



# Coprophagy

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Vetsuisse Faculty



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# **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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ASOCIAL

DETritIVORY,  
GENERAL  
COPROPHAGY





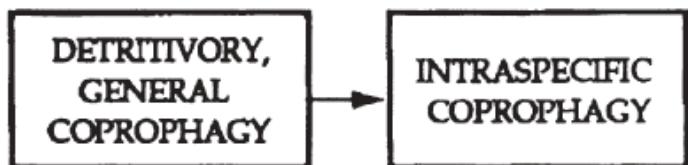
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ASOCIAL

GREGARIOUS

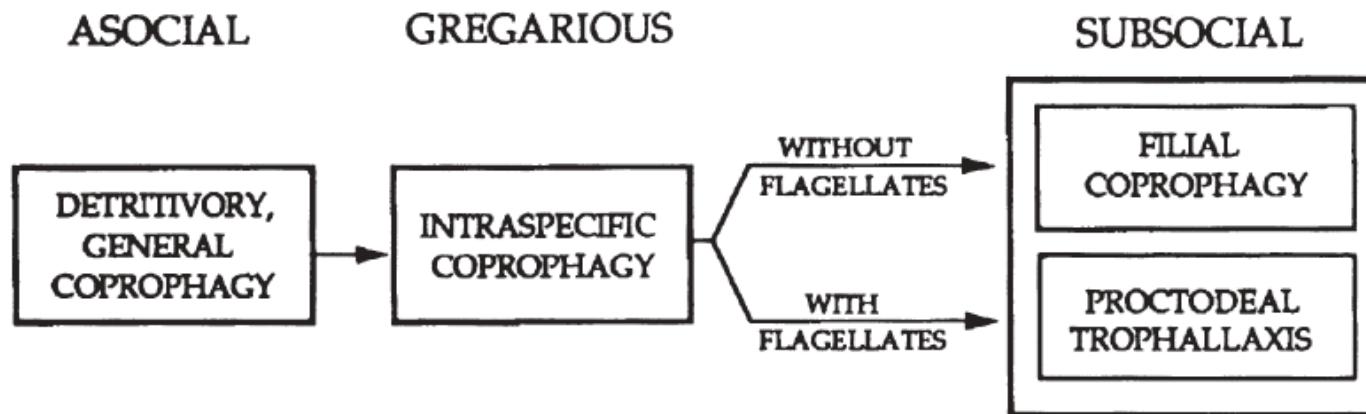




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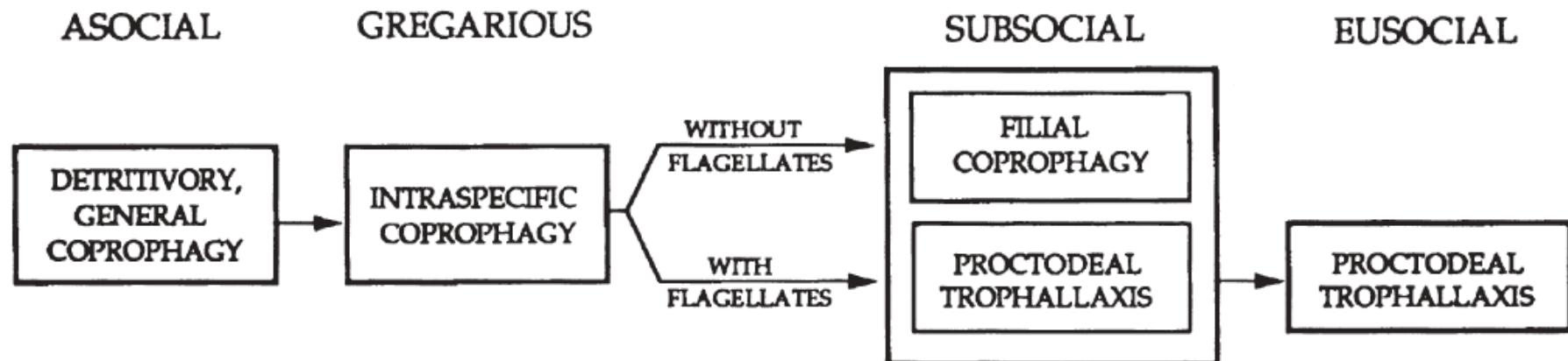




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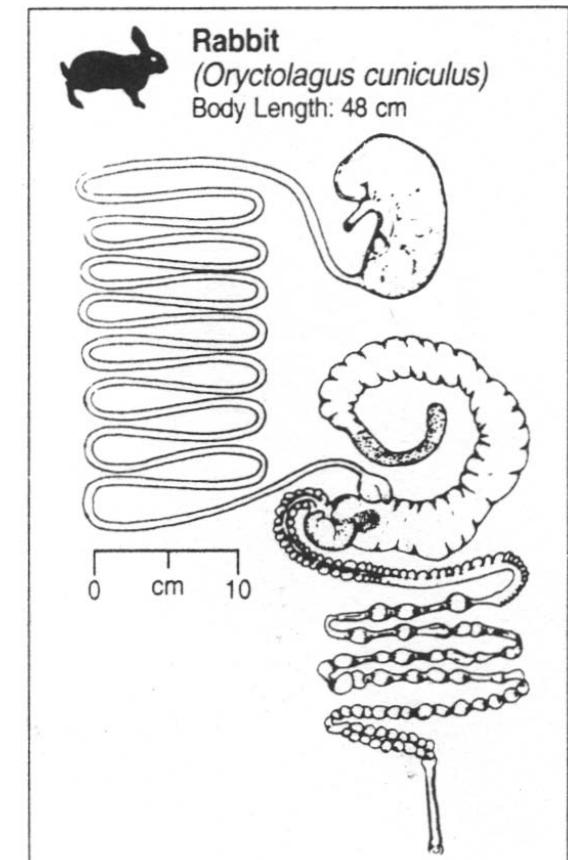
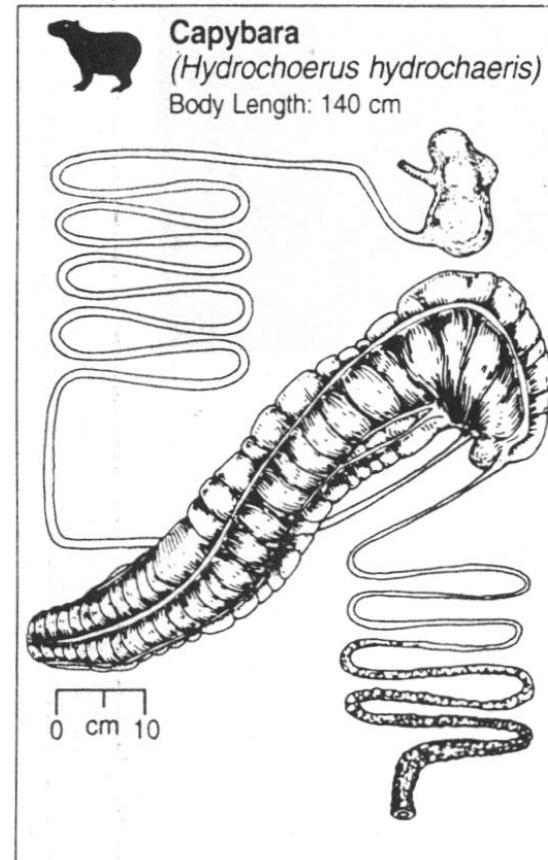
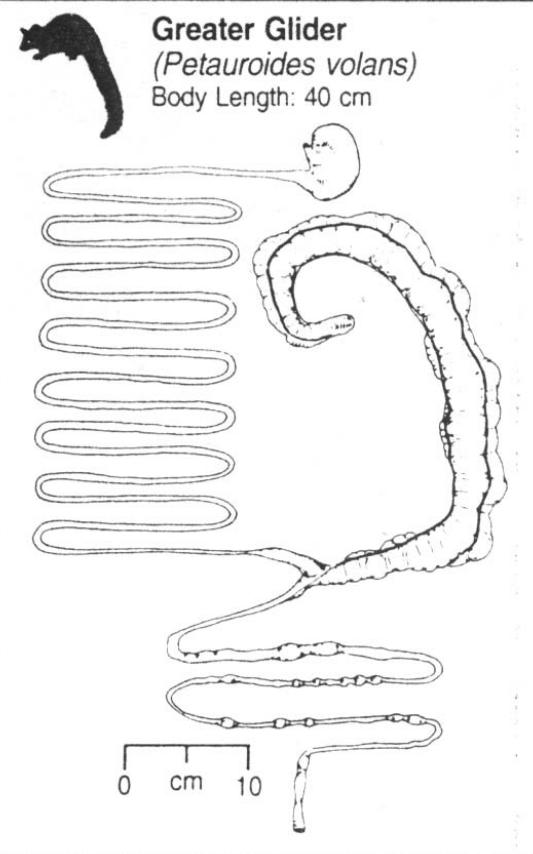
C. A. Nalepa<sup>1</sup>, D. E. Bignell<sup>2</sup> and C. Bandi<sup>3</sup>

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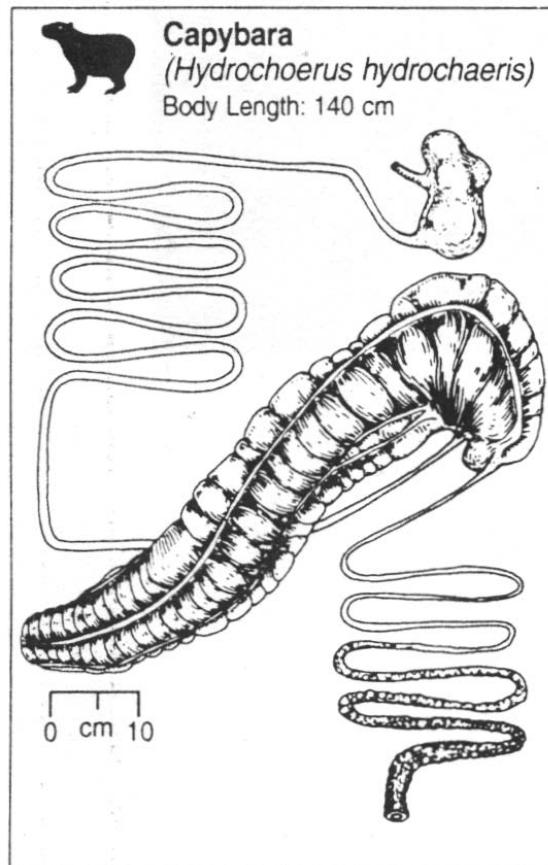
# Caecum fermenters



from Stevens und Hume (1995)



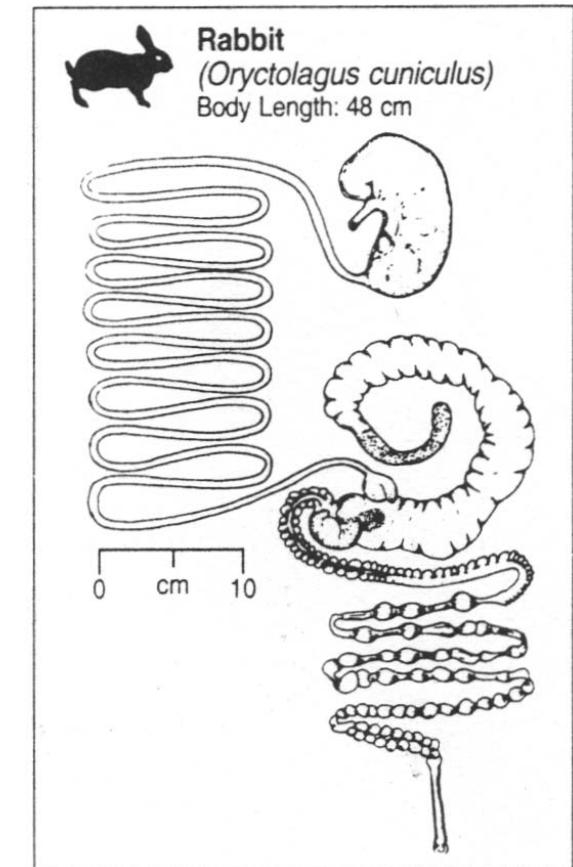
# Caecum fermenters



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



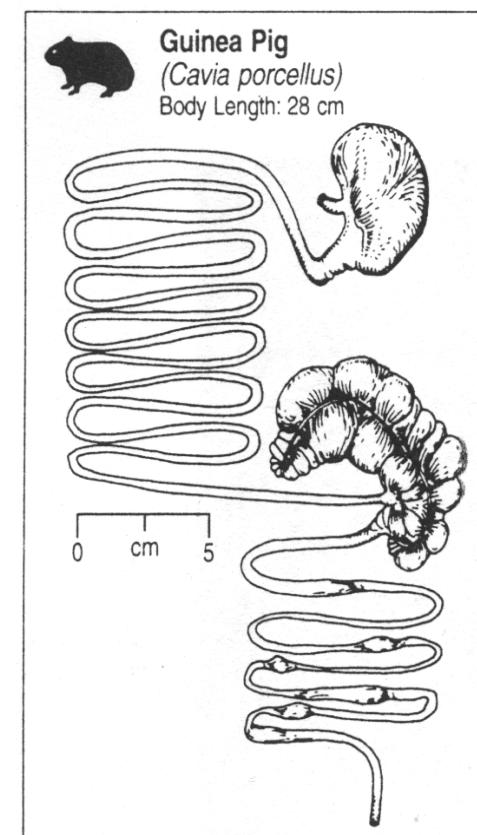
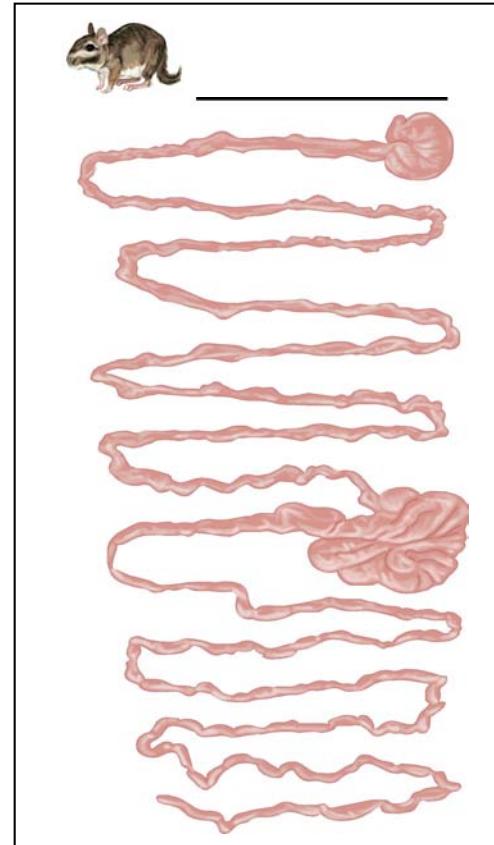
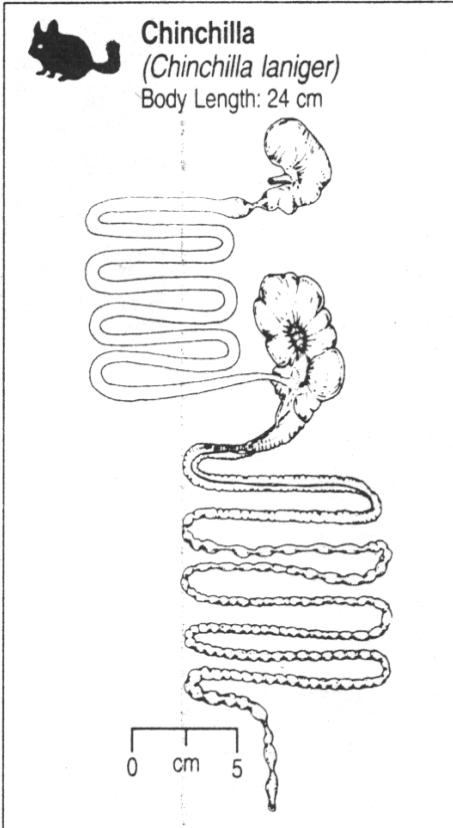
# Caecum fermenters



