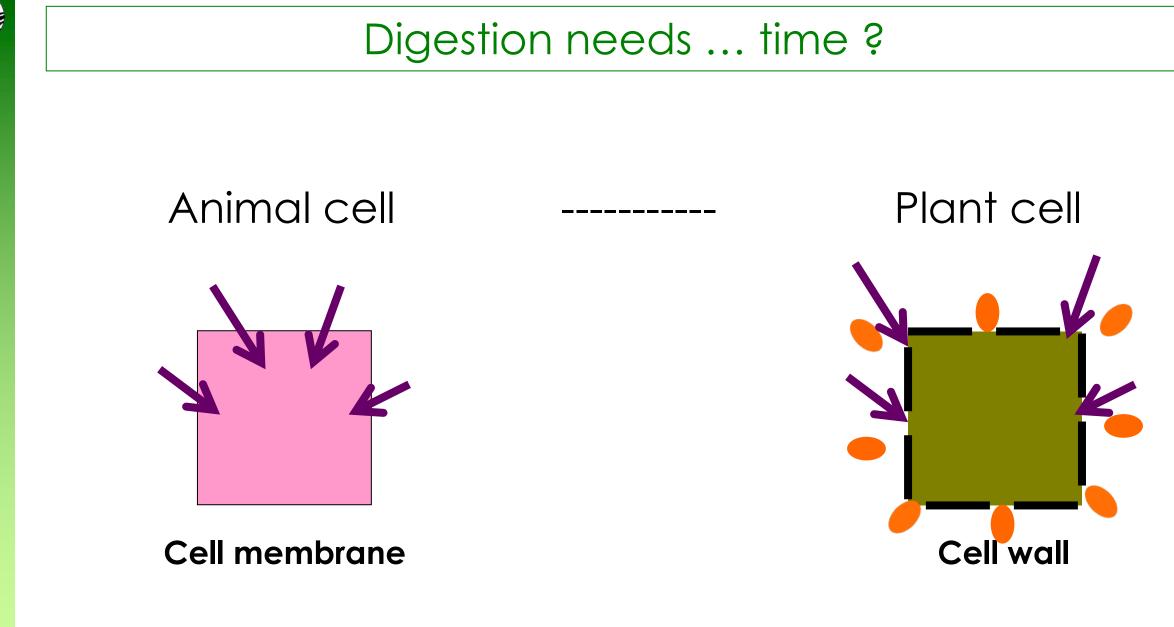




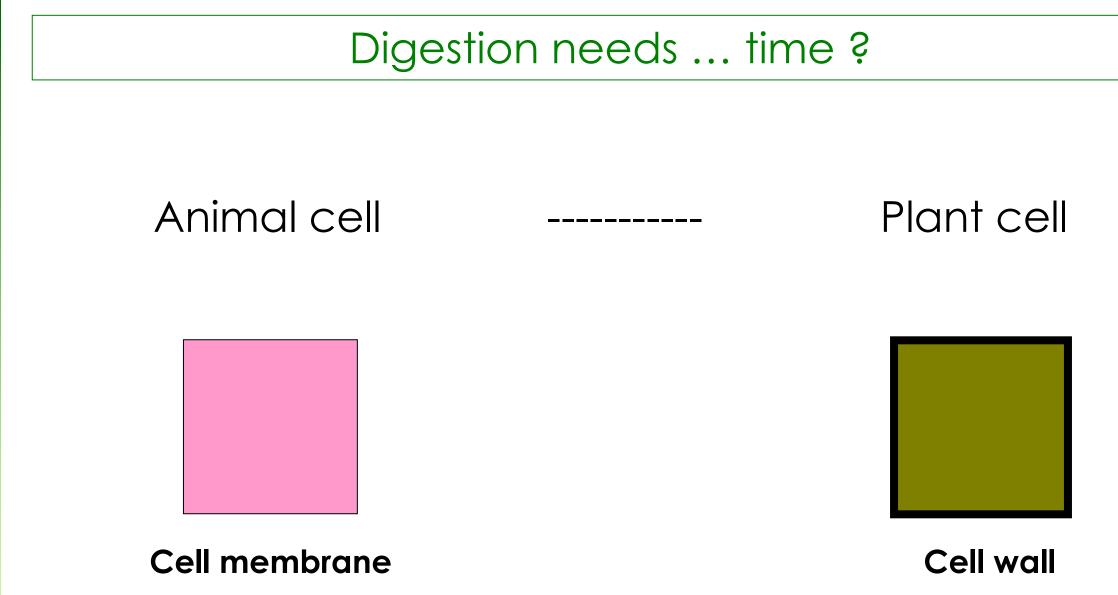




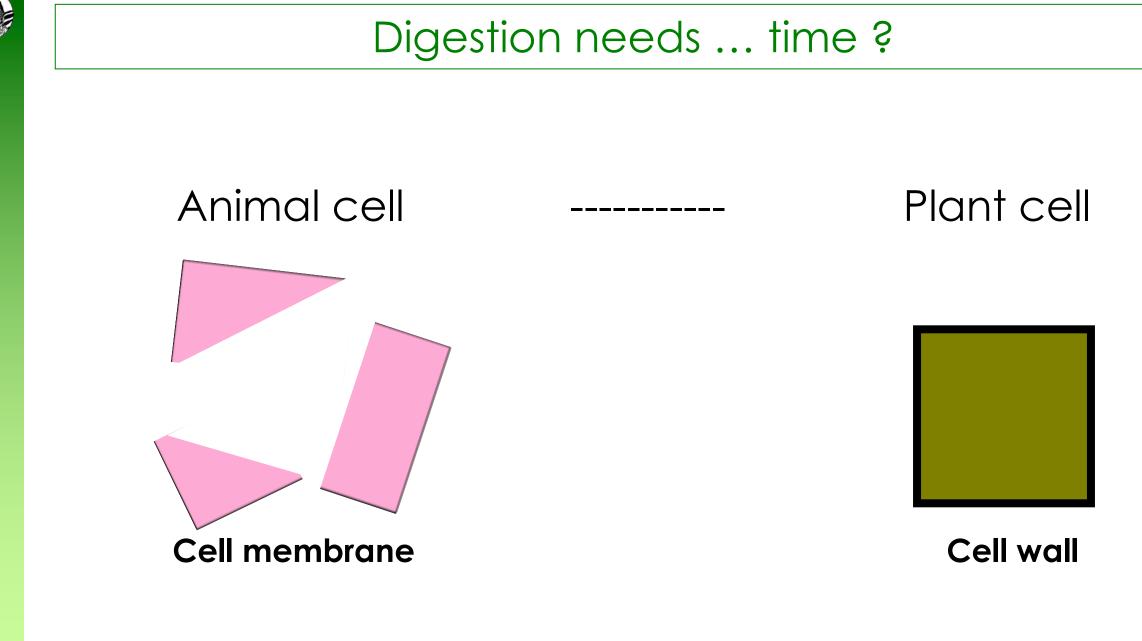






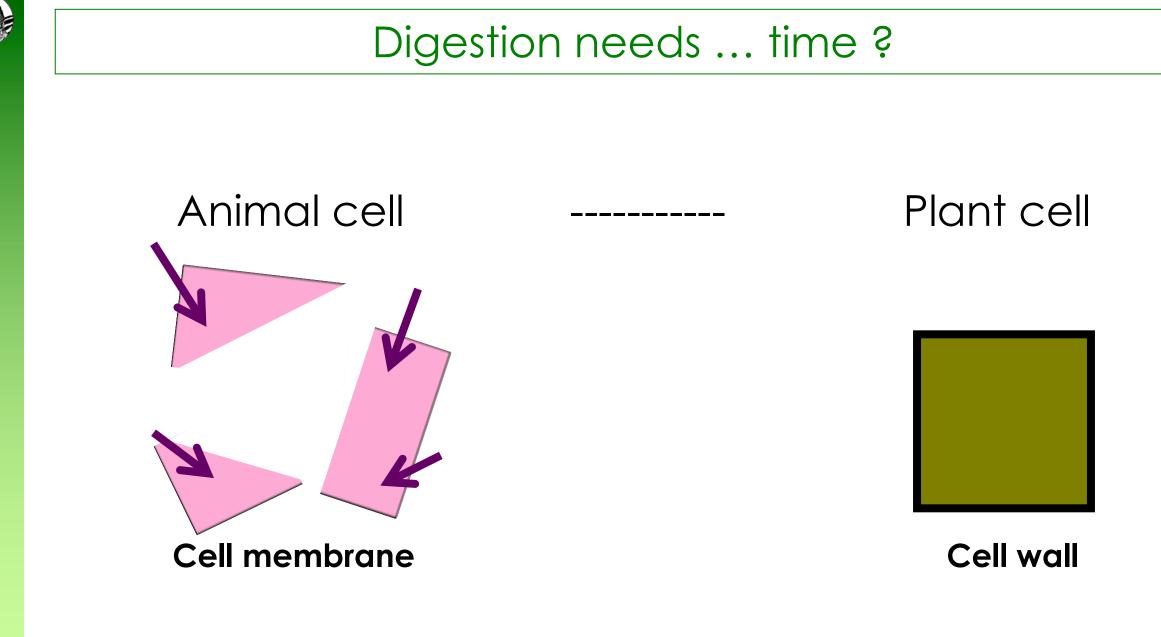




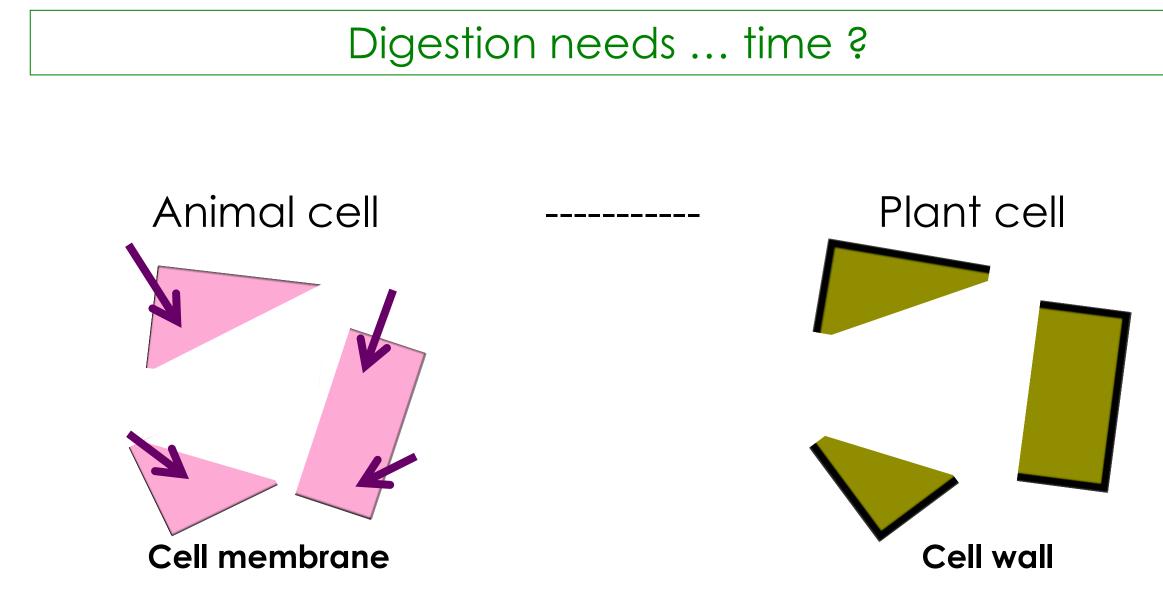


Hummel et al. (2020)

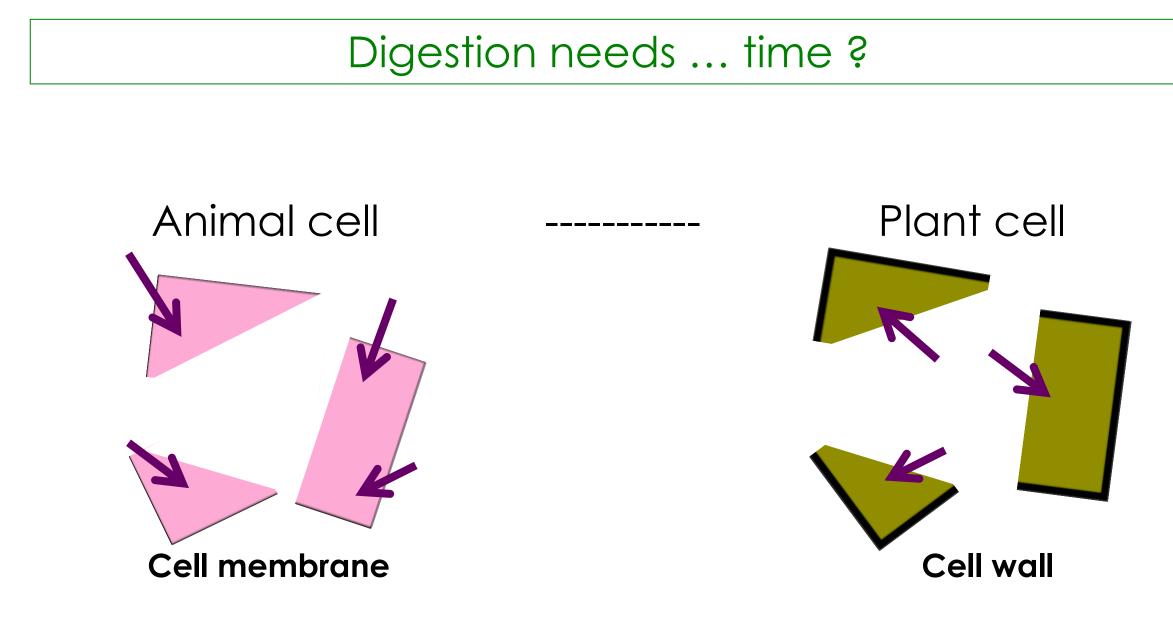




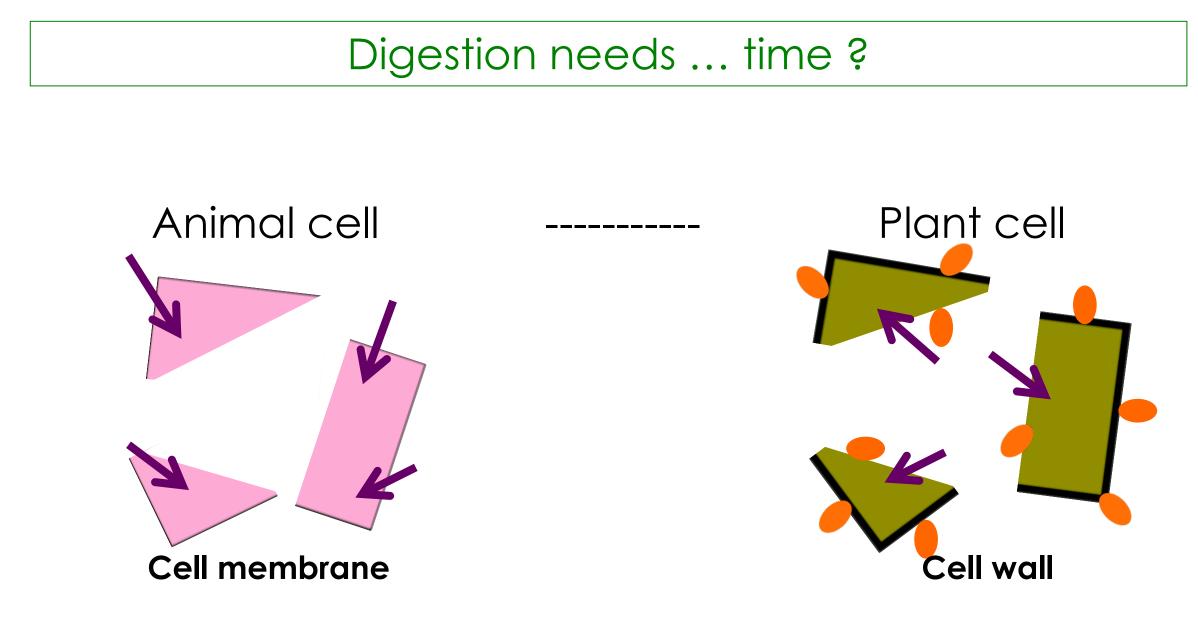




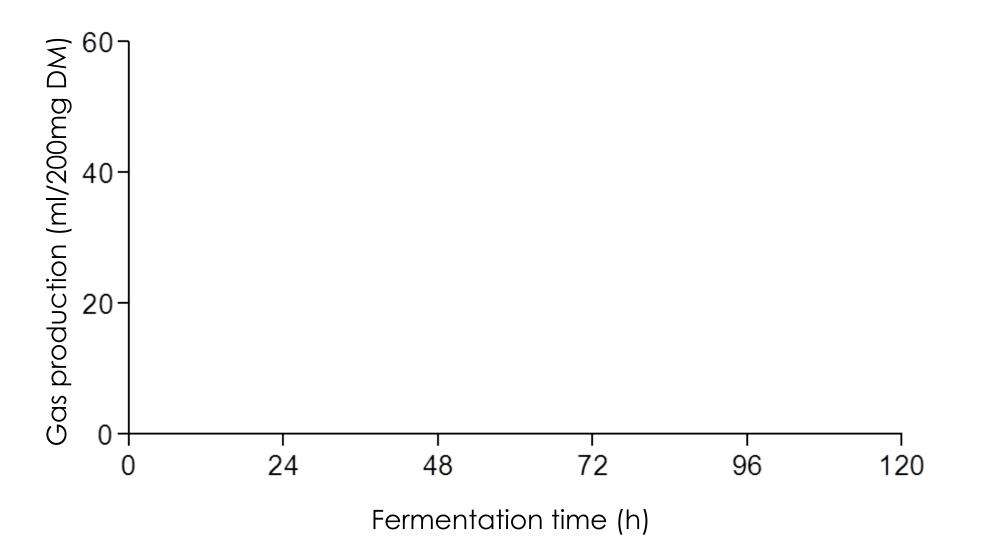








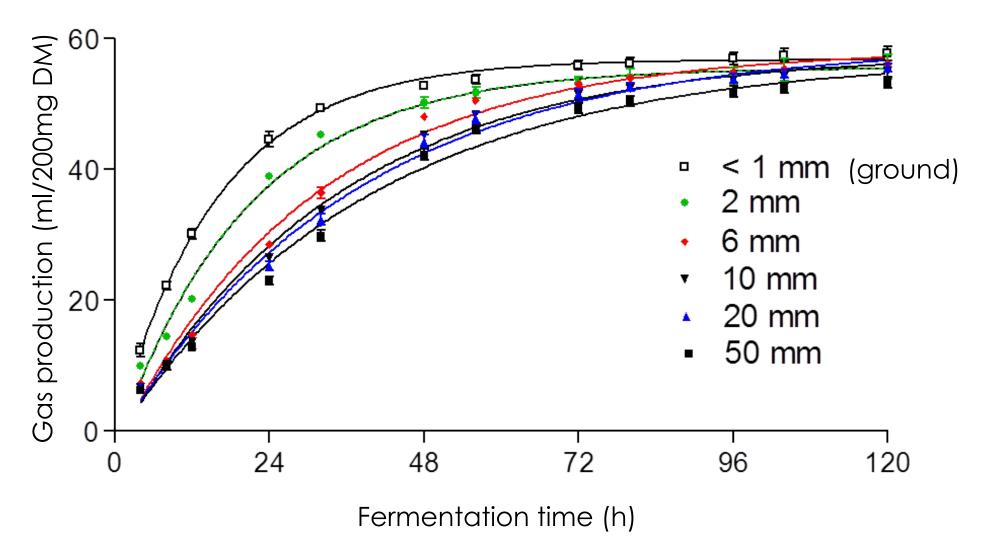




Hummel (unpubl.)

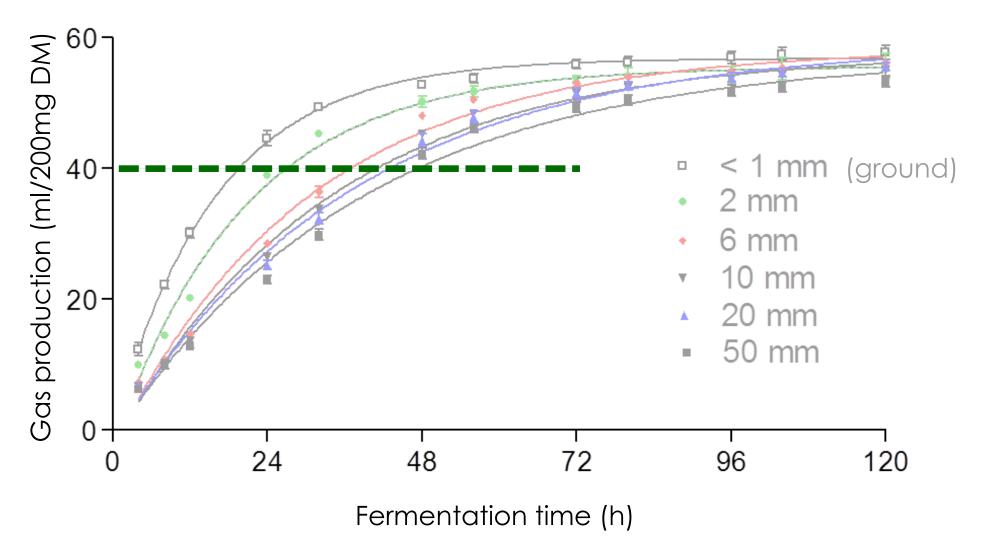


Maize leaves



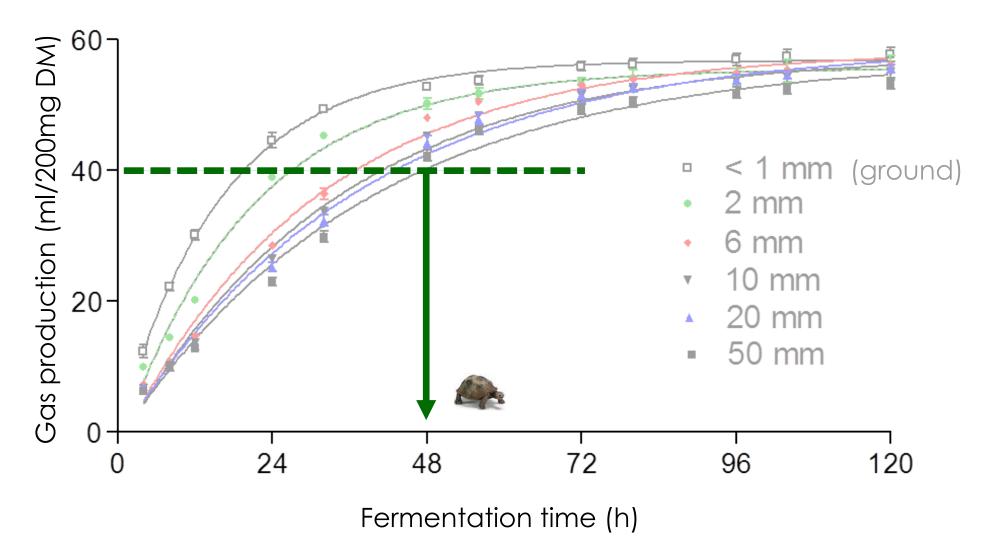


Maize leaves



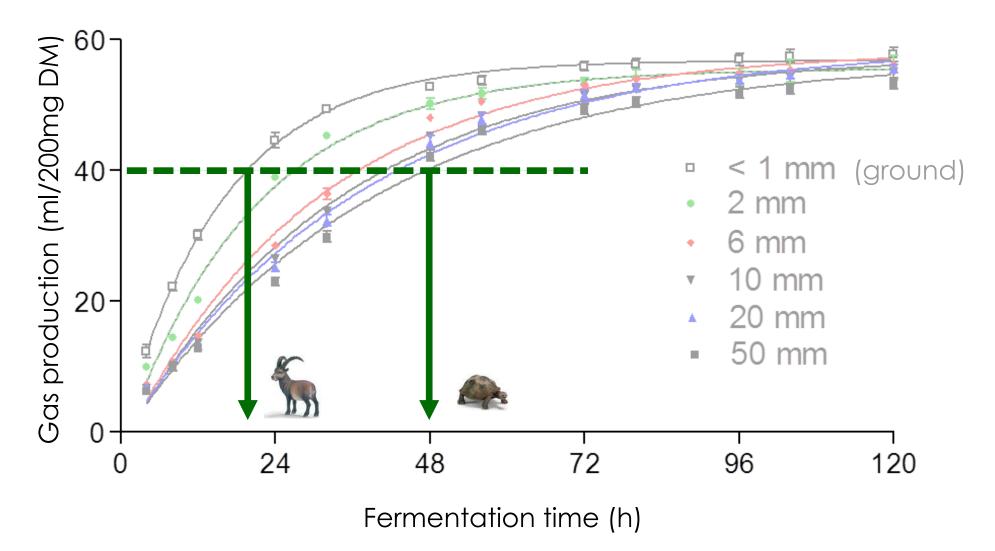


Maize leaves





Maize leaves





# Particle size reduction in terrestrial vertebrates



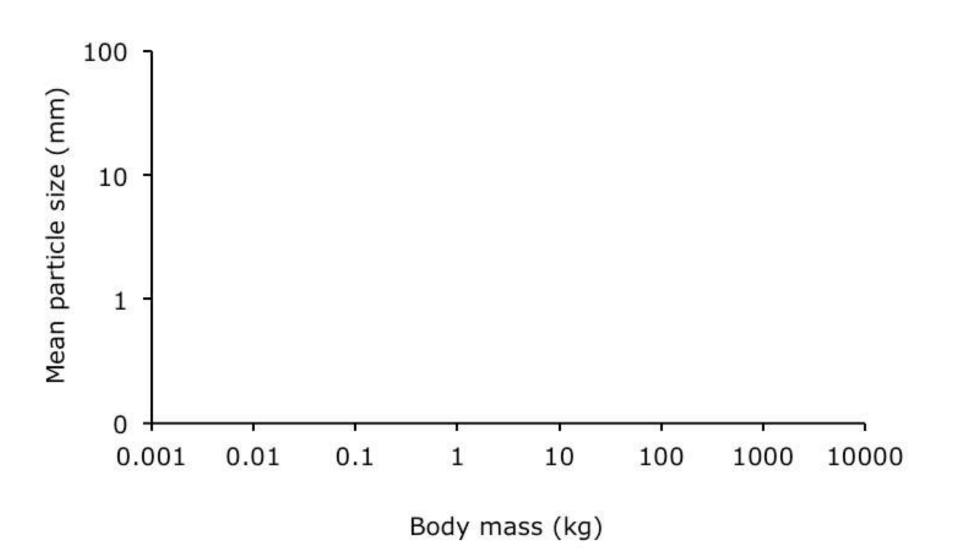
#### **Comparative chewing efficiency in mammalian herbivores**

Julia Fritz, Jürgen Hummel, Ellen Kienzle, Christian Arnold, Charles Nunn and Marcus Clauss Oikos 118: 1623–1632, 2009



#### Comparative chewing efficiency in mammalian herbivores

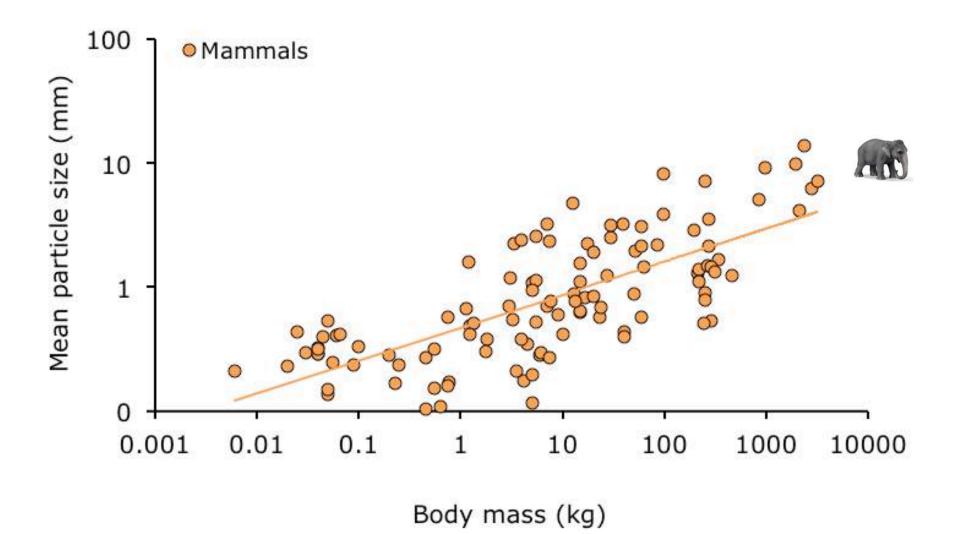
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### To Chew





#### To Chew or Not to Chew





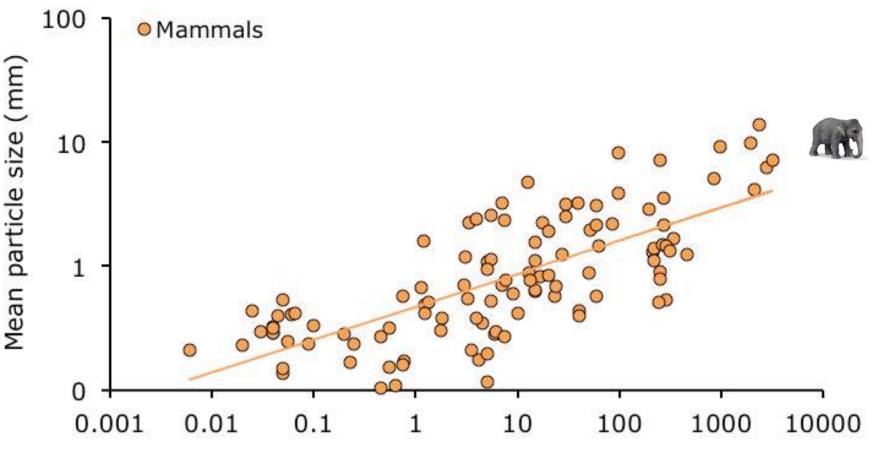
#### To Chew or Not to Chew: Fecal Particle Size in Herbivorous Reptiles and Mammals

JULIA FRITZ<sup>1\*</sup>, JÜRGEN HUMMEL<sup>2</sup>, ELLEN KIENZLE<sup>1</sup>, W. JÜRGEN STREICH<sup>3</sup>, AND MARCUS CLAUSS<sup>4</sup> J. Exp. Zool. 313A:579–586, 2010



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Body mass (kg)

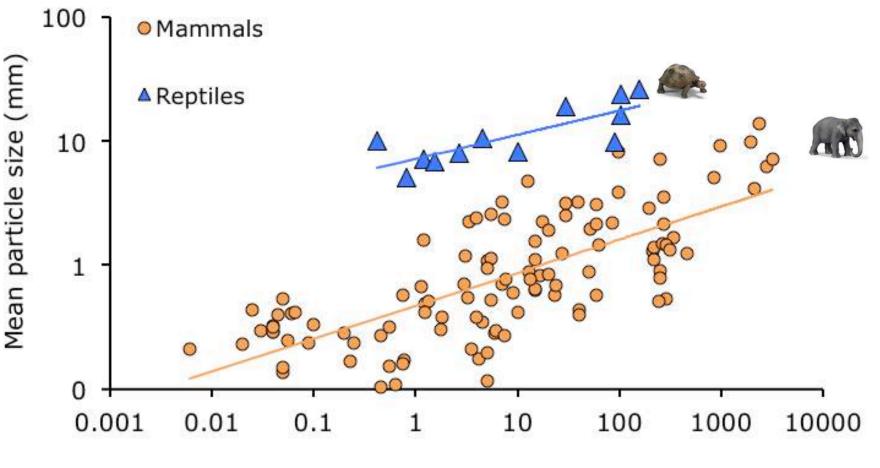
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### To Chew or Not to Chew: Fecal Particle Size in Herbivorous Reptiles and Mammals

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Body mass (kg)



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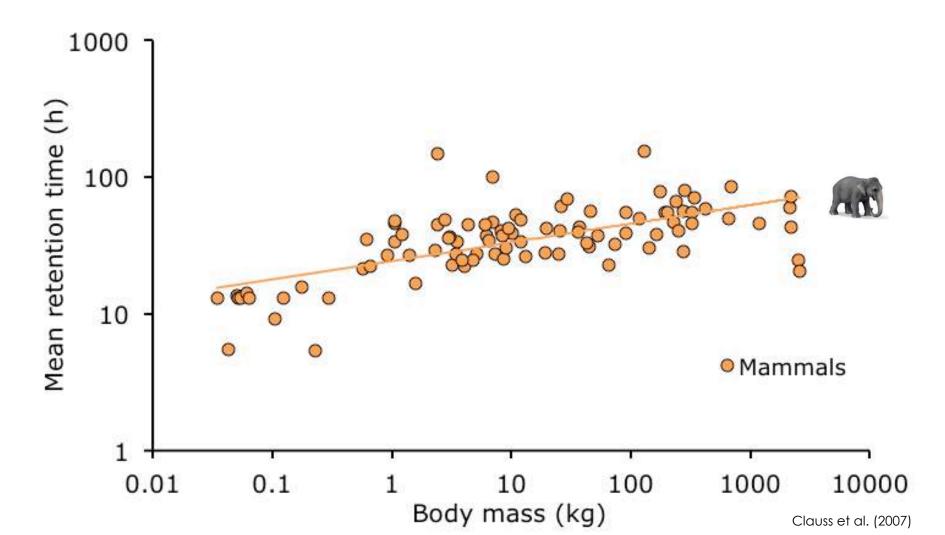
J. Exp. Zool. 313A:579–586, 2010

