

Particularidades da Digestão em Ruminantes

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Factores determinantes do processo digestivo nos ruminantes

- Papel central da digestão microbiana e localização das câmaras fermentativas
 - Implicações anatómicas
 - Implicações no transito digestivo
 - Implicações na eficiência e estratégias digestiva
 - Implicações da localização pré- ou pós-gástrica das câmaras de fermentação

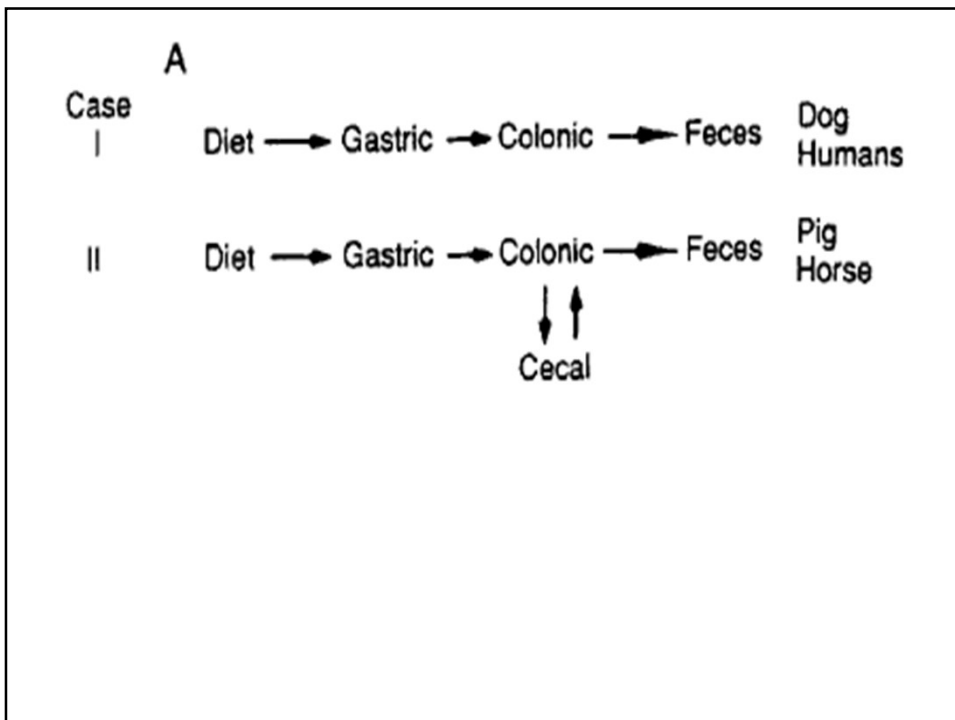
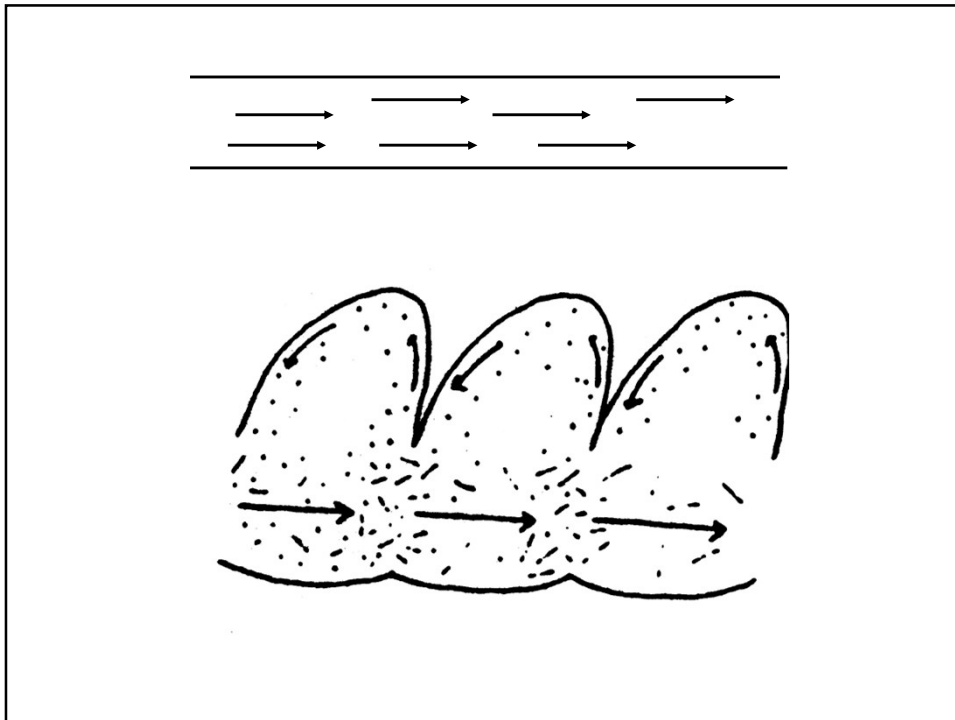
Table 3.2. Occurrence of enzymatic systems for degradation