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



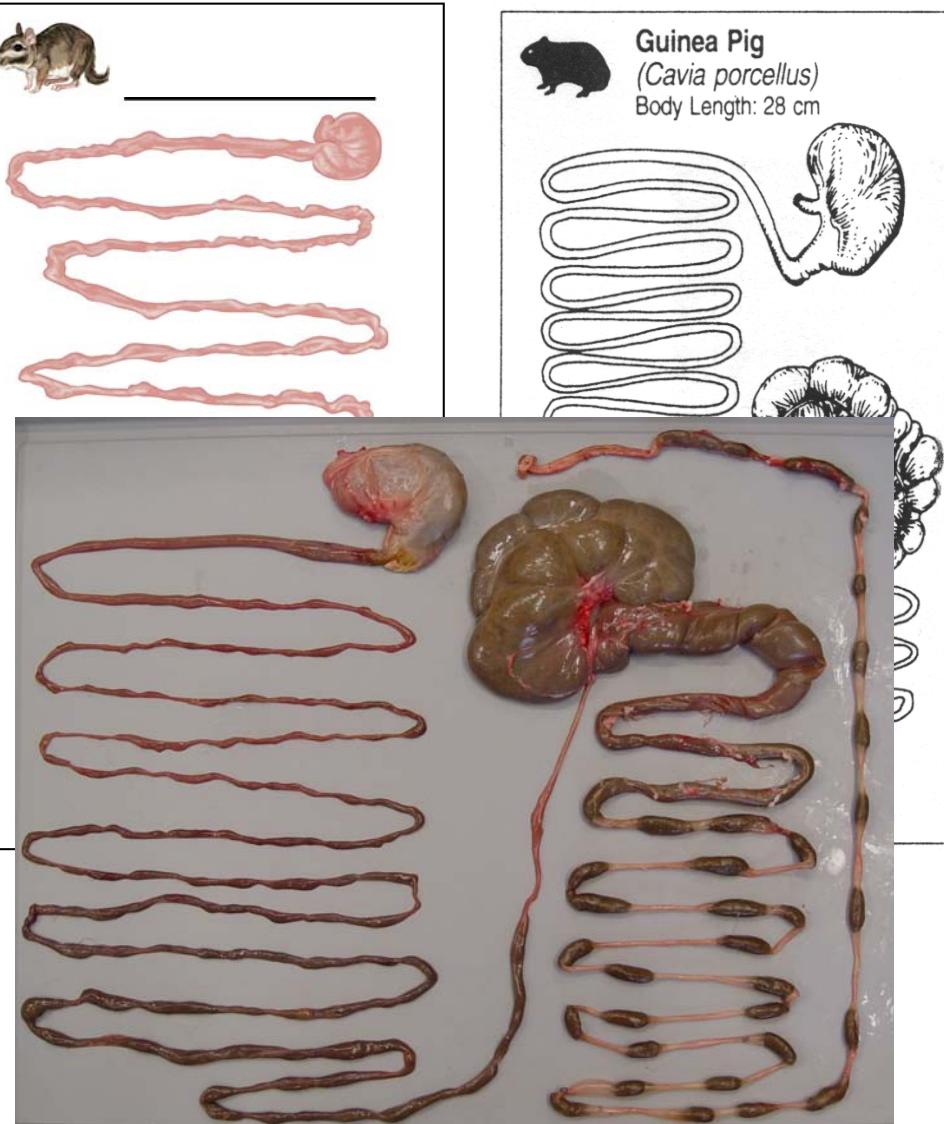
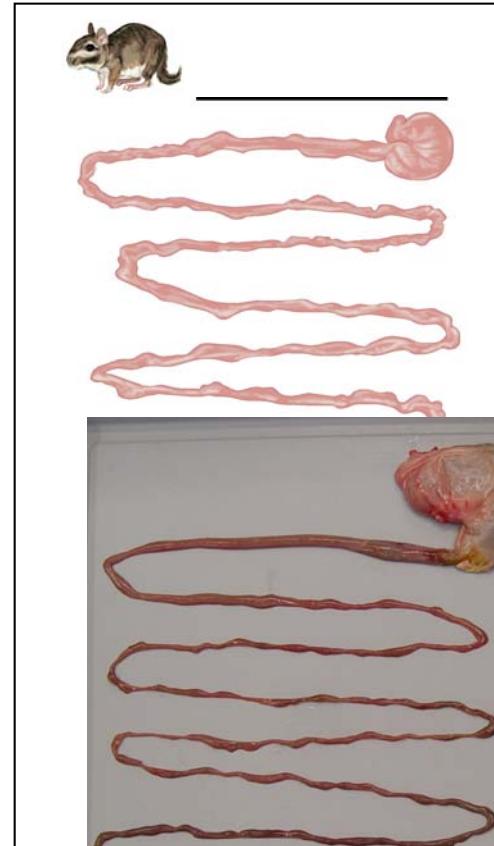
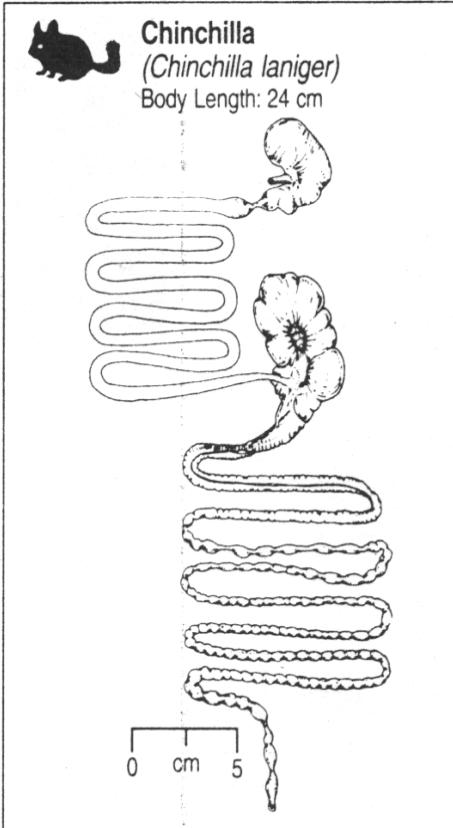
# Caecum fermenters



from Stevens und Hume (1995)  
Besselmann (2005)



# Caecum fermenters



from Stevens und Hume (1995)  
Besselmann (2005), Photo: A. Hug



# Caecum fermenters

Agouti



Mara



Photo: D. Müller, M. Clauss



# Caecum fermenters

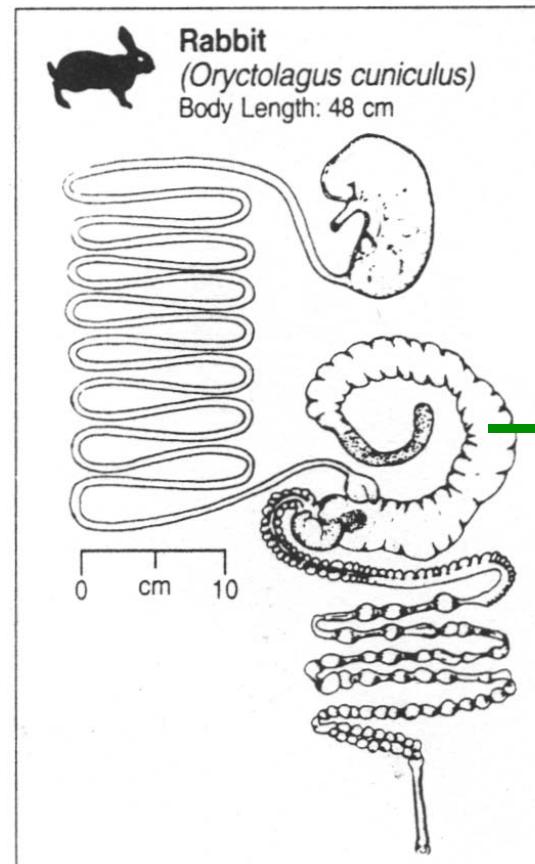
Mara



Photo: M. Clauss



# Caecum fermenters

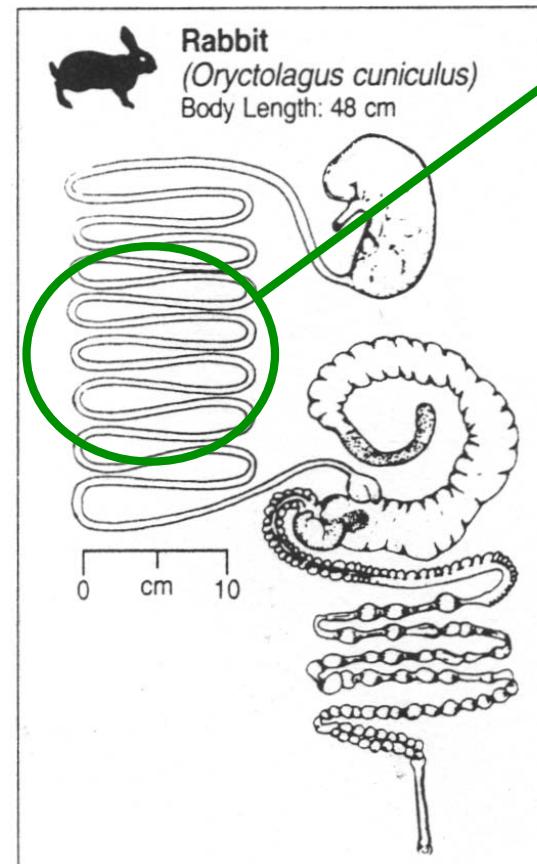


Fermentation:  
Production of VFA  
Acetate  
Propionate  
Butyrate

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



# Caecum fermenters

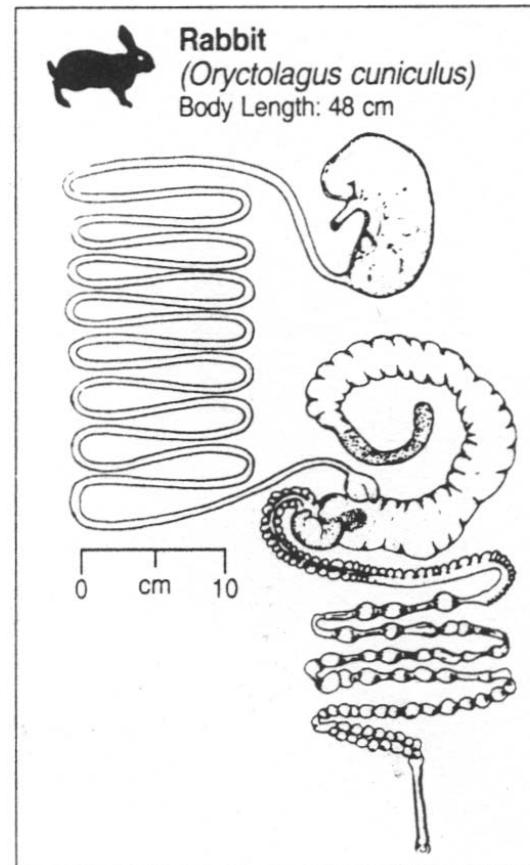


Fermentation after sites of aut-enzymatic digestion and absorption:

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



# Caecum fermenters



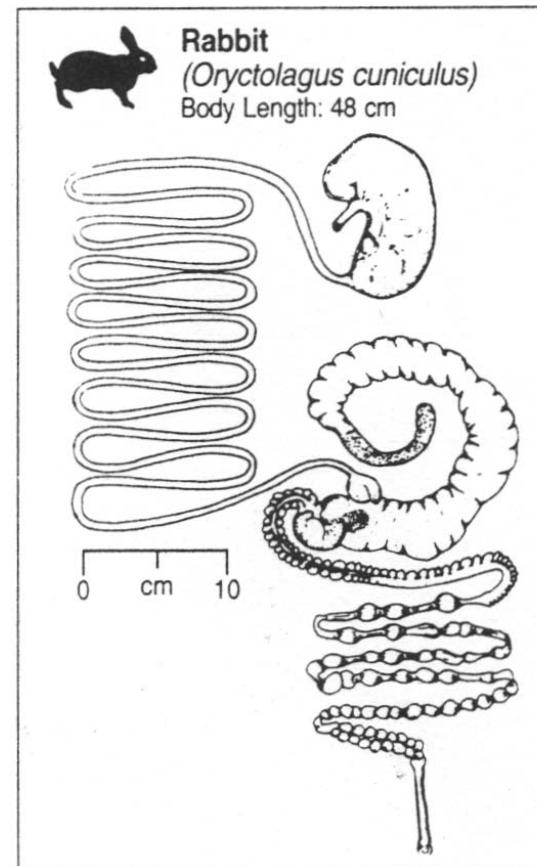
Fermentation after sites of aut-enzymatic digestion and absorption:

Use of easily digestible substances prior to fermentation

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



# Caecum fermenters



Fermentation after sites of aut-enzymatic digestion and absorption:

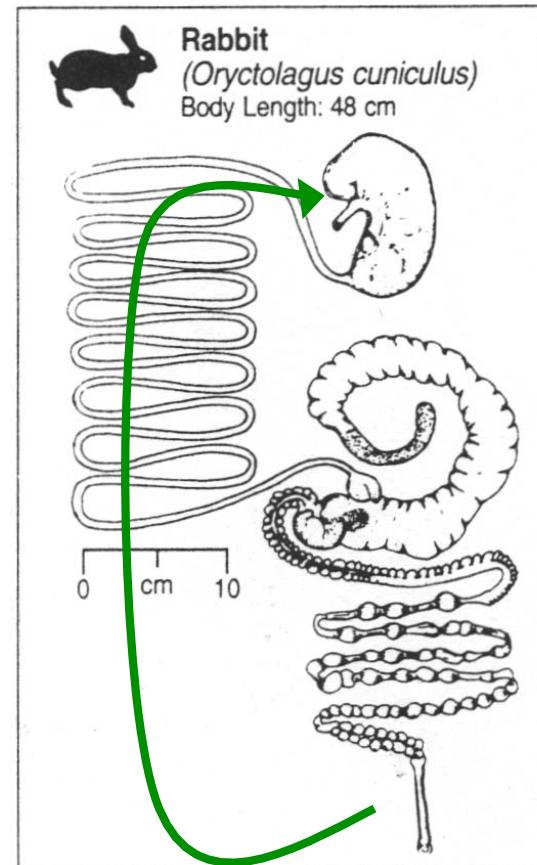
Use of easily digestible substances prior to fermentation

Loss of bacterial protein and bacterial products (B-Vitamins)

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



# Caecum fermenters



Fermentation after sites of aut-enzymatic digestion and absorption:

Use of easily digestible substances prior to fermentation

Loss of bacterial protein and bacterial products (B-Vitamins)