JULIA FRITZ<sup>1\*</sup>, JÜRGEN HUMMEL<sup>2</sup>, ELLEN KIENZLE<sup>1</sup>, W. JÜRGEN STREICH<sup>3</sup>, AND MARCUS CLAUSS<sup>4</sup> 100 Mammals Leaf recovered from the feces of an I. iguana. Note that he shape of the leaf and the vascular bundles are nearly intact Mean particle size (mm) Reptiles 10 00 1 0 0.001 0.01 0.1 10 100 1000 10000 1

Body mass (kg)

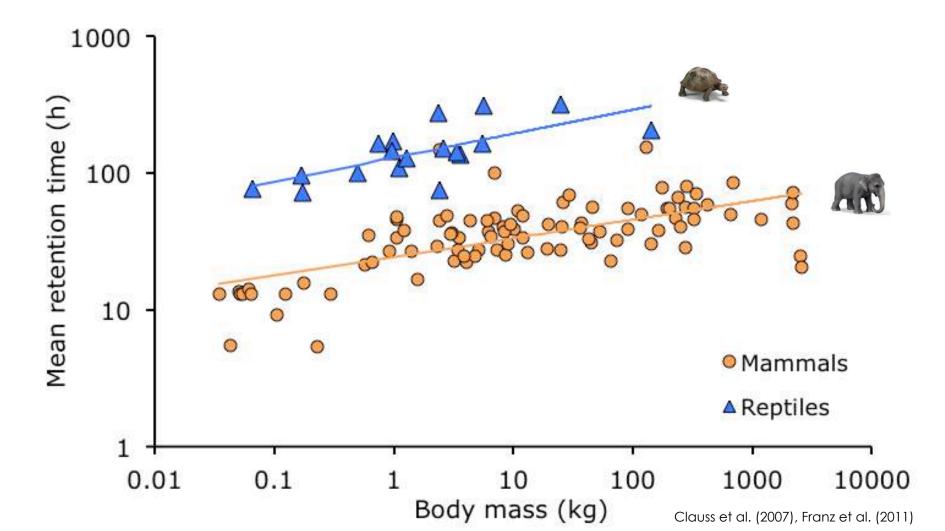


# Retention time in the digestive tract



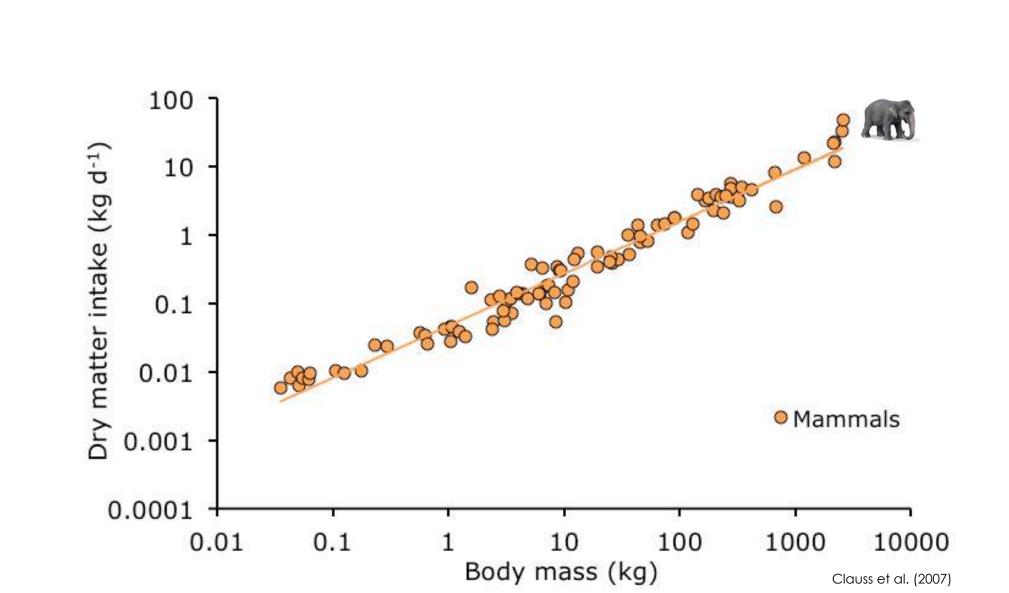


# Retention time in the digestive tract



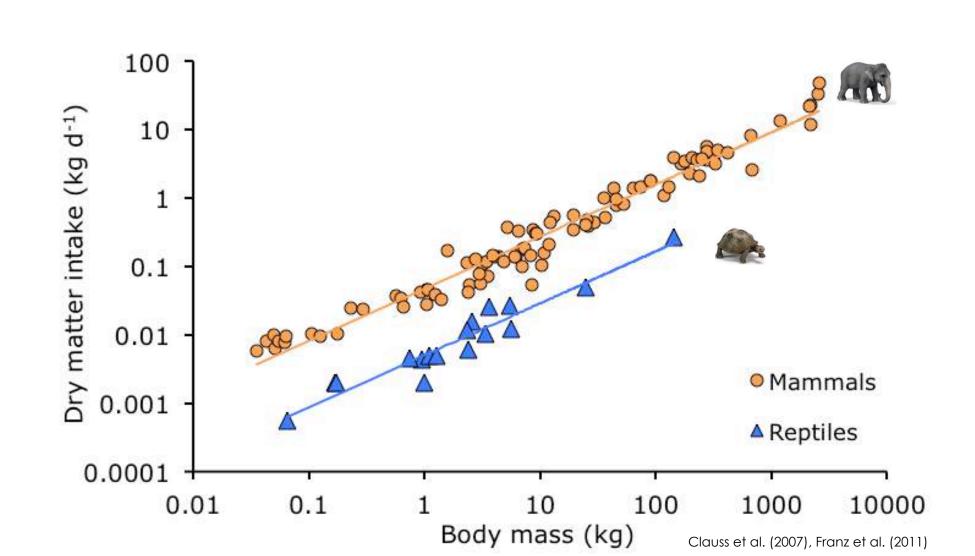


### Food intake



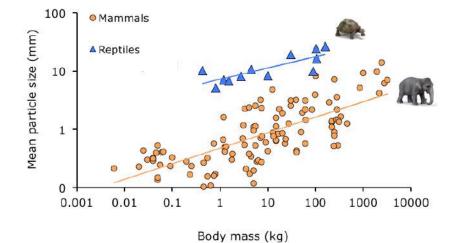


### Food intake



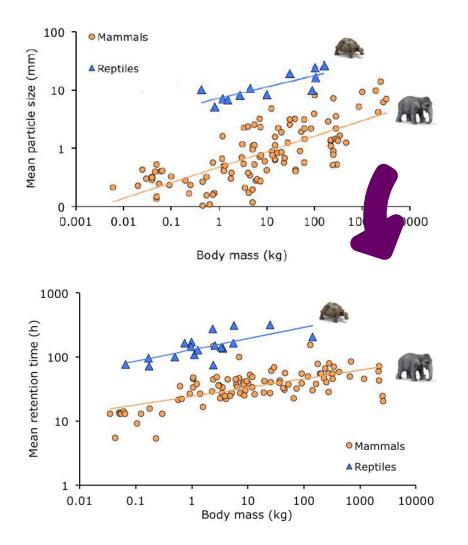


# Chewing ...





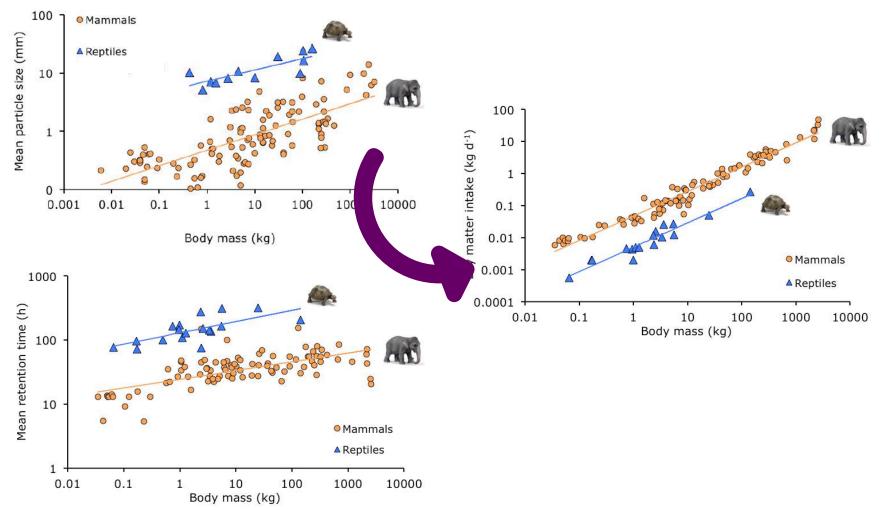
# Chewing ... facilitates shorter retention times



Clauss et al. (2007), Fritz et al. (2009, 2010), Franz et al. (2011)



# Chewing ... facilitates higher intakes

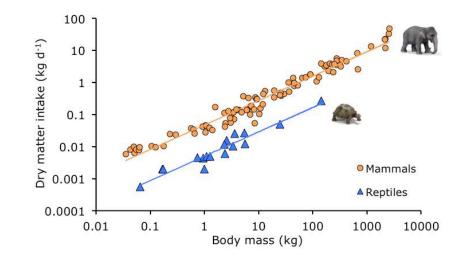


Clauss et al. (2007), Fritz et al. (2009, 2010), Franz et al. (2011)



# Chewing ... facilitates higher intakes

#### for herbivores particle size reduction is a precondition for endothermy !

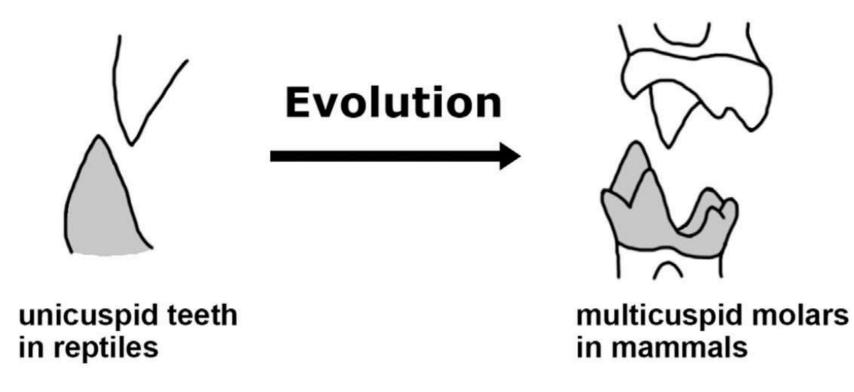




# Teeth evolve for ...



# Evolution and development of the mammalian multicuspid teeth Atsushi Yamanaka Journal of Oral Biosciences 64 (2022) 165–175

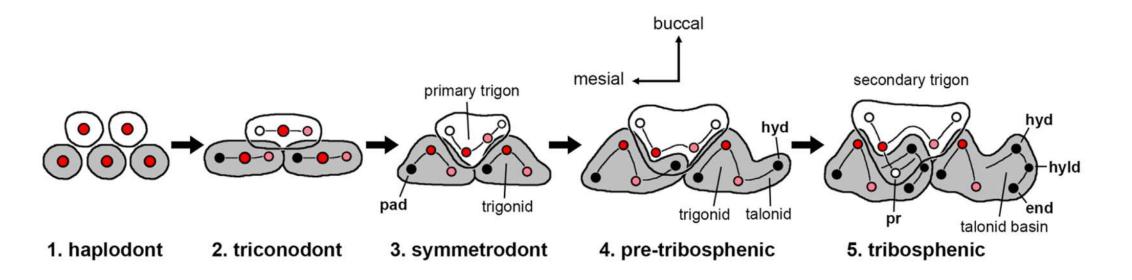




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#### Atsushi Yamanaka

Journal of Oral Biosciences 64 (2022) 165-175

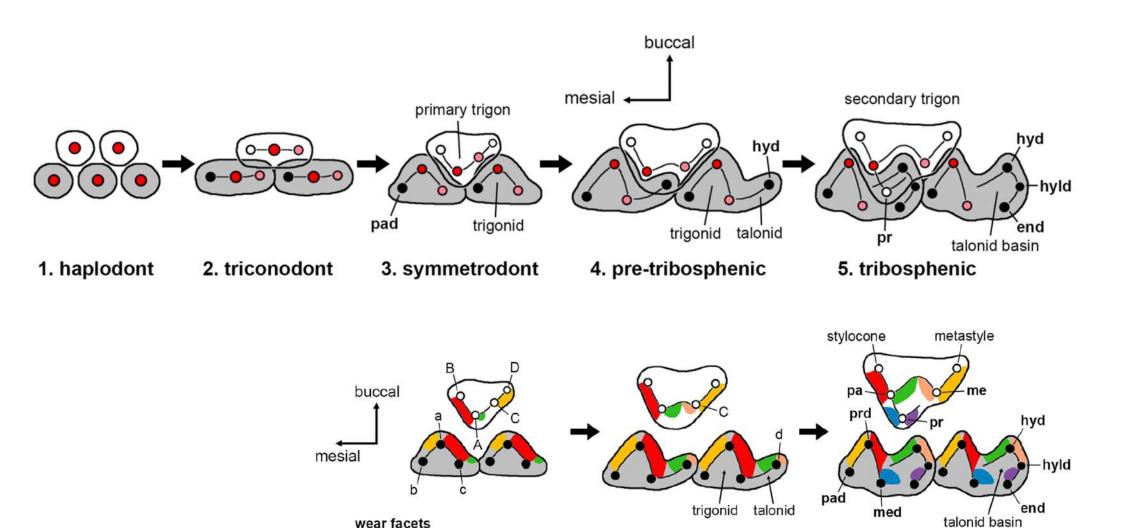




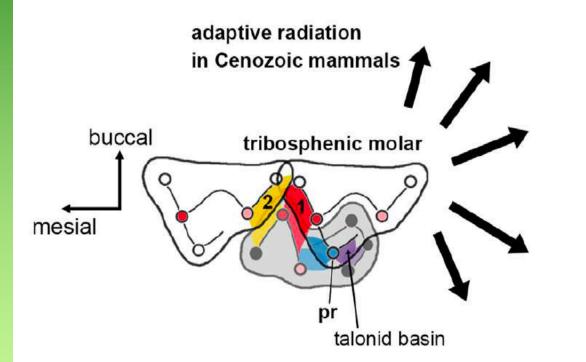
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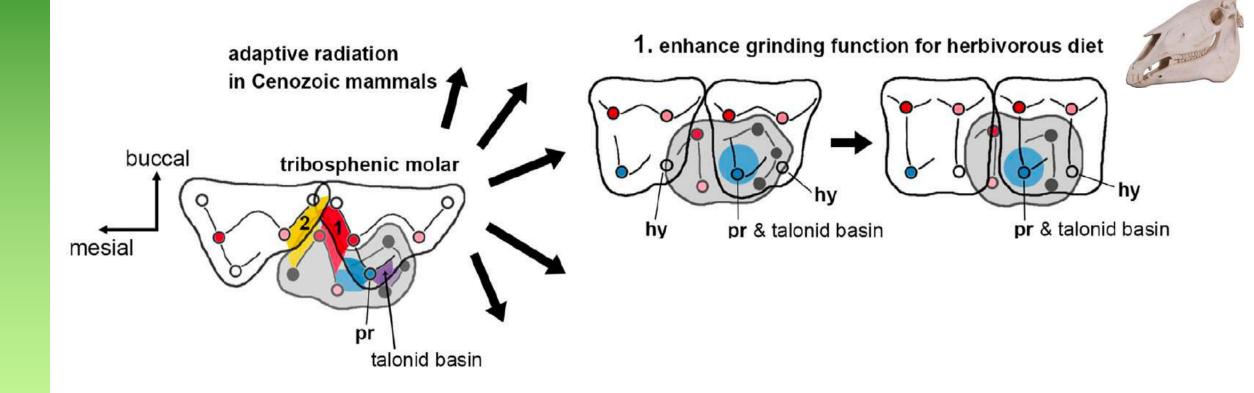






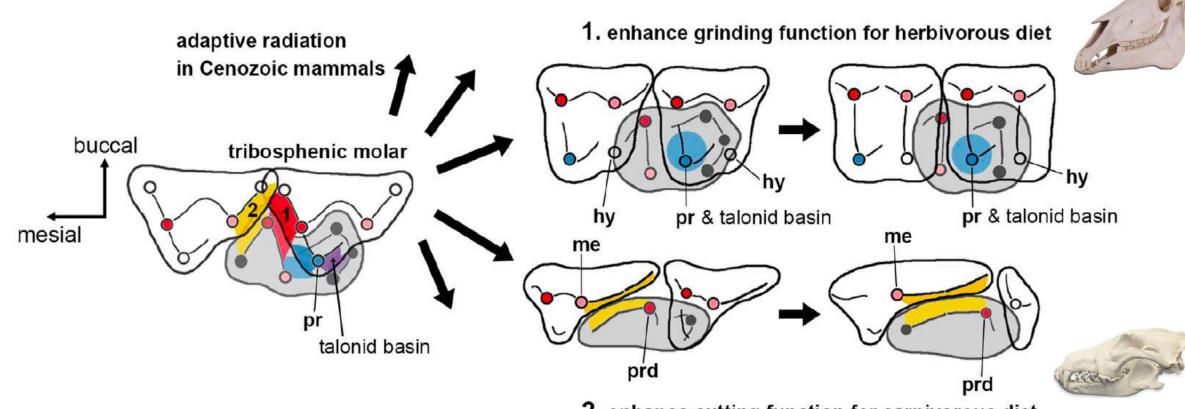


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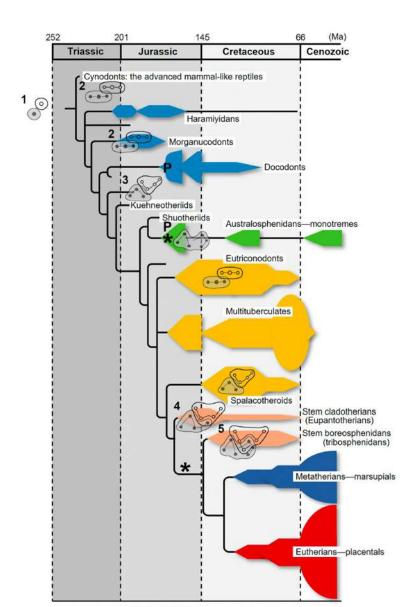
**2.** enhance cutting function for carnivorous diet



# Evolution and development of the mammalian multicuspid teeth

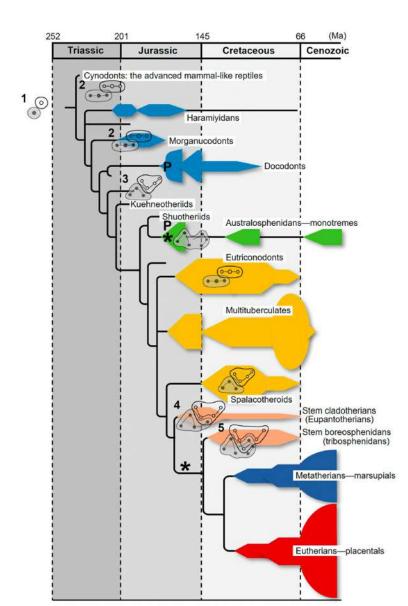
#### Atsushi Yamanaka

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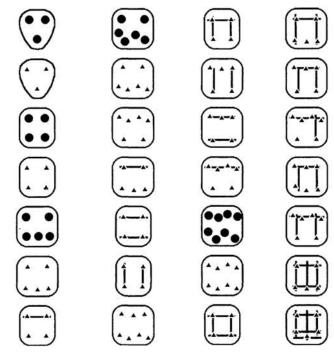


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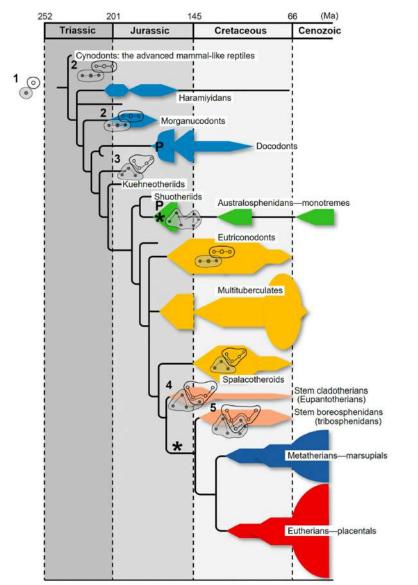
### Molar Tooth Diversity, Disparity, and Ecology in **Cenozoic Ungulate Radiations**

Jukka Jernvall, John P. Hunter,\* Mikael Fortelius





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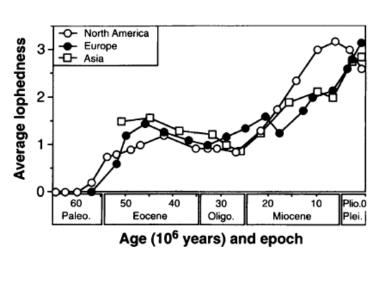
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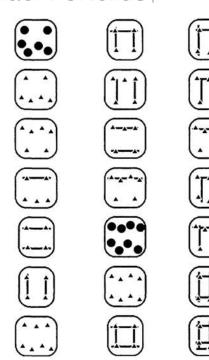
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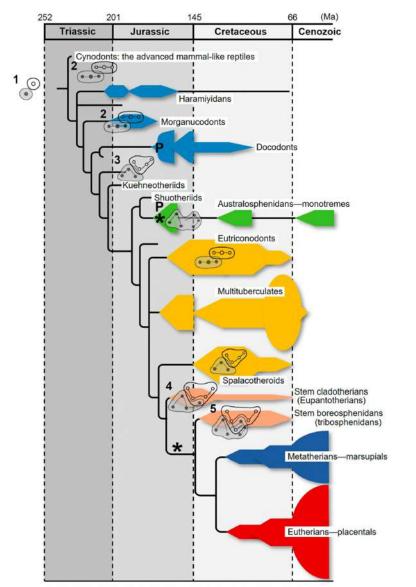
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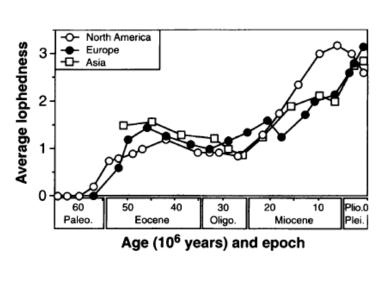
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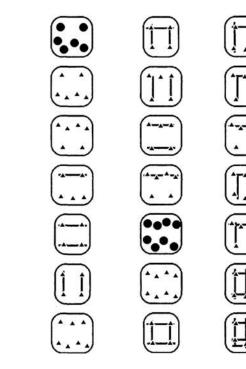
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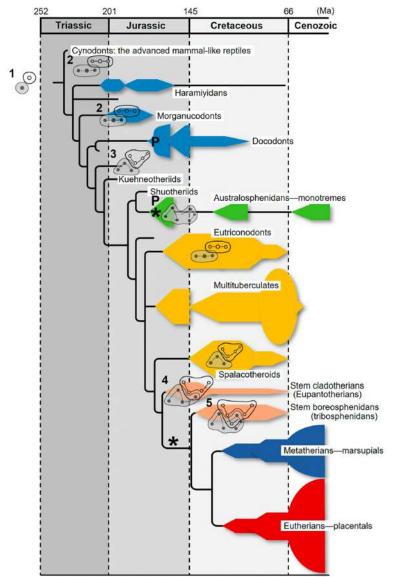
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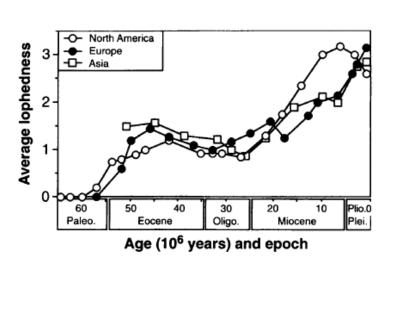
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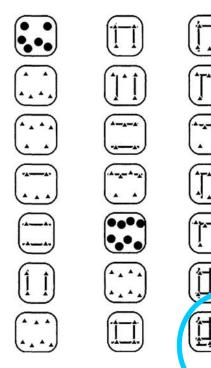
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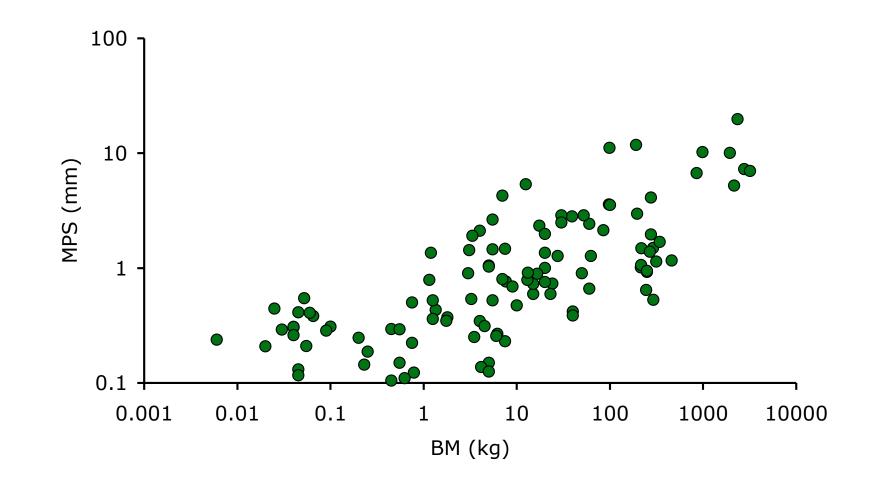
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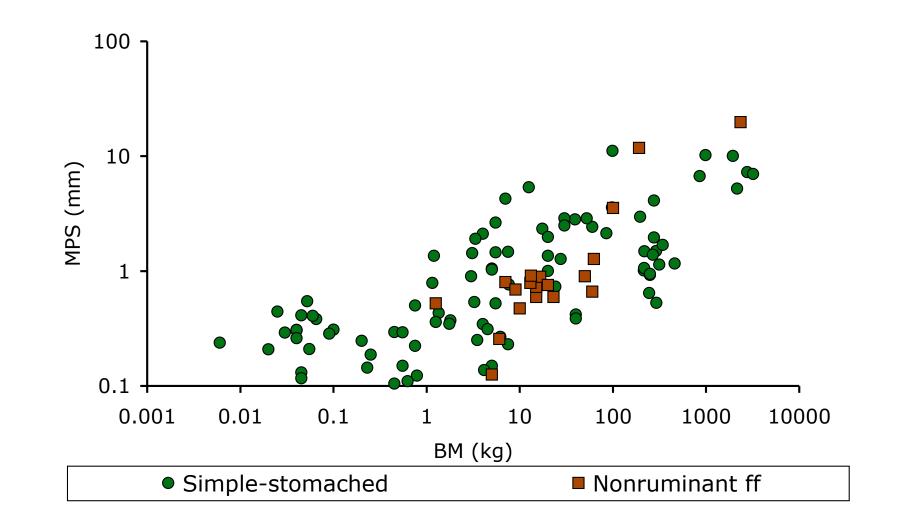


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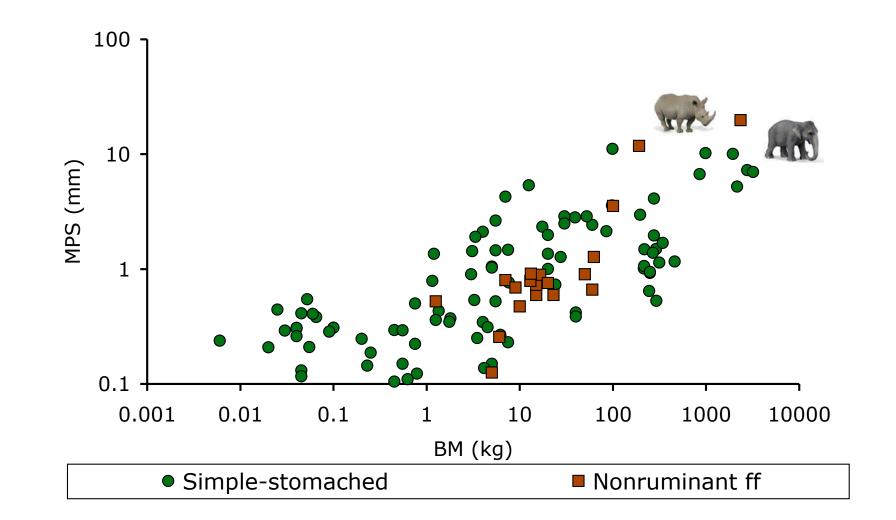


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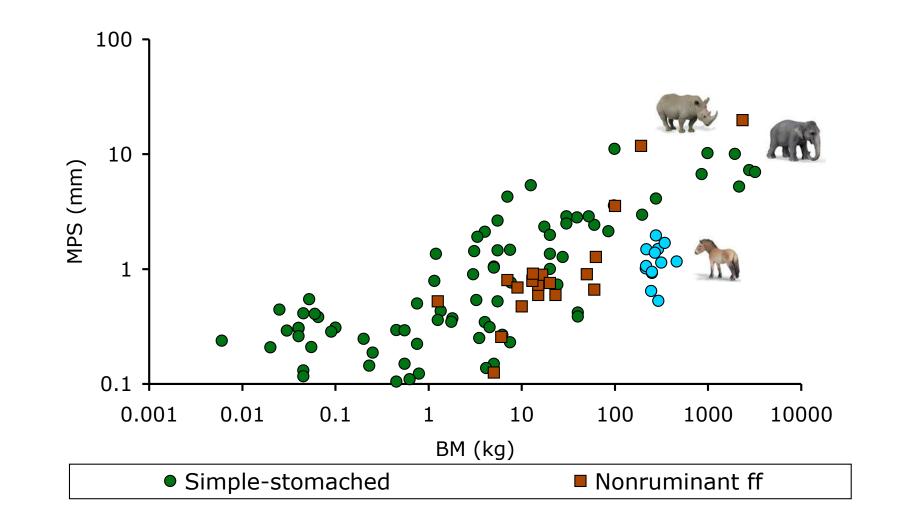


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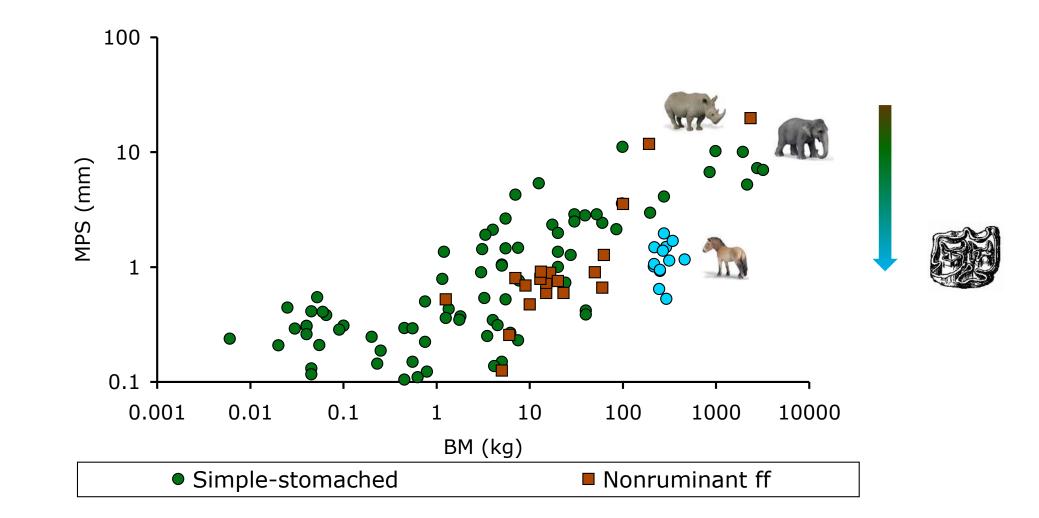
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# Teeth evolve for ... efficiency





Vagan Tapaltsyan,<sup>1,8</sup> Jussi T. Eronen,<sup>2,3,8</sup> A. Michelle Lawing,<sup>4</sup> Amnon Sharir,<sup>1</sup> Christine Janis,<sup>5</sup> Jukka Jernvall,<sup>6,\*</sup> and Ophir D. Klein<sup>1,7,\*</sup>

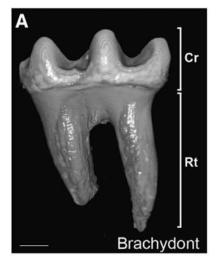


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#### Brachydont

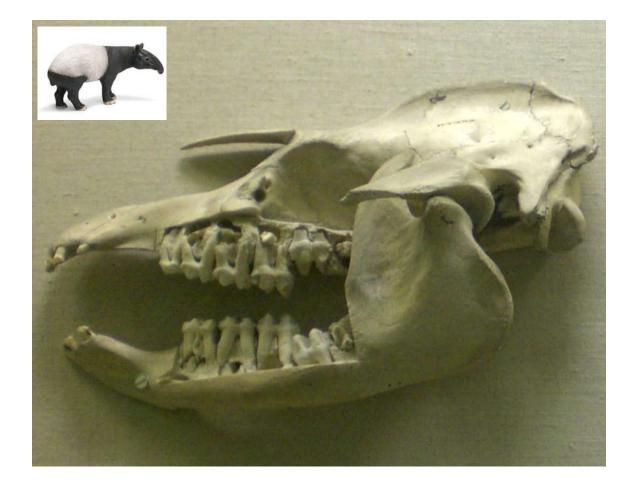








# Brachydonty





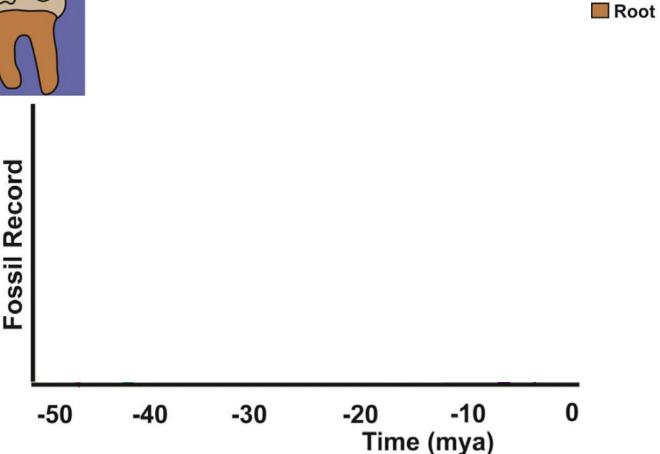
Vagan Tapaltsyan,<sup>1,8</sup> Jussi T. Eronen,<sup>2,3,8</sup> A. Michelle Lawing,<sup>4</sup> Amnon Sharir,<sup>1</sup> Christine Janis,<sup>5</sup> Jukka Jernvall,<sup>6,\*</sup> and Ophir D. Klein1,7,\*