Material	Aerobic		Anaerobic (microbial)	
	Bacterial and fungal	Animal (mammalian)	GI tract	Sludge or soil
Sugar	+	+	+	+
Starch	+	+	+	+
Cellulose	+	-	+	+
Lignin	+	-	-	+
Keratin protein	+	-	-	+
Fats	+	+	-	+
Fossil				
Oil	+	-	-	-
Coal	-	-	-	-

Table 5.1. Mammals classified by gastrointestinal anatomy

Class	Species	Dietary habit	
Pregastric fermenters			
Ruminants	Cattle, sheep	Grazing herbivores	
	Deer, antelope, camel	Selective herbivores, including folivores and frugivores	
Nonruminants	Colobine monkey	Selective herbivore	
	Hamster, vole	Selective herbivores	
	Kangaroo, hippopotamus	Grazing and selective herbivores	
	Hoatzin	Folivore	
Hindgut fermenters			
Cecal digesters	Capybara	Grazer	
	Rabbit (lemming)	Selective herbivores	
	Rat, mice	Omnivores	
Colonic digesters	Sacculated	Elephant, horse, zebra	Grazers
		New World monkeys	Folivores
	Pig, human	Omnivores	
	Unsacculated	Panda	Herbivore
		Dog, cat	Carnivore

Sources: Parra, 1978; Hume, 1982; C. E. Stevens, 1988.