**Coprophagy/  
Caecotrophy**

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



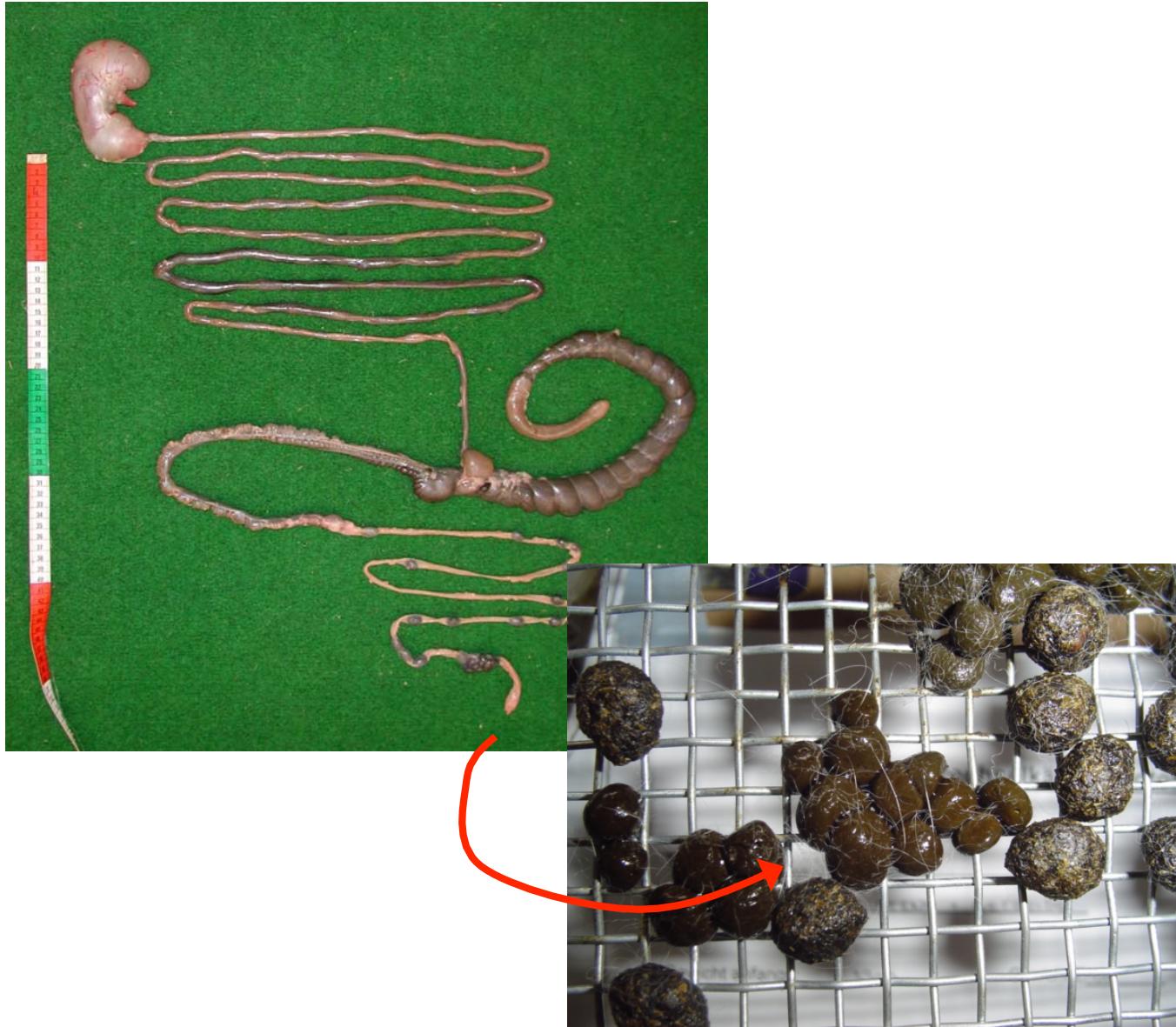
# Coprophagy/Caecotrophy



Photos: B. Burger



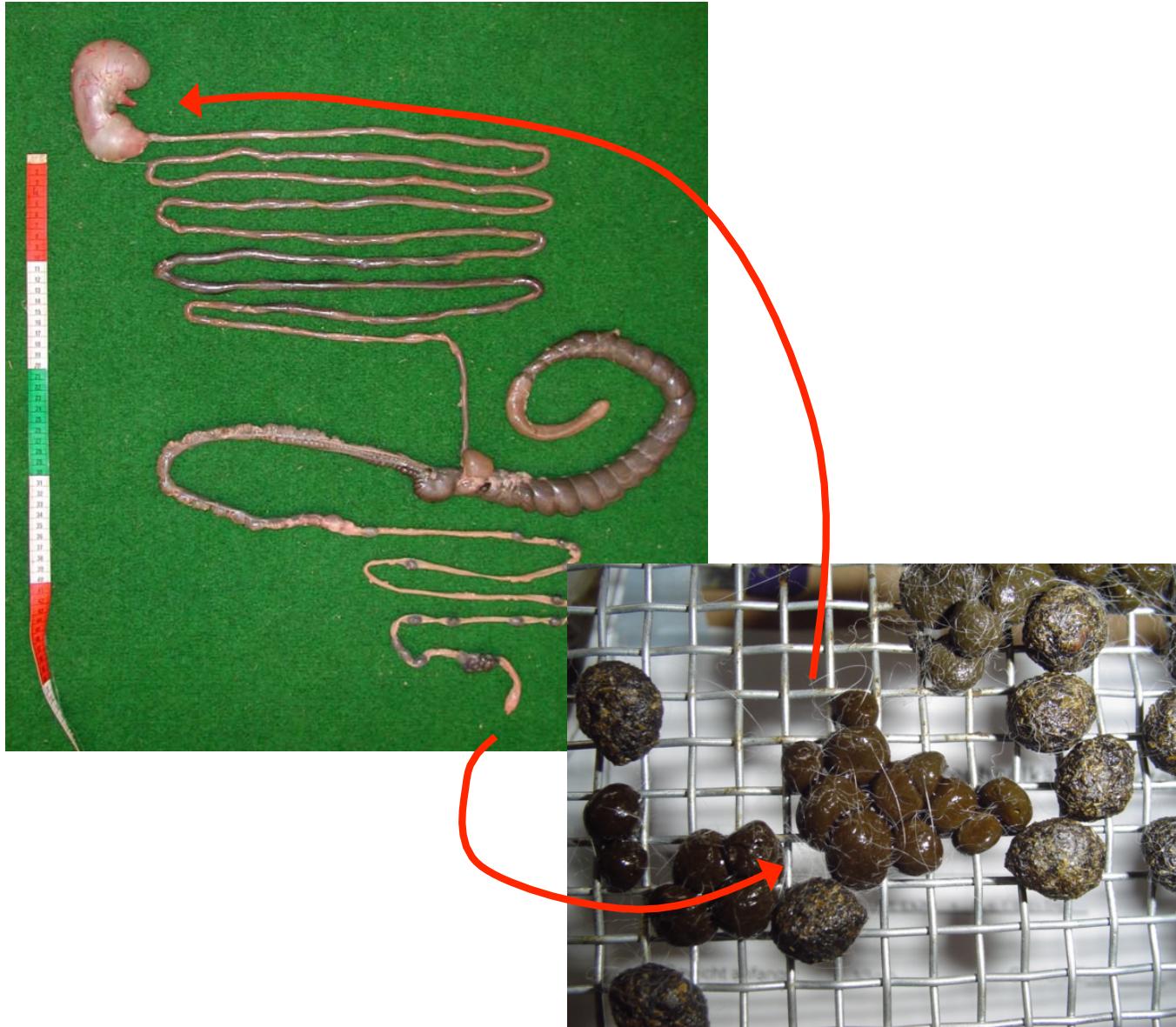
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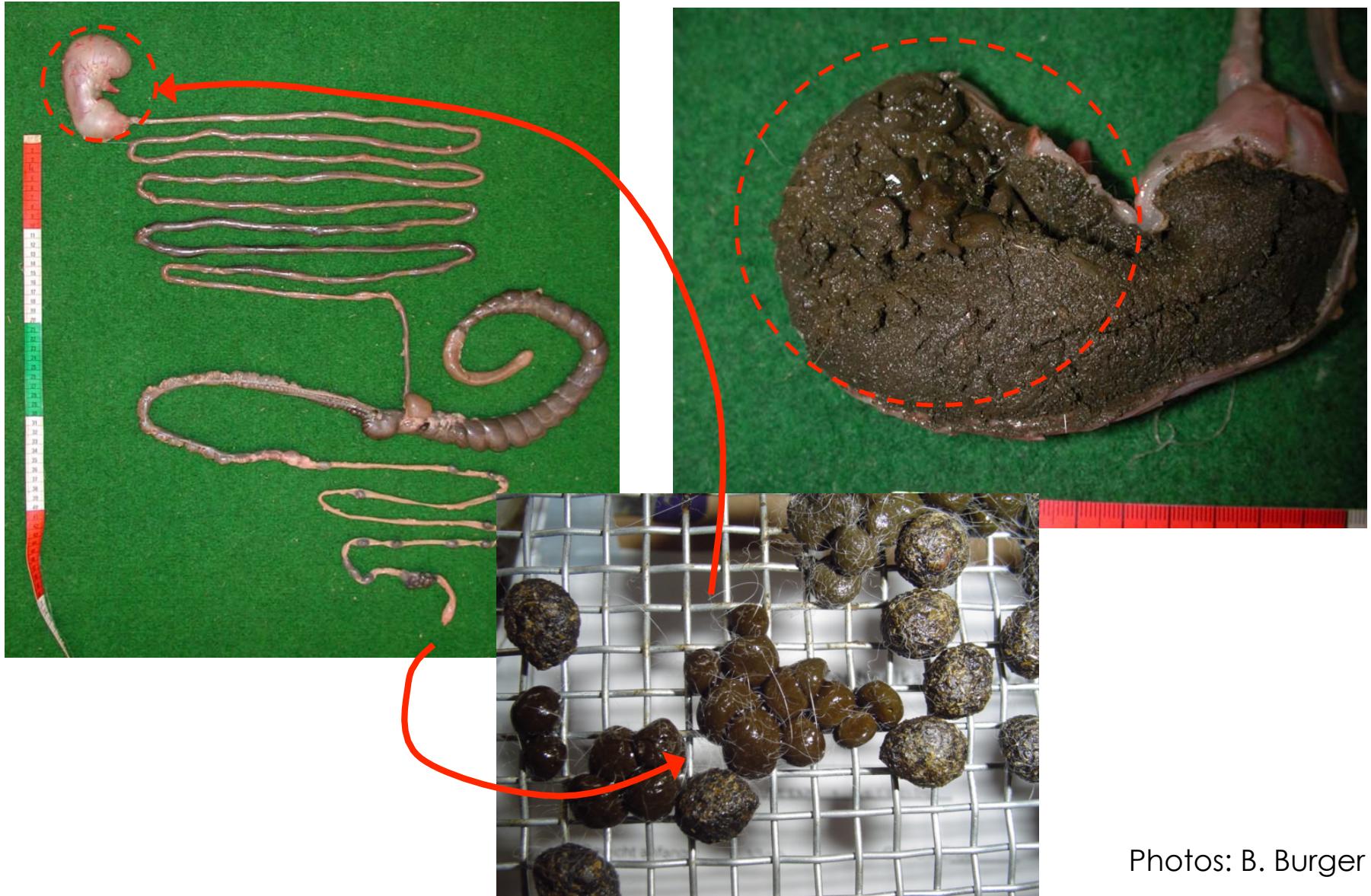
# Coprophagy/Caecotrophy



Photos: B. Burger



# Coprophagy/Caecotrophy



Photos: B. Burger



# Coprophagy/Caecotrophy



Photos: B. Burger, M. Clauss



# Coprophagy/Caecotrophy



*Ctenomys talarum*



Martino et al. (2007)



# Three kinds of faeces (*Myocastor coypus*)



Soft feces

The black part



The green part

Hard feces

from Takahashi & Sakaguchi (1998)



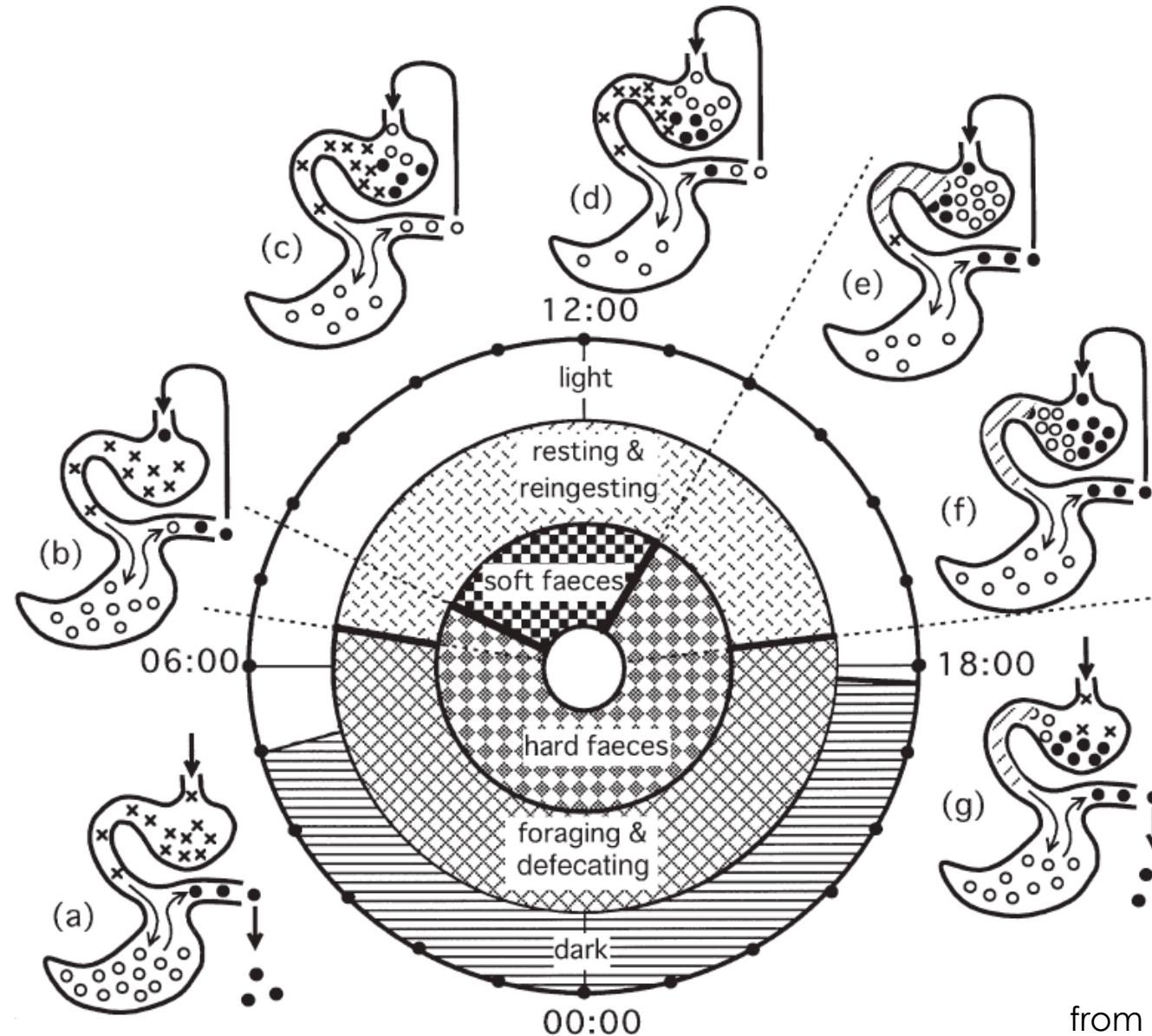
# Coprophagy/Caecotrophy



Photo: Pablo Rodríguez López del Río



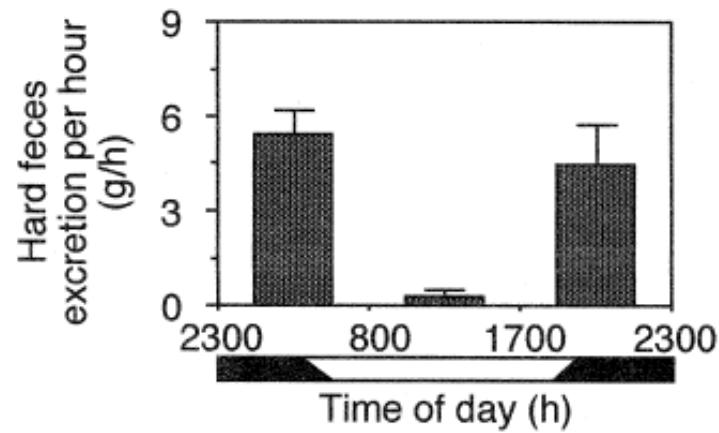
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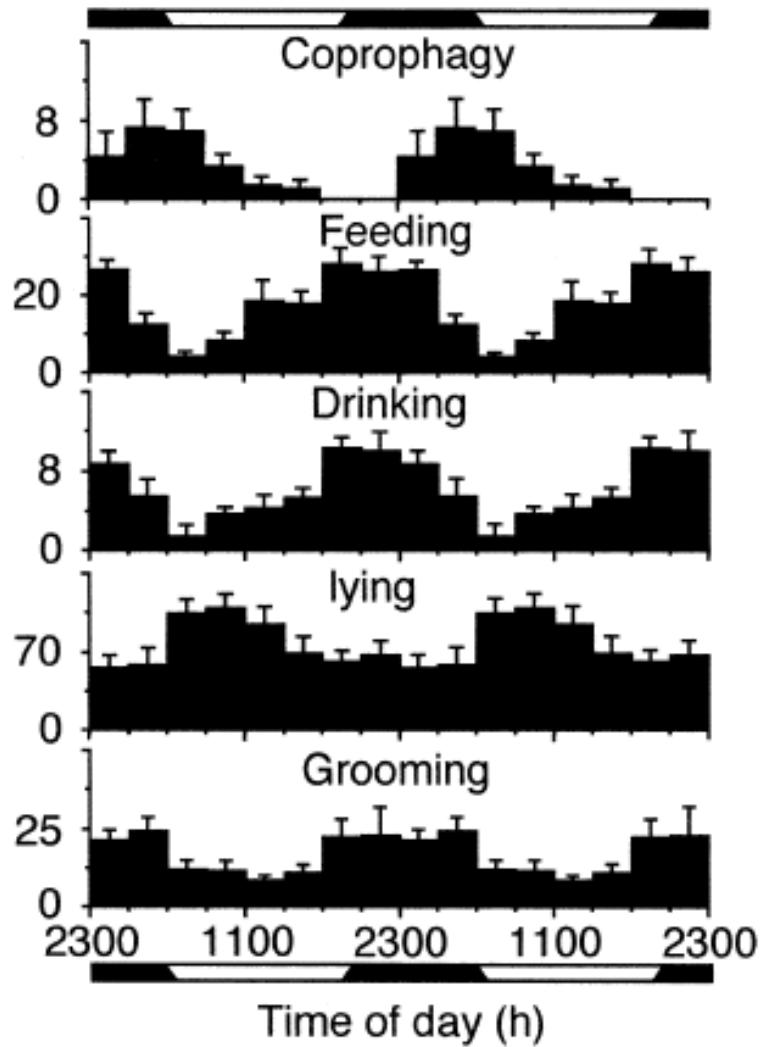
from Hirakawa (2001)