#### Brachydont



Prevalence

Phenotype



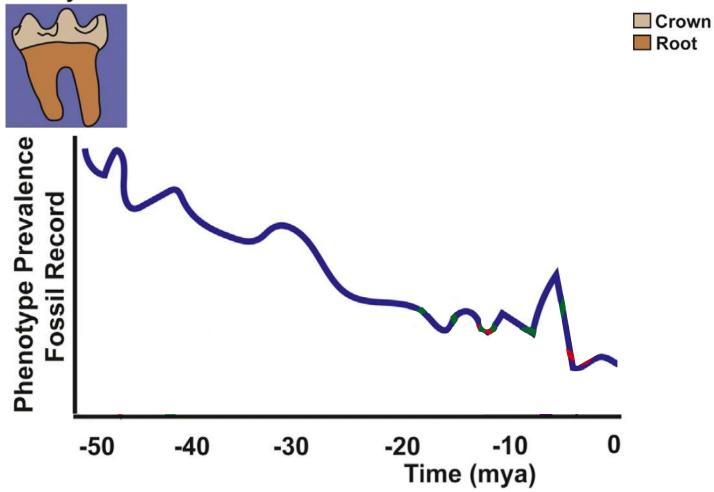


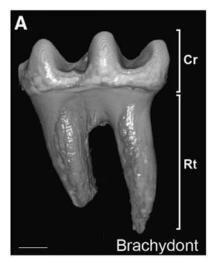
Crown



Vagan Tapaltsyan,<sup>1,8</sup> Jussi T. Eronen,<sup>2,3,8</sup> A. Michelle Lawing,<sup>4</sup> Amnon Sharir,<sup>1</sup> Christine Janis,<sup>5</sup> Jukka Jernvall,<sup>6,\*</sup> and Ophir D. Klein<sup>1,7,\*</sup>

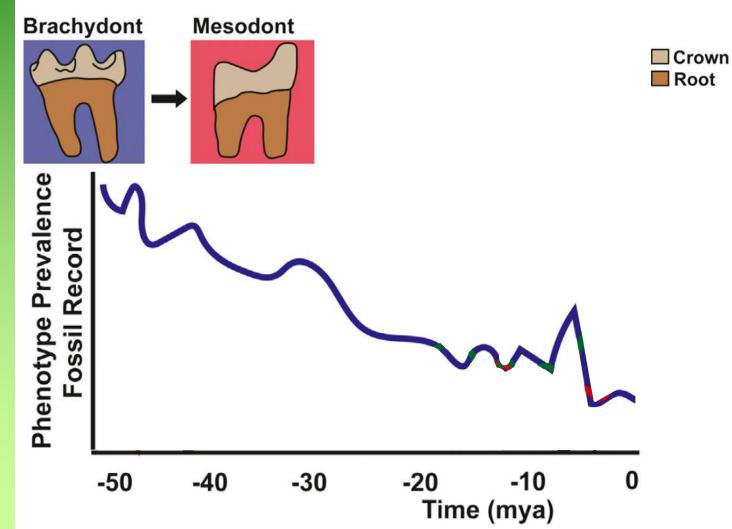
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Vagan Tapaltsyan,<sup>1,8</sup> Jussi T. Eronen,<sup>2,3,8</sup> A. Michelle Lawing,<sup>4</sup> Amnon Sharir,<sup>1</sup> Christine Janis,<sup>5</sup> Jukka Jernvall,<sup>6,\*</sup> and Ophir D. Klein<sup>1,7,\*</sup>



Cell Reports 11, 673-680, May 5, 2015

Rt

Mesodont

в

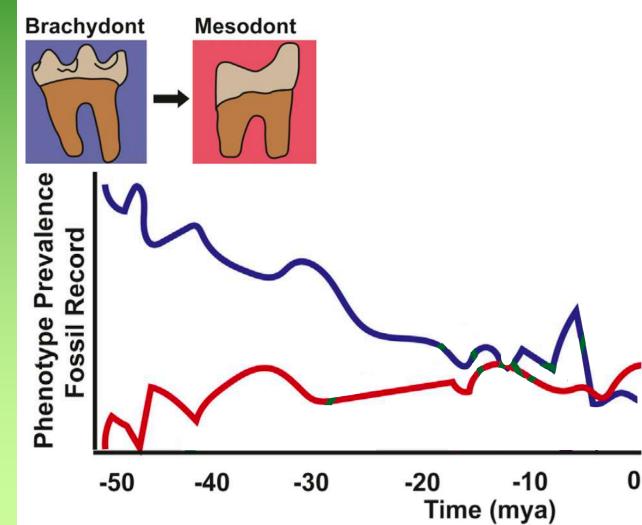
Rt

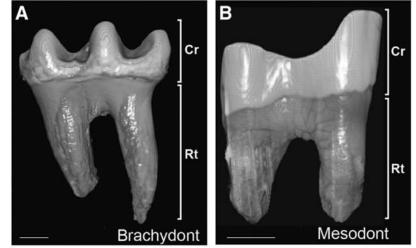
Brachydont



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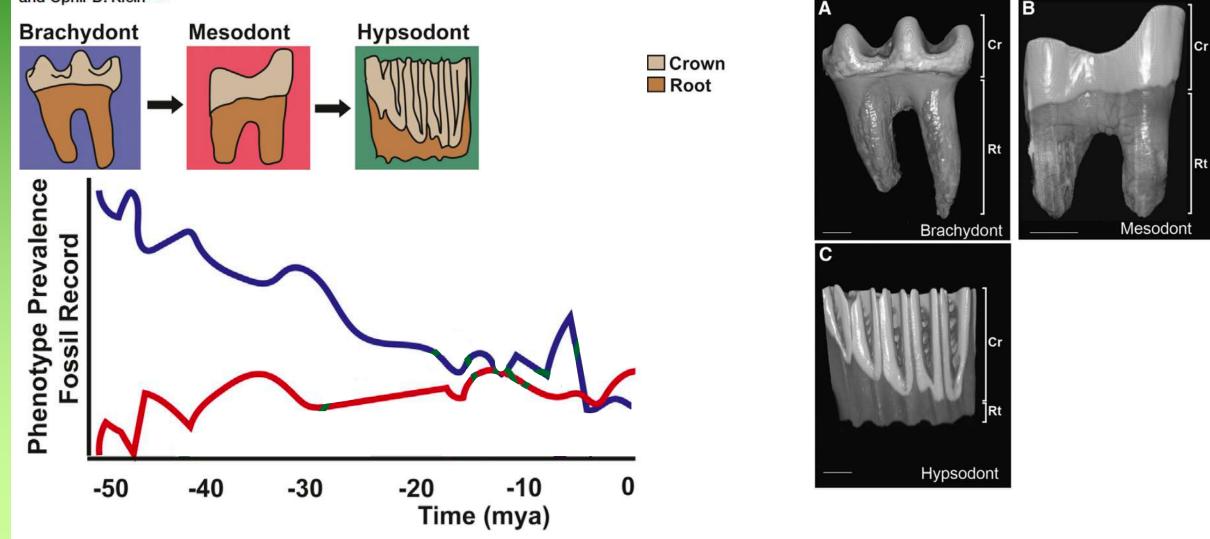
Crown Root







Vagan Tapaltsyan,<sup>1,8</sup> Jussi T. Eronen,<sup>2,3,8</sup> A. Michelle Lawing,<sup>4</sup> Amnon Sharir,<sup>1</sup> Christine Janis,<sup>5</sup> Jukka Jernvall,<sup>6,\*</sup> and Ophir D. Klein<sup>1,7,\*</sup>



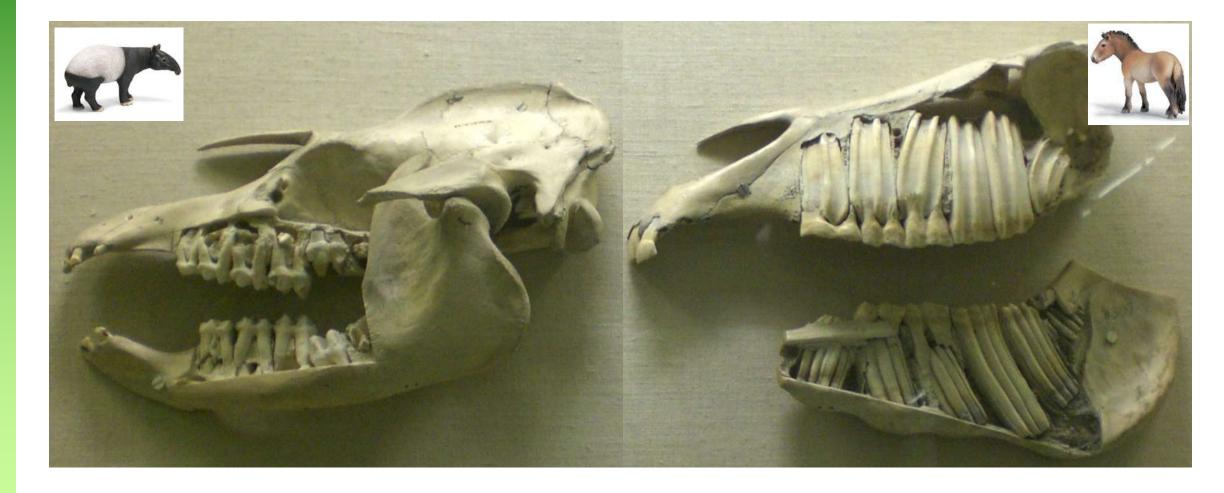
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### Brachydonty

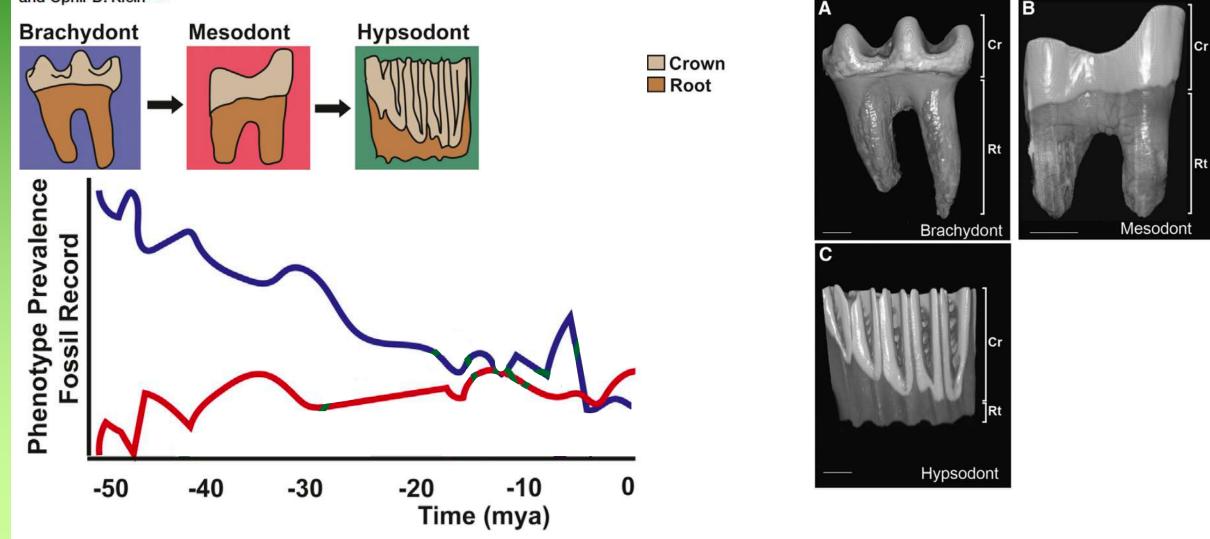
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### Hypsodonty





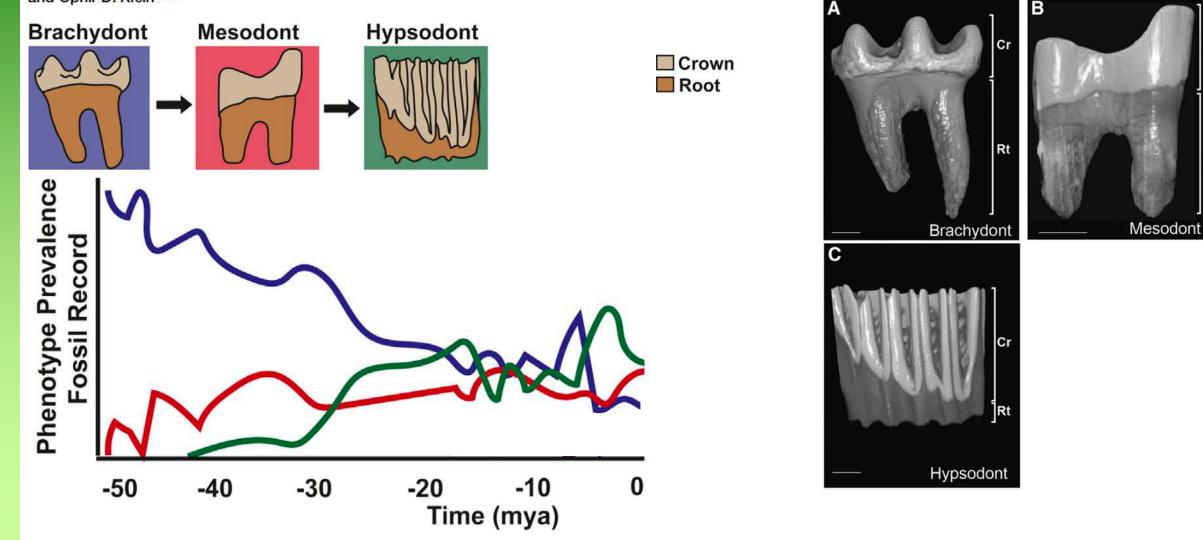
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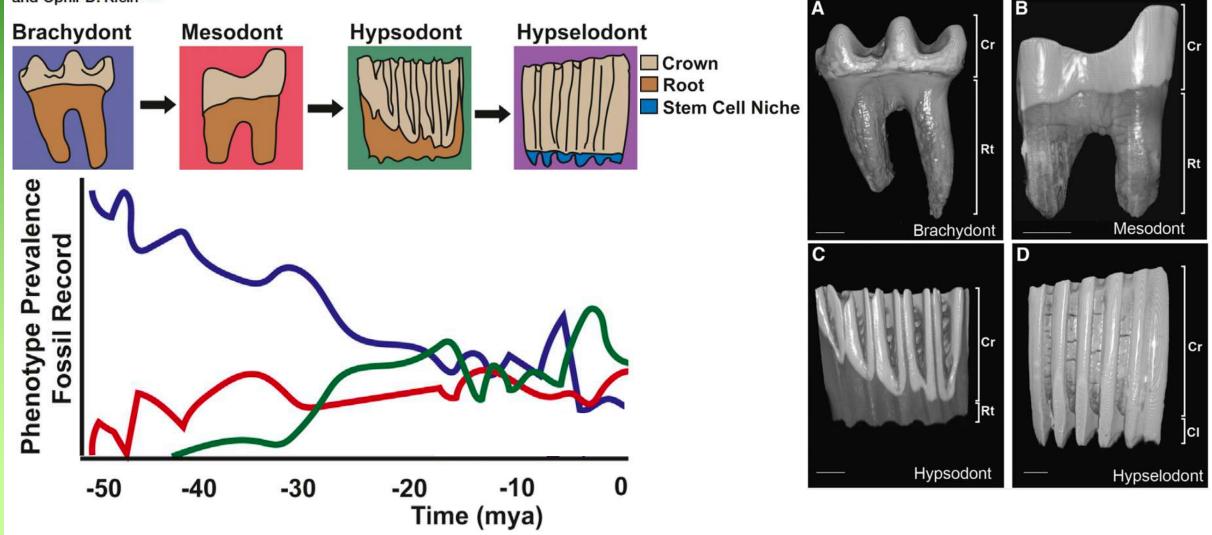
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Rt



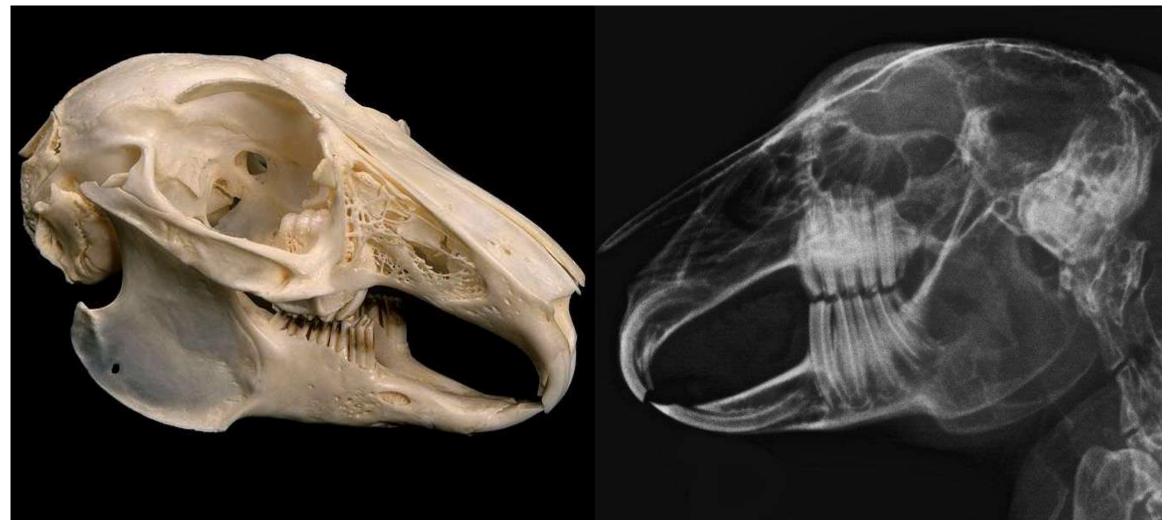
Vagan Tapaltsyan,<sup>1,8</sup> Jussi T. Eronen,<sup>2,3,8</sup> A. Michelle Lawing,<sup>4</sup> Amnon Sharir,<sup>1</sup> Christine Janis,<sup>5</sup> Jukka Jernvall,<sup>6,\*</sup> and Ophir D. Klein<sup>1,7,\*</sup>





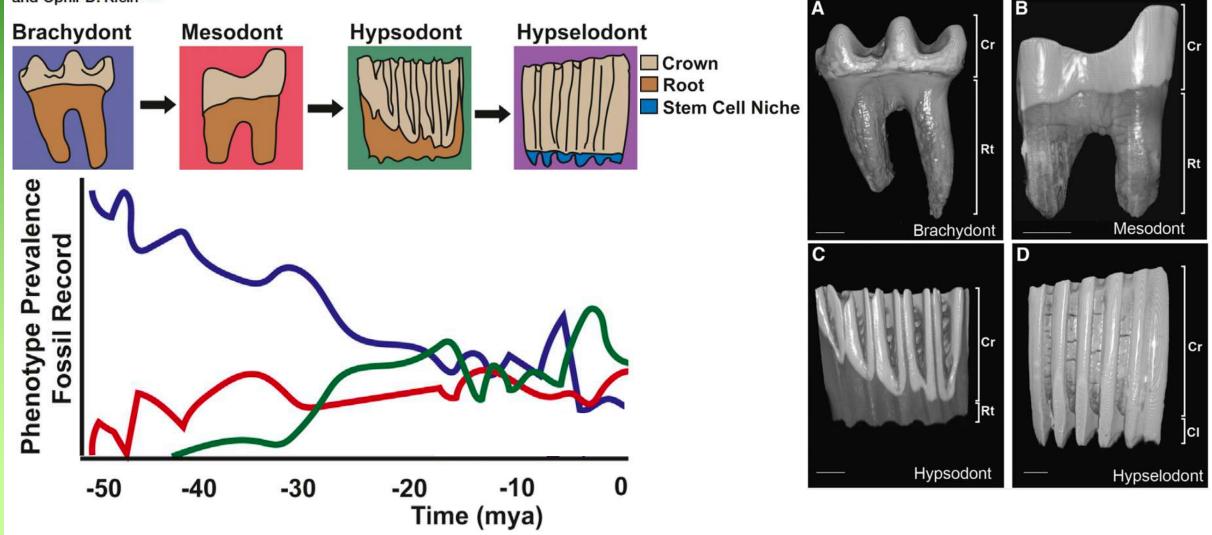
### Ever-growing teeth – 'Hypselodonty'





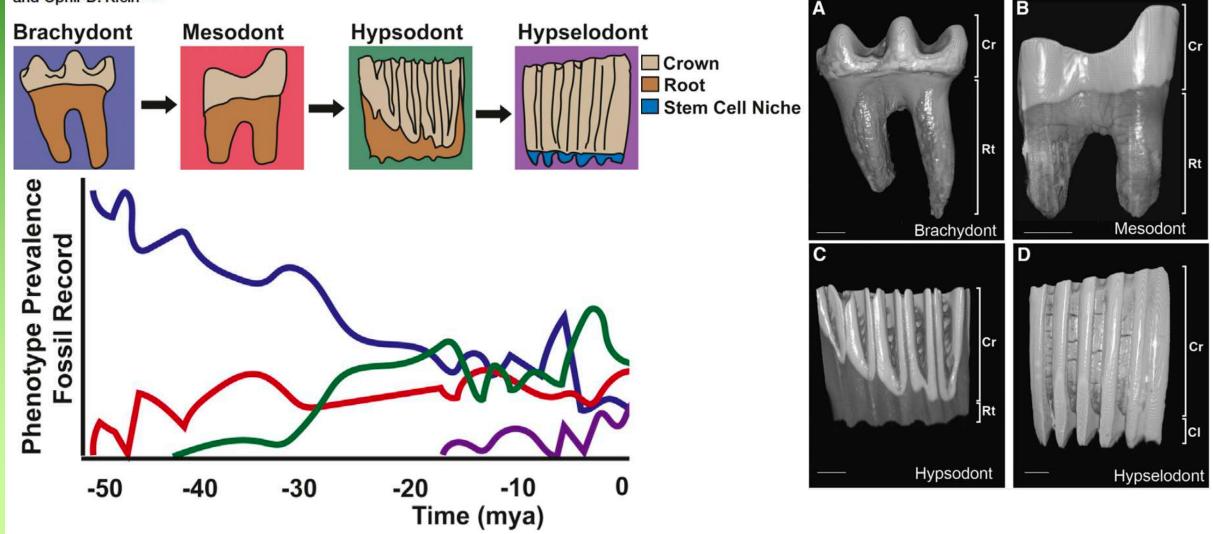


Vagan Tapaltsyan,<sup>1,8</sup> Jussi T. Eronen,<sup>2,3,8</sup> A. Michelle Lawing,<sup>4</sup> Amnon Sharir,<sup>1</sup> Christine Janis,<sup>5</sup> Jukka Jernvall,<sup>6,\*</sup> and Ophir D. Klein<sup>1,7,\*</sup>





Vagan Tapaltsyan,<sup>1,8</sup> Jussi T. Eronen,<sup>2,3,8</sup> A. Michelle Lawing,<sup>4</sup> Amnon Sharir,<sup>1</sup> Christine Janis,<sup>5</sup> Jukka Jernvall,<sup>6,\*</sup> and Ophir D. Klein<sup>1,7,\*</sup>





## Teeth evolve for ...



& durahil

durability



# Faunivory – Omnivory – Herbivory



# Faunivory – Omnivory – Herbivory

## and microbe farming

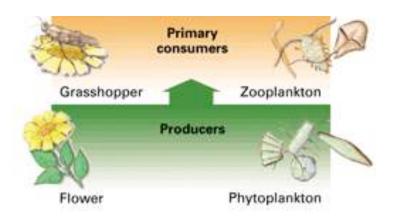


A terrestrial food chain A marine food chain



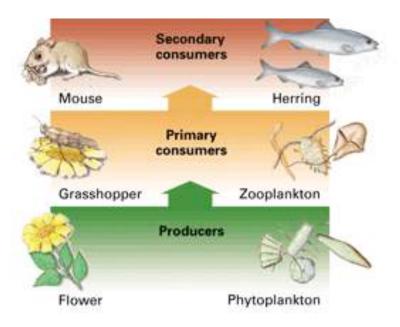


A terrestrial food chain A marine food chain



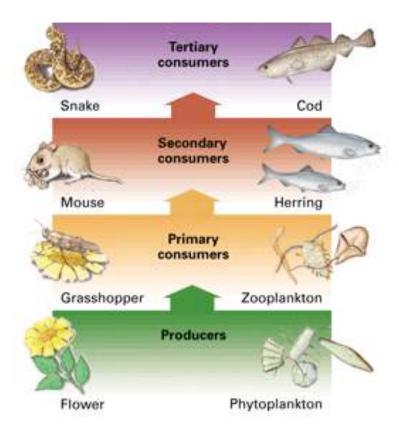


A terrestrial food chain A marine food chain

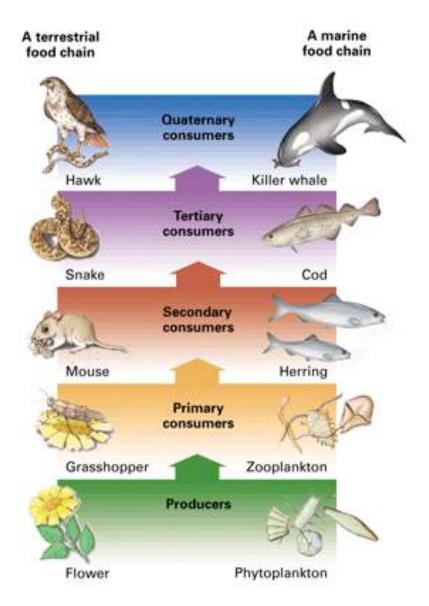




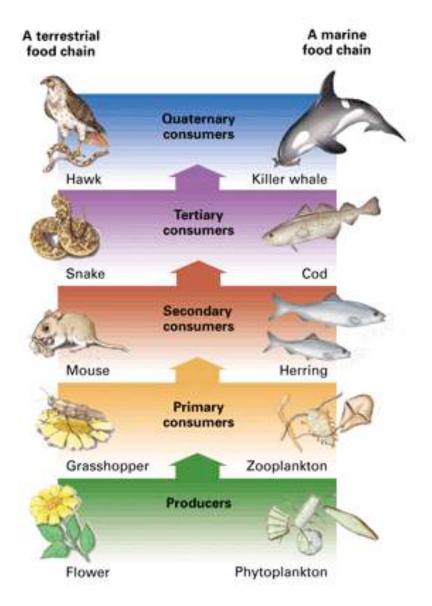
A terrestrial food chain A marine food chain



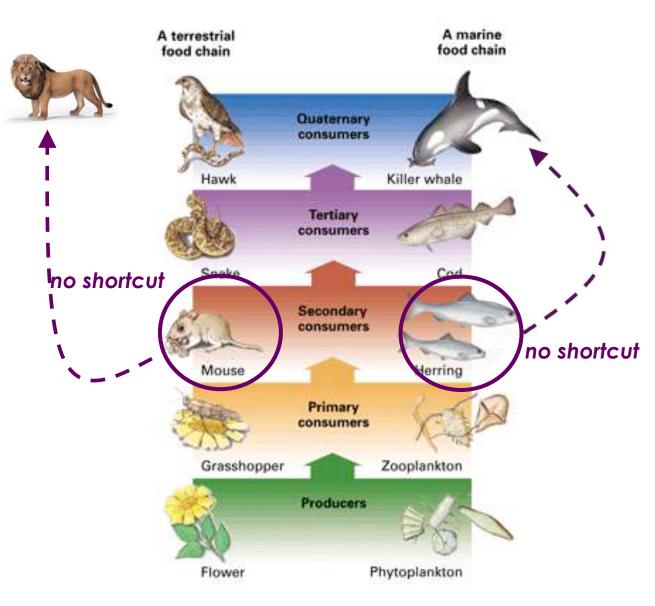




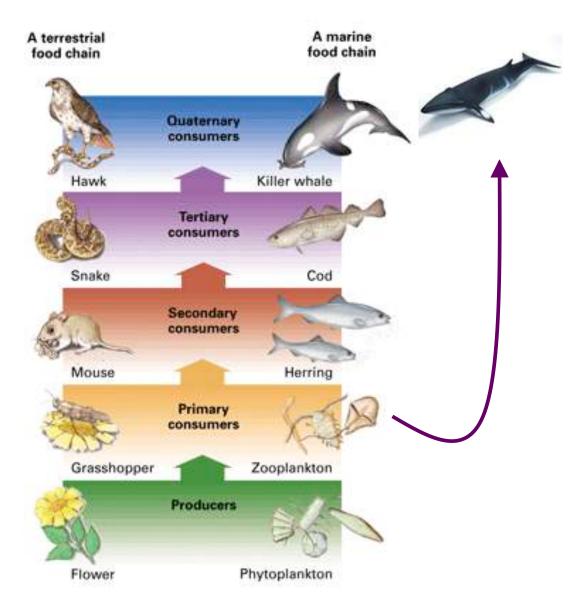










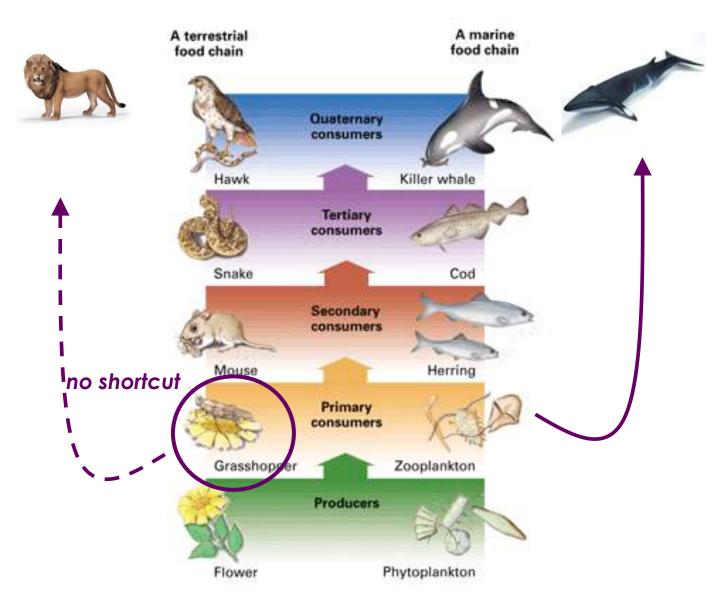




#### Easy-to-harvest packages of tiny invertebrates – krill clouds



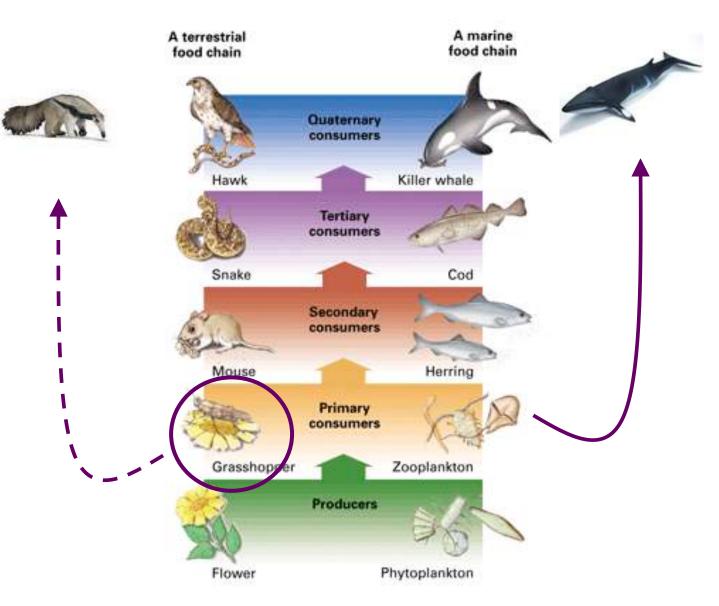




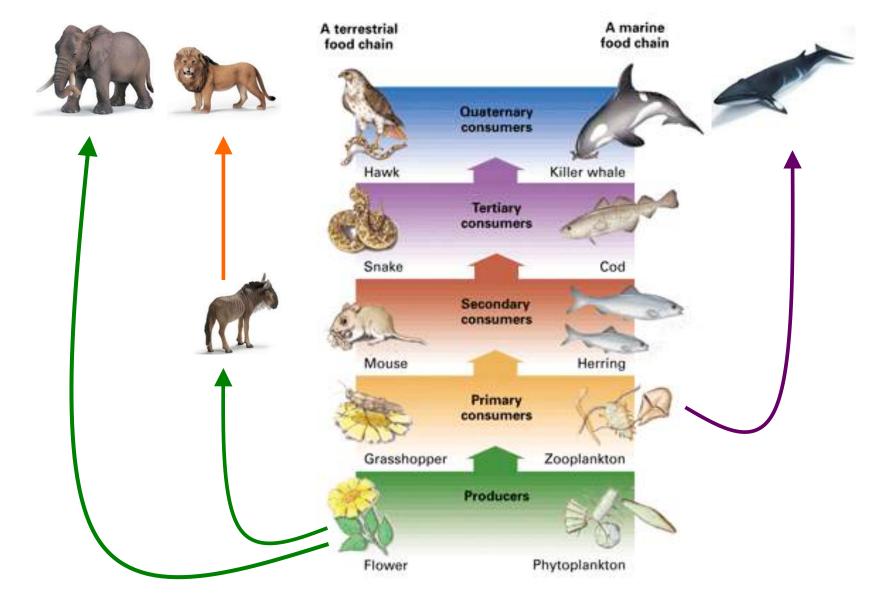
### No easy-to-harvest packages of tiny vertebrates