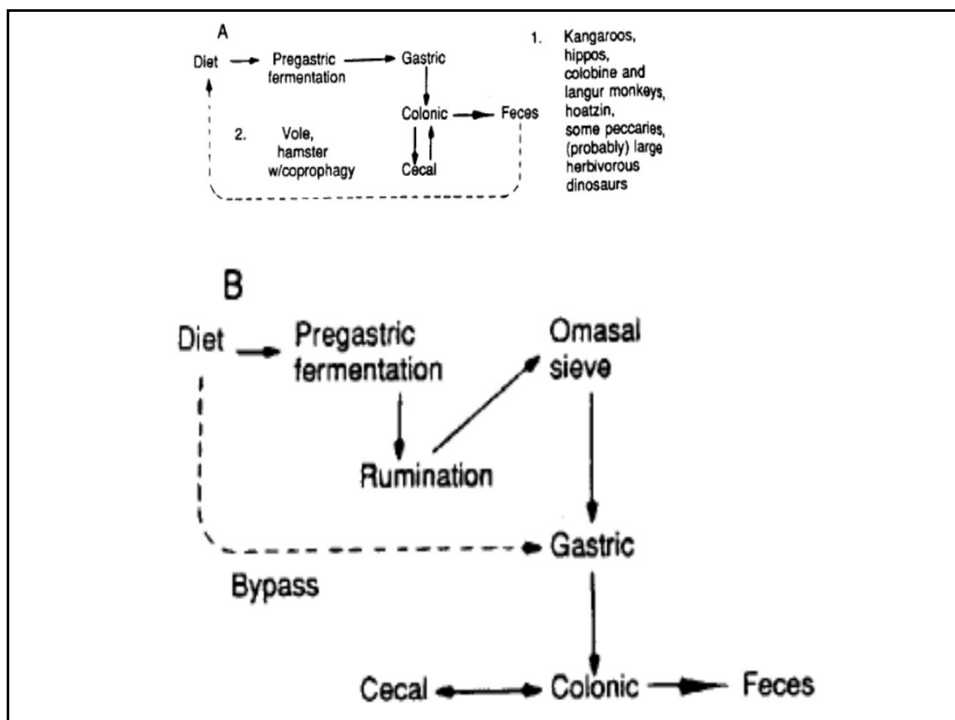
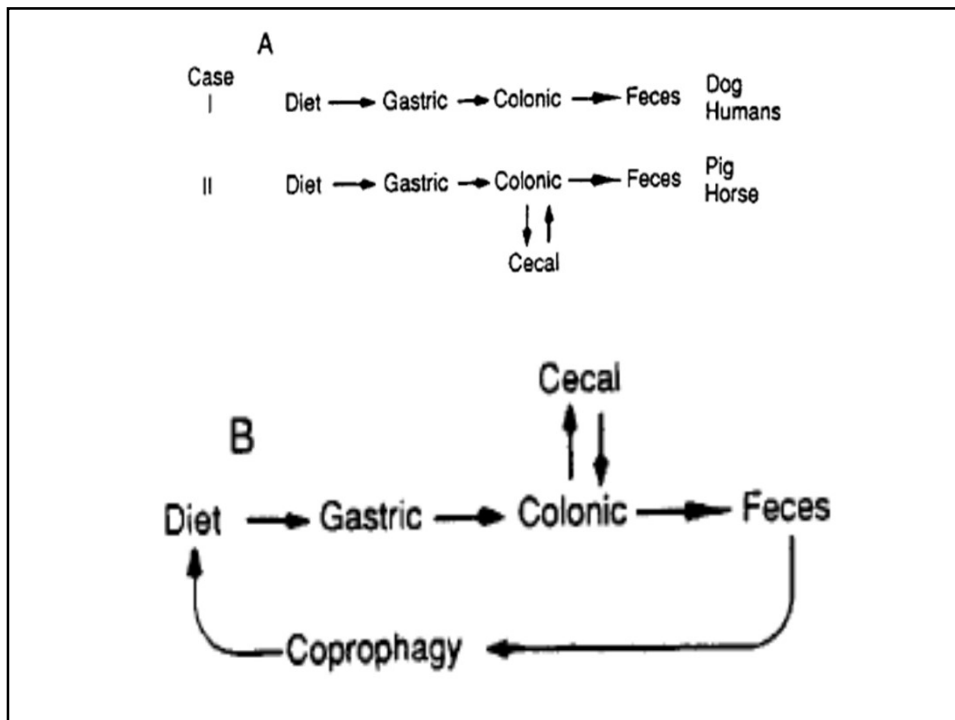


Table 5.3. Fermentative capacity expressed as percentage of the total digestive tract for mammal species

Species	Reticulorumen (%)	Cecum (%)	Colon and rectum (%)	Total fermentative capacity (%)
Sheep	71	8	4	83
Capybara	—	71	9	80
Cattle	64	5	5-8	75
Horse	—	15	54	69
Guinea pig	—	46	20	66
Rat	—	32	29	61
Rabbit	—	43	8	51
Pig	—	15	33	48
Human	—	—	17	17
Cat	—	—	16	16
Dog	—	1	13	14

Source: Parra, 1978.