# Coprophagy/Caecotrophy



Time spent of each behavior (min/3 hours)



from Takahashi & Sakaguchi (1998)



# Coprophagy/Caecotrophy



Photo: A. Tschudin



# Coprophagy/Caecotrophy



Photo: D. Besselmann

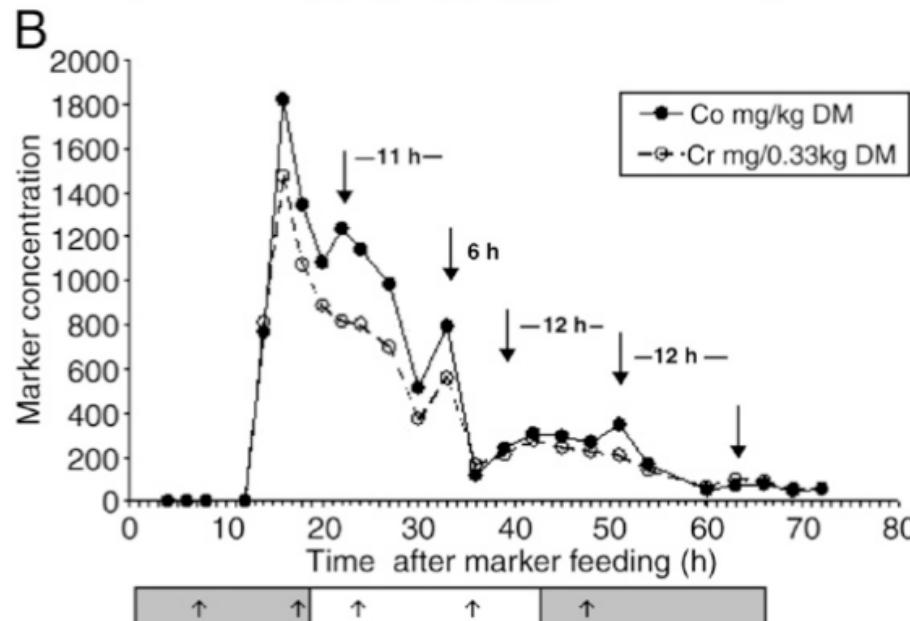
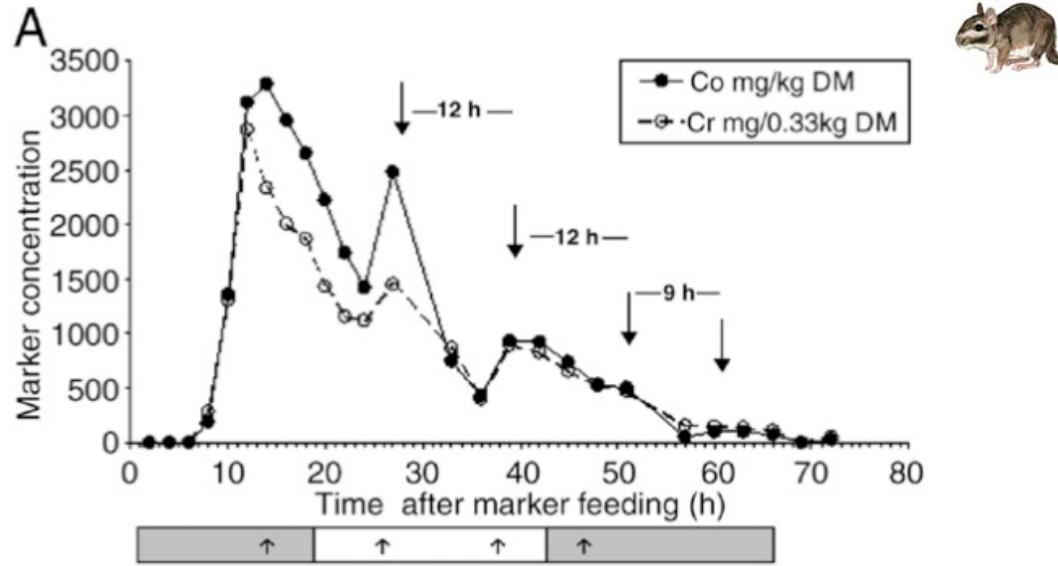


# Coprophagy/Caecotrophy





# Coprophagy and ingesta passage patterns



from Clauss et al. (2007)



# Why coprophagy?





## Comparative Composition of Hard Feces and Cecotropes

Constituent (%)	Hard feces	Cecotropes	References
Crude protein	9.2	28.5	Eden (1940)
Ether extract	1.7	1.1	
Crude fiber	28.9	15.5	
Nitrogen free extract	52.0	43.7	
Ash	8.2	11.2	
Phosphorus	1.3	2.2	
Sodium	0.11	0.22	
Potassium	0.57	1.80	
Dry matter	52.7	38.6	Fekete and Bokori (1985)
Ash	13.7	15.2	
Crude fiber	30.0	17.8	
Crude protein	15.4	25.7	
Gross energy (kcal/kg)	4350	4540	
Crude protein	14.8	37.8	Huang <i>et al.</i> (1954)
Fat	1.8	1.5	
Ash	14.8	14.3	
Crude fiber	27.8	14.3	
Crude protein	18.7	37.4	Thacker and Brandt (1955)
Ether extract	4.3	3.5	
Ash	13.2	13.1	
Lignin	12.3	7.5	
Cellulose	46.6	27.2	
Other carbohydrates	4.9	11.3	
Cell wall constituents	78.1	45.1	Uden and Van Soest (1982)
Cellulose	35.8	20.3	
Hemicellulose	31.1	19.1	
Acid detergent fiber	47.0	26.0	
Lignin	11.0	5.8	



Table 1: The concentrations of nitrogen (% in dry matter) in food, caecal contents, caecotrophes, and faeces of nine hindgut fermentors

	Food	Caecal contents	Faeces	Caecotrophes
Scandinavian lemming				
<i>Lemmus lemmus</i>	1.8	5.2	1.7	nm
Water vole				
<i>Arvicola terrestris</i>	nm	6.0	1.9	6.3
Rat				
<i>Rattus norvegicus</i>	2.1	3.1	1.9	3.5
Guinea pig				
<i>Cavia porcellus</i>	1.9	3.1	1.7	4.7
Chincilla				
<i>Chincilla laniger</i>	2.0	2.7	1.8	3.4
Nutria				
<i>Myocaster coypus</i>	2.7	3.3	2.7	nm
Rabbit				
<i>Oryctolagus cuniculus</i>	2.4	4.2	1.5	4.6
Common ringtail possum				
<i>Pseudochirus peregrinus</i>	1.3	3.9	1.2	4.6
Donkey				
<i>Equus asinus</i>	1.3	1.2	0.9	-

nm = not measured



# Effect of coprophagy on fibre digestion

Diet	Coprophagy <sup>a</sup>	Digestibility (%)		References
		DM	ADF	
High-alfalfa pellets	+	48.3	13.1	Robinson <i>et al.</i> (1985)
High-alfalfa pellets	-	45.3	14.2	
Fresh grass	+	49.8	20.4	Robinson <i>et al.</i> (1985)
Fresh grass	-	52.6	8.7	
Laboratory diet	+	60.8	15.7	Stephens (1976)
Laboratory diet	-	58.2	12.1	

<sup>a</sup> +, Coprophagy permitted; -, coprophagy prevented.



## Effect of coprophagy on protein digestion

Dietary protein source	Coprophagy <sup>b</sup>	Nitrogen digestibility (%)	Nitrogen retention (g/day)
Alfalfa meal	+	64.9	1.10
Alfalfa meal	-	50.8	0.93
Soybean meal	+	76.9	0.78
Soybean meal	-	64.0	0.65
Fresh grass	+	77.6	0.78
Fresh grass	-	67.6	0.44

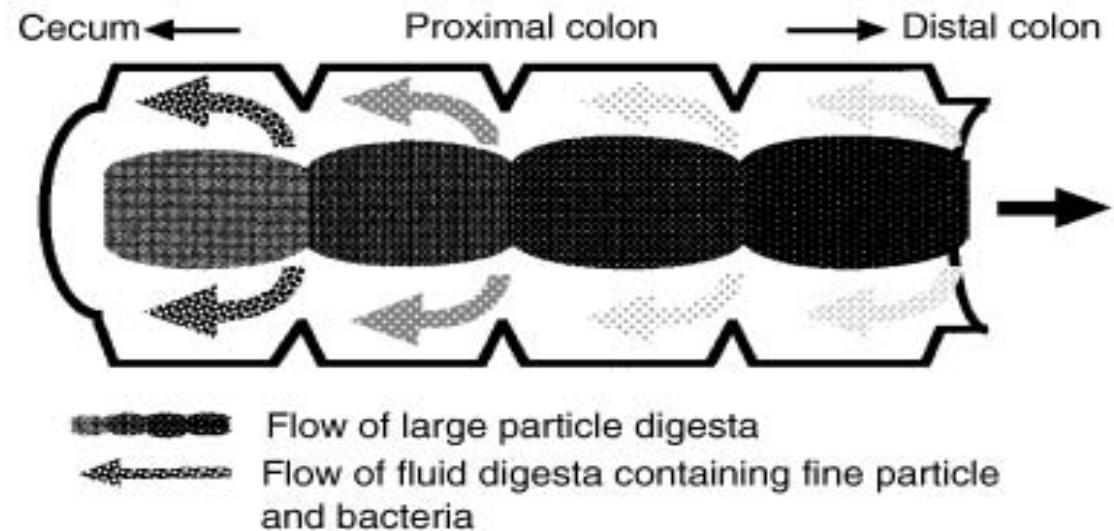
<sup>a</sup> From Robinson *et al.* (1985).

<sup>b</sup> +, Coprophagy allowed; -, coprophagy prevented by a collar.



# Sorting of ingesta for caecotroph formation

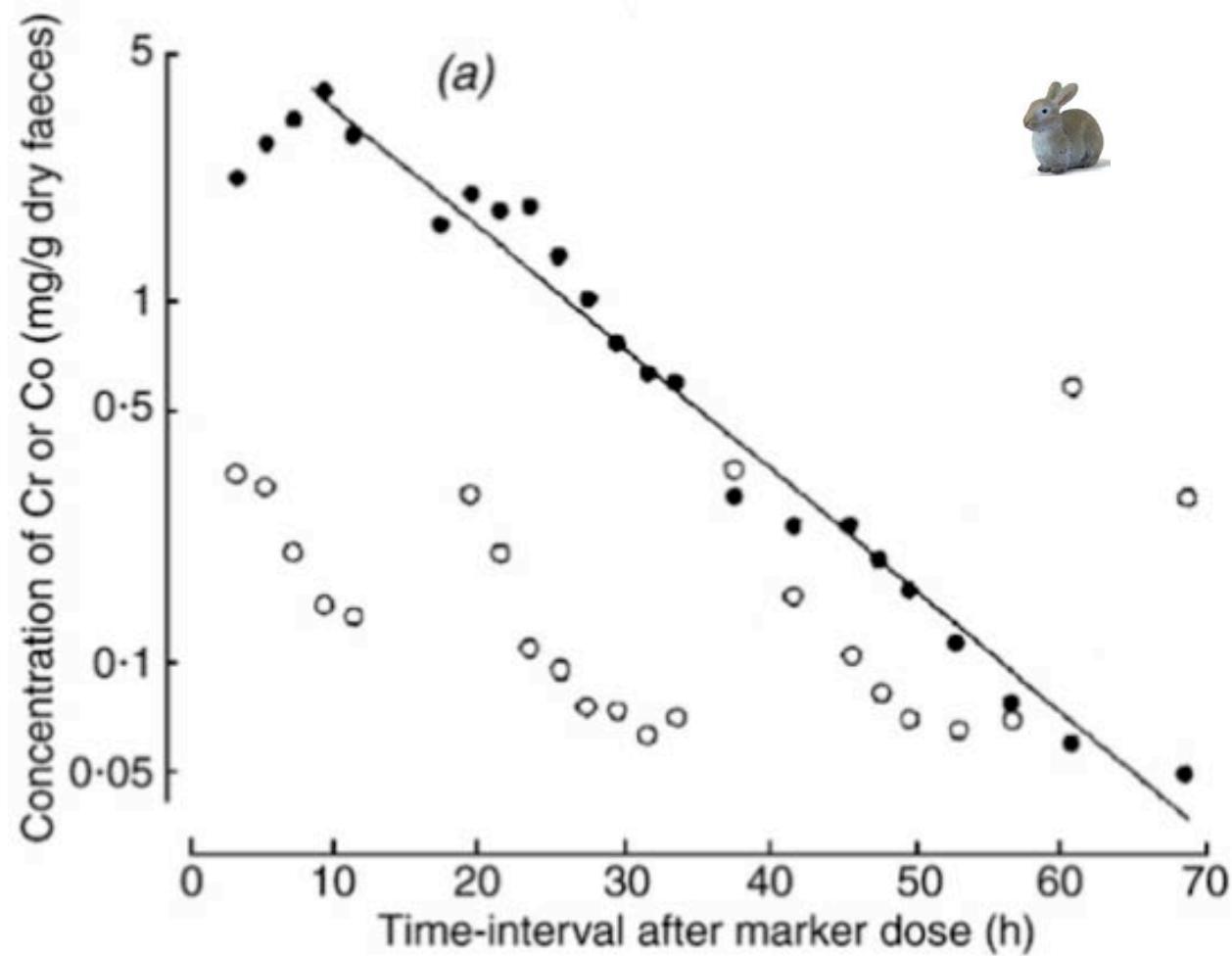
**Wash back mechanism**  
(Rabbit)



from Sakaguchi (2003)



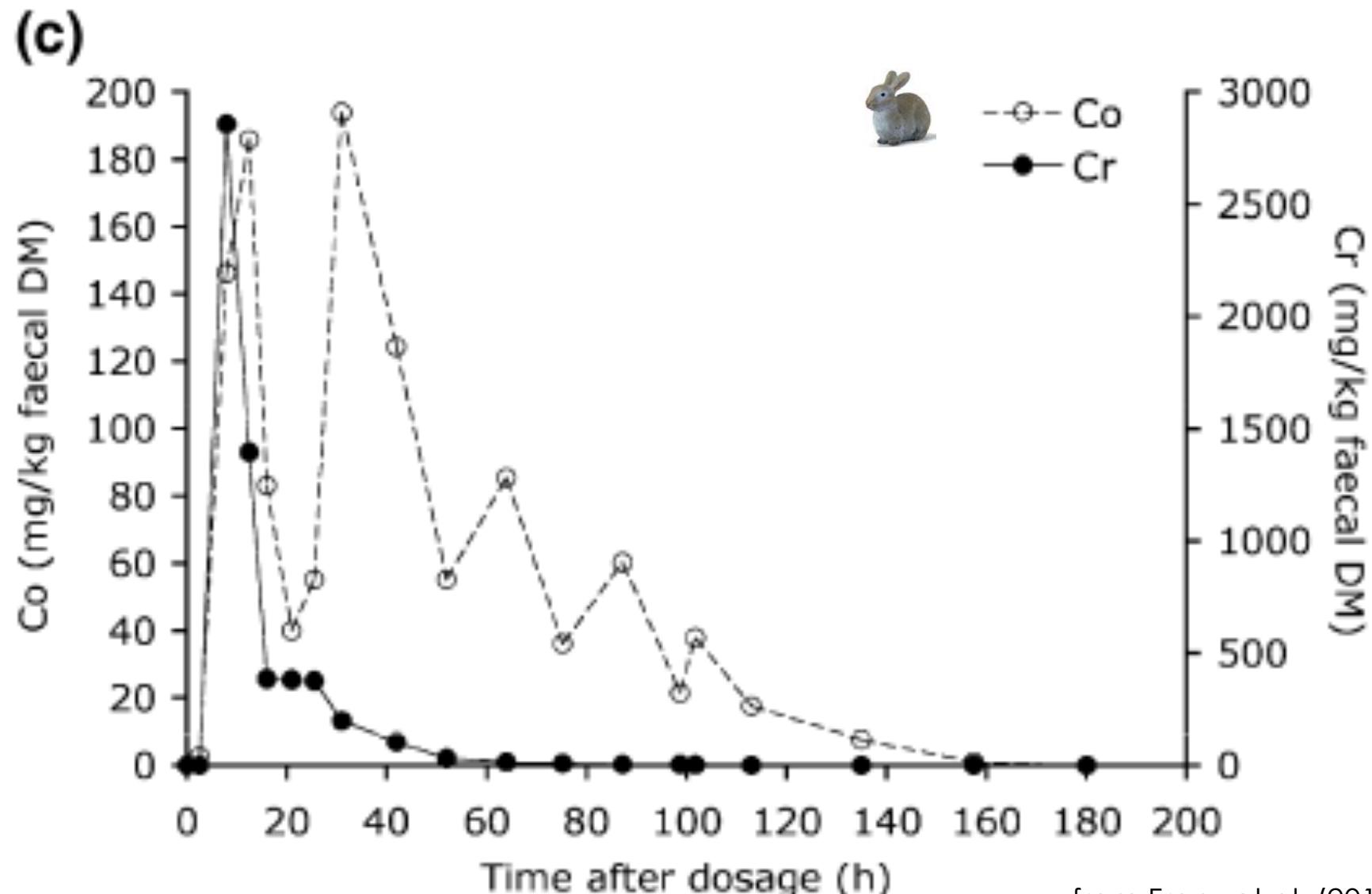
# Coprophagy and ingesta passage patterns



from Sakaguchi et al. (1987)