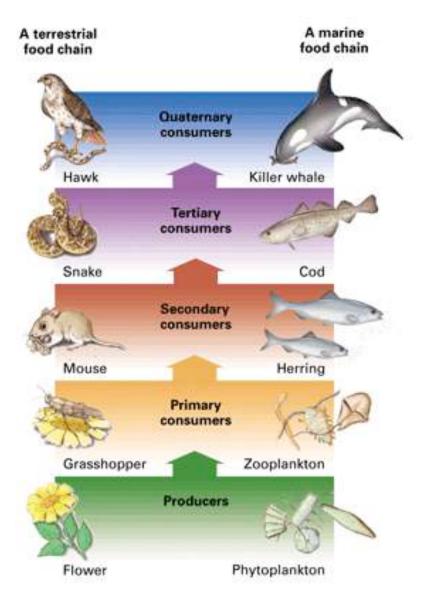




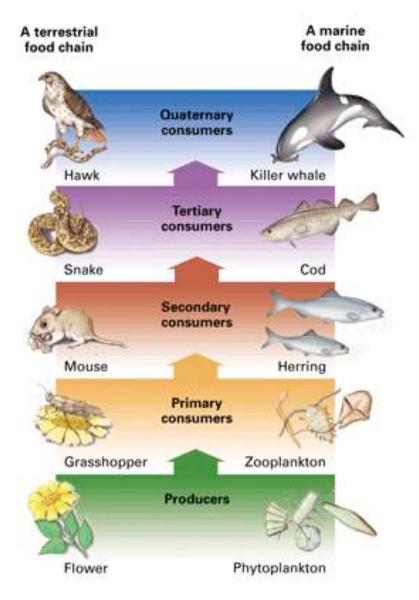
#### Ubiquitous dense large packages of plant food in terrestrial systems







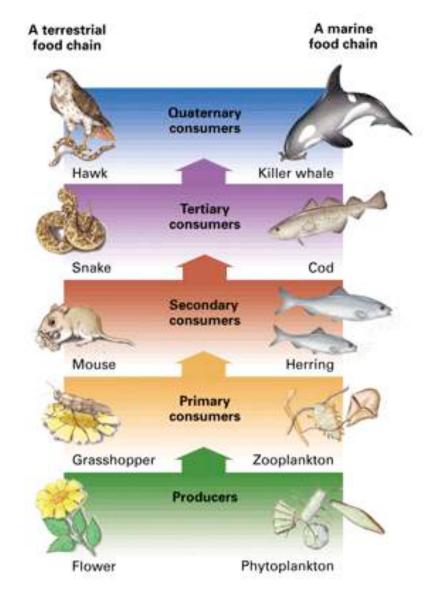




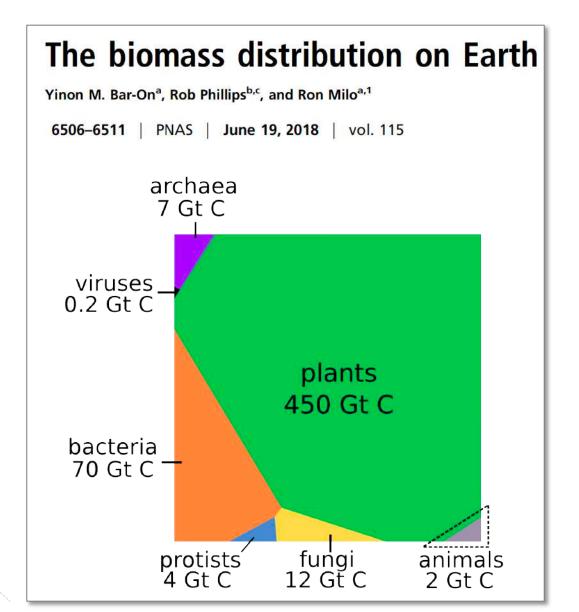




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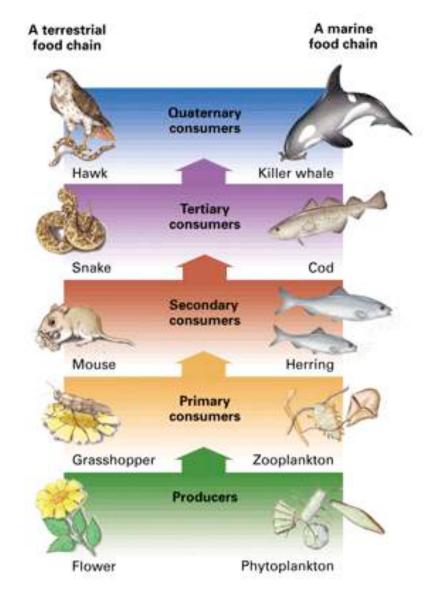




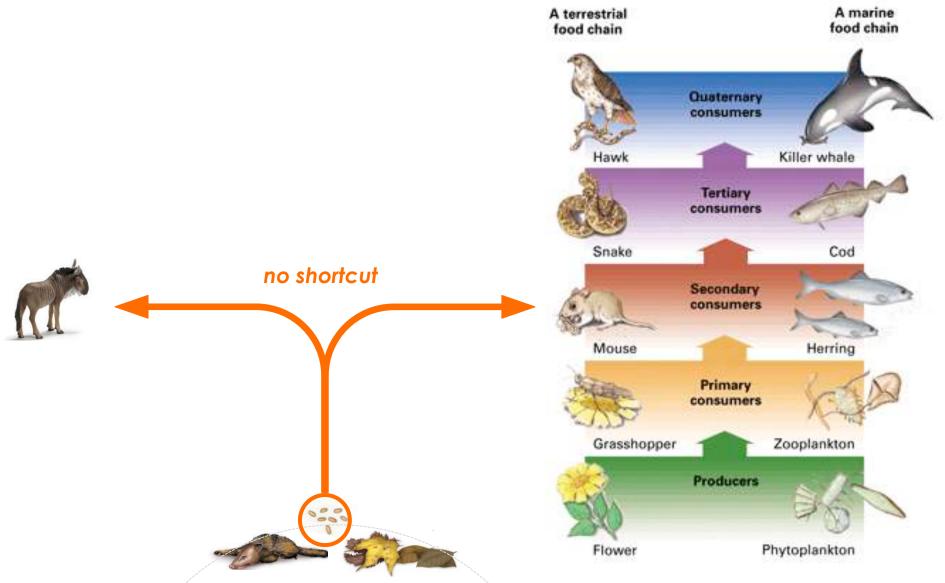




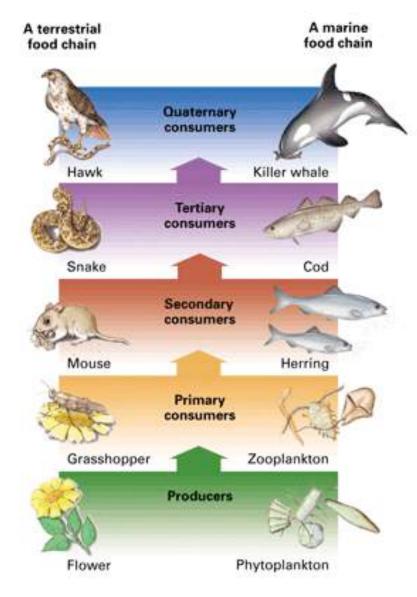
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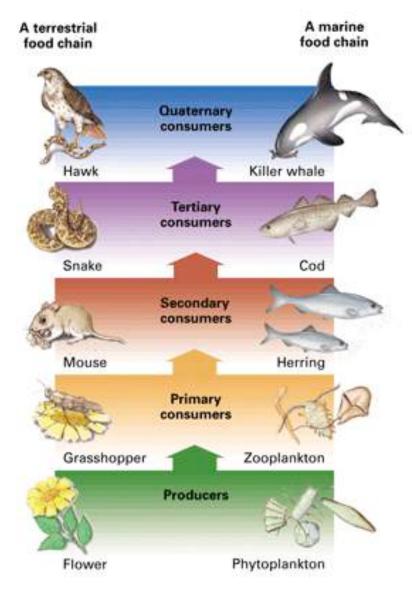






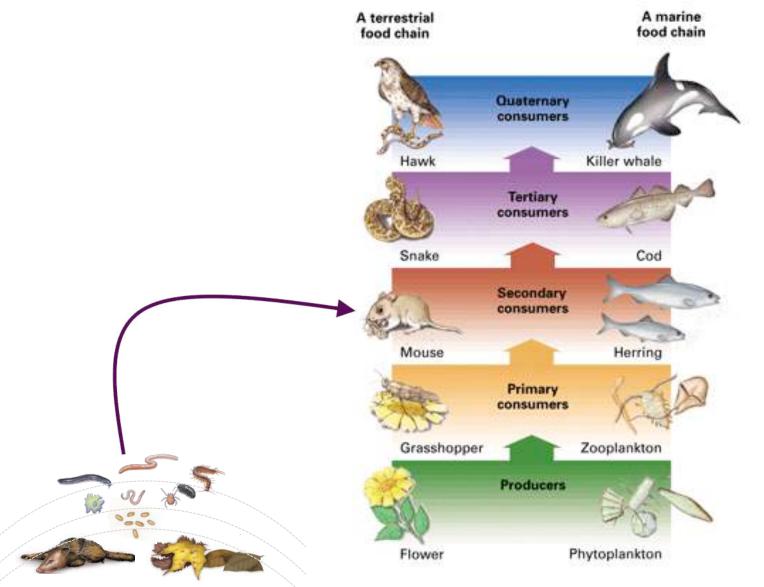














### Microbes in the digestive tract











### Microbes in the digestive tract

... "provide a service":



### Microbes in the digestive tract

... "provide a service":

- they 'ferment' carbohydrates and produce volatile fatty acids



... "provide a service":

- they 'ferment' carbohydrates and produce volatile fatty acids

- they may detoxify certain substances



... "provide a service":

- they may detoxify certain substances
- they produce vitamins



... "provide a service":

- they may detoxify certain substances
- they produce vitamins
- they 'produce microbial protein'



... "provide a service":

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- they produce vitamins
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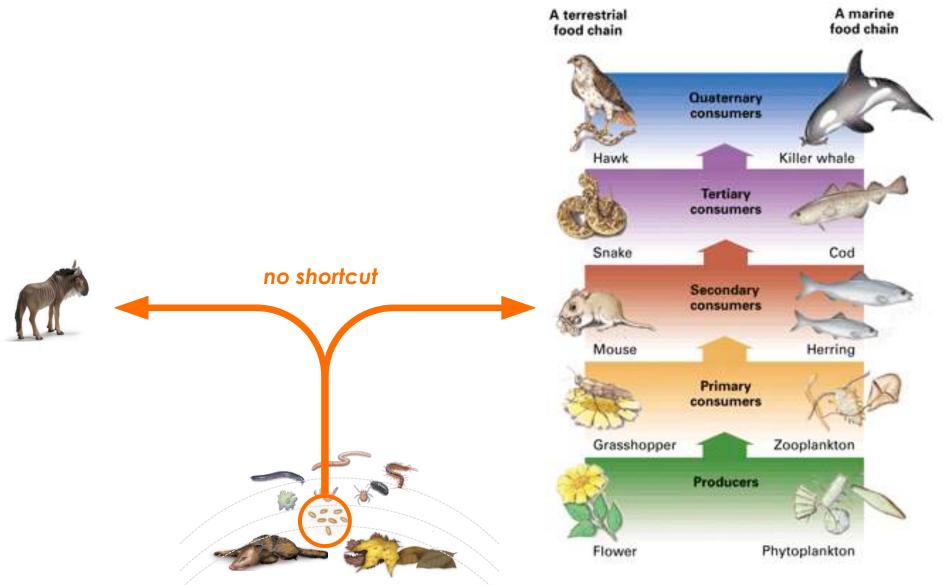


... "provide a service":

- they may detoxify certain substances
- they produce vitamins
- they 'produce microbial protein' = microbes are (potential) prey in a trophic chain



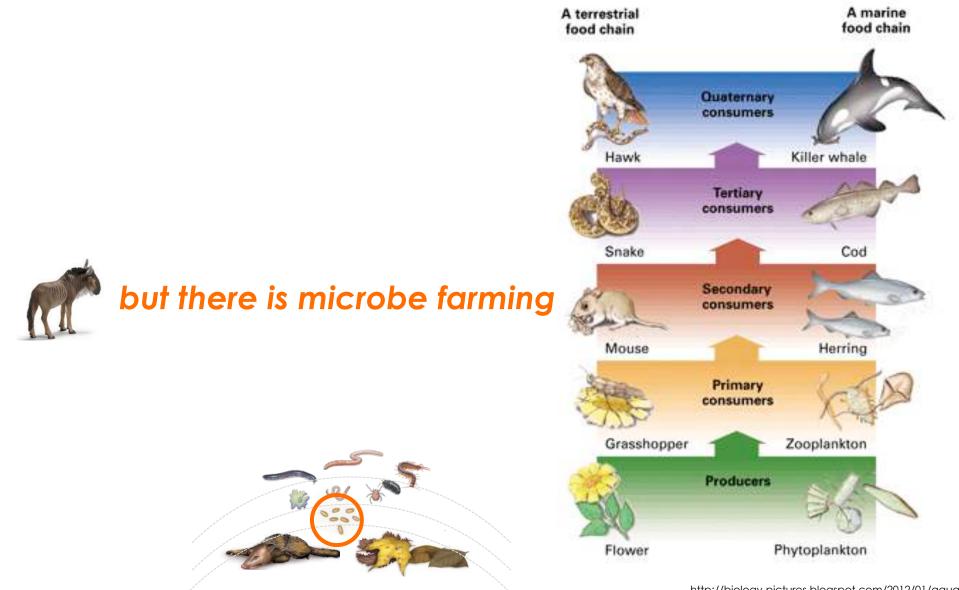
#### Food chains ... & shortcuts



http://biology-pictures.blogspot.com/2012/01/aquatic-and-terrestrial-food-chains.html



#### Food chains ... & shortcuts



http://biology-pictures.blogspot.com/2012/01/aquatic-and-terrestrial-food-chains.html



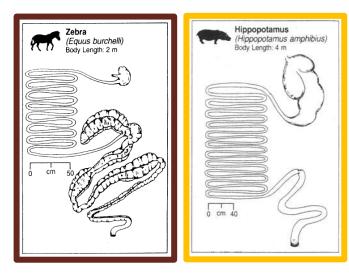
#### Farming: contain, nurture, harvest





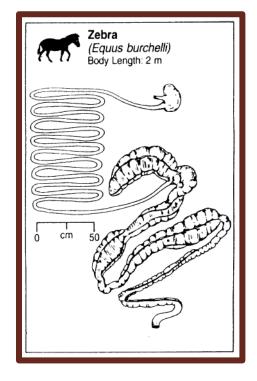
#### Farming: contain, nurture, harvest

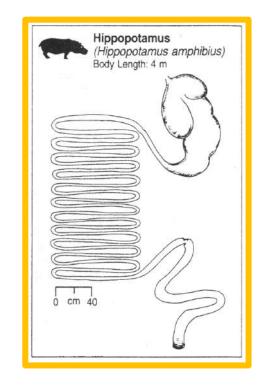




Stevens & Hume (1995)









#### Farming: contain, nurture, harvest

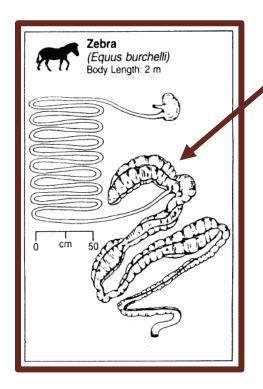


Hippopotamus (Hippopotamus amphibius) Body Length: 4 m Equus burchelli) Body Length: 2 m cm 40

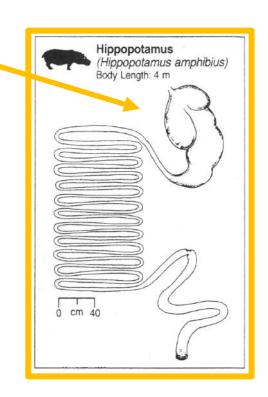




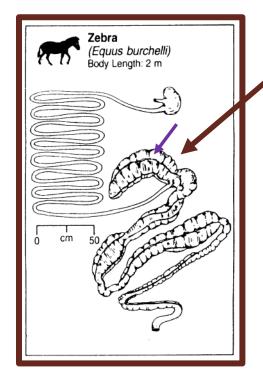




Microbes live and grow by fermenting the diet (rest) ... ... and produce volatile fatty acids

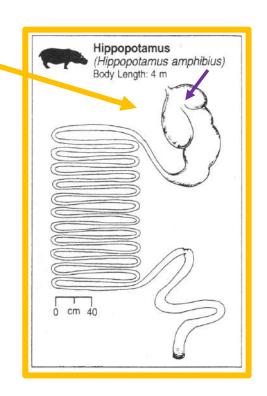






Microbes live and grow by fermenting the diet (rest) .... ... and produce volatile fatty acids

... and are supplied with **urea** via saliva / **blood** 





#### Farming: contain, nurture, harvest



Hippopotamus (Hippopotamus amphibius) Body Length: 4 m Equus burchelli) Body Length: 2 m cm 4



+ supplemental (endogenous) nitrogen



#### Farming: contain, nurture, harvest



Hippopotamus (Hippopotamus amphibius) Body Length: 4 m Zebra (Equus burchelli) Body Length: 2 m cm 4

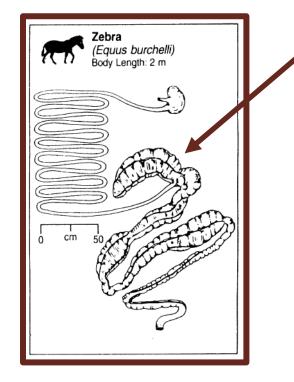


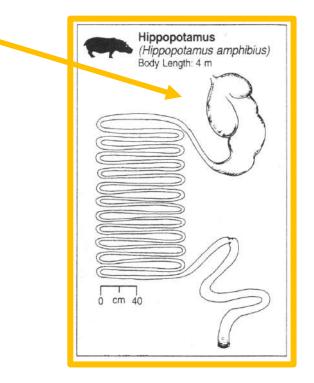
+ supplemental (endogenous) nitrogen



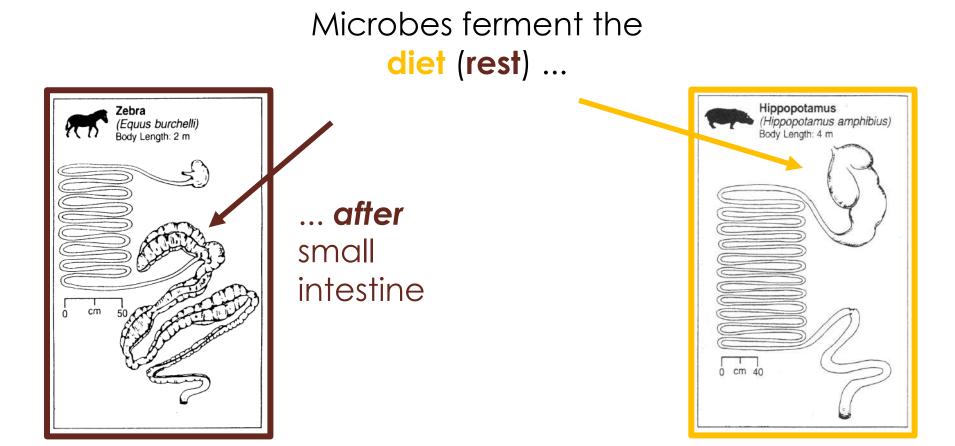


diet (rest) ...

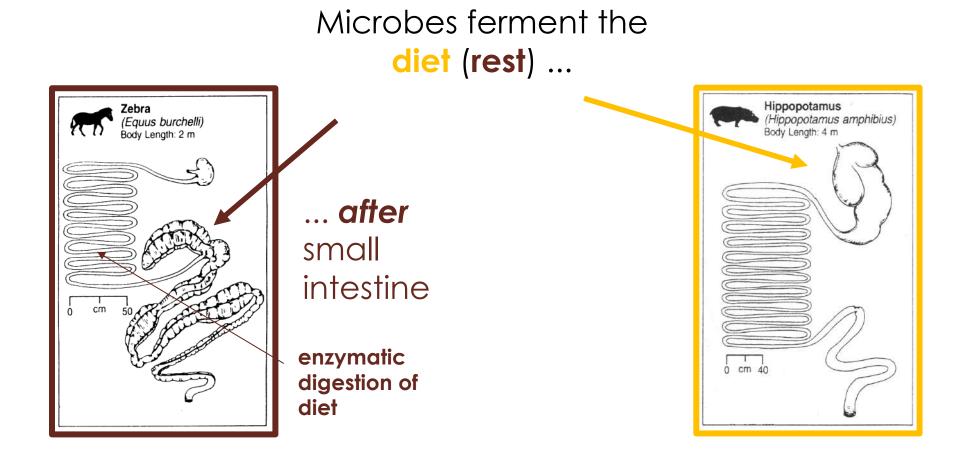




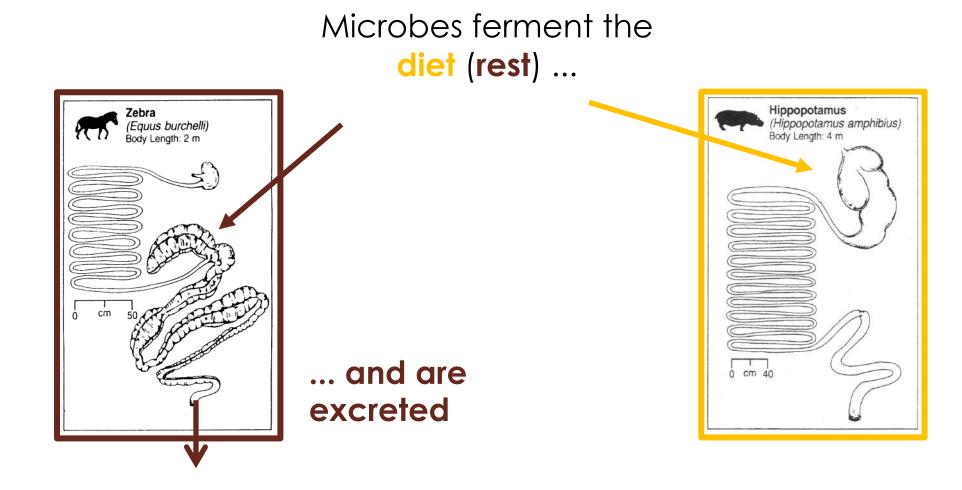














### Extraction not possible ?



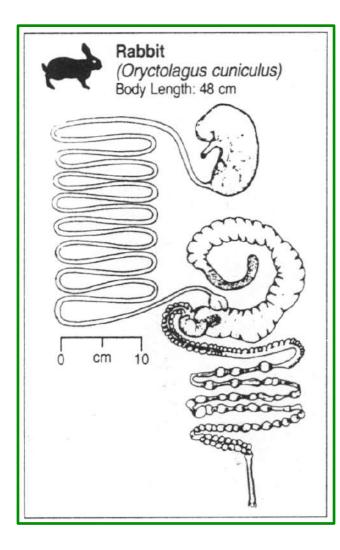


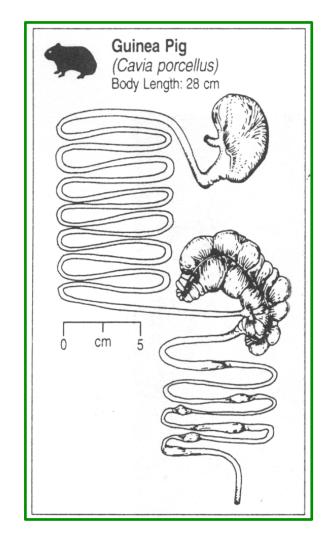
#### Extraction not possible ?

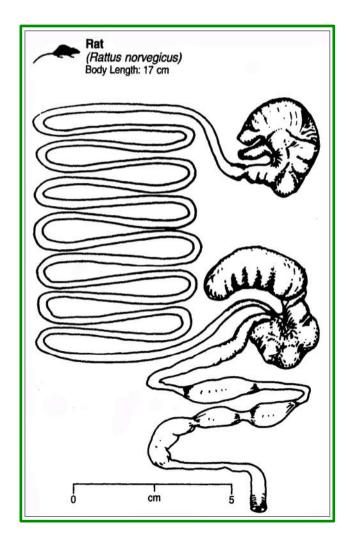




#### Small hindgut fermenters





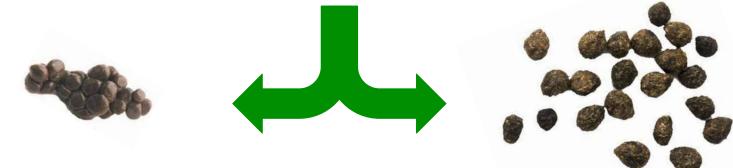




#### Separating microbes from indigestible material



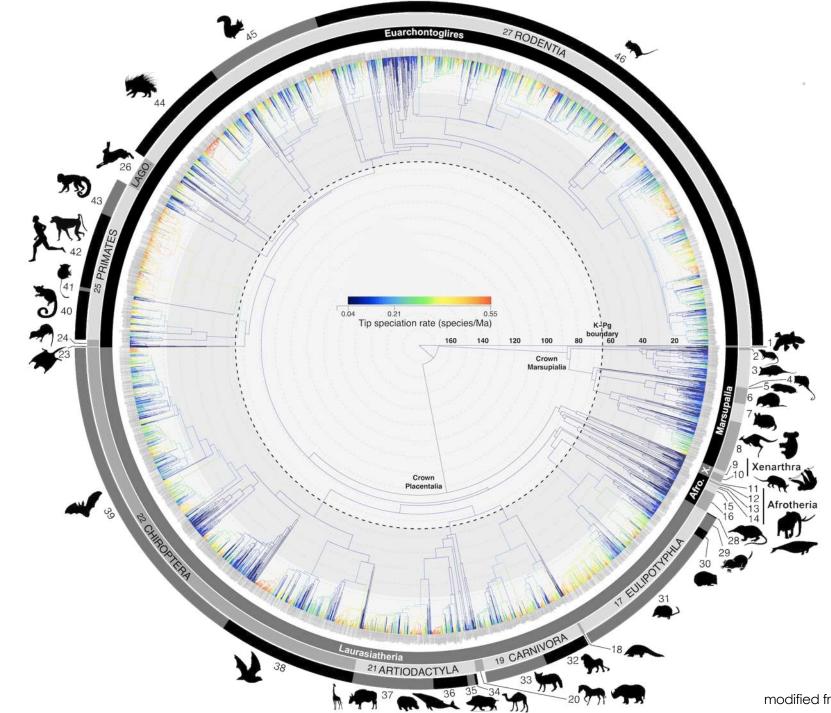
# "Colonic separation mechanism"



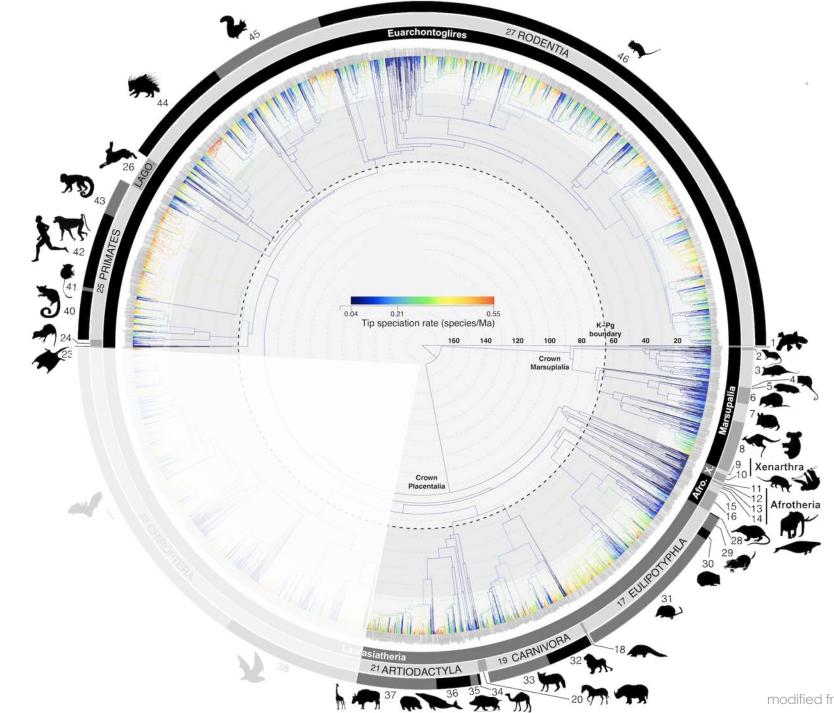
more microbial matter, measurable as protein