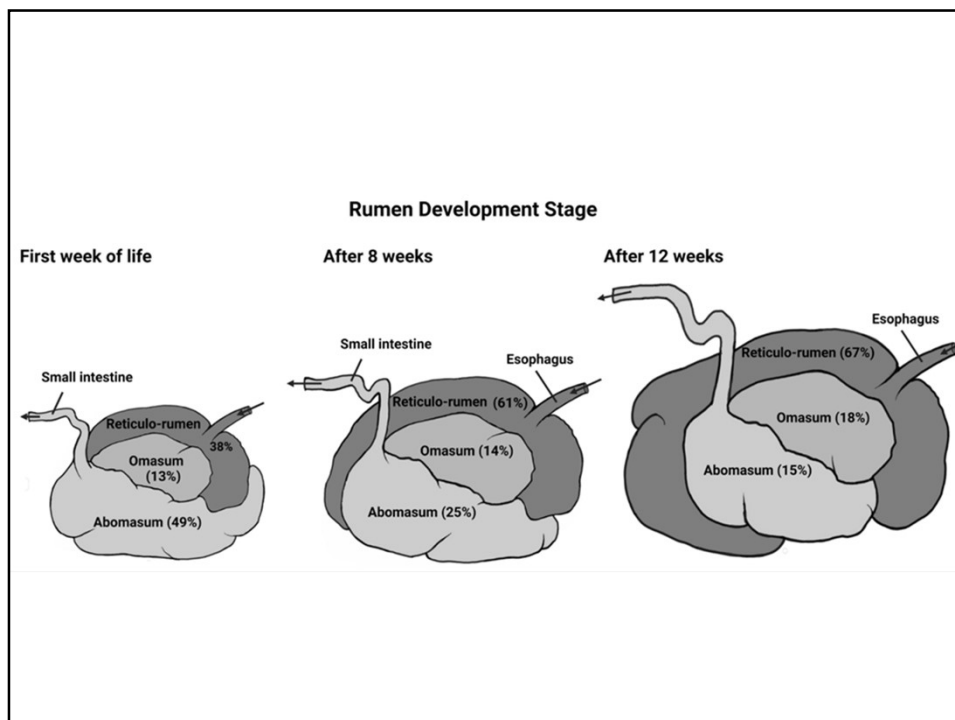


Table 17.7. Sites of disappearance of digestible cellulose and hemicellulose

Site	Species	Diet	Cellulose	Hemicellulose	Reference
Rumen-abomasum	Sheep	Restricted to grass	93	86	Beever et al., 1972
Small intestine			2	0	
Cecum + colon			5	14	
Rumen-abomasum	Sheep	Ad lib hay	93	83	Beever et al., 1972
Small intestine			2	8	
Cecum + colon			5	9	
Rumen-abomasum	Sheep	Pelleted	80	71	Beever et al., 1972
Small intestine			2	5	
Cecum + colon			18	24	
Postrumen	Cattle	Restricted alfalfa	9	34	Waldo, 1970
Postrumen		Ad lib alfalfa	10	31	
Postrumen	Sheep	Alfalfa	10	20 ^a	Hogan and Weston, 1967
Postrumen		Ground alfalfa	10	33 ^a	
Postrumen		Wheaten hay	10	0 ^a	
Postrumen		Ground wheaten hay	31	41 ^a	

Note: Values are percentages of total disappearance.

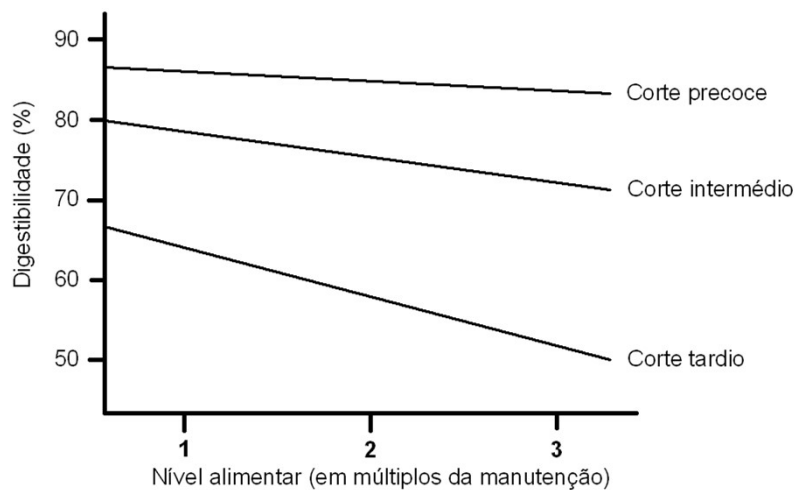
^aCalculated from original cell wall values.