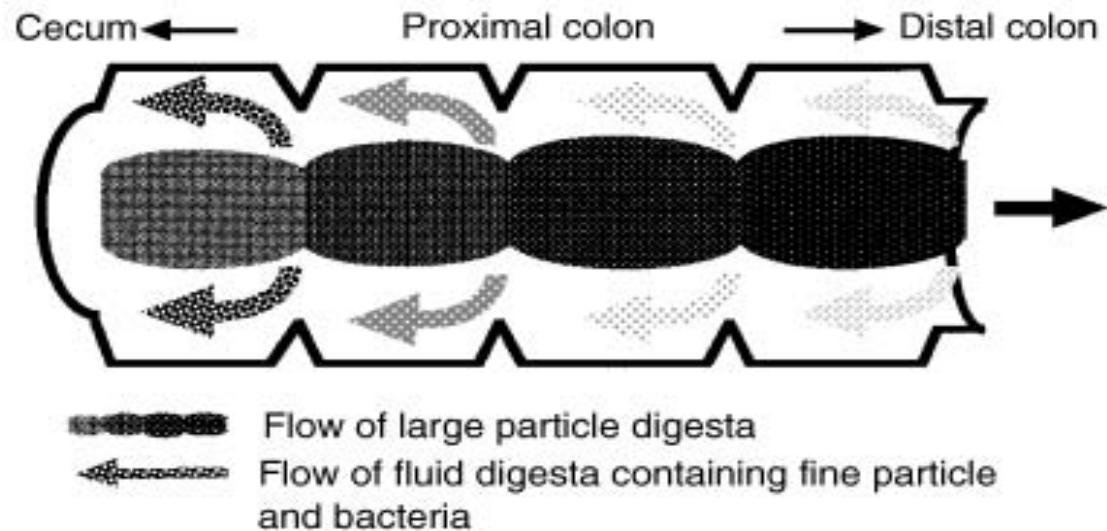
## Coprophagy and ingesta passage patterns



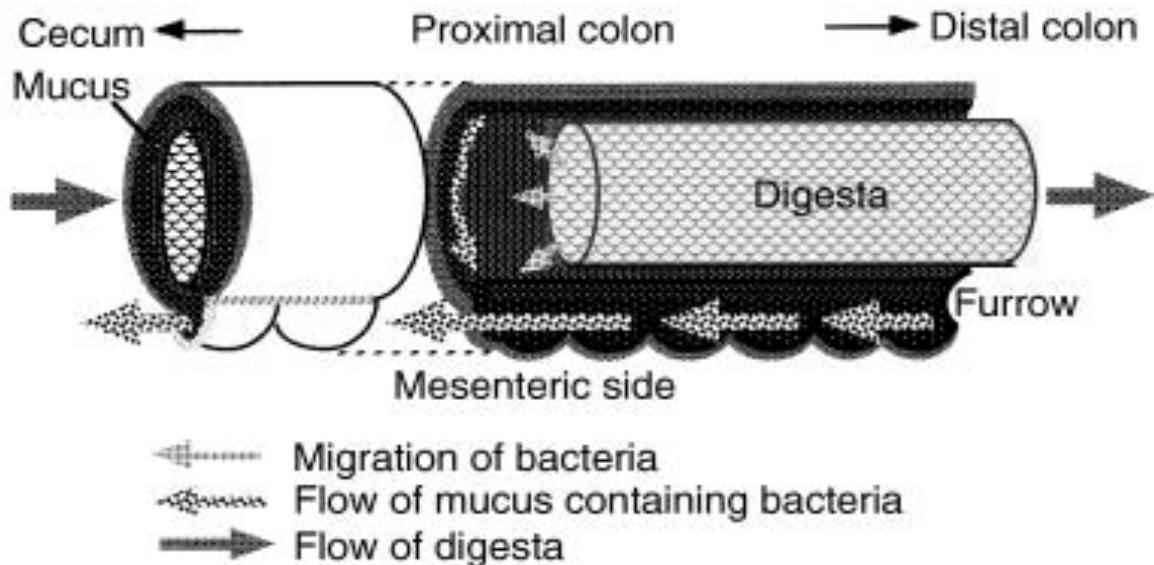


# Sorting of ingesta for caecotroph formation

**Wash back** mechanism  
(Rabbit)



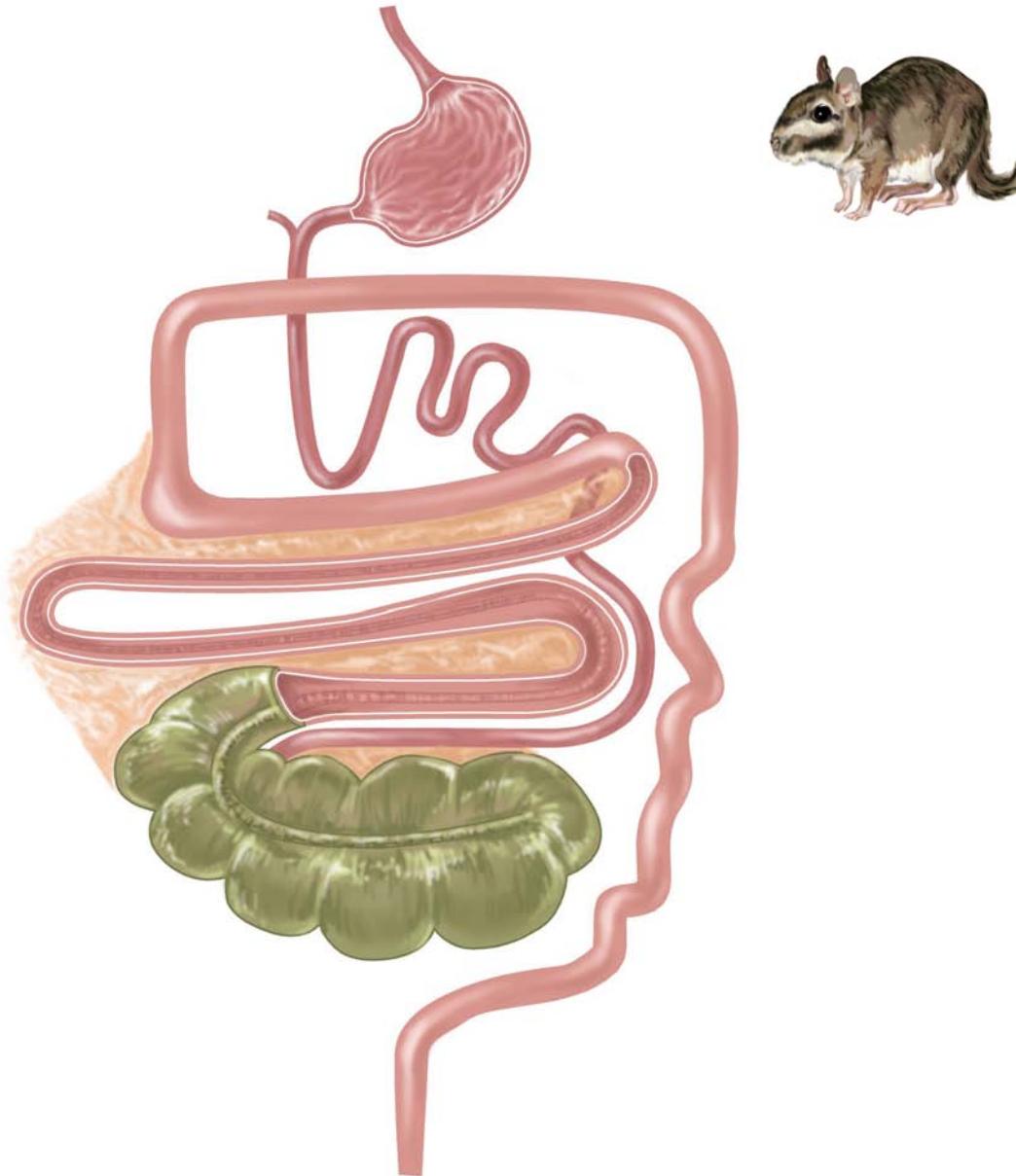
**Mucus trap** mechanism  
(Guinea pig, Chinchilla)



from Sakaguchi (2003)



# The colonic groove / furrow



from Besselmann (2005)



## The colonic groove / furrow



from Besselmann (2005)



## The colonic groove / furrow

Mara



Photo: M. Clauss



# The colonic groove / furrow

Capybara

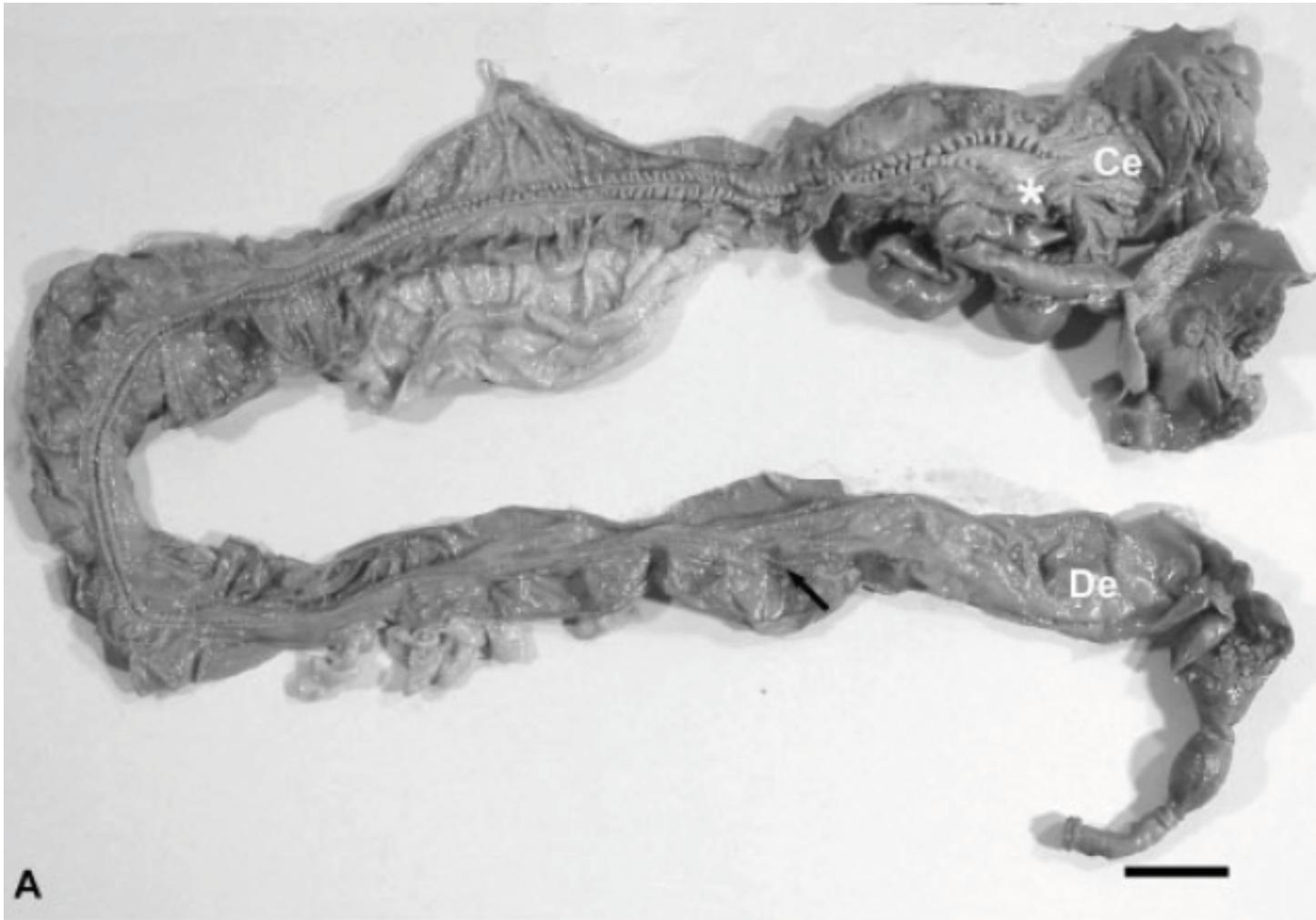


Photo: M. Clauss



# The colonic groove / furrow

Mole-rat (*Bathyergus suillus*)

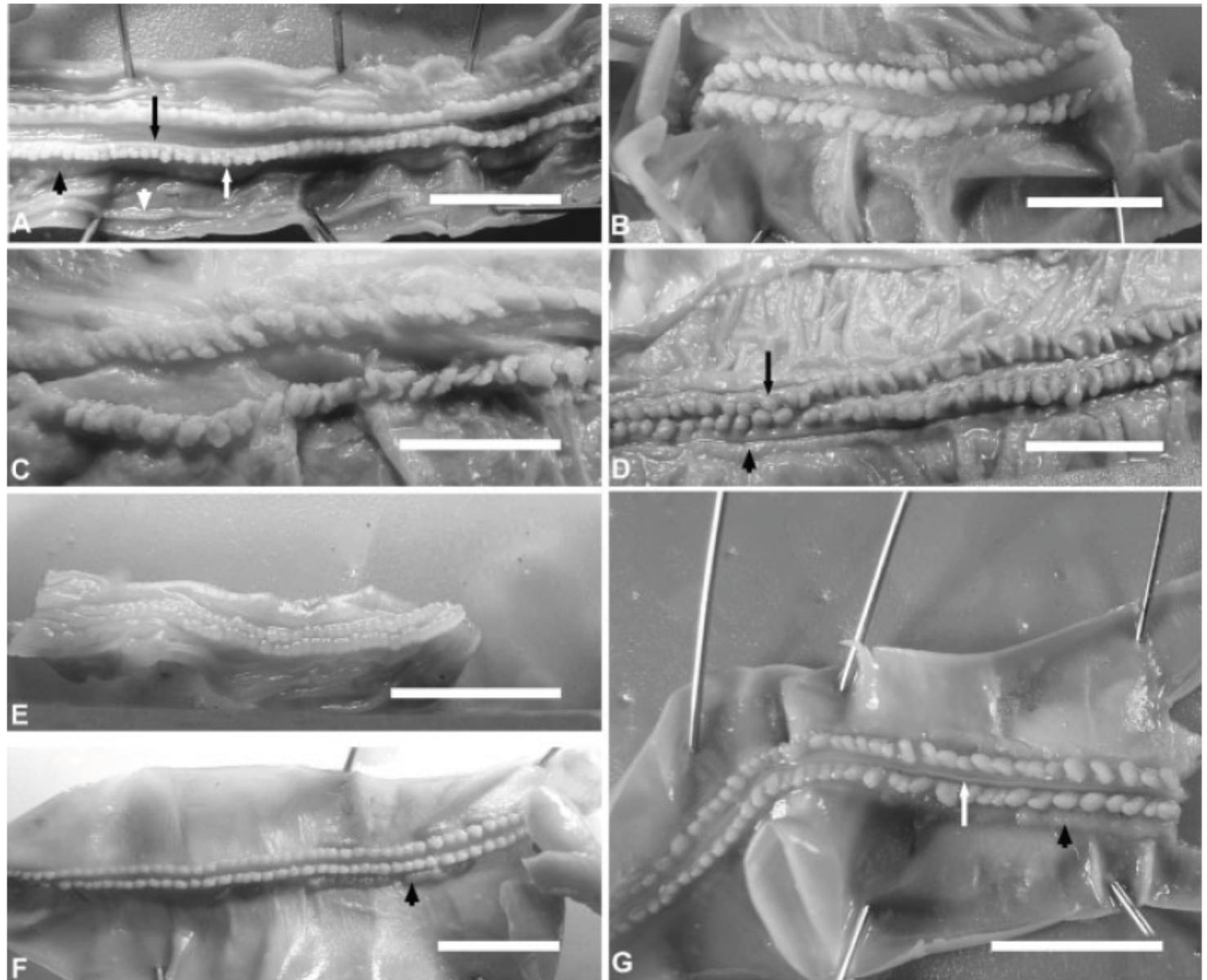


from Kotze et al. (2009)