more indigestible material, especially fibre

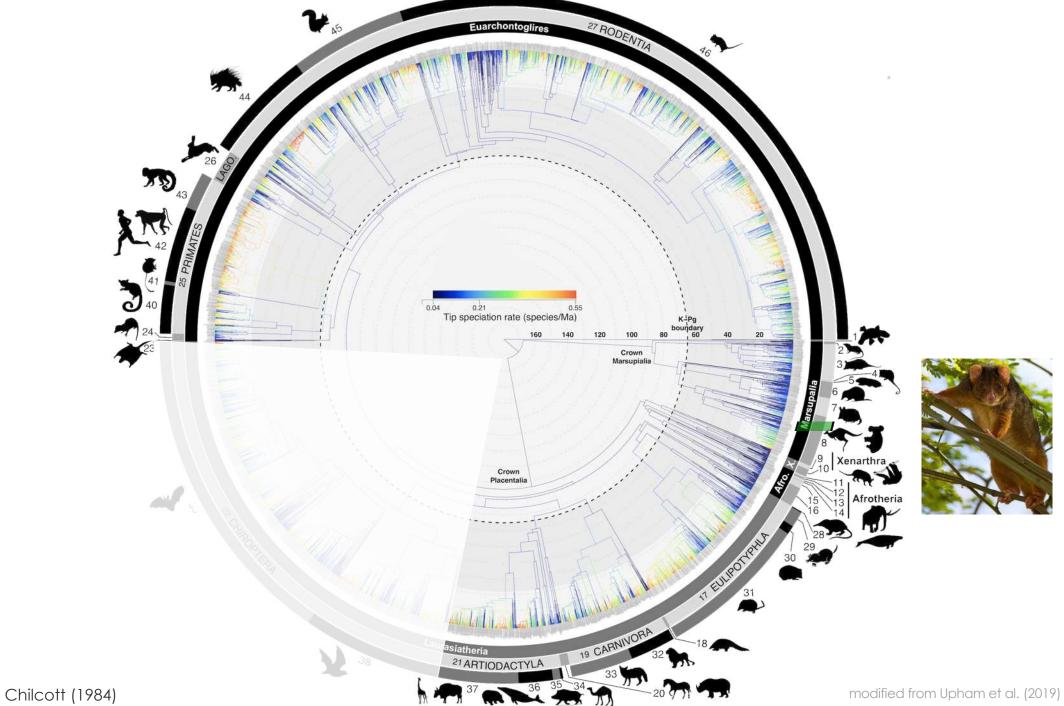




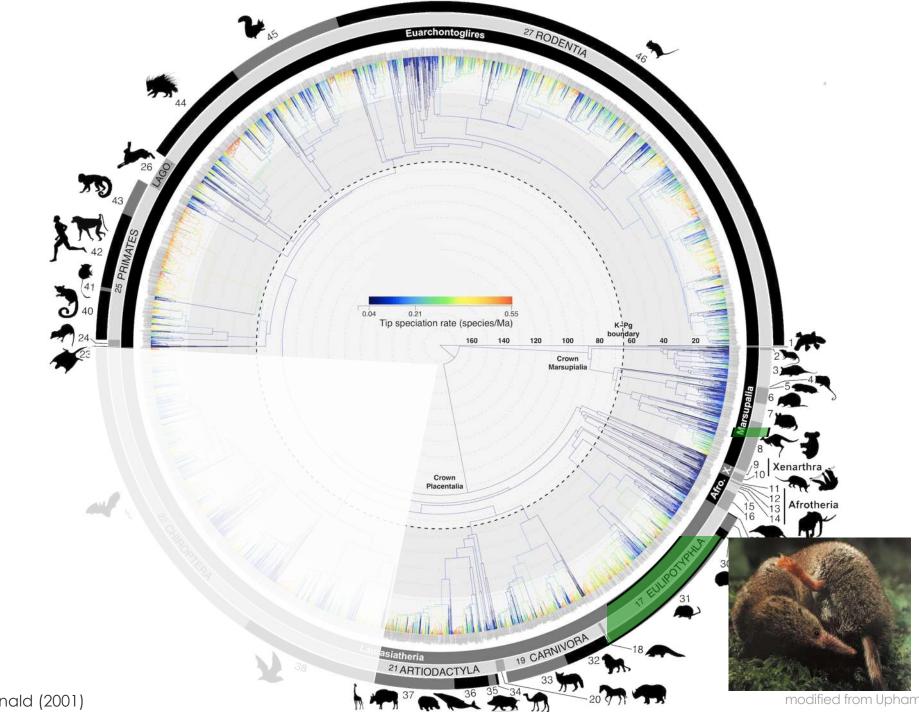




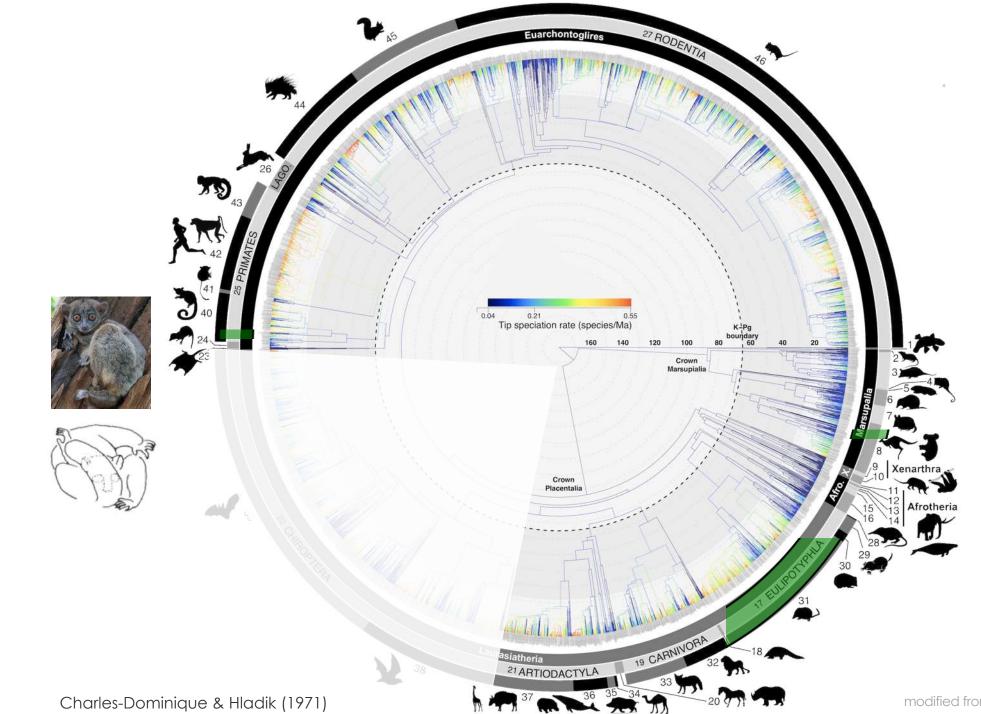




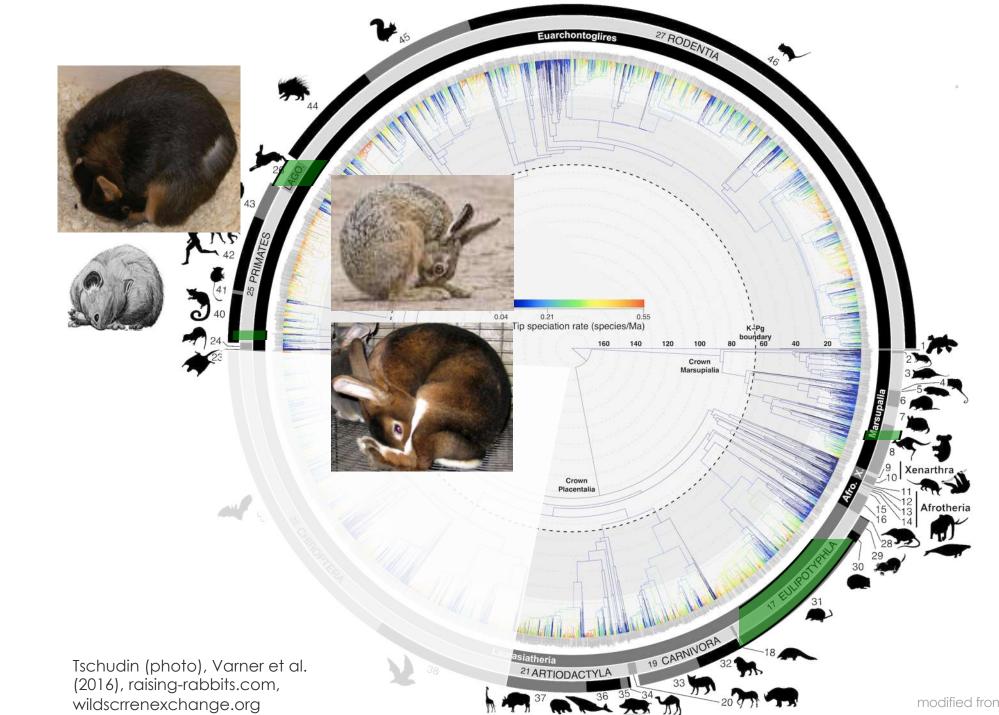




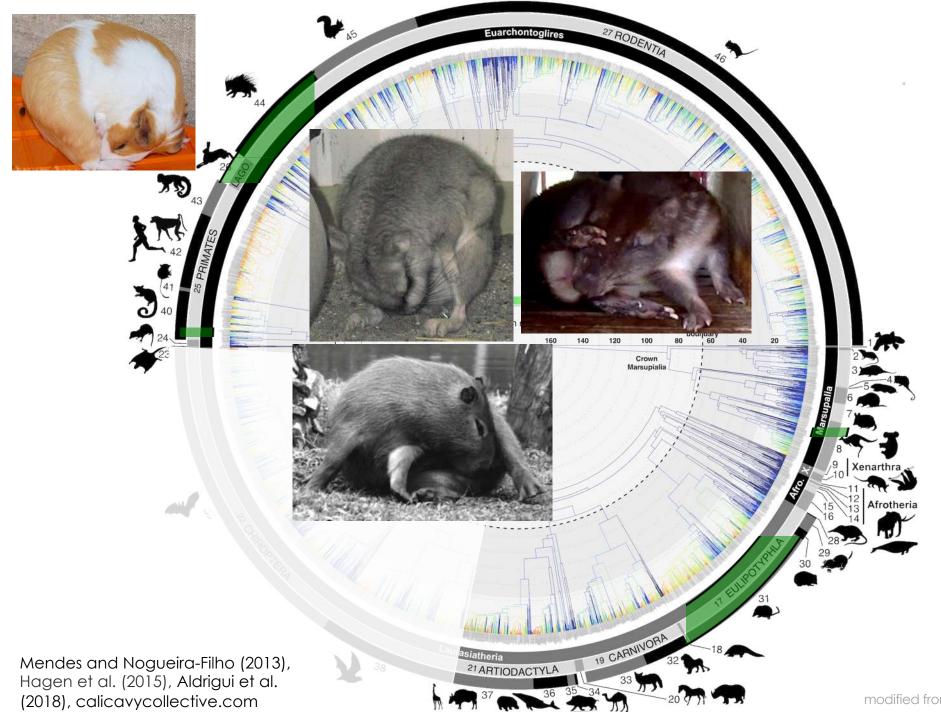
Macdonald (2001)



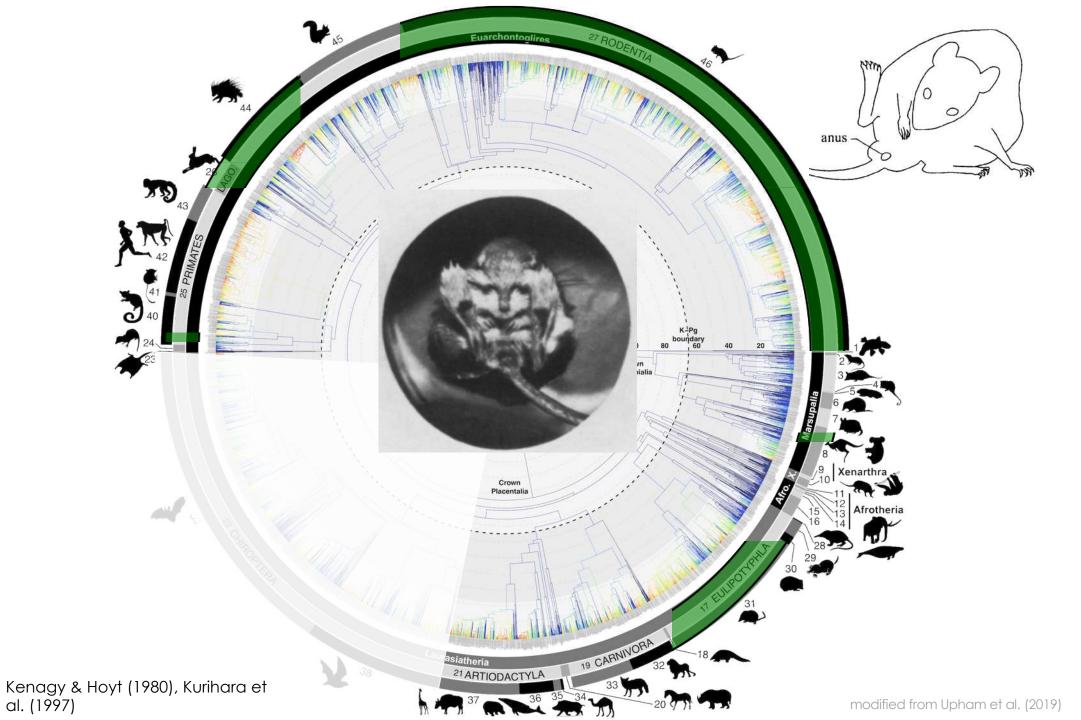
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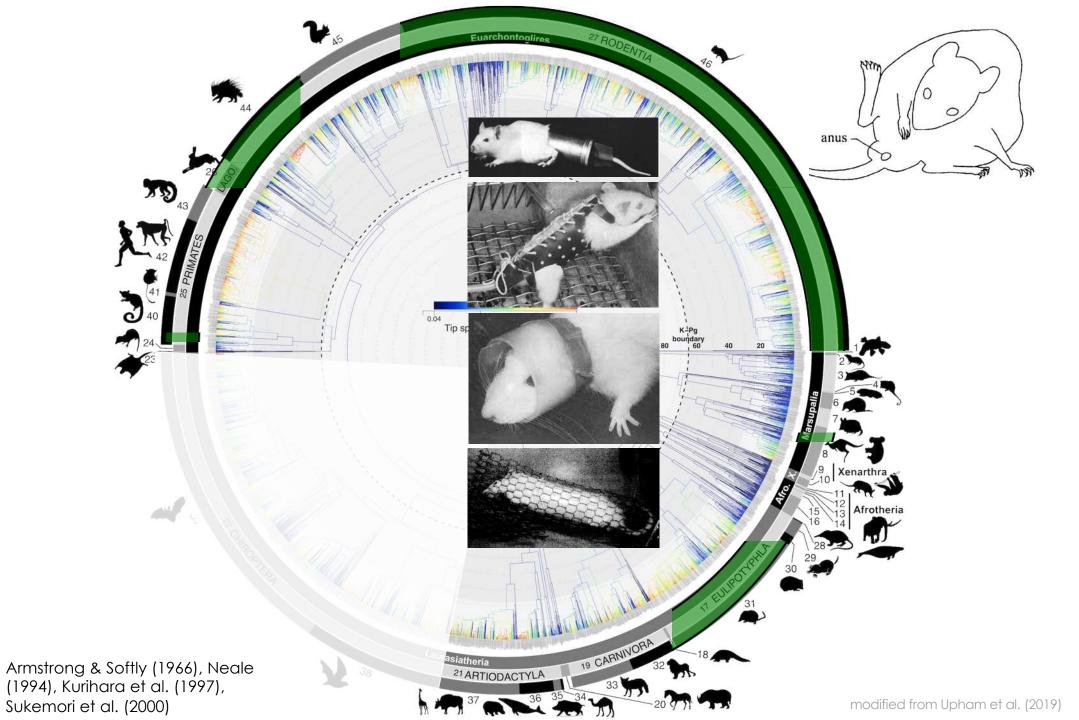




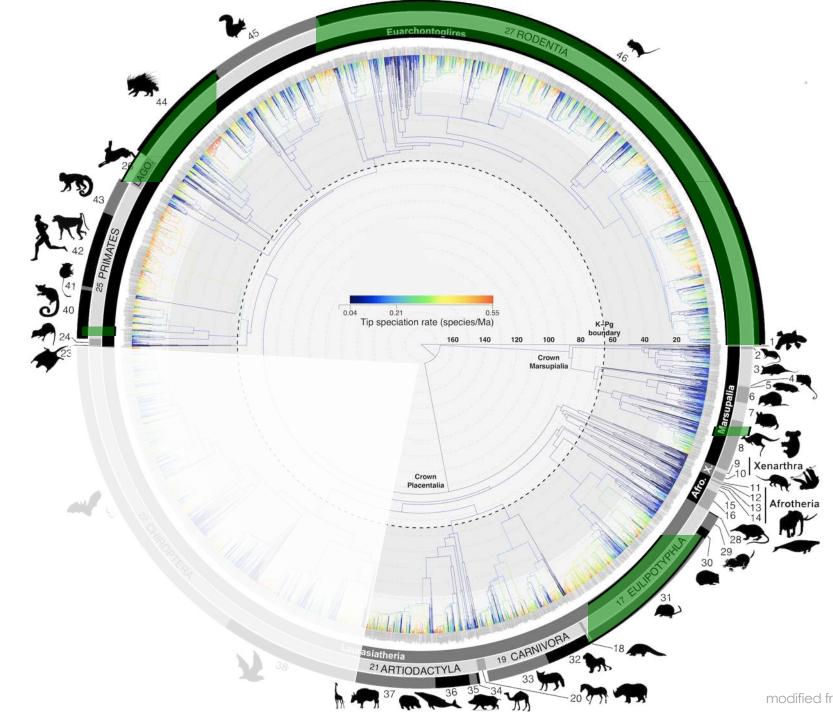














#### Limited menus: an ecological challenge

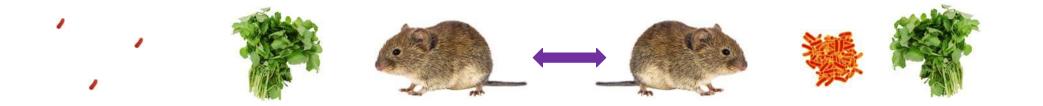


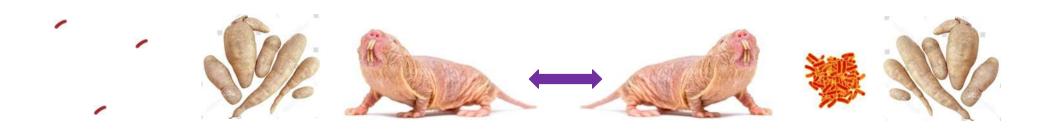


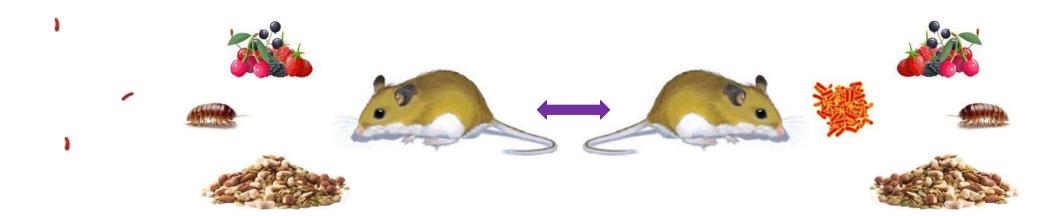




## Expanded menus: an ecological opportunity



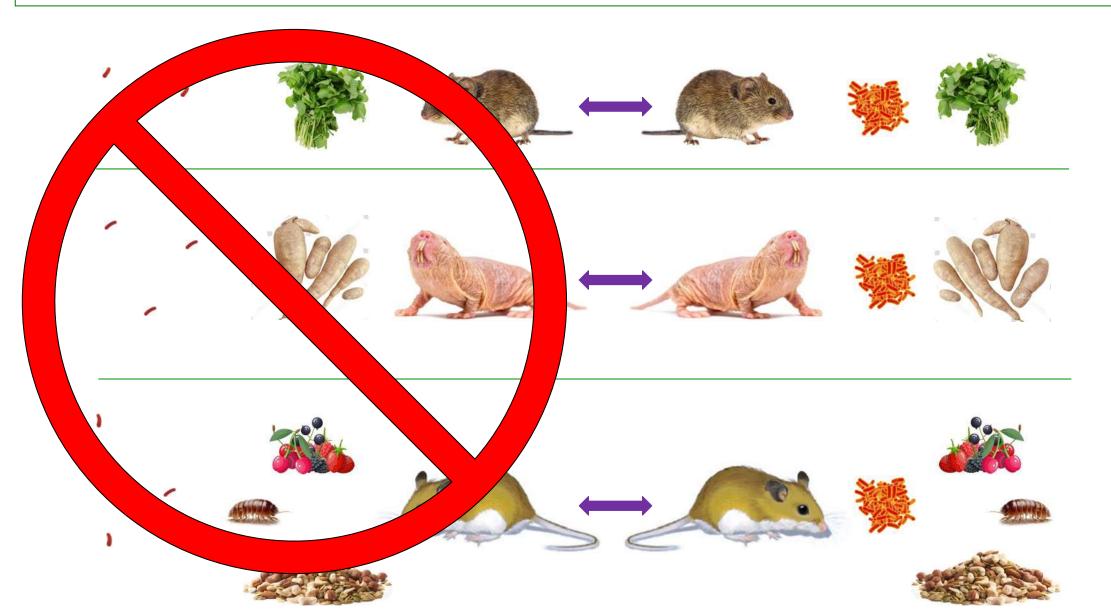






# Expanded menus: an ecological opportunity

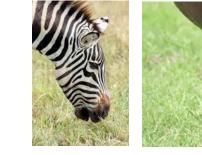
(without alternative)







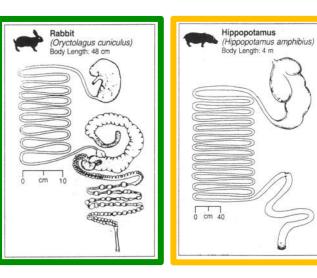
Hippopotamus (Hippopotamus amphibius) Body Length: 4 m Zebra (Equus burchelli) Body Length: 2 m cm 4

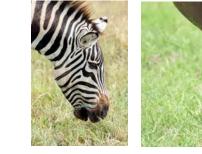


+ supplemental (endogenous) nitrogen not possible ?









+ supplemental (endogenous) nitrogen colonic separation & coprophagy





Hippopotamus (Hippopotamus amphibius) Body Length: 4 m Rabbit (Oryctolagus cuniculus) Body Length: 48 cm house 0 cm 40 00000000

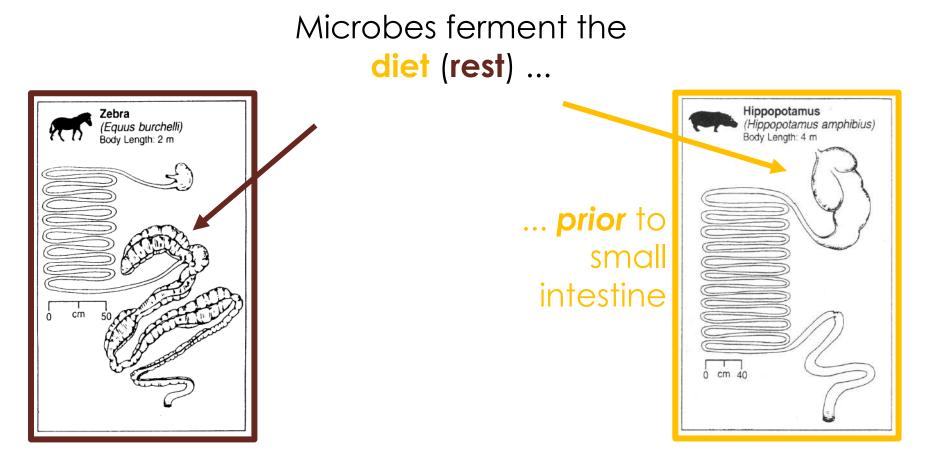




feasible at small body size (and few extant small species do not do it)

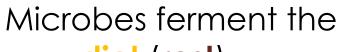


#### Hindgut and Foregut fermenters





#### Hindgut and Foregut fermenters

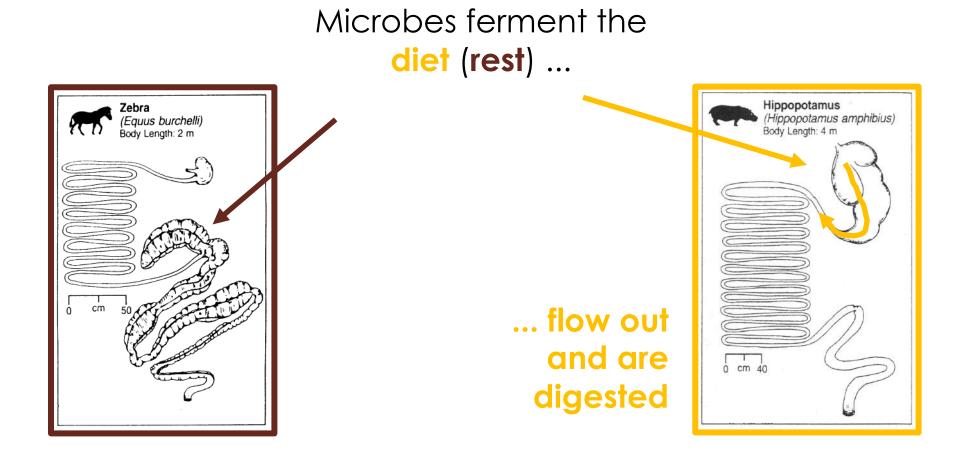


diet (rest) ...





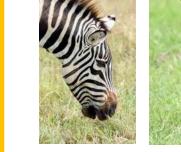
#### Hindgut and Foregut fermenters







Hippopotamus (Hippopotamus amphibius) Body Length: 4 m Rabbit (Oryctolagus cuniculus) Body Length: 48 cm 0 cm 40 000000



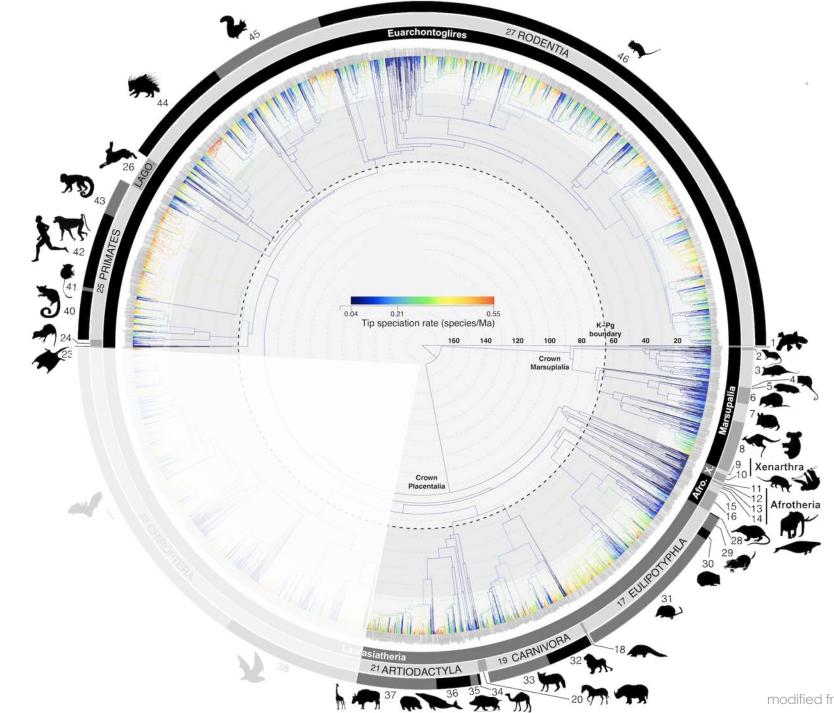


+ supplemental (endogenous) nitrogen feasible at small body size (and few extant small species do not do it)

#### no effort required ?

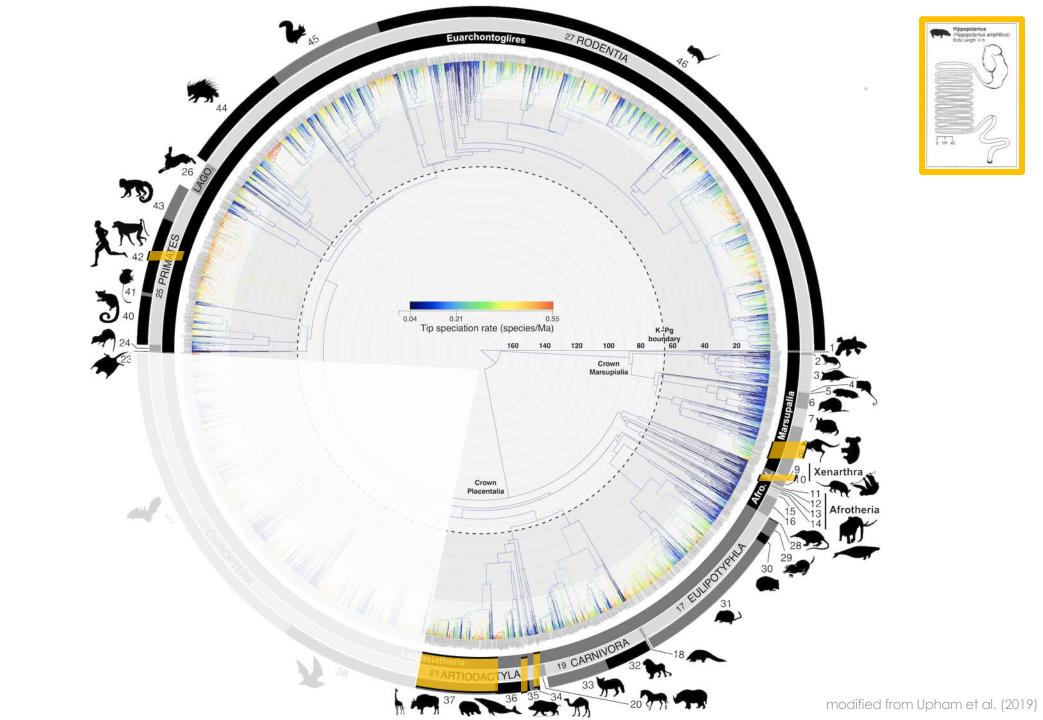
Stevens & Hume (1995)



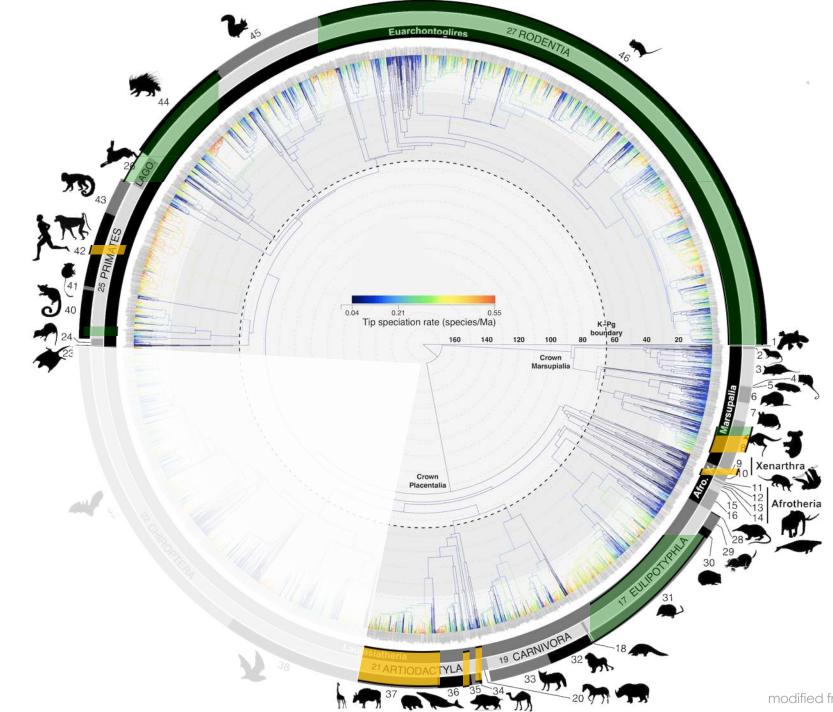


modified from Upham et al. (2019)









modified from Upham et al. (2019)

# How do you increase the yield of a growing system ?





### How do you increase the yield of a growing system ?



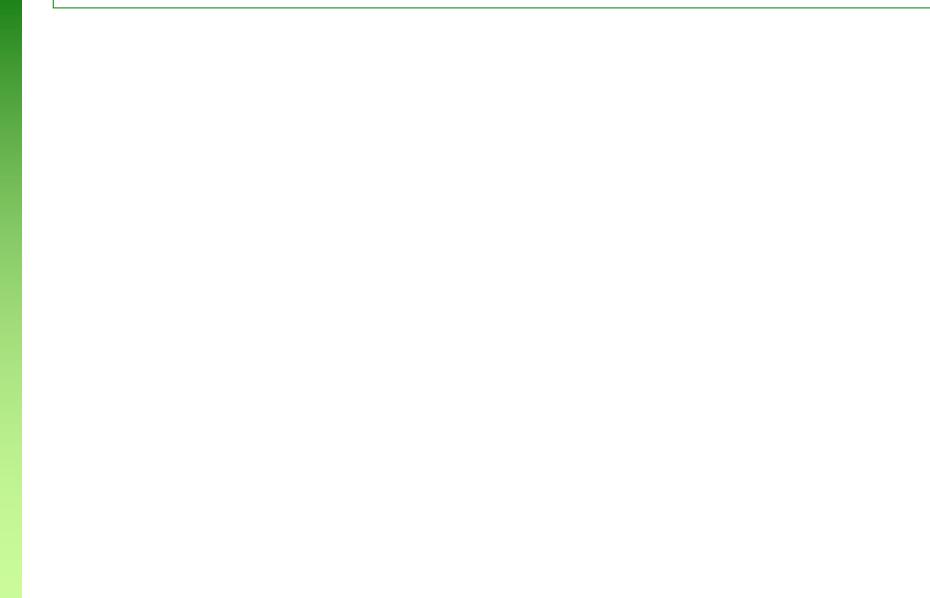


#### How do you increase the yield of a growing system ?

# frequent harvest to keep the population in the growth stage



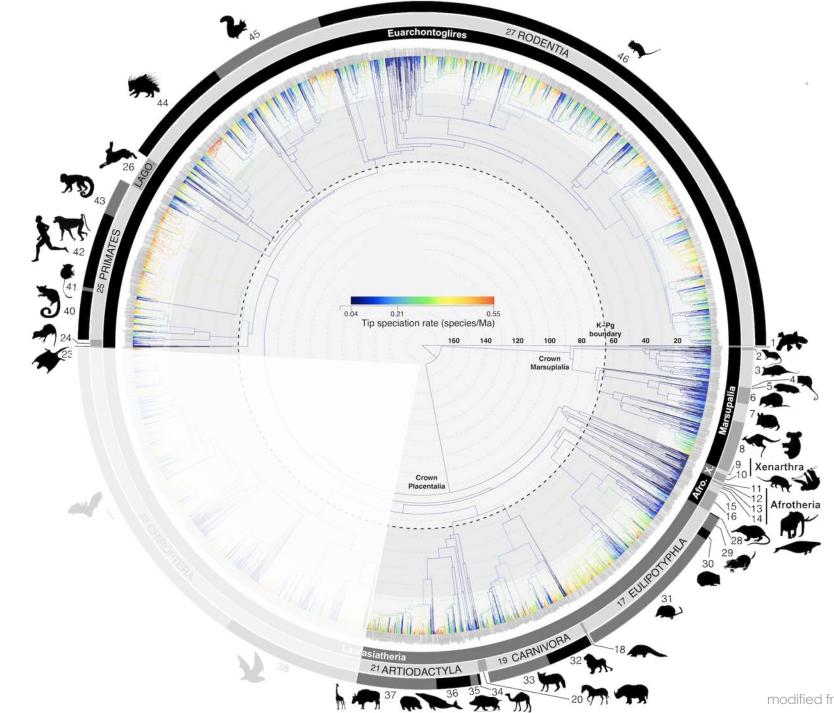
#### How do you harvest microbes ?