Table 5.7. Comparative passage rates of liquid and particles

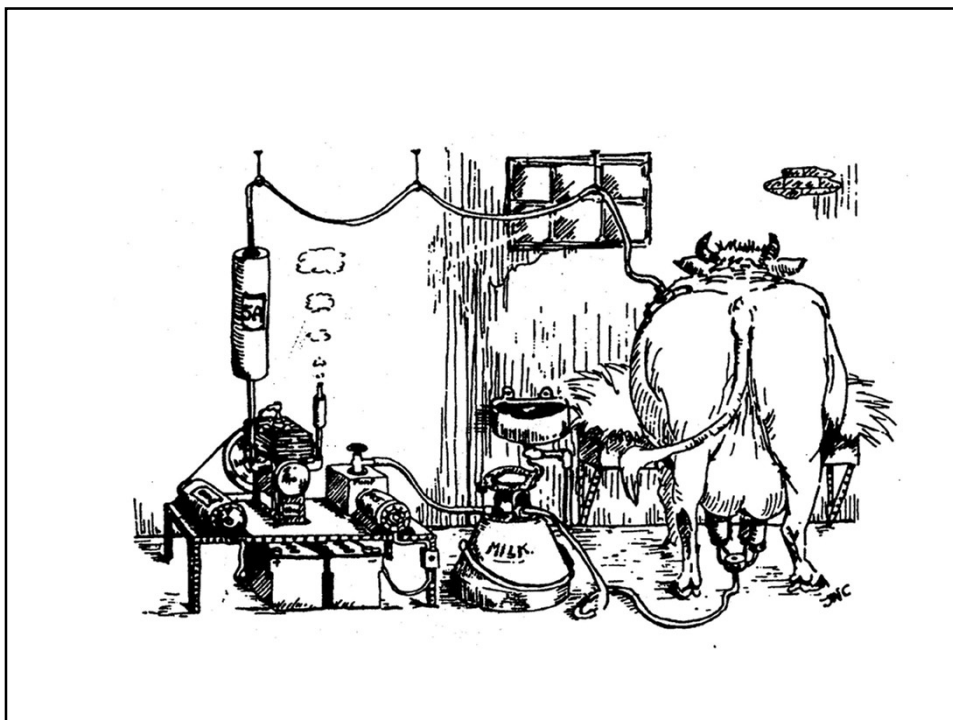
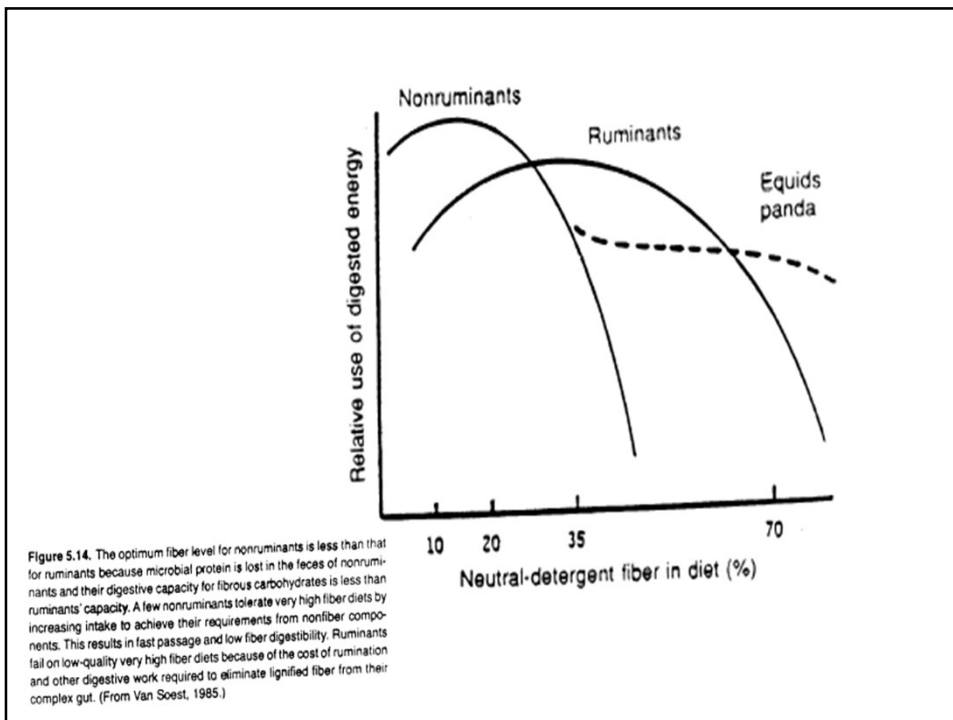
Species	Body weight (kg)	Whole tract retention ^a		Retention in fermentation compartments	
		Particles ^c (h)	Liquid (h)	Particles (h)	Liquid (h)
Ruminants					
Large heifers	555	79	29	47	15
Small heifers	243	62	30	38	16
Sheep	30	70	38	35	19
Goats	29	52	39	28	19
Nonruminants					
Horses	388	29	29	10	11
Ponies	132	34	26	10	9
Human	70	41	39	12	12
Rabbit	3	9	193 ^d	4	180 ^e