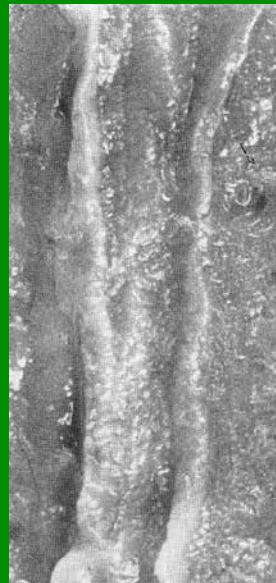


# The colonic groove / furrow

Mole-rats



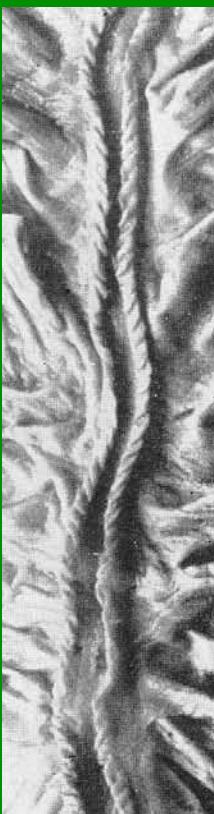
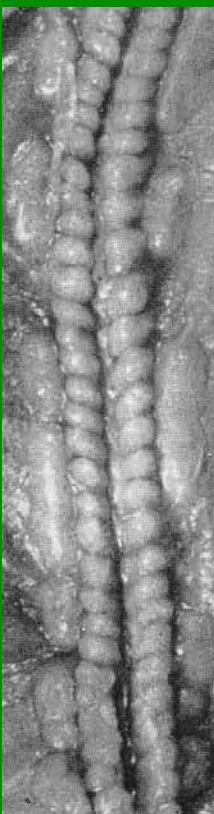
from Kotze et al. (2009)



Nutria (*Myocastor coypus*)

Brush-tailed porcupine (*Atherurus africanus*)

Springhare (*Pedetes capensis*)



Bocage's mole rat (*Cryptomys bocagei*)

Hutia (*Capromys prehensilis*)

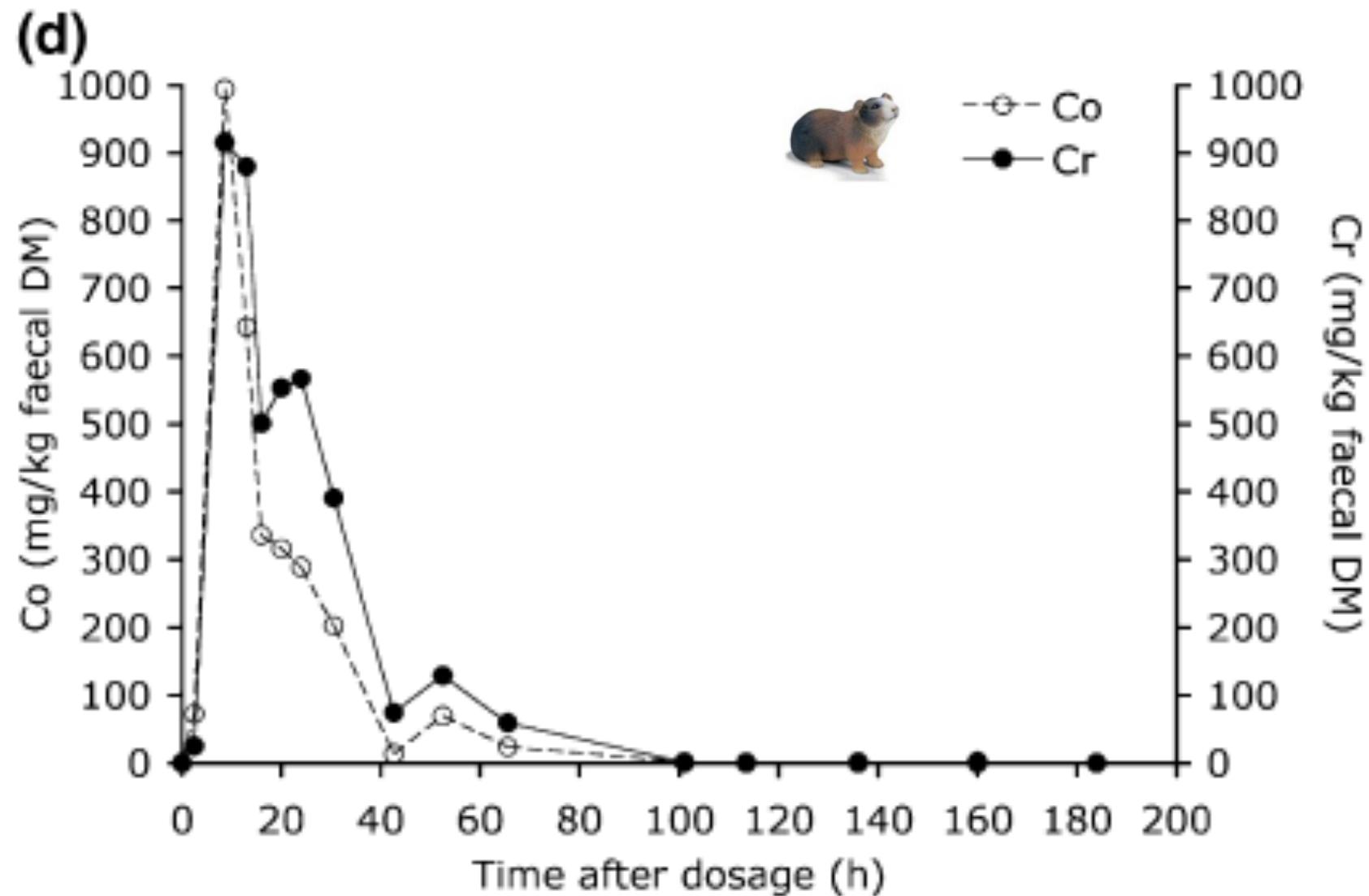
Cape mole rat (*Georychus capensis*)

Grasscutter (*Thryonomys swinderinus*)

from Gorgas (1967)



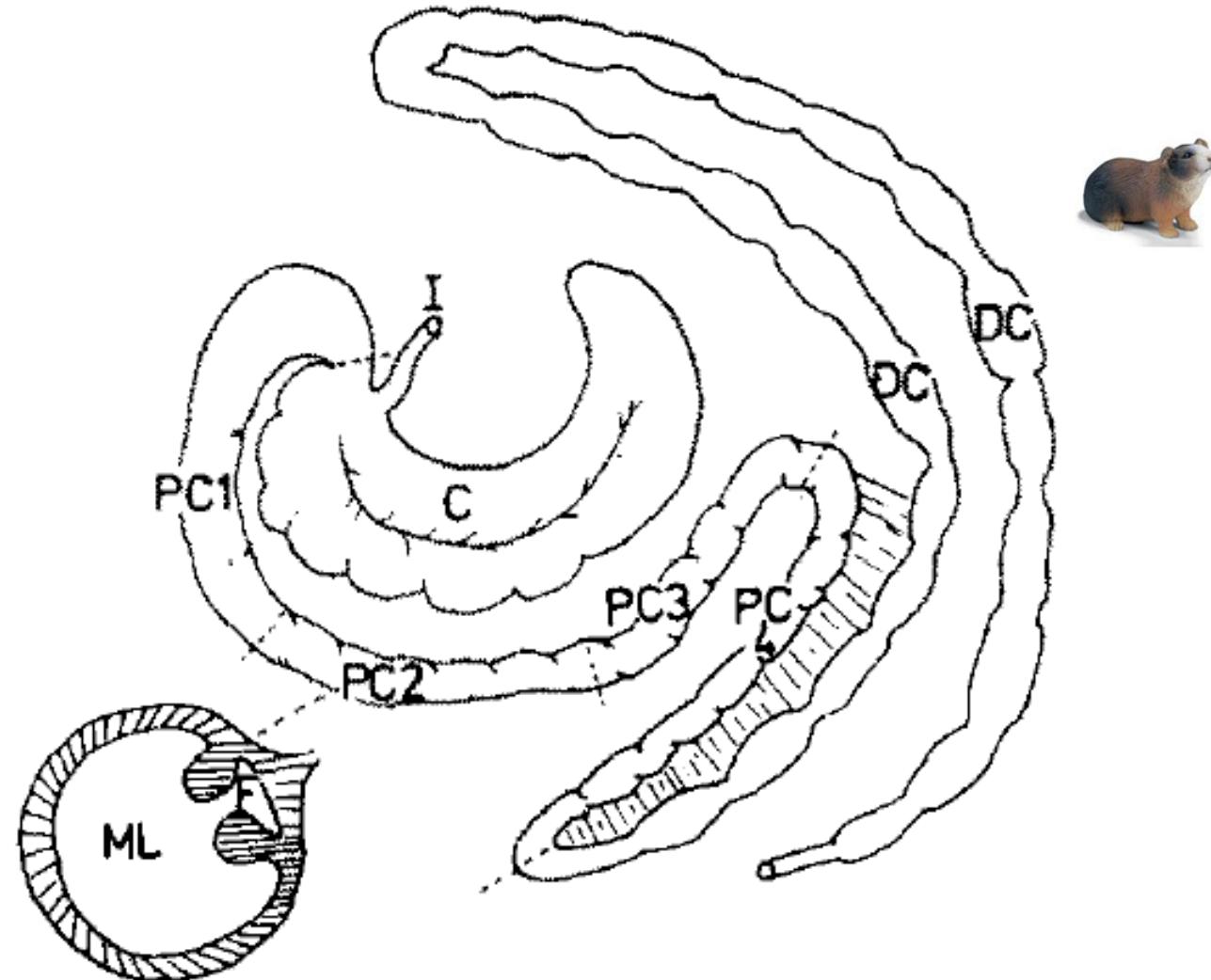
## Coprophagy and ingesta passage patterns



from Franz et al. (2011)



# The colonic groove / furrow



from Holtenius & Björnhag (1985)



## The colonic groove / furrow

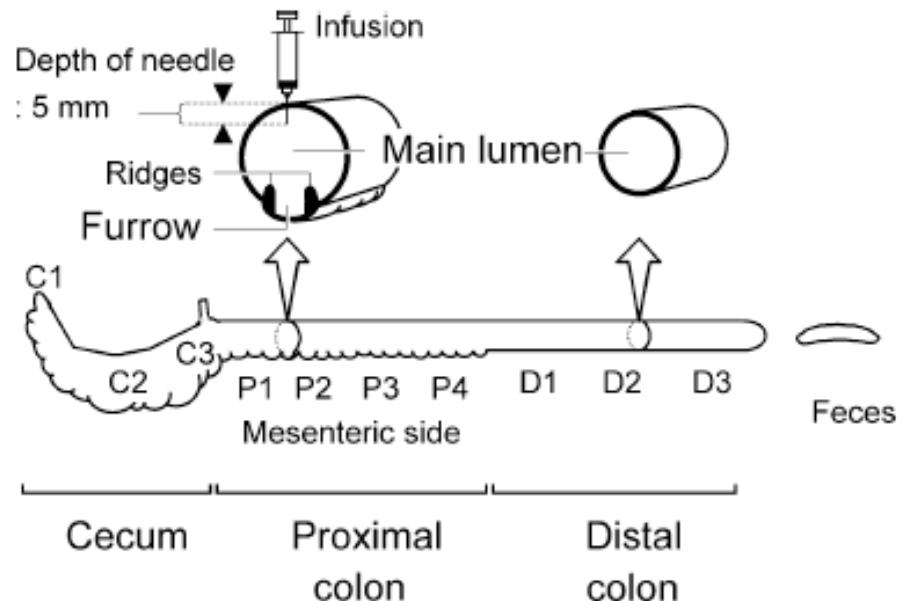
Table 2. The concentration of nitrogen, ATP and dry matter (DM) in contents of the main lumen and of the furrow in proximal colon of guinea-pigs

	Main lumen		Furrow		
	Mean	SD	Mean	SD	
<b>Nitrogen mg/g DM, N = 39</b>					
Colon, proximal part 1	30.3	6.3	43.0	11.9	P < 0.001
Colon, proximal part 2	25.9	6.2	43.4	11.2	P < 0.001
Colon, proximal part 3	23.8	5.7	39.3	9.4	P < 0.001
<b>ATP µg/g DM, N = 22</b>					
Colon, proximal part 1	298	188	512	300	P < 0.001
Colon, proximal part 2	194	144	270	148	P < 0.001
Colon, proximal part 3	88	56	165	66	P < 0.005
<b>Dry matter %, N = 43</b>					
Colon, proximal part 1	18.3	2.0	19.2	4.7	P < 0.05
Colon, proximal part 2	19.9	2.4	22.8	4.8	P < 0.001
Colon, proximal part 3	20.7	2.1	23.2	4.4	P < 0.001

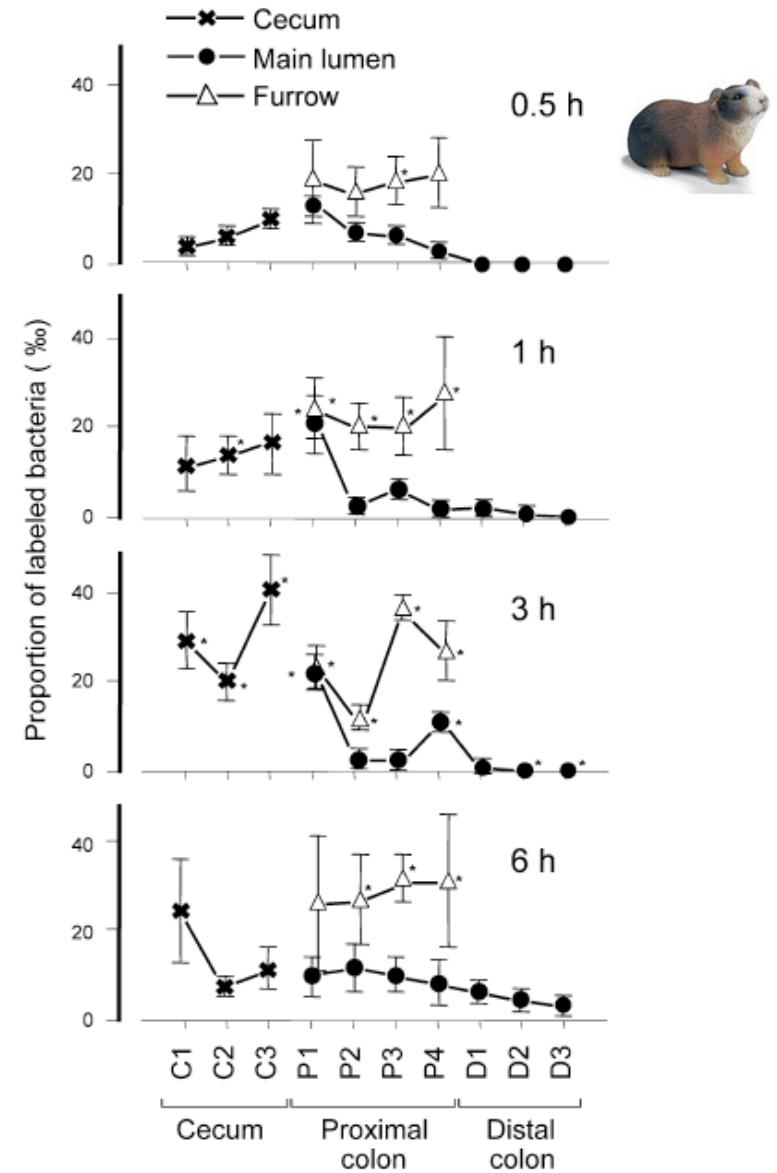
from Holtenius & Björnhag (1985)



# The colonic groove / furrow



from Takahashi & Sakaguchi (2006)