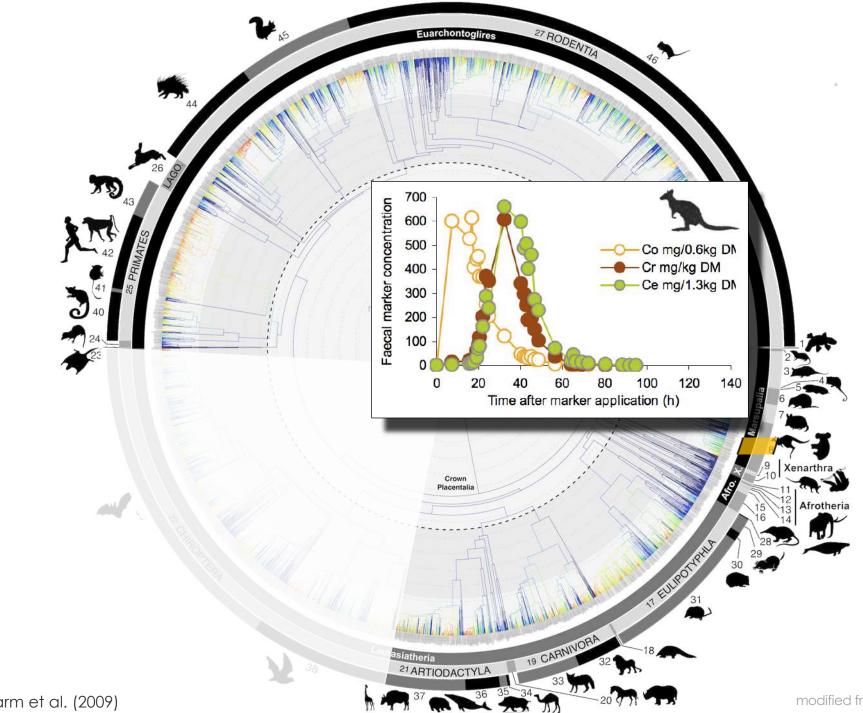
# by flushing them out of the fermenter while retaining the substrate





modified from Upham et al. (2019)

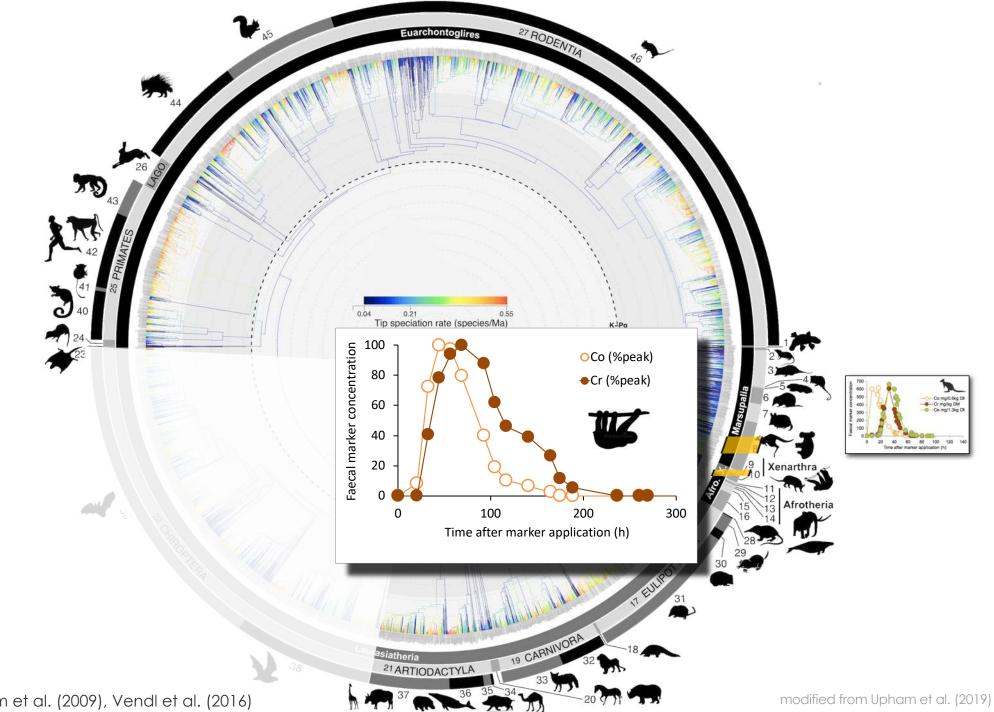




Schwarm et al. (2009)

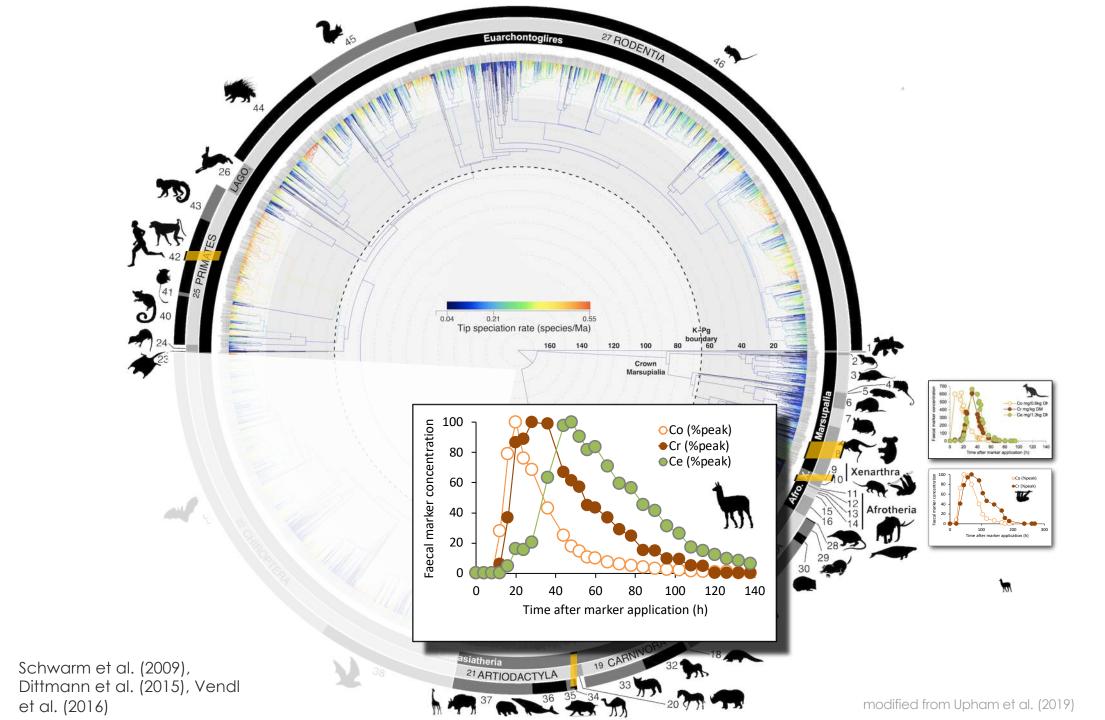
modified from Upham et al. (2019)



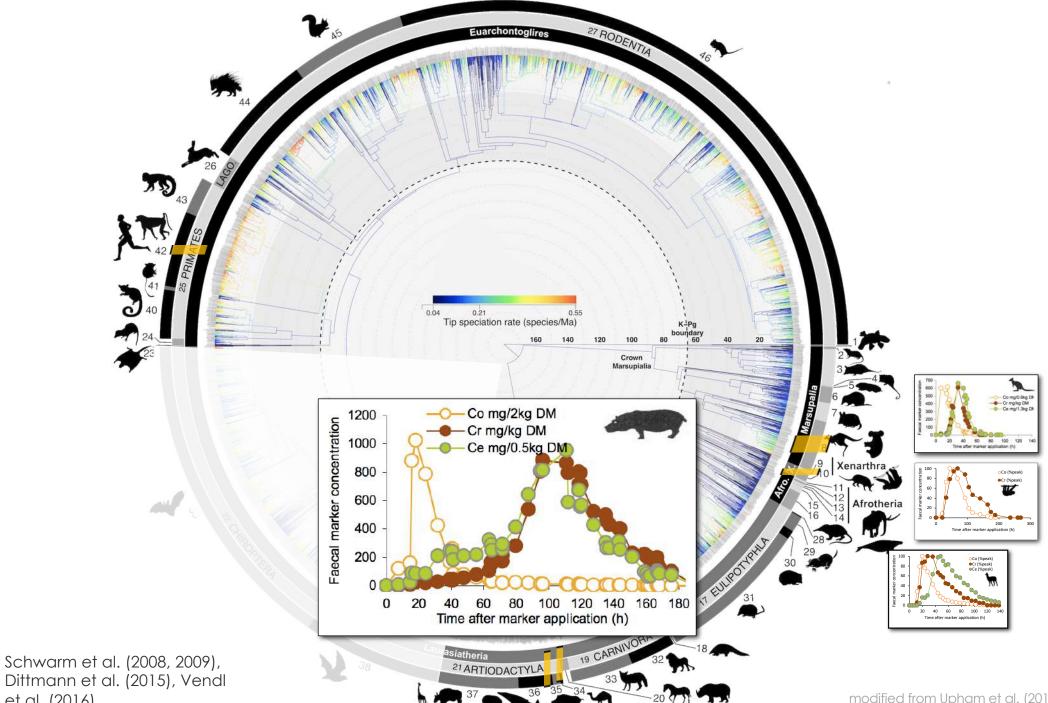


Schwarm et al. (2009), Vendl et al. (2016)



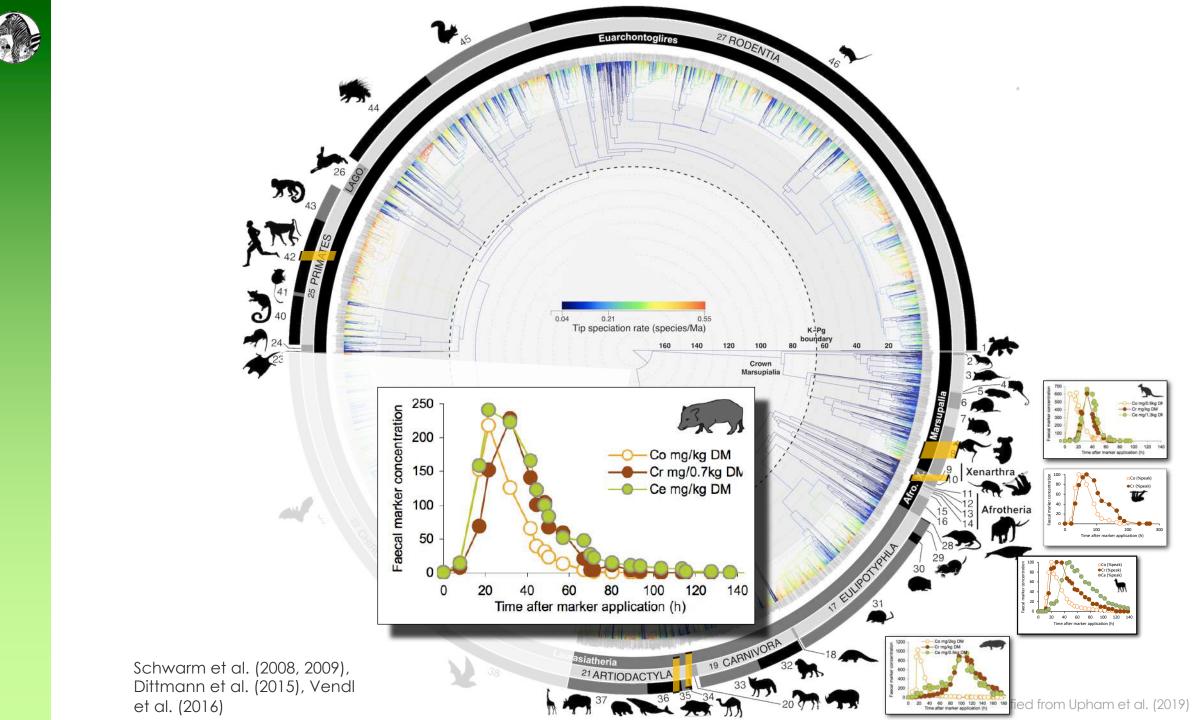


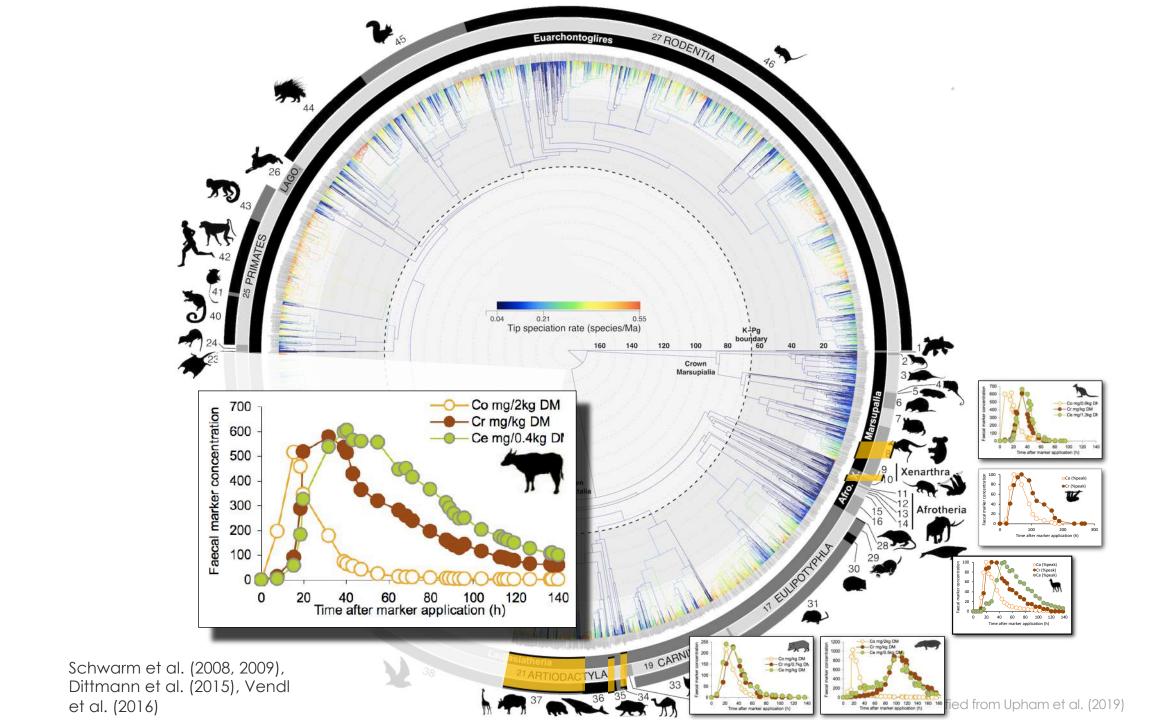




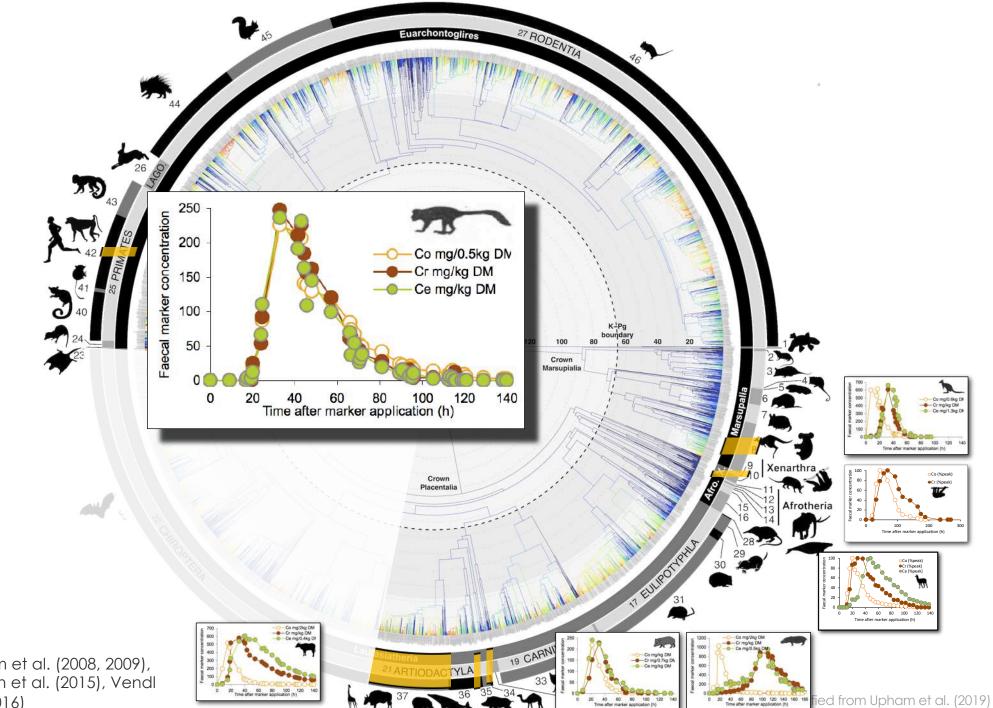
Dittmann et al. (2015), Vendl et al. (2016)

modified from Upham et al. (2019)

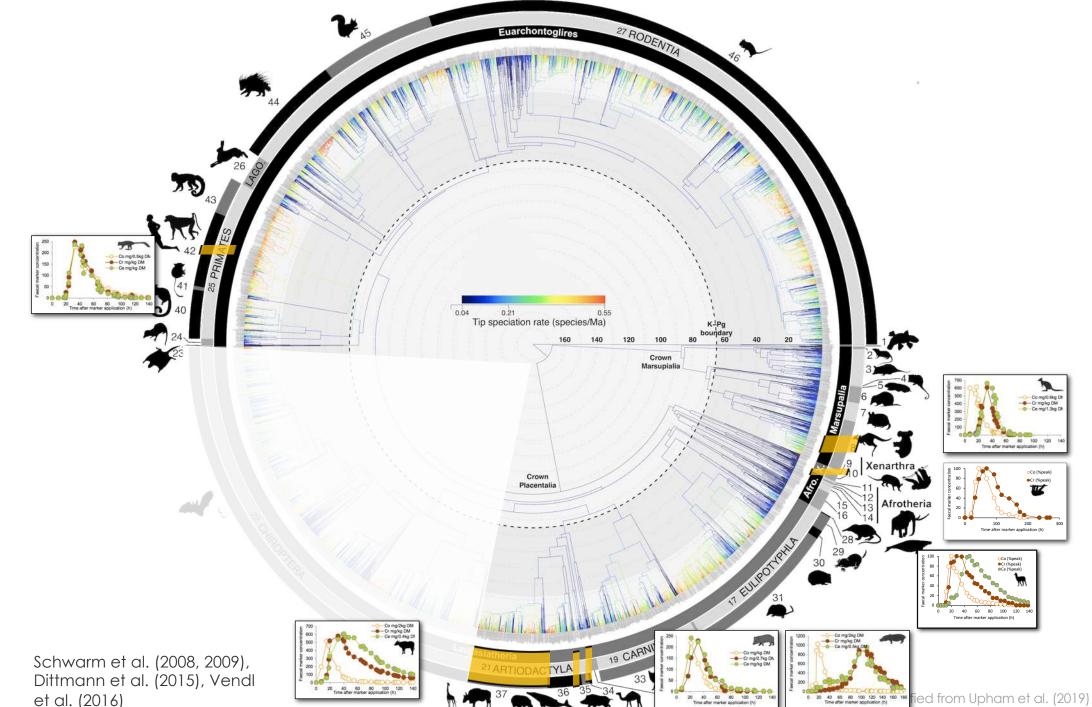








Schwarm et al. (2008, 2009), Dittmann et al. (2015), Vendl et al. (2016)

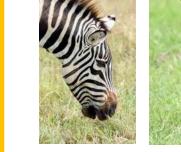


et al. (2016)





Hippopotamus (Hippopotamus amphibius) Body Length: 4 m Rabbit (Oryctolagus cuniculus) Body Length: 48 cm 0 cm 40 000000





+ supplemental (endogenous) nitrogen feasible at small body size (and few extant small species do not do it)

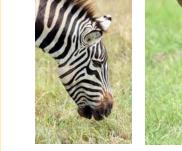
#### no effort required ?

Stevens & Hume (1995)





Hippopotamus (Hippopotamus amphibius) Body Length: 4 m Rabbit (Oryctolagus cuniculus) Body Length: 48 cm 0 cm 40 000000





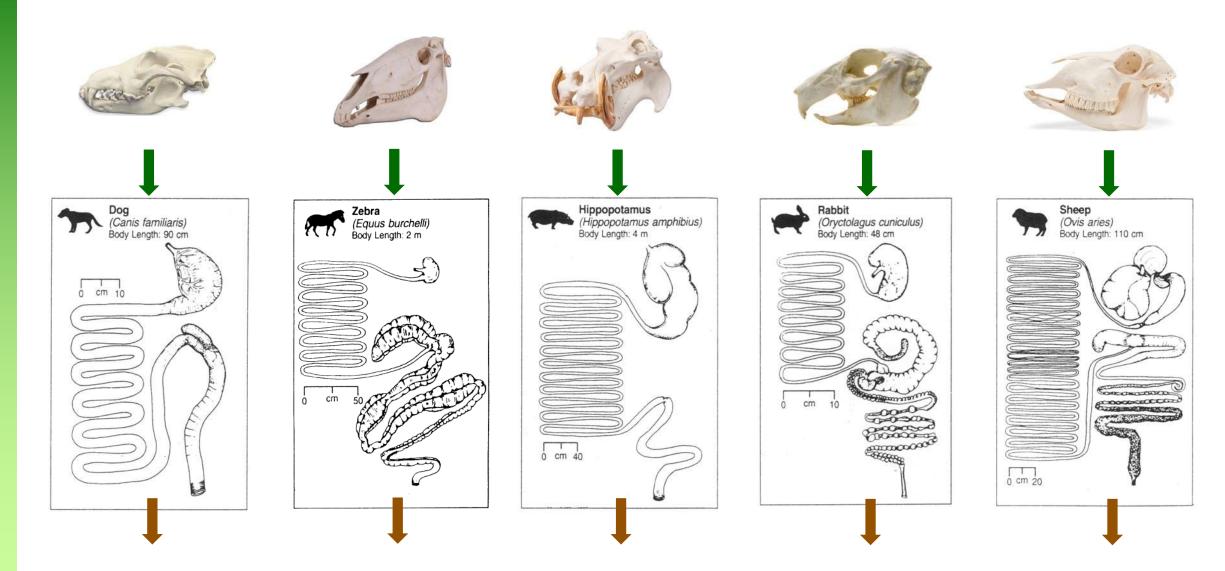
+ supplemental (endogenous) nitrogen feasible at small body size (and few extant small species do not do it)

optimize via flushing (saliva)

Stevens & Hume (1995)

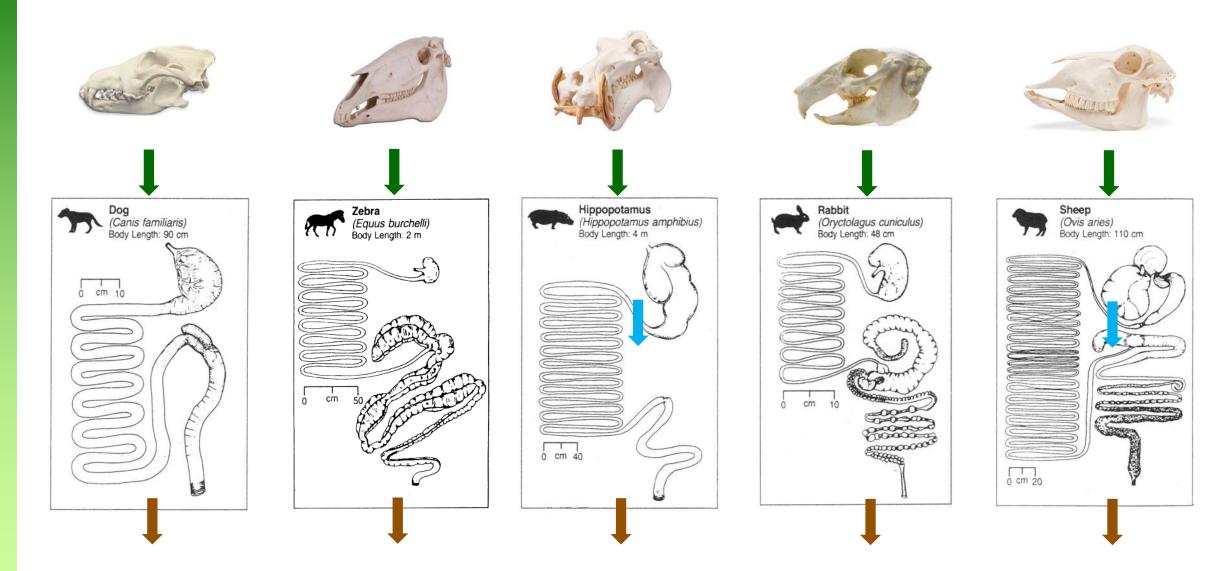


#### Teeth and gut do their own thing



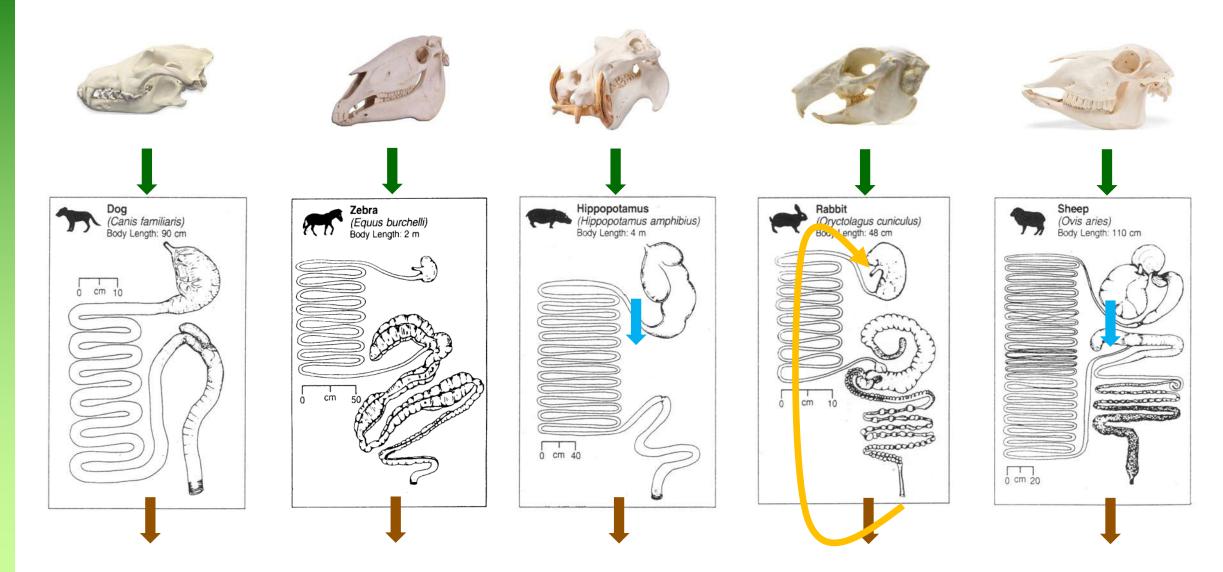


# Teeth and gut do their own thing





# Teeth and gut do their own thing





# What happens if there is a lot of fluid ?

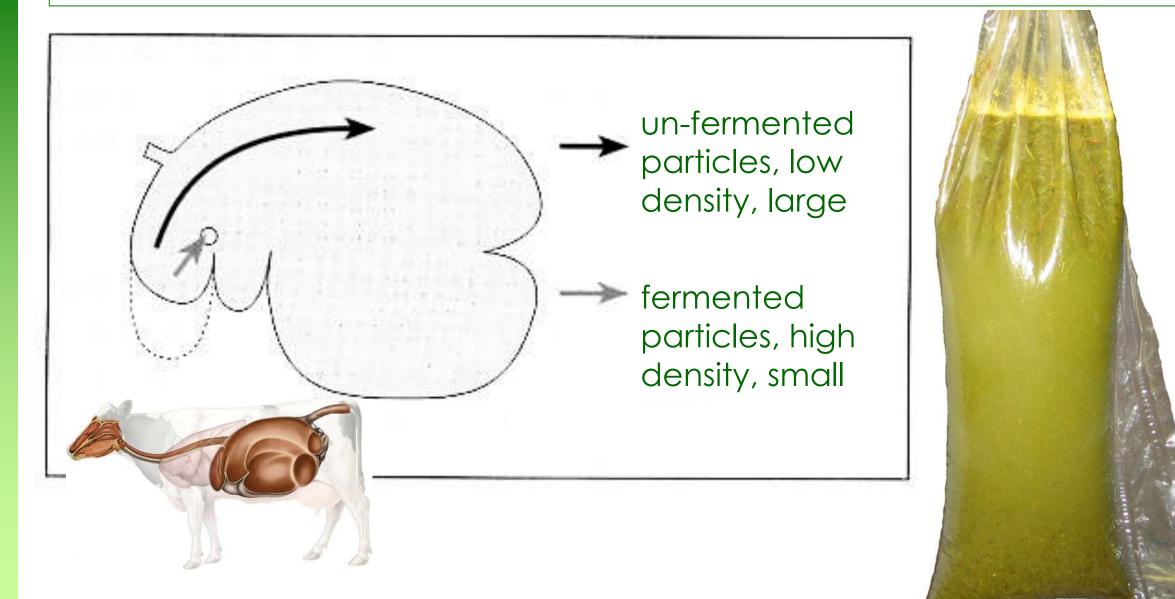


### Particles separate in fluid





#### Particles separate in fluid: Sorting





#### Faecal particles in a ruminant and a nonruminant





### Faecal particles in a ruminant and a nonruminant

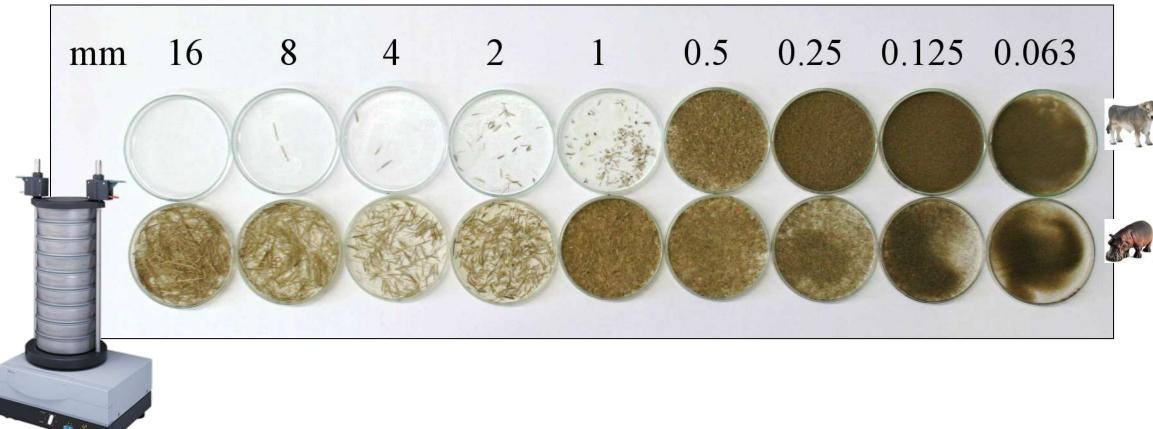


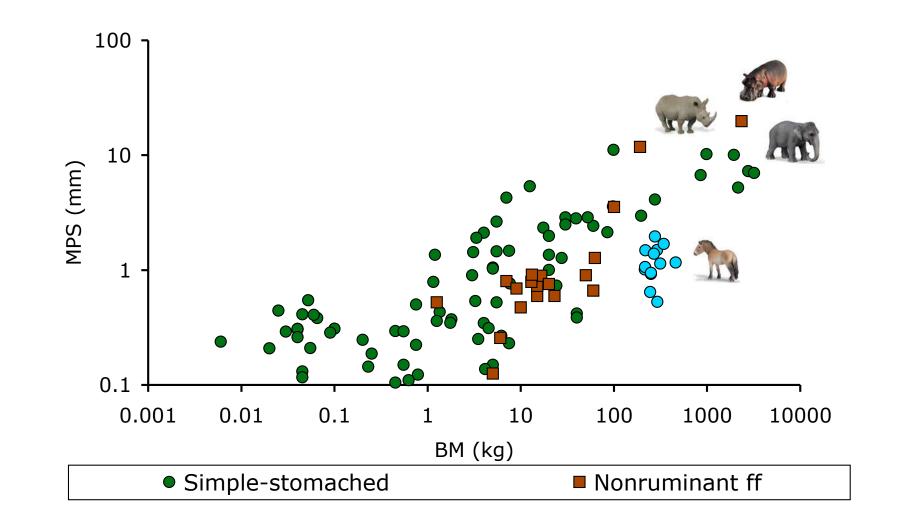
Photo A. Schwarm



# **Comparative chewing efficiency in mammalian herbivores**

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

Oikos 118: 1623-1632, 2009

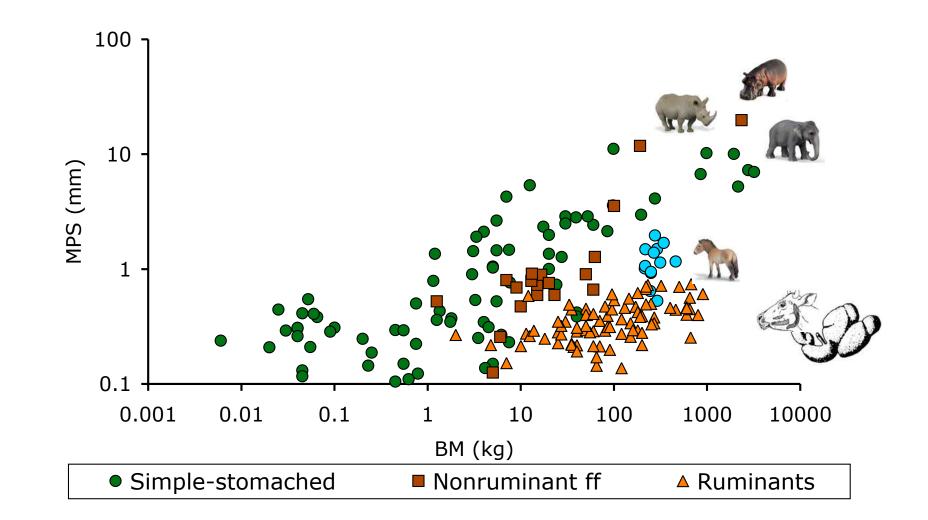




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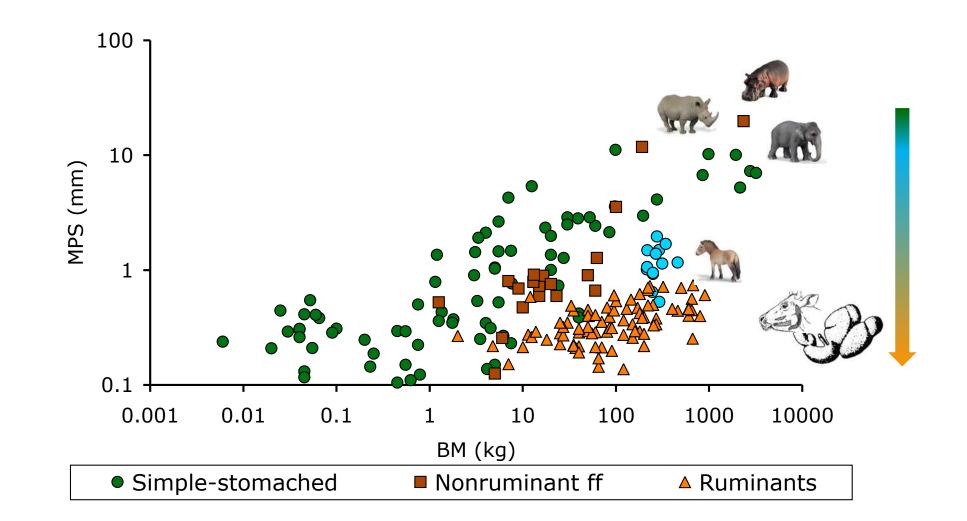




## Comparative chewing efficiency in mammalian herbivores

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Oikos 118: 1623-1632, 2009





# Teeth evolve for efficiency ...

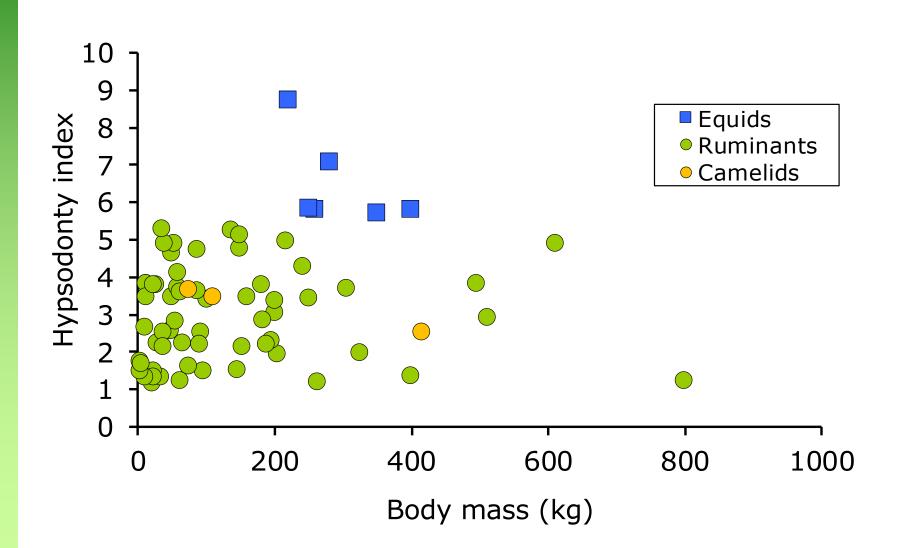


## Teeth evolve for efficiency ...

... but achieve the highest efficiency with the help of a gut-based sorting mechanism.