Table 15.3. Effects of alfalfa hay particle size on retention time and fiber digestibility

Feed	Mean size (μm)	5% transit (h)	Retention 80 – 5 (h) ^a	Fiber digestibility (%)
Long hay	—	22	54	44
Coarse grind	434	16	39	34
Medium grind	393	16	44	31
Finely ground	280	13	27	22



Efeito do nível de ingestão alimentar em ovinos na digestibilidade de azevém cortado em diversas fase do seu desenvolvimento (Demarquilly e Jarrige, 1981).



Hospedeiro condiciona o ecossistema ruminal:

- Ingestão de alimento (intermitente)
- Fluxo e diluição (saliva, ingestão de água, parede ruminal, passagem)
- Ruminação e movimentos ruminais
- Temperatura, pH, potencial redox
- Imunidade ou outras forma de controlo da micropopulação ?!!

Componentes presentes no rúmen:

- Partículas alimentares
- População microbiana
- Material endógeno
- Produtos finais da fermentação

Simbiose hospedeiro aeróbio e comunidade microbiana ruminal anaeróbia

Vantagens para o hospedeiro:

- possibilidade de aproveitar abundantes recursos alimentares celulósicos obtendo :
 - AGV (fontes de energia em aerobiose e esqueletos carbonados)
 - Biomassa microbiana (proteína, lípidos e vitaminas)

Vantagens para a comunidade microbiana ruminal:

- habitat sustentável no tempo com:
 - Ambiente aquoso com dinâmica suficiente para promover a mistura mas permitindo o tempo necessário para a celulólise.
 - Abastecimento regular de água e de substrato (alimento) já sujeito a maceração mecânica.
 - Eliminação de produtos finais do seu metabolismo.
 - Condições ambientais estáveis (pH, temperatura, potencial redox e pressão osmótica).

Ecossistema retículo-ruminal

Condições ambientais

- Anaerobiose
- Excesso de H (pressão redutora)
- Temperatura (38 a 40°C)
- pH
- Pressão osmótica
- Taxas de passagem da fase líquida e sólida
- Substratos disponíveis
- Inúmeros nichos especializados

Alguns dados sobre o ecossistema retículo-ruminal	Retículo-Rumen	
	Ovinos	Bovinos
Volume, L	7 (5-10)	70 (40-100)
Fluxo, L/d		
Saliva	10 (8-16)	120 (60-160)
Água (bebida)	2 (1-3)	35 (20-40)
Água (alimentos)	2,5 (2-3)	4,5 (3,-5,5)
Concentrações		
MS (g/l)	60 (50-100)	
Bactérias (nº/ml)	10 ¹⁰ - 10 ¹¹	
Protozoários	10 ⁵ - 10 ⁶	
Propriedades		
PH	7 (5,0 - 7,5)	
Eh (mv)	-350 (-200 - -400)	
Pressão osmótica (mosmol)	250 - 350	