# Three kinds of faeces (*Myocastor coypus*)



The black part



The green part

Soft feces

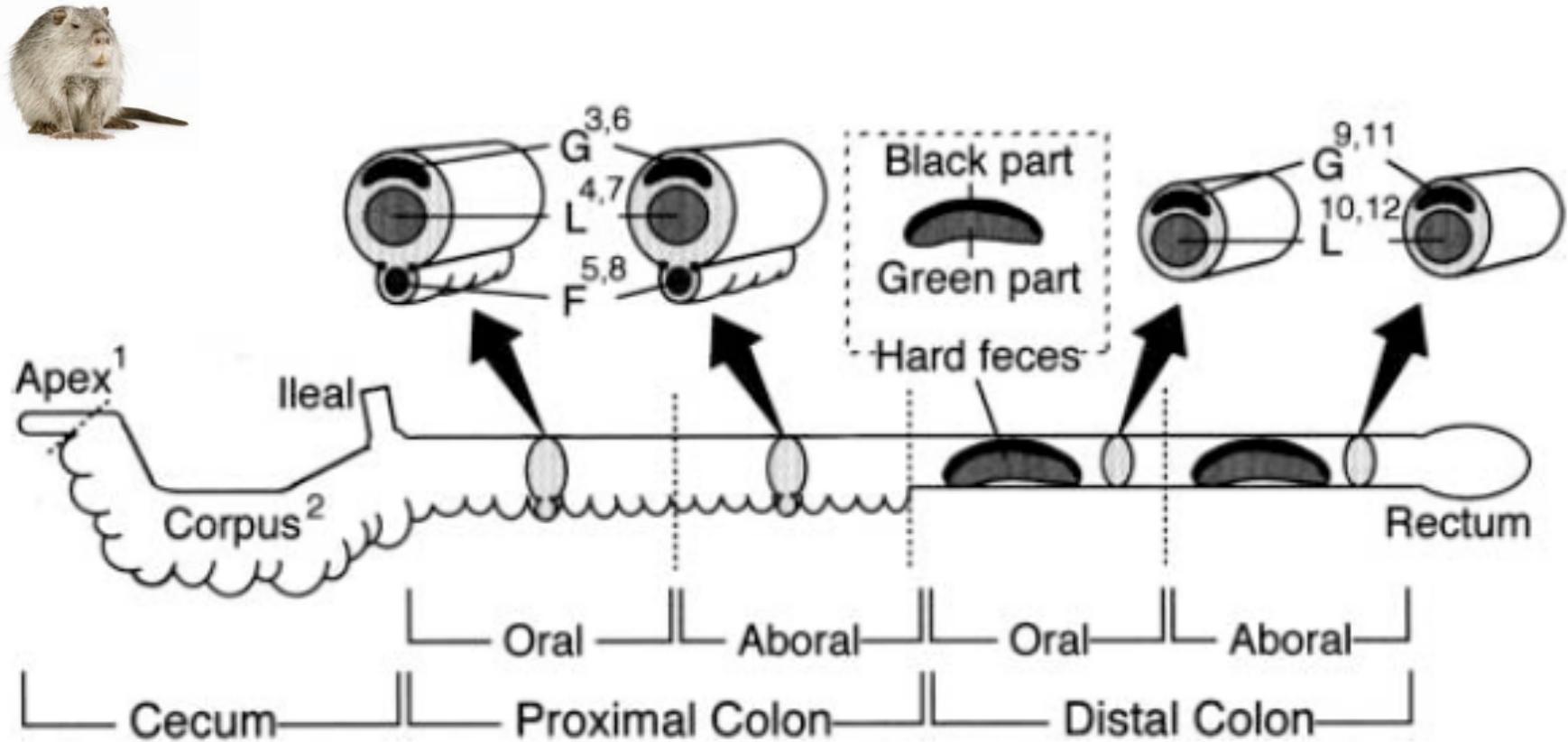
Hard feces

	Type of feces			Part of hard feces		
	Soft	Hard	SE	Black <sup>a</sup>	Green	SE
Moisture (% of fresh feces)	67.4*	59.3	2.0	61.9	58.7	1.9
Organic matter	85.3	85.1	1.1	84.0	87.0	1.2
Crude protein (n × 6.25)	19.1**	13.4	0.8	18.0 <sup>††</sup>	10.9	1.1
Ether extracts	3.55*	2.77	0.20	3.05 <sup>†</sup>	2.45	0.15
NEE <sup>b</sup>	23.5**	25.8	0.4	26.4	27.3	1.4
ADF	29.5**	33.6	0.7	26.6 <sup>††</sup>	36.7	0.8
Crude ash	14.7	14.9	1.1	16.0	13.0	1.2

from Takahashi & Sakaguchi (1998)



# The colonic groove / furrow (*Myocastor coipus*)



from Takahashi & Sakaguchi (2000)



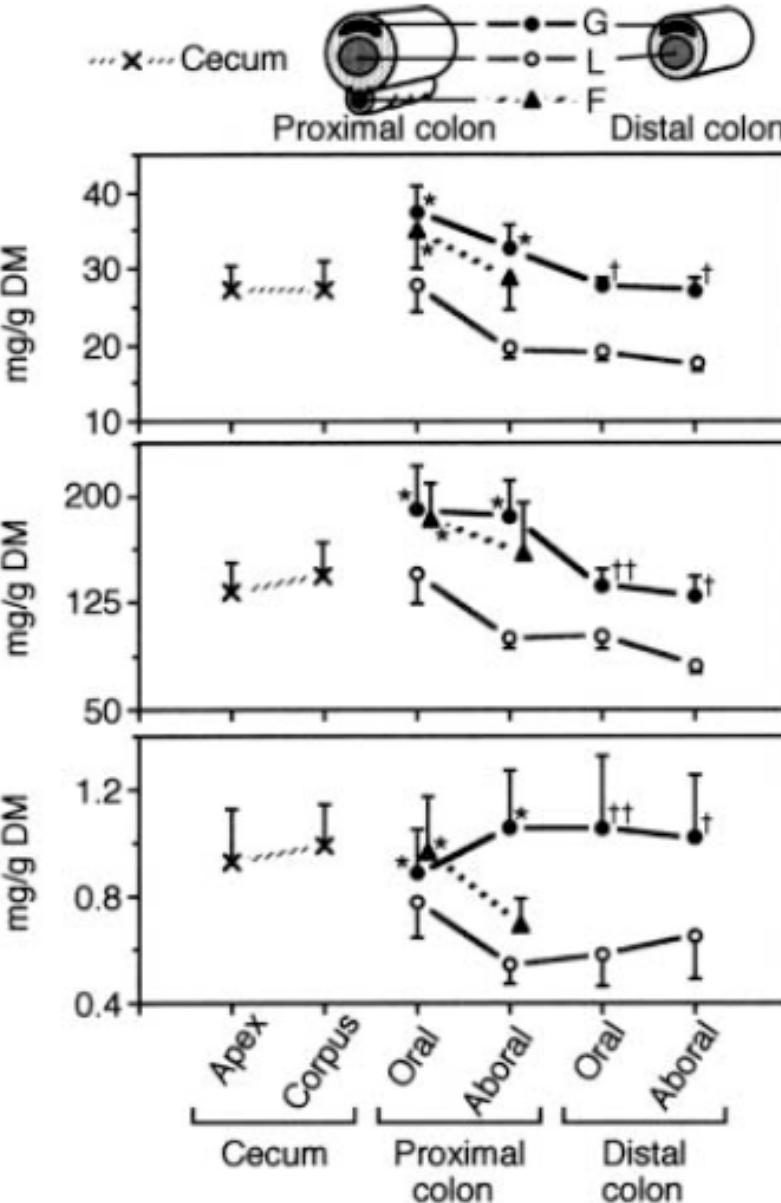
# Three kinds of faeces (*Myocastor coipus*)



Soft feces



The black part  
The green part  
Hard feces

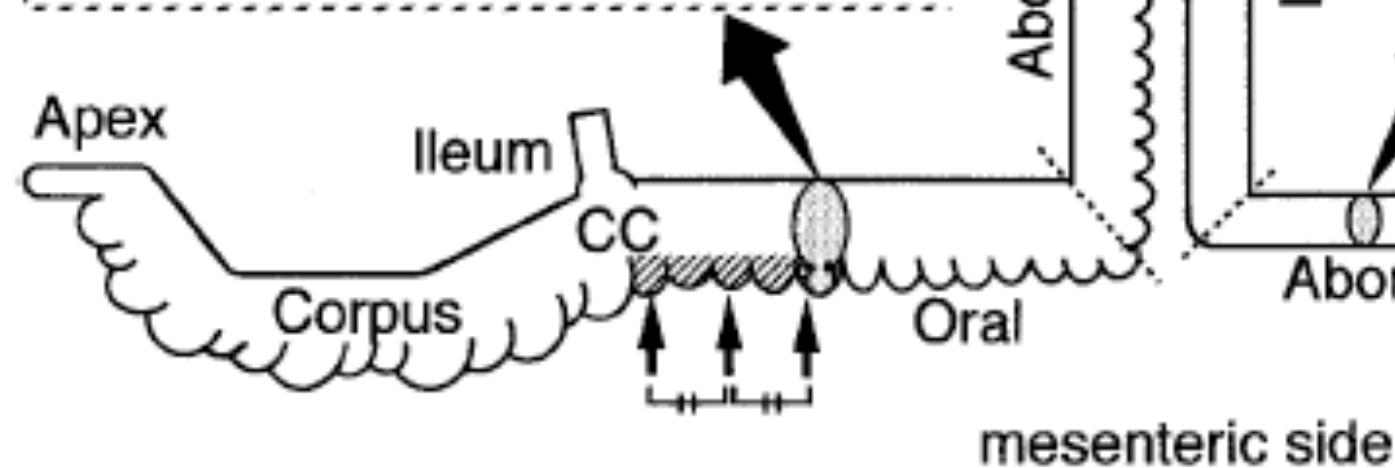
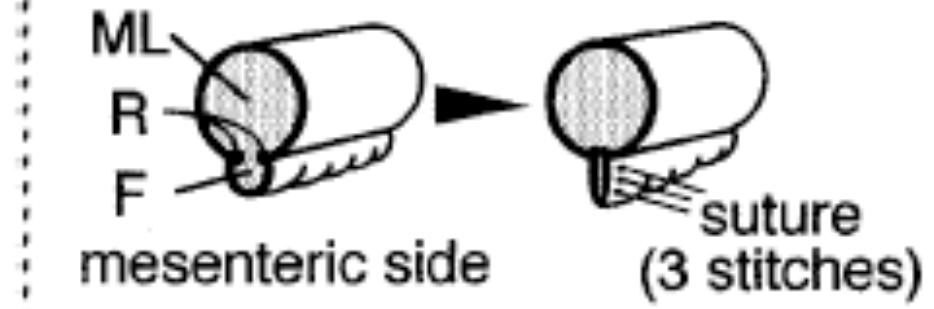


from Takahashi & Sakaguchi (1998)



# The colonic groove / furrow (*Myocastor coipus*)

## --- Expt 1. Closing the furrow ---

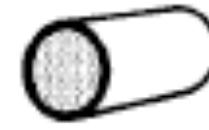


Parallel loop

Flexure

Aboral

Oral



Rectum

Aboral

Cecum      Proximal Colon      Distal Colon

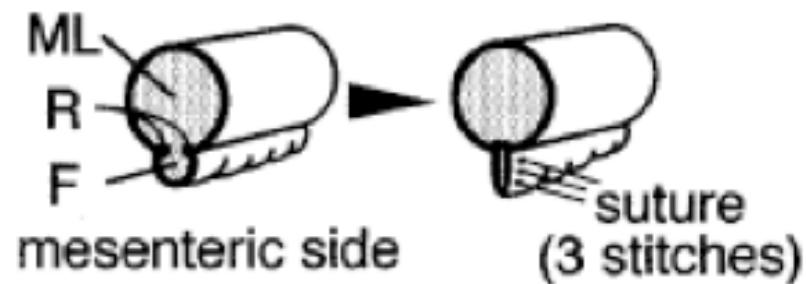
from Takahashi & Sakaguchi (2000)



## The colonic groove / furrow (*Myocastor coipus*)



	Intact (n = 5)		Sutured (n = 3)		Sham (n = 3)	
	Soft	Hard	Soft	Hard	Soft	Hard
N	30.6 <sup>a</sup>	21.4 <sup>b</sup>	25.2 <sup>b</sup>	24.3 <sup>b</sup>	38.8 <sup>a</sup>	25.4 <sup>b</sup>
TAA	150.8 <sup>a</sup>	76.9 <sup>b</sup>	109.7 <sup>b</sup>	104.8 <sup>b</sup>	148.0 <sup>a</sup>	76.4 <sup>b</sup>
DAP	0.92 <sup>a</sup>	0.62 <sup>a,b</sup>	0.80 <sup>a</sup>	0.74 <sup>a</sup>	1.03 <sup>a</sup>	0.58 <sup>b</sup>

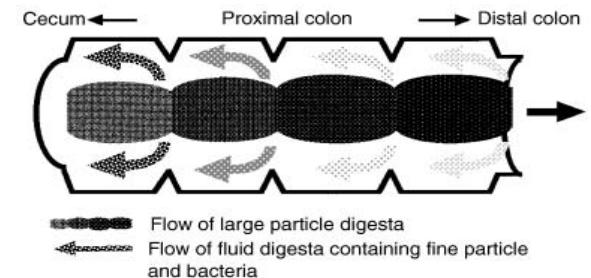


from Takahashi & Sakaguchi (2000)

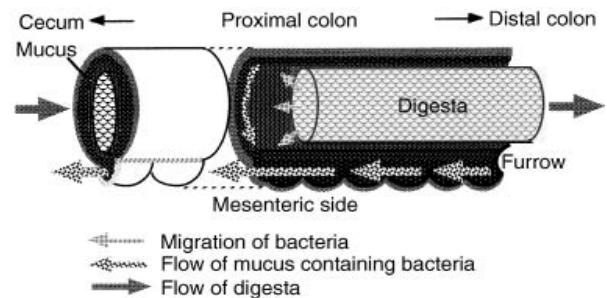


# Sorting of ingesta for caecotroph formation

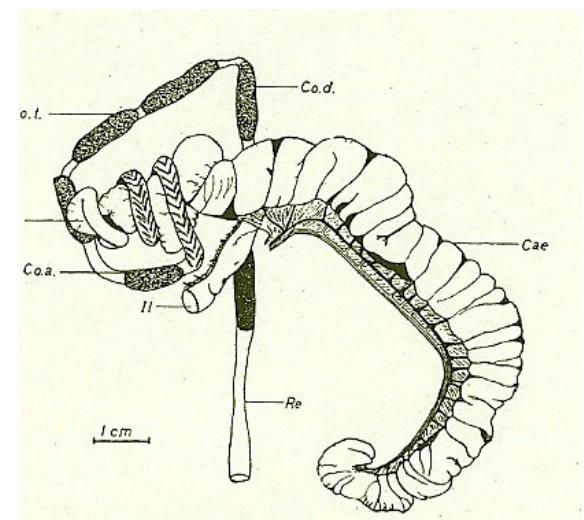
**Wash back** mechanism  
(Lagomorphs)



**Mucus trap** mechanism  
(Hystricomorph rodents)



**Mucus trap** mechanism ?  
(Myomorph rodents)

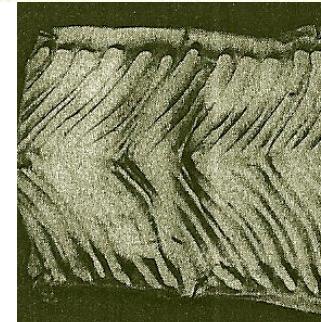
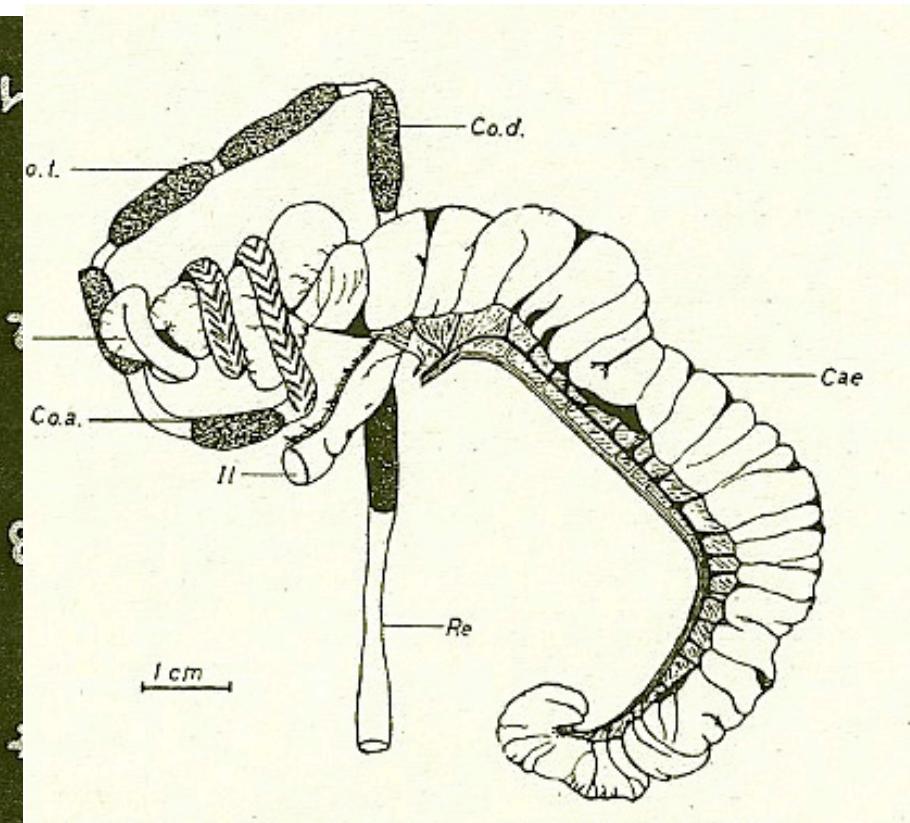


from Sakaguchi (2003) & Behmann (1972)