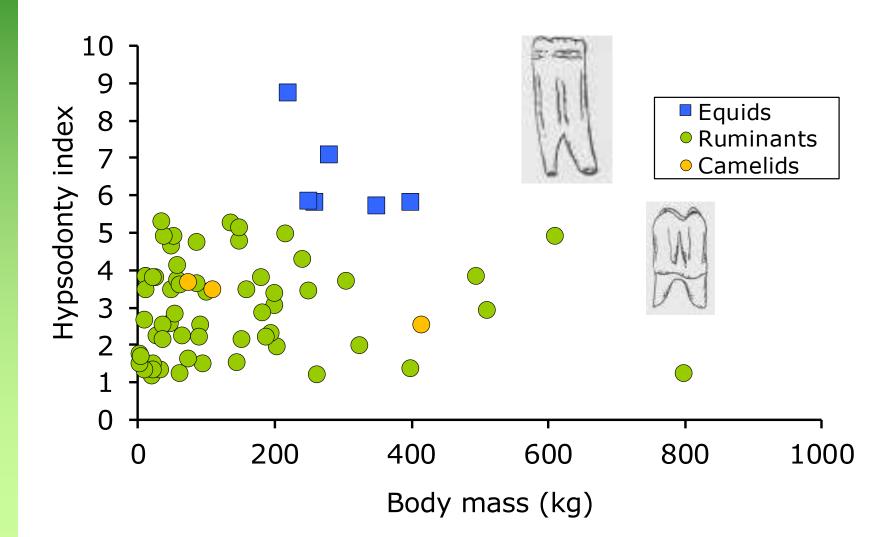


#### Ruminants are not super-hypsodont



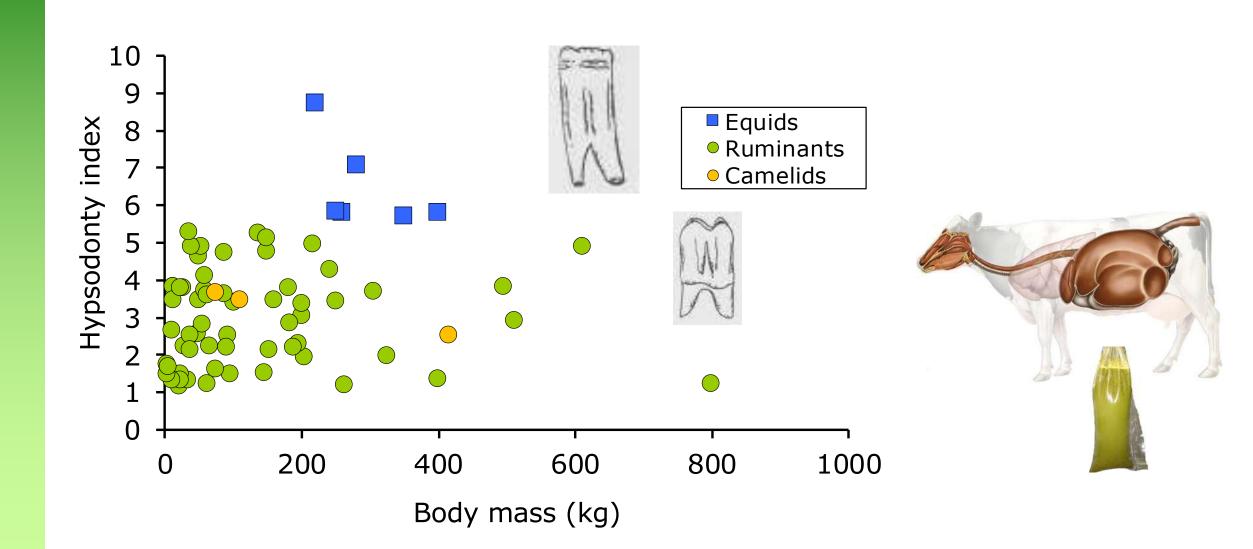


#### Ruminants are not super-hypsodont

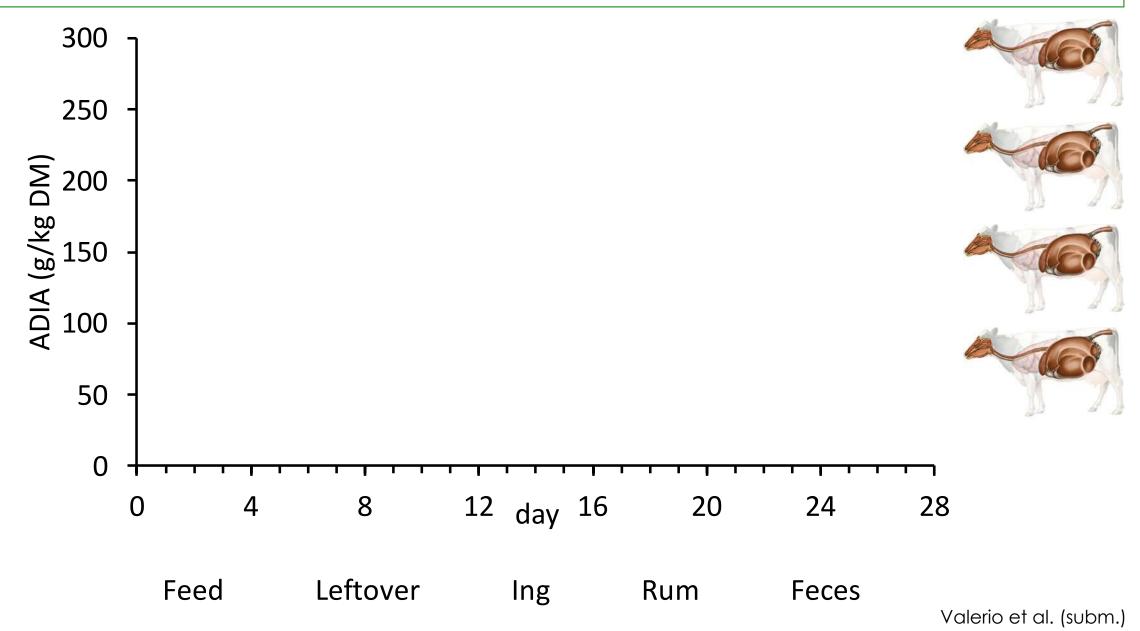




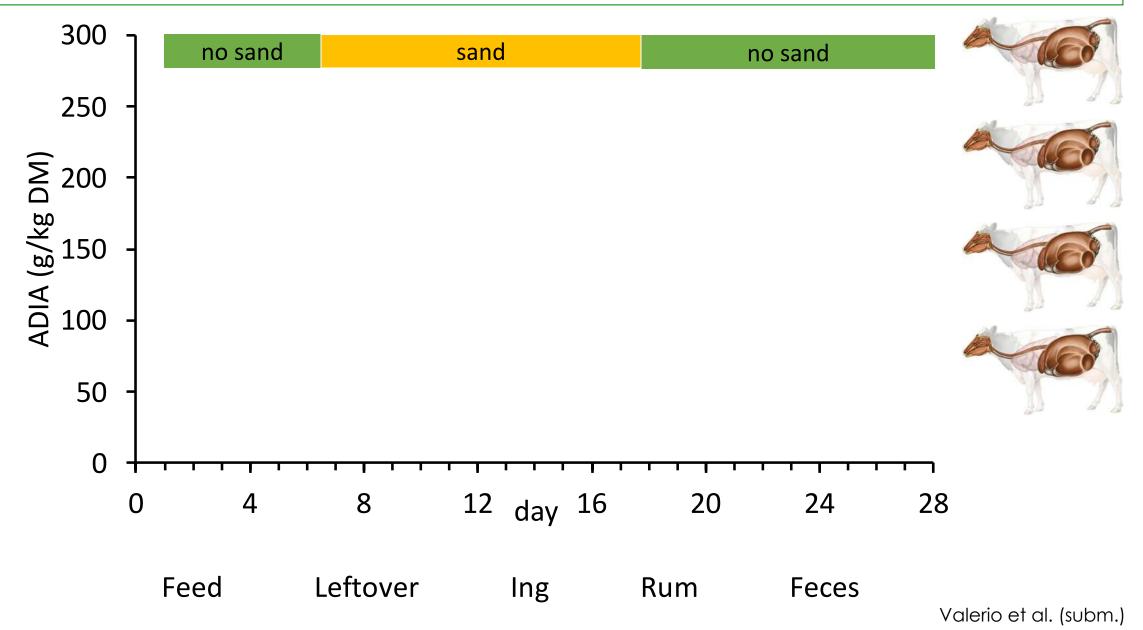
#### Ruminants are not super-hypsodont



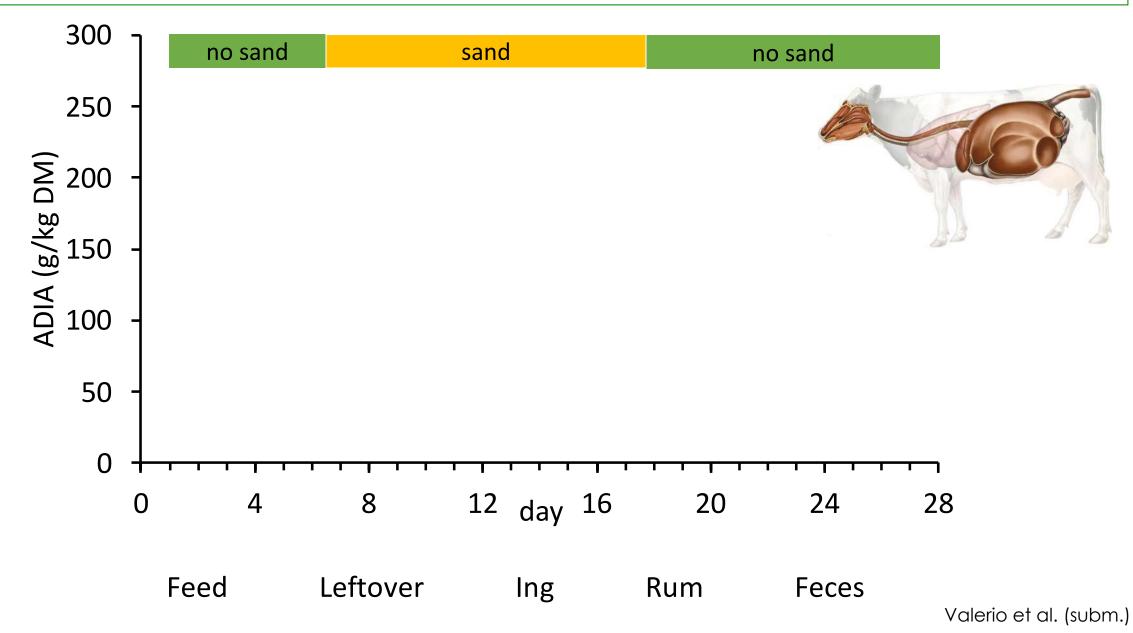




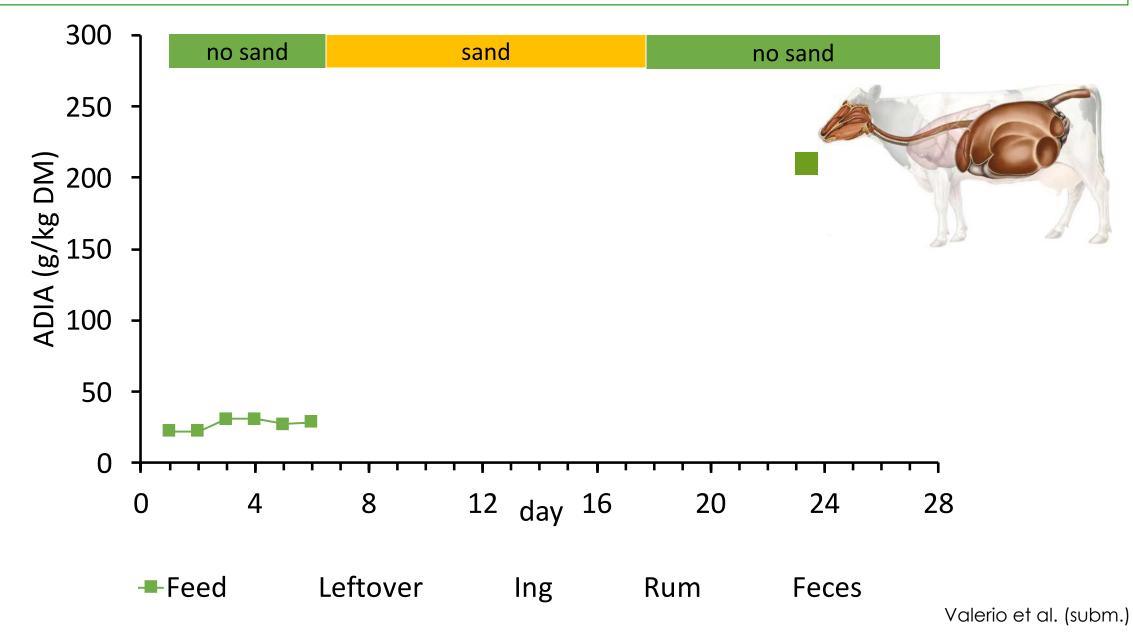




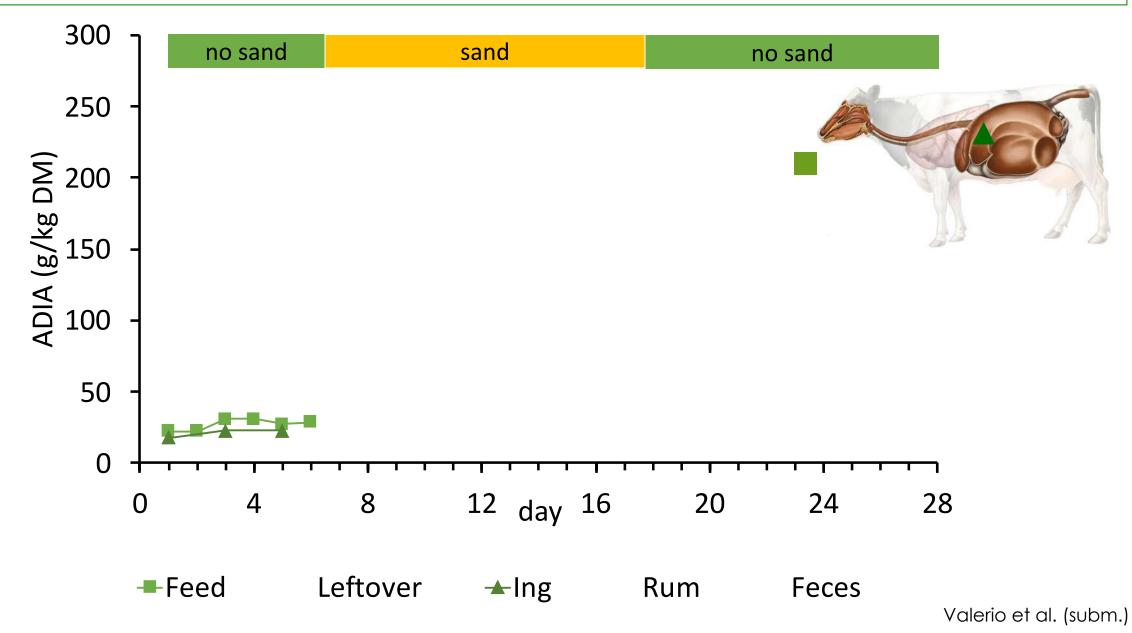




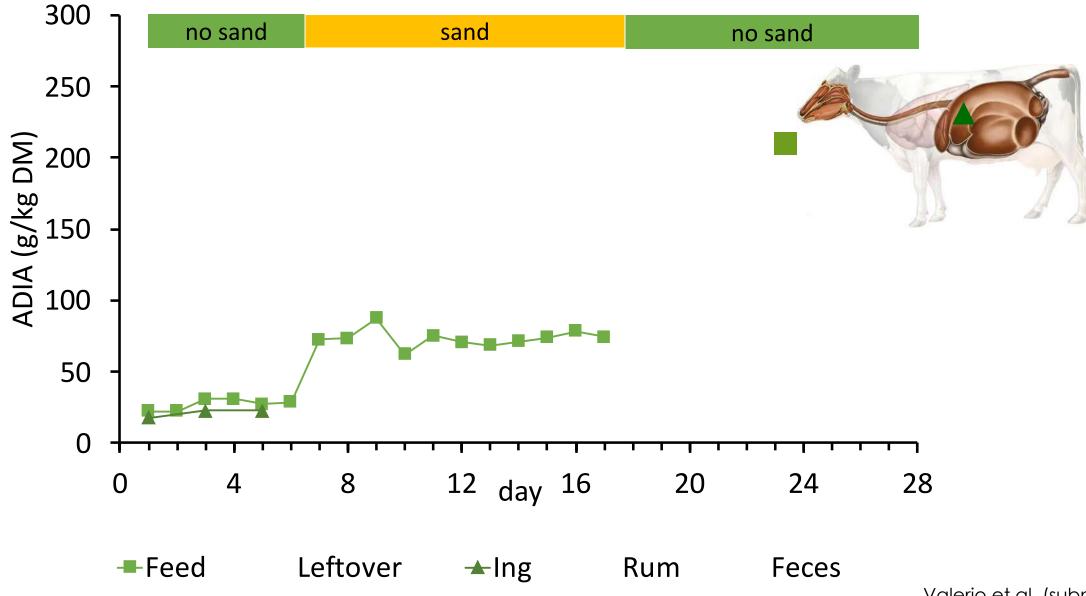






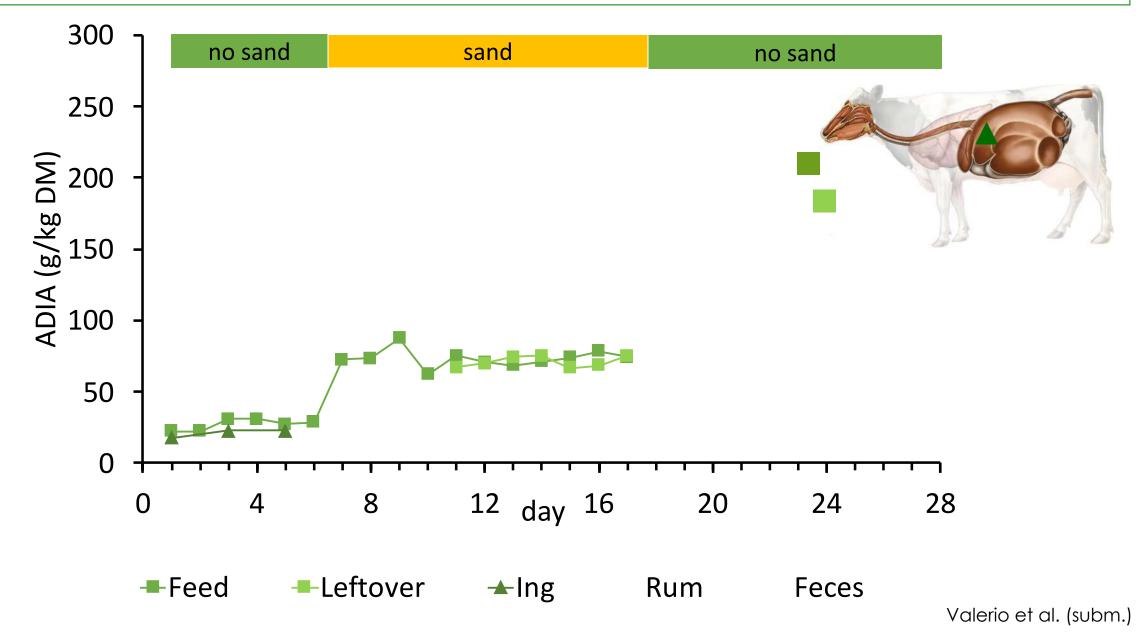




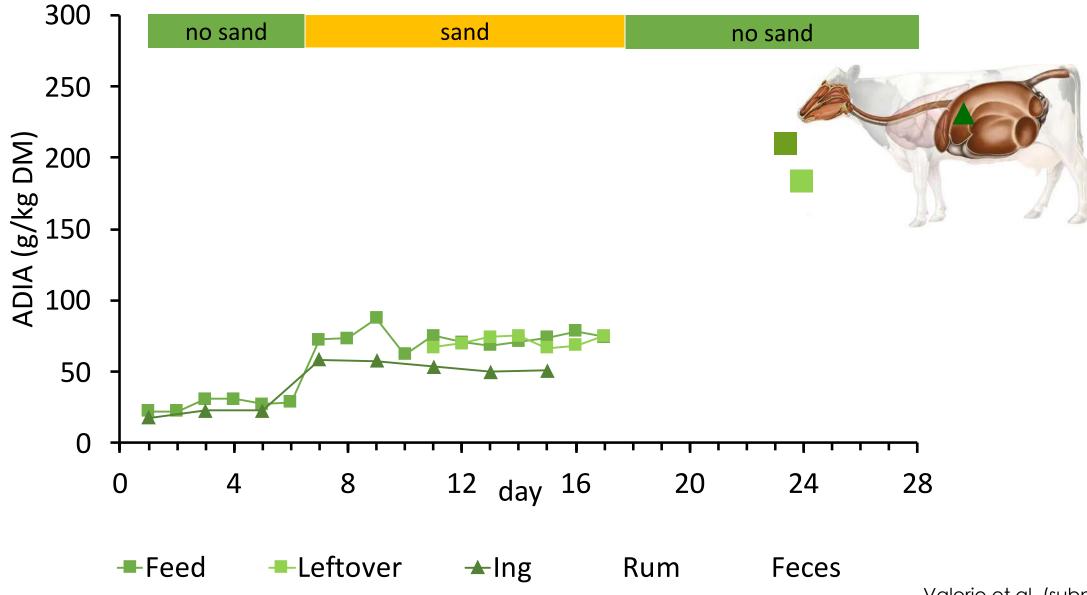


Valerio et al. (subm.)



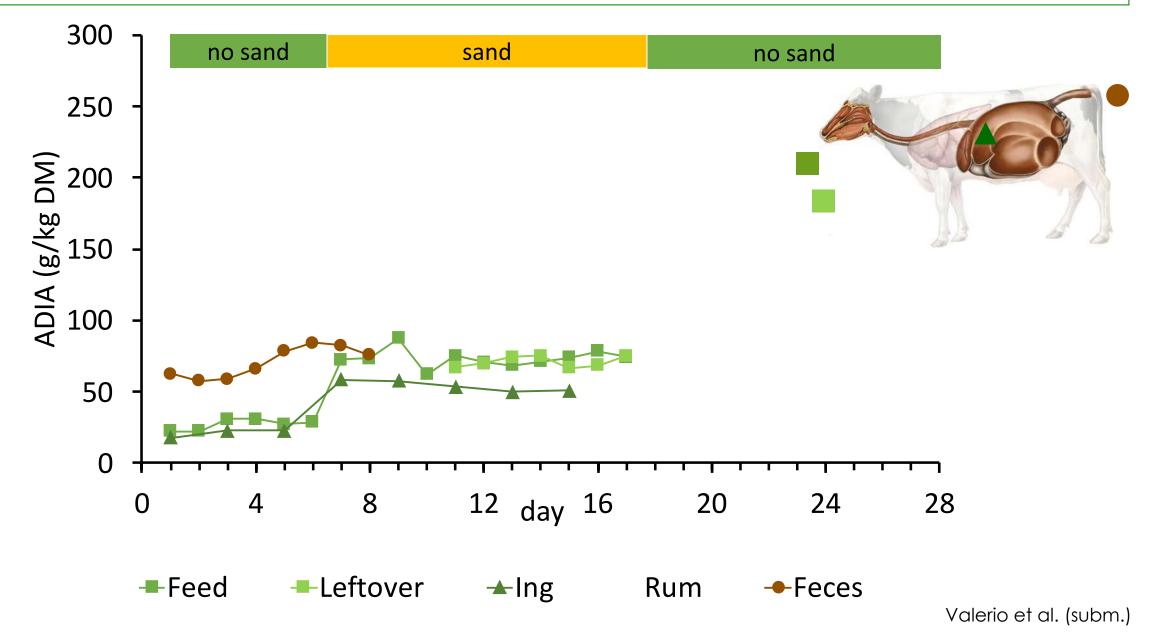




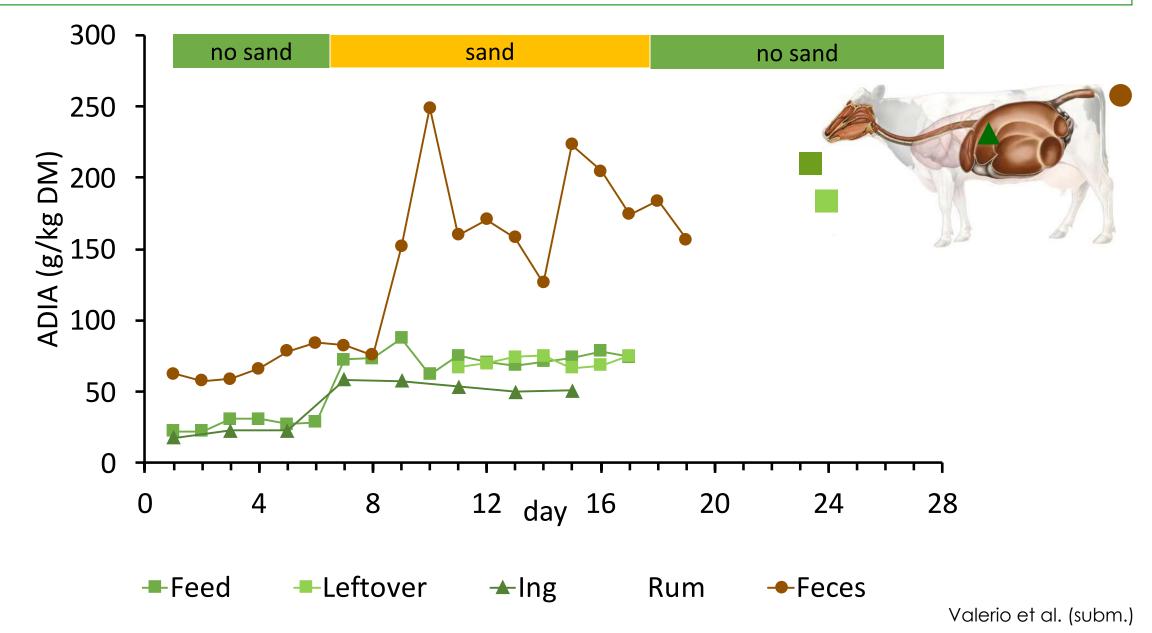


Valerio et al. (subm.)