# Sorting of ingesta for caecotroph formation

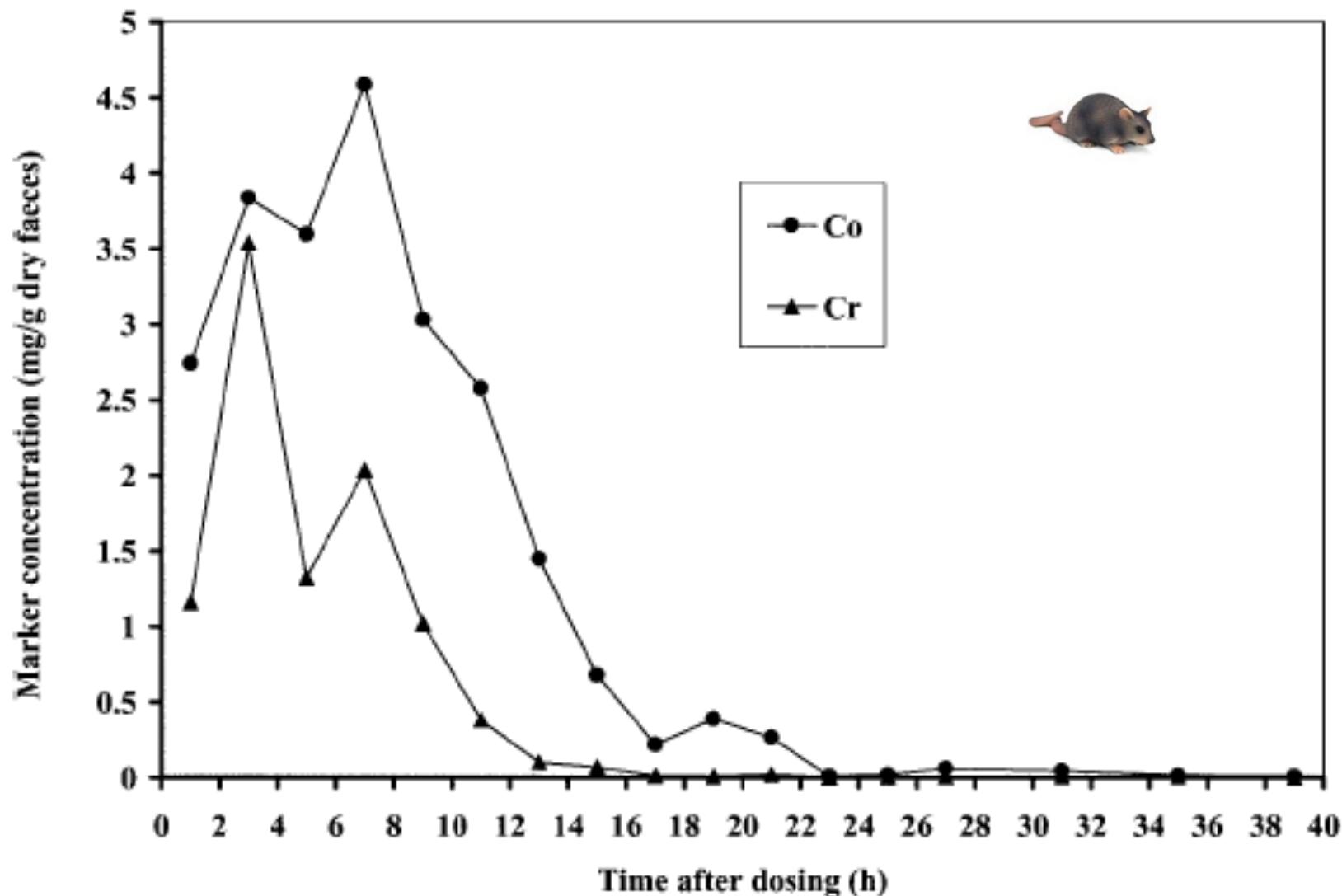
**Mucus trap** mechanism ?  
(Myomorph rodents)



from Behmann (1972)



# Coprophagy and ingesta passage patterns

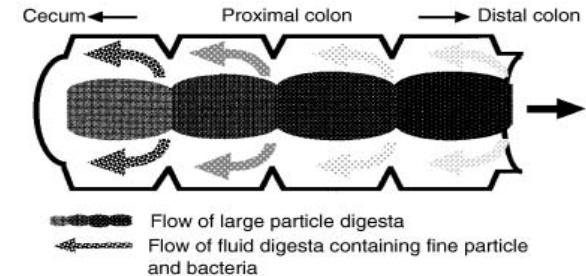
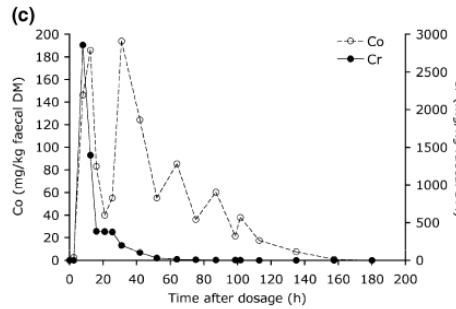


from Pei et al. (2001)

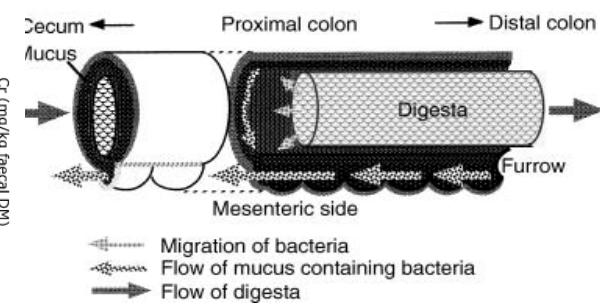
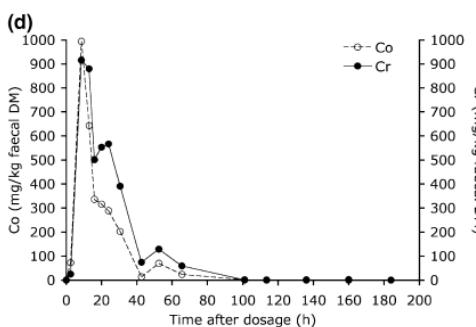


# Sorting of ingesta for caecotroph formation

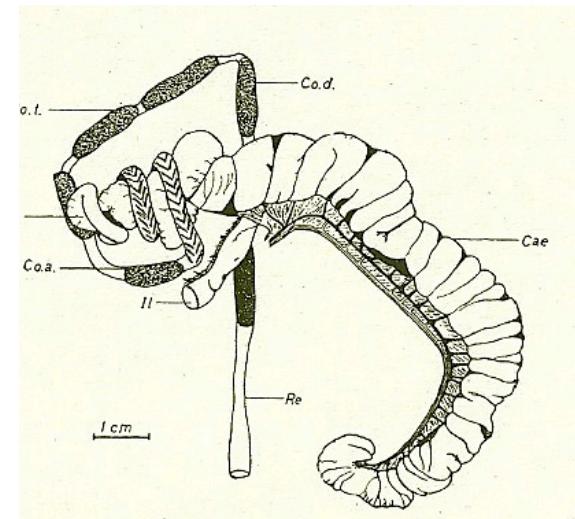
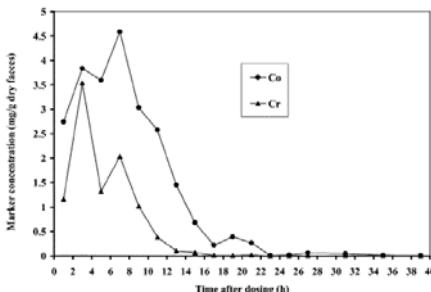
**Wash back mechanism**  
(Lagomorphs)



**Mucus trap mechanism**  
(Hystricomorph rodents)



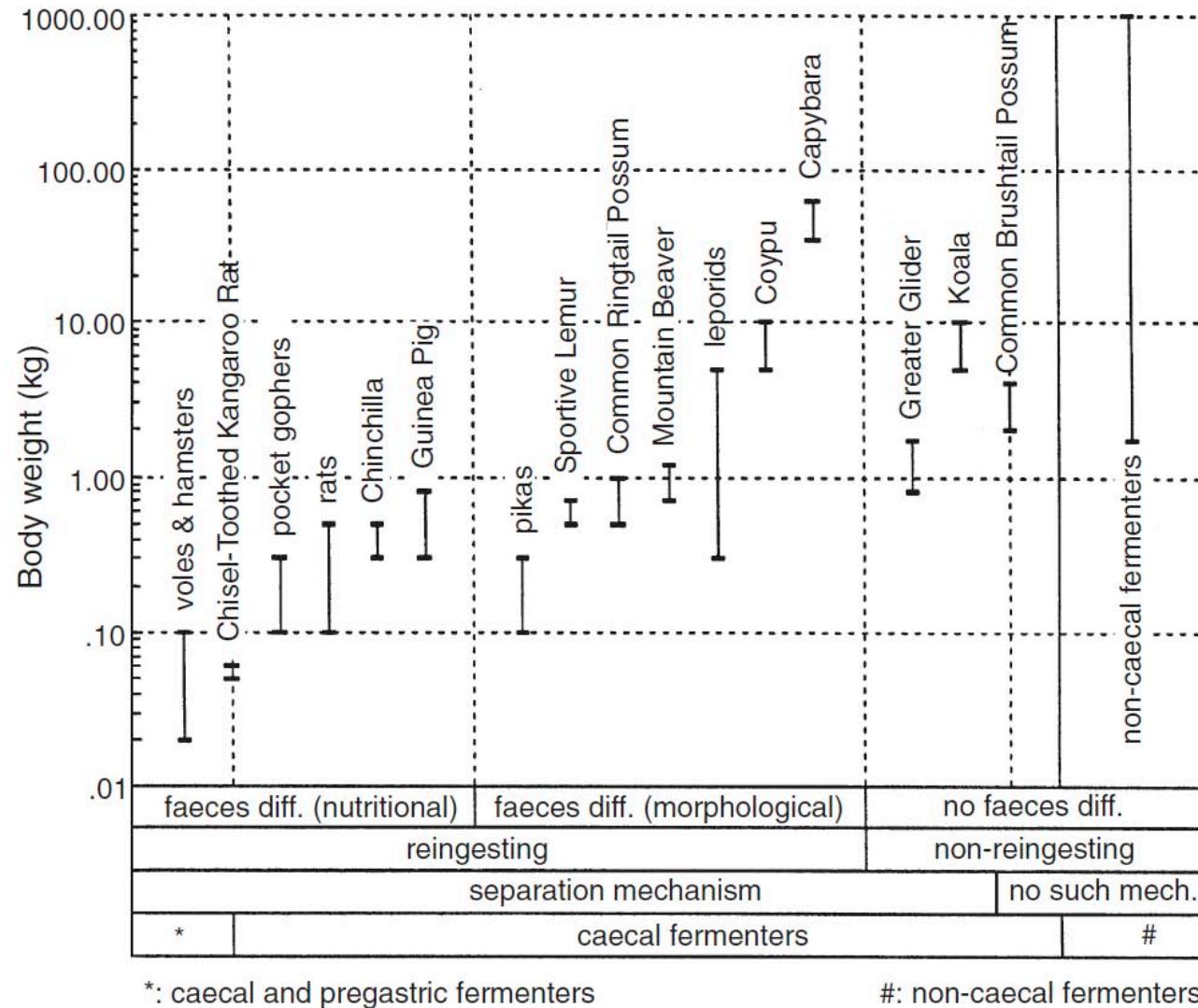
**Mucus trap mechanism ?**  
(Myomorph rodents)



from Sakaguchi (2003) & Behmann (1972)



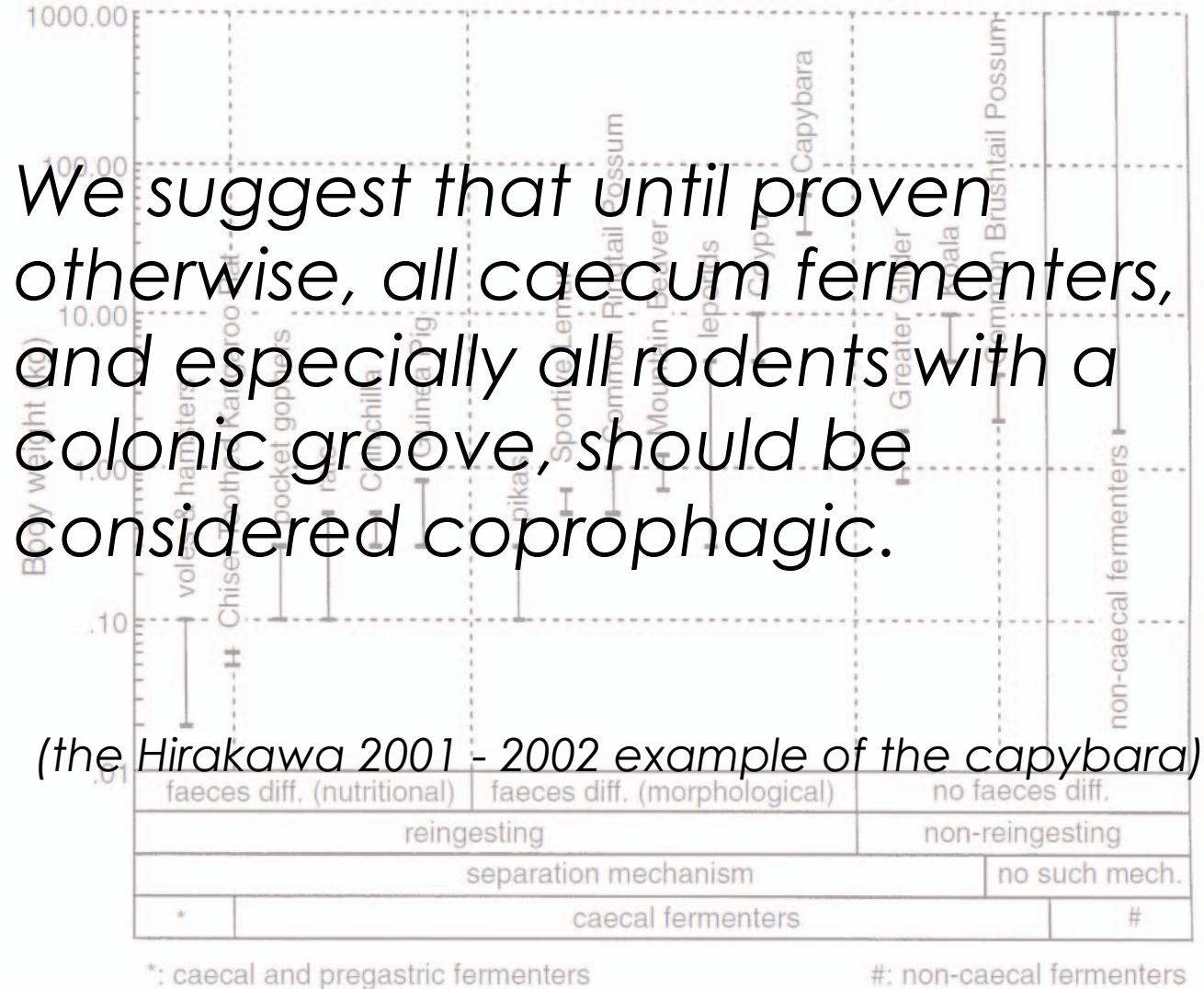
# Who practices coprophagy?



from Hirakawa (2002)



# Who practices coprophagy?



from Hirakawa (2002), Clauss et al. (2007)



# Coprophagy / Trophallaxis



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