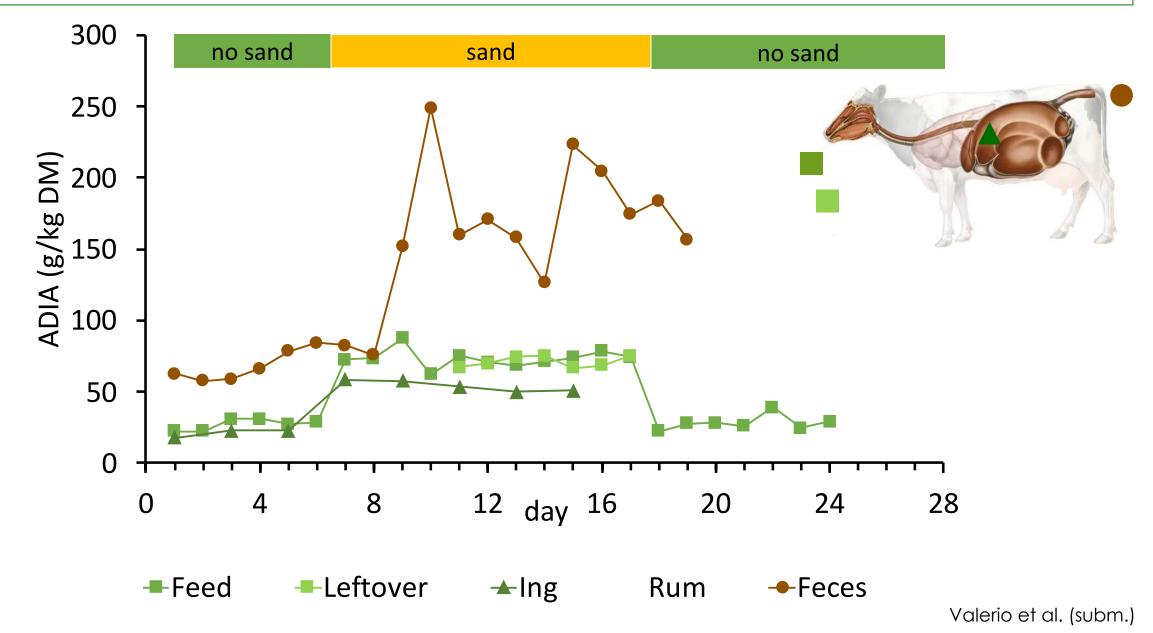




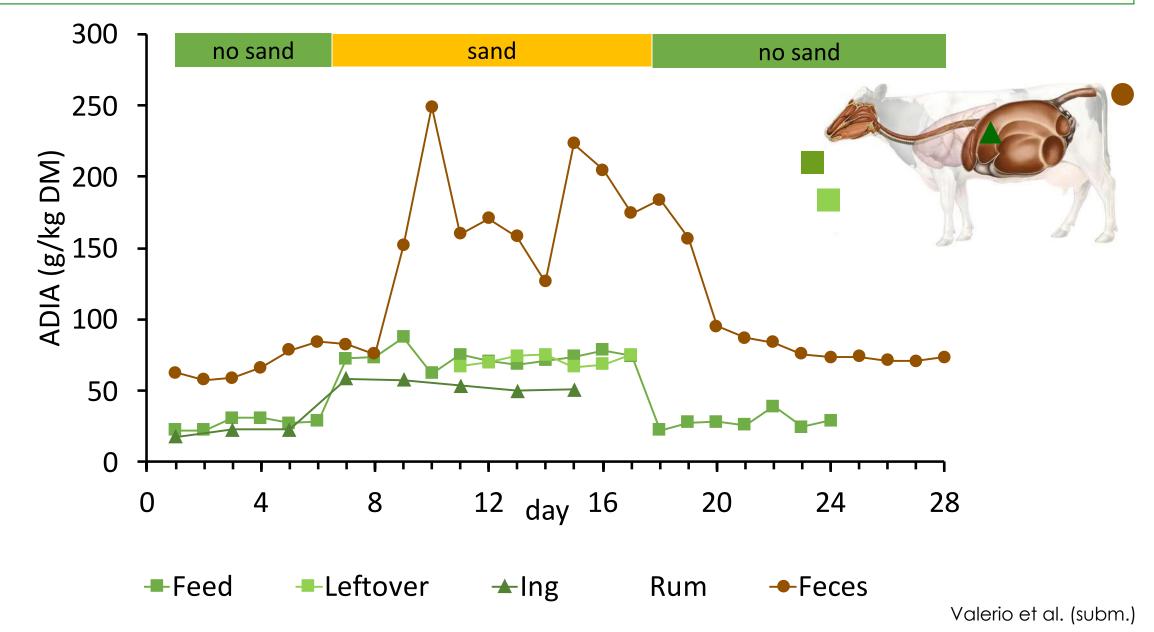




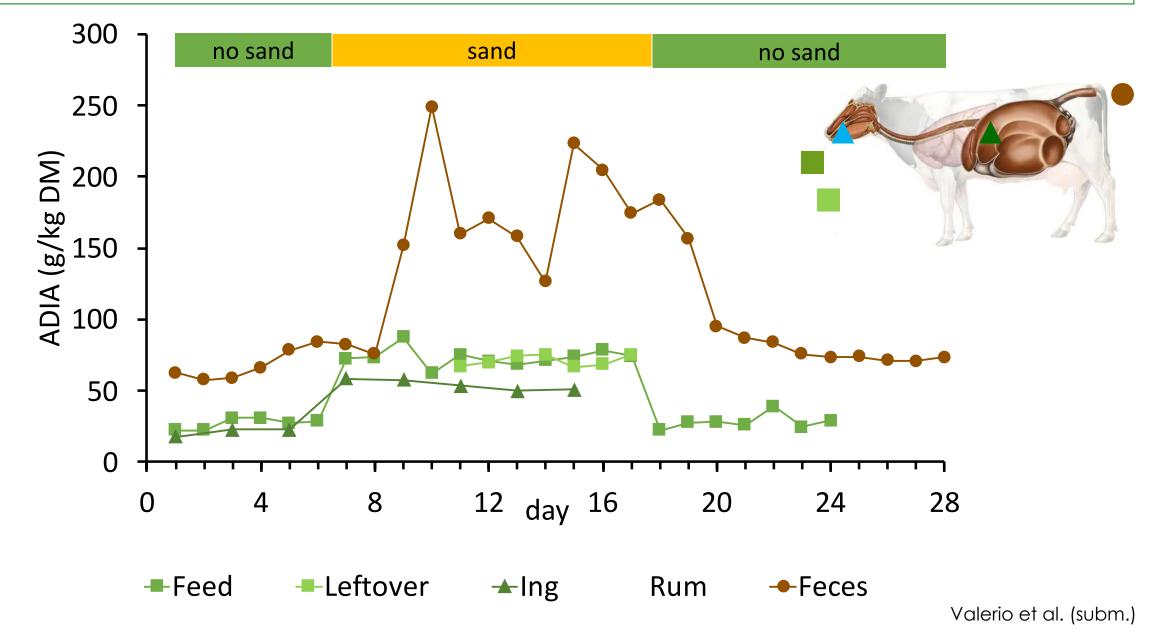




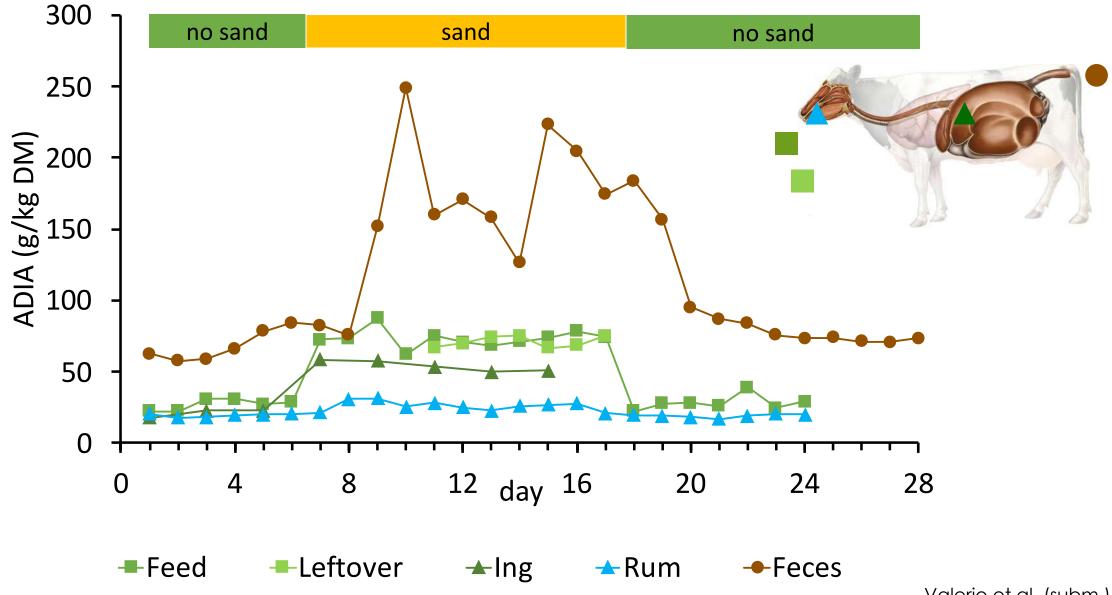












Valerio et al. (subm.)



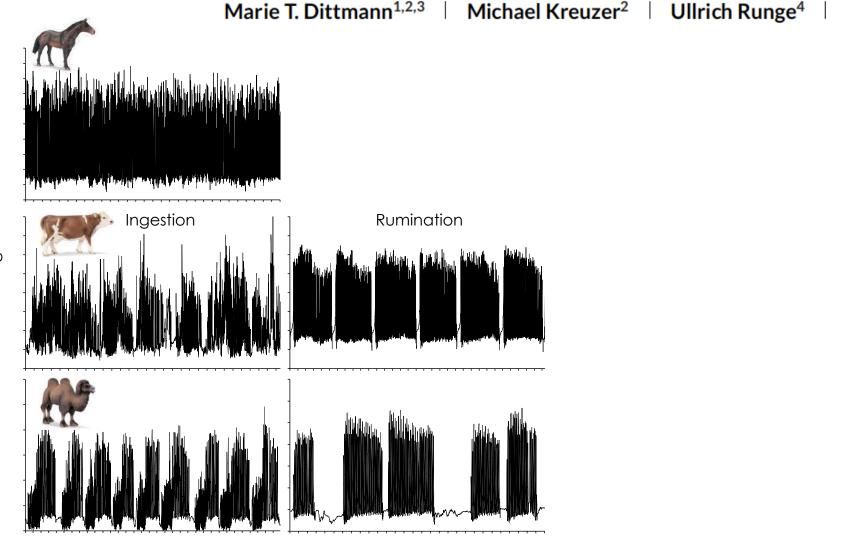
# Teeth evolve for durability ...



## Teeth evolve for durability ...

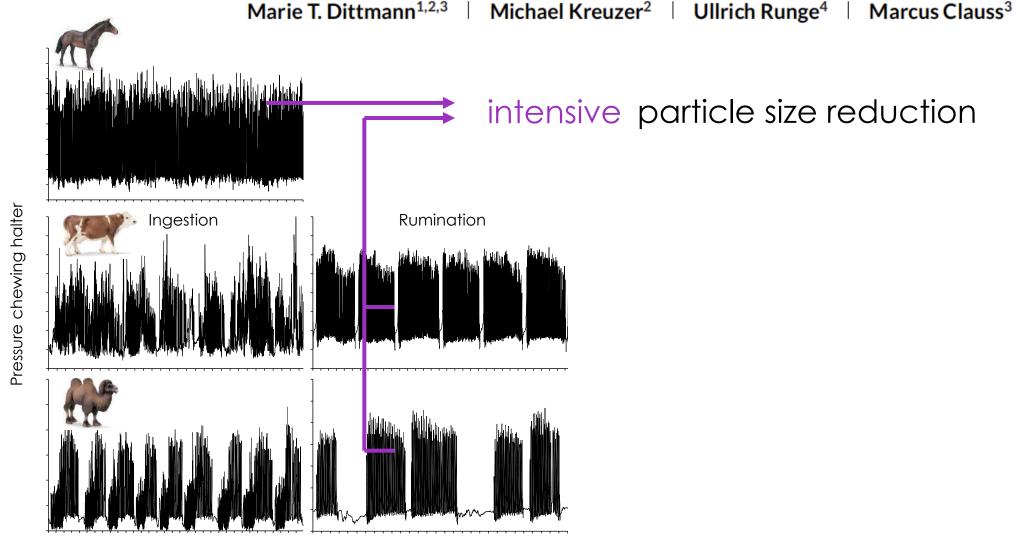
... but receive particular protection by a gut-based washing mechanism.

Marcus Clauss<sup>3</sup>

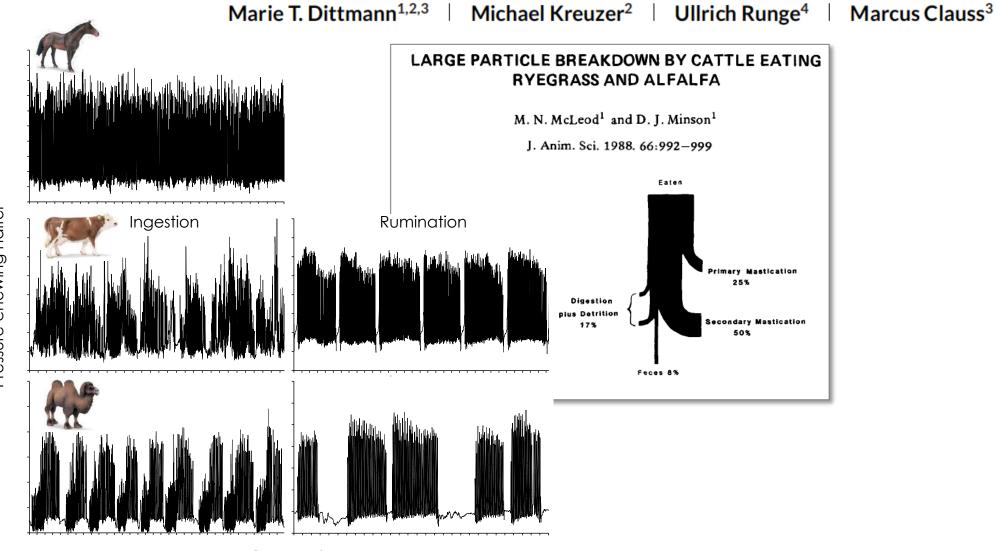


Pressure chewing halter

<sup>10</sup> seconds

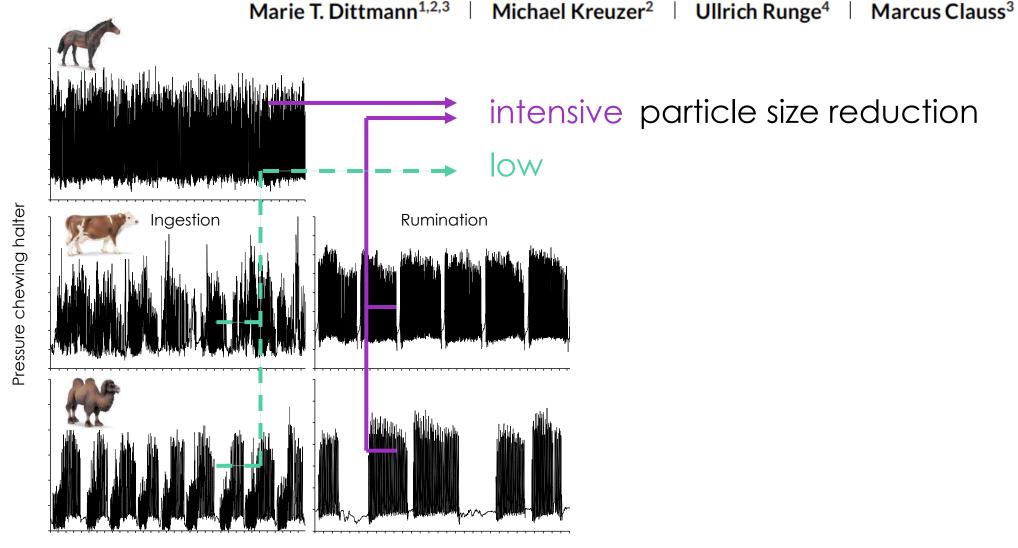


<sup>10</sup> seconds



Pressure chewing halter

10 seconds



10 seconds

Marie T. Dittmann<sup>1,2,3</sup> | Michael Kreuzer<sup>2</sup> | Ullrich Runge<sup>4</sup> | Marcus Clauss<sup>3</sup>

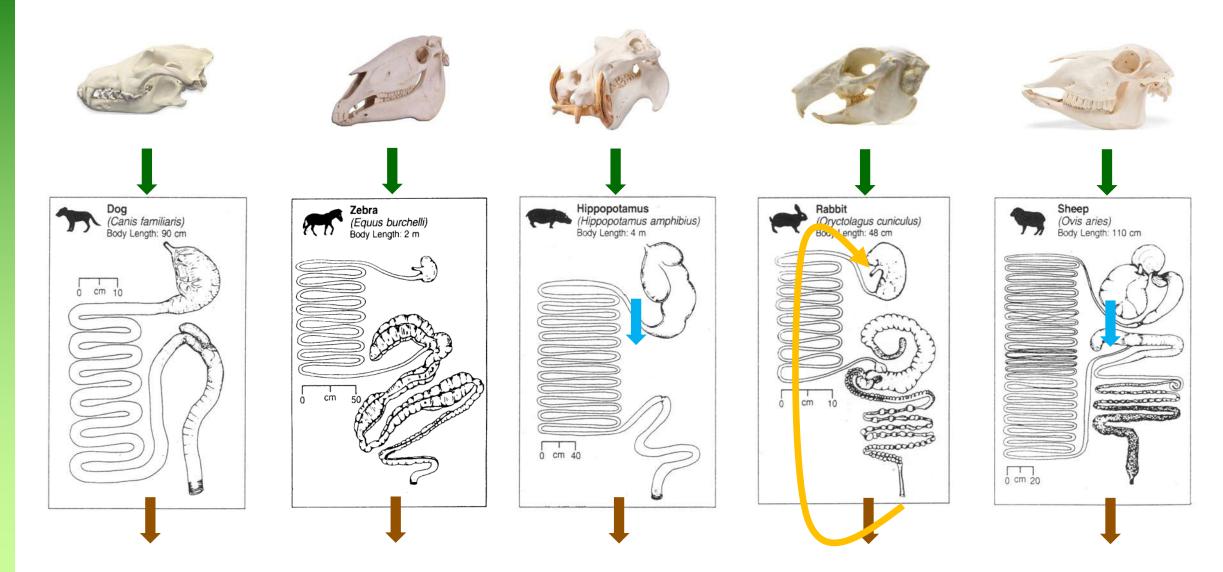
low particle size reduction Ingestion why chew so 'sloppily' during ingestion ?

Pressure chewing halter

<sup>10</sup> seconds

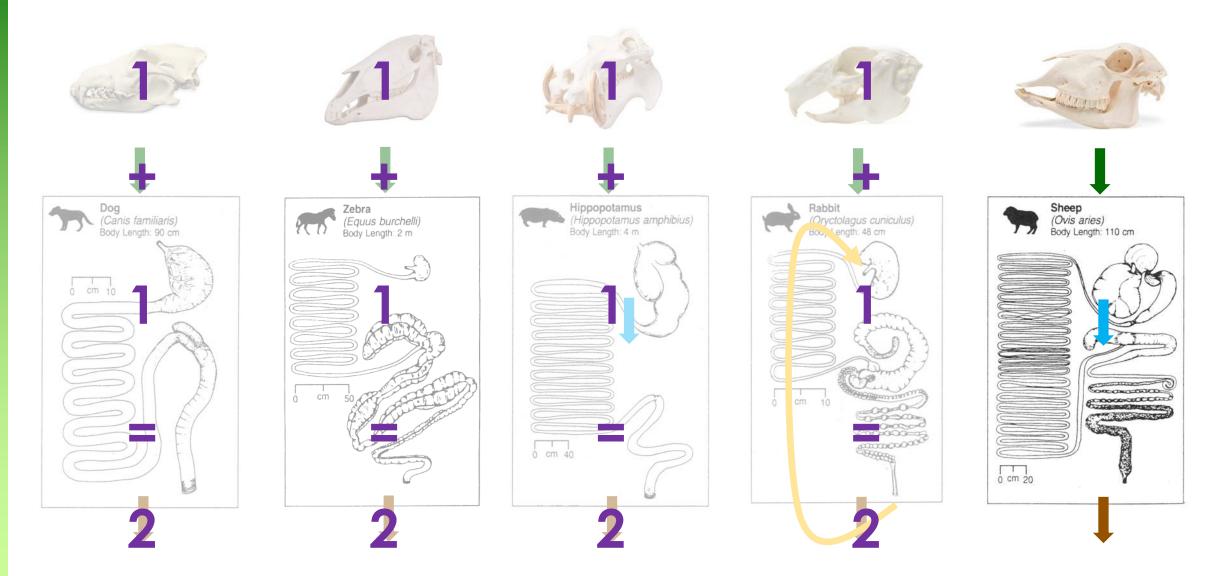


### Teeth and gut do their own thing



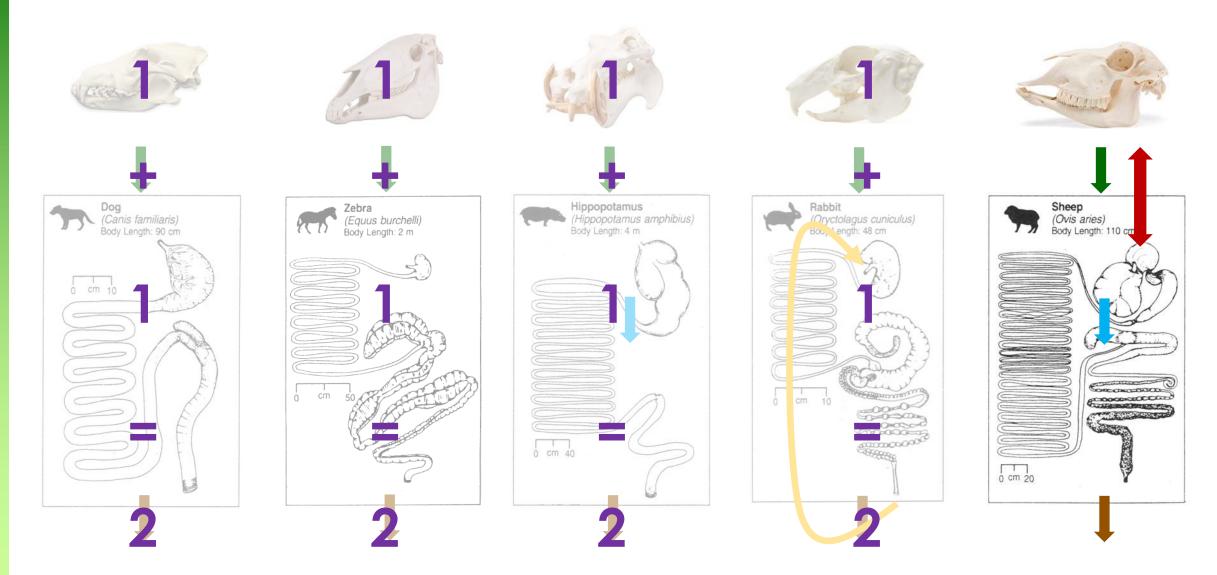


#### Teeth and gut do their own thing





#### Teeth and gut do their own thing





#### Teeth and gut work together

100

10 (mm) SdM

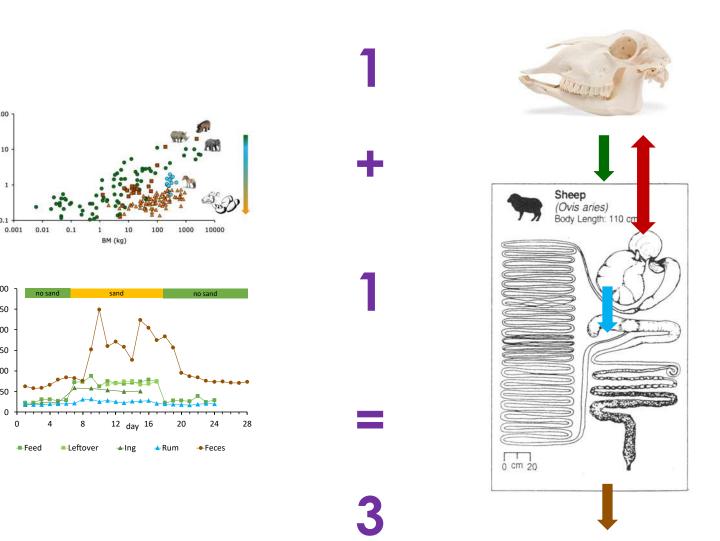
0.1

300

250

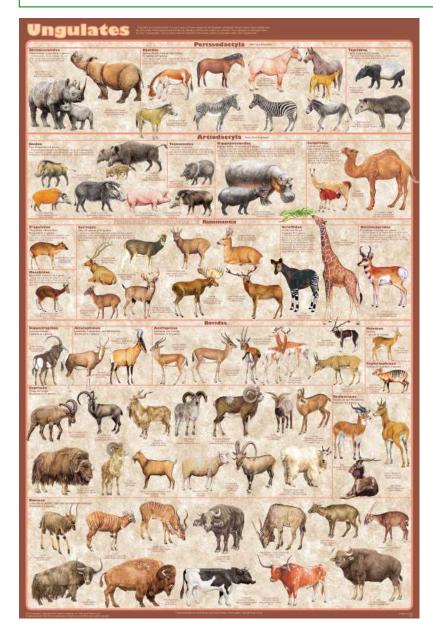
(WQ 200 B/g) 150 100

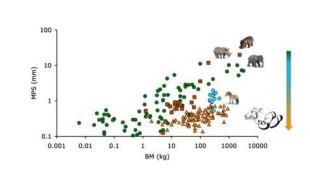
50 0

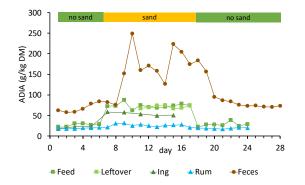


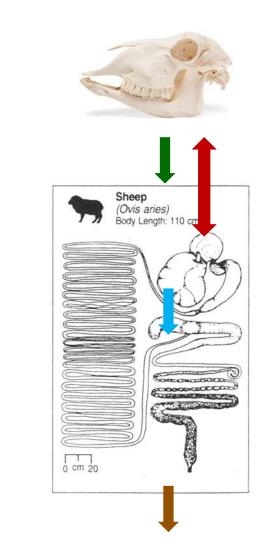


#### Teeth and gut work together

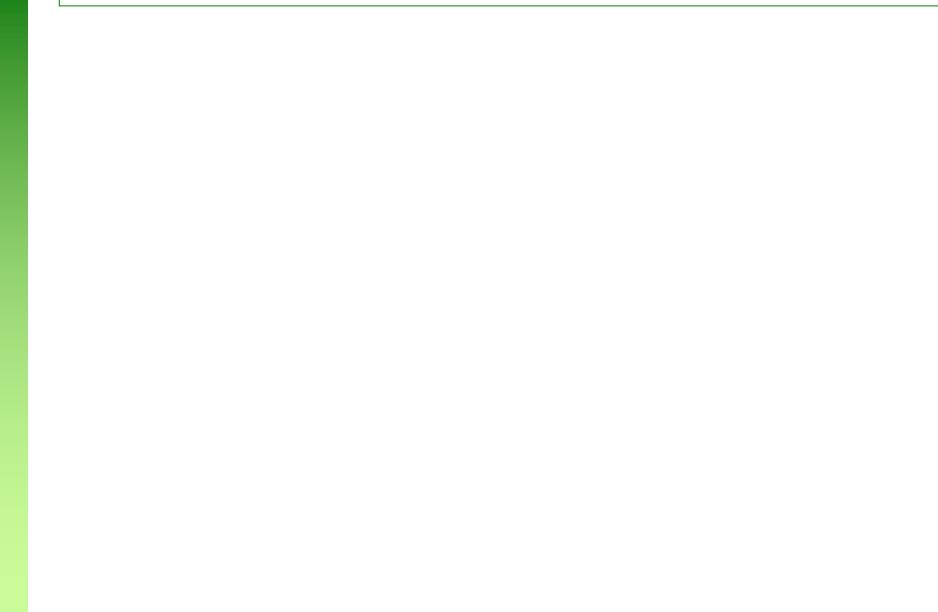






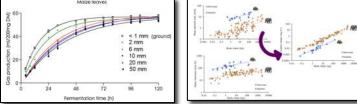








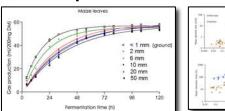
Particle size reduction is a prerequisite for fast digestion, high intake, and endothermy

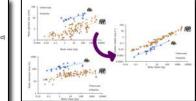


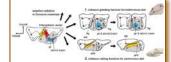


Particle size reduction is a prerequisite for fast digestion, high

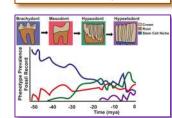
intake, and endothermy





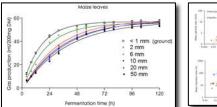


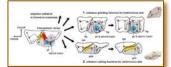
Teeth evolved for increasing efficiency and durability





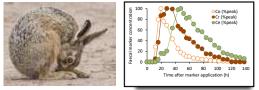
Particle size reduction is a prerequisite for fast digestion, high intake, and endothermy





Teeth evolved for increasing efficiency and durability

Digestive tract evolution: various adaptations to microbe farming





## Summary

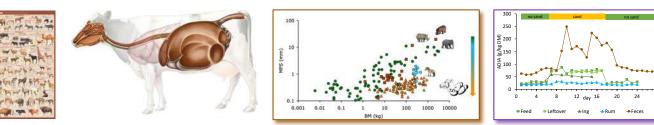
Particle size reduction is a prerequisite for fast digestion, high intake, and endothermy

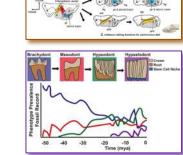
Molte leaves Molte leaves 40 - 40 - 2 mm 6 mm 2 mm 6 mm 10 mm 20 mm20

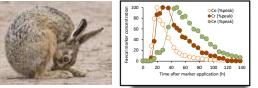
Teeth evolved for increasing efficiency and durability

Digestive tract evolution: various adaptations to microbe farming

Rumination: the ultimate tooth-gut interplay









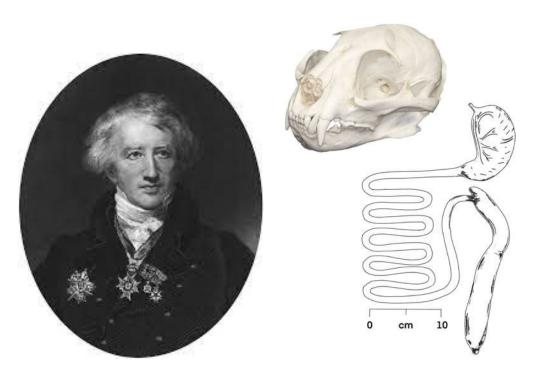
# thank you for your attention



# Interplay of organ systems



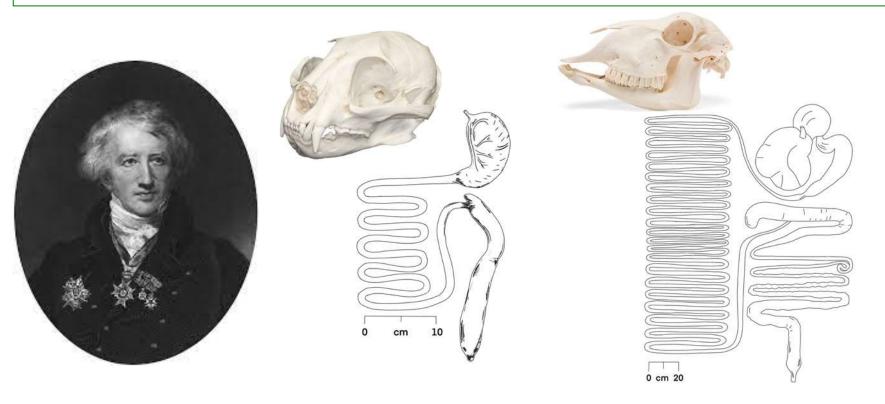
## Principle of the correlation of parts



If an animal's teeth are such as they must be, in order for it to nourish itself with flesh, we can be sure without further examination that the whole system of its digestive organs is appropriate for that kind of food, and that its whole skeleton and locomotive organs, and even its sense organs, are arranged in such a way as to make it skillful at pursuing and catching its prey. For these relations are the necessary conditions of existence of the animal; if things were not so, it would not be able to subsist. (Cuvier)



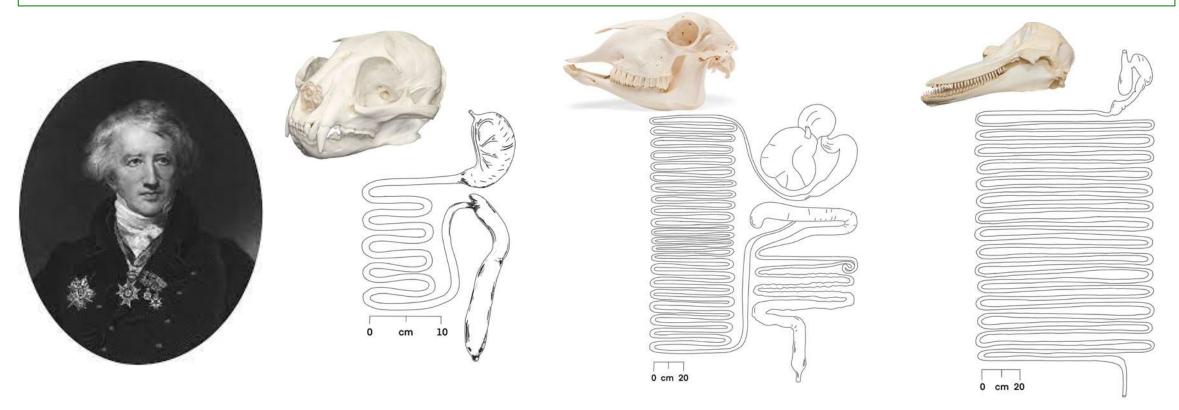
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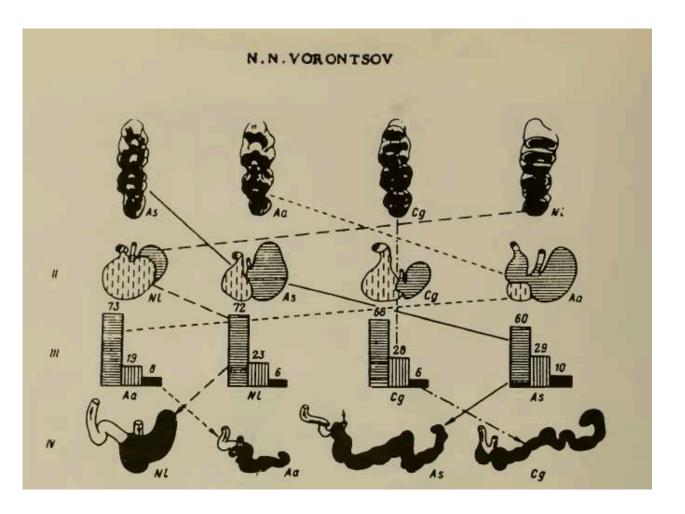
## Principle of the compensation of parts ?

#### EVOLUTION OF THE ALIMENTARY SYSTEM IN MYOMORPH RODENTS

#### N.N. VORONTSOV

TRANSLATED FROM RUSSIAN

Published for the Smithsonian Institution and the National Science Foundation, Washington, D.C. by the Indian National Scientific Documentation Centre, New Delhi.







## What separates a creationist from an evolutionist ?

Not so much the agency (the old man with the white beard)



but the narrative of the adaptation ('perfect' vs. 'adequate at the time')



## The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme

BY S. J. GOULD AND R. C. LEWONTIN Proc. R. Soc. Lond. B 205, 581-598 (1979)

An adaptationist programme has dominated evolutionary thought in England and the United States during the past 40 years. It is based on faith in the power of natural selection as an optimizing agent. It proceeds by breaking an organism into unitary 'traits' and proposing an adaptive story for each considered separately. Trade-offs among competing selective demands exert the only brake upon perfection; non-optimality is thereby rendered as a result of adaptation as well. We criticize this



Principle of contingency and adequacy

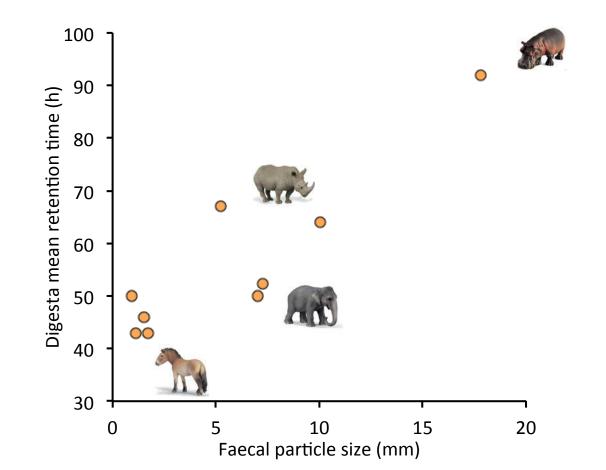
# Stuff works until a better solution really kicks off.

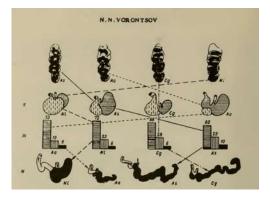


## Chewing – Retention tradeoff ?

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

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







## How do you increase the yield of a growing system ?