Teores em Vitaminas na Dieta e Rúmen

	Dieta	Rúmen
Tiamina	2- 18	3 - 29
Riboflavina	5- 27	7 - 37
Niacina	11- 91	46 - 233
Pantothenic	23- 42	17 - 56
Biotina	0,04 - 0,47	0,13 - 1,16
B ₁₂	Residual	1,1 - 3,0

Ecossistema Retículo-ruminal

A Summary of the Relationships Between the Microorganisms and the Host Animal

Process	Outcome
Salivary output	Dilution and flow Buffering action Steady supply of nitrogen
Rumination	Breakdown of food Aeration? Increased salivation?
Rumen movement	Mixing of contents Emptying Sequestration
Gas production	Eructation Surface tension effects Absorption
Absorption through wall	Removal of end products Maintenance of pH Maintenance of temperature

Secreção Salivar e Sua Função

Funções:

- Humedecimento e lubrificação dos alimentos
- Constitui 70 a 90 % dos líquidos contidos no rúmen
- Neutralização da acidez provocada pela produção de ácidos orgânicos
- Manter o pH entre 5,8 e 7
- Possui substâncias anti-espumantes
- Neutralização de taninos
- Reciclagem de N (ureia)

Secreção Salivar e Sua Função

Table 15.6. Effect of ration on saliva production and eating rate

Feed	Eating rate (g food/min)	Salivary production	
		(ml/min)	(ml/g food)
Pelleted ration	357	243	0.68
Fresh grass	283	266	0.94
Silage	248	280	1.13
Dried grass	83	270	3.25
Hay	70	254	3.63

Source: C. B. Bailey, 1958.

Tamponamento

Reticulo-ruminal

Table 15.7. Factors contributing to rumen buffering

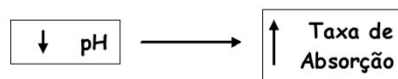
	Promoted by	Buffer source
Washout (passage)	Osmotic pressure Feed intake	Dilution
Absorption	VFA concentration	Removal of free acid
Saliva	Coarse fiber and rumination	Bicarbonate Phosphate
Fiber	Cation exchange	Neutralization
Mineral salts of plant organic acids	Forage composition	Fermenting of plant acids to CO ₂
Protein	NH ₃ production	Neutralization
Microbial efficiency	Microbial growth	Diversión of carbon to cells instead of acids

Absorção da mucosa retículo-ruminal

Absorção de AGV

A maioria dos AGV é absorvida no retículo-rúmen

pH 6 - 7 , 95 % dos AGV estão sob a forma ionizada



- Difusão simples das formas não ionizadas
- Difusão facilitada das formas ionizadas

Metabolismo dos AGV no epitélio ruminal

Acetato (C2)

→ pouco metabolizado no ep. ruminal (1 a 30%)

Propionato (C3)

→ pouco metabolizado no ep. ruminal (5 a 30%)

→ convertido a lactato

Butirato (C4)

→ extensa metabolização (90%)

→ conversão a acetoacetato, β -hidroxibutirato

Absorção através da mucosa retículo-ruminal

Absorção de ácidos gordos cadeia média e longa

- Até C10 são absorvidos
- A partir de C12 já não são absorvidos

Ácidos gordos voláteis (AGV)

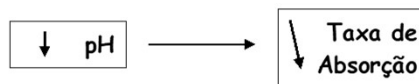
	Peso molecular	pKa	E.B. (kcal/mol)	Concentrações molares		
				Concen- trado	Fornagem	Mista
C2	60,05	4,75	209,4	55	70	65
C3	74,08	4.87	367,2	25	15	20
C4	88,10	4.81	524,3	15	10	10

Absorção através da mucosa retículo-ruminal

Absorção de Amónia

Base fraca com pKa = 9

pH 6 - 7 , 99 % da amónia está sob a forma ionizada



Difusão simples da forma não ionizada

Absorção através da mucosa retículo-ruminal

Absorção de Amino ácido e peptideos

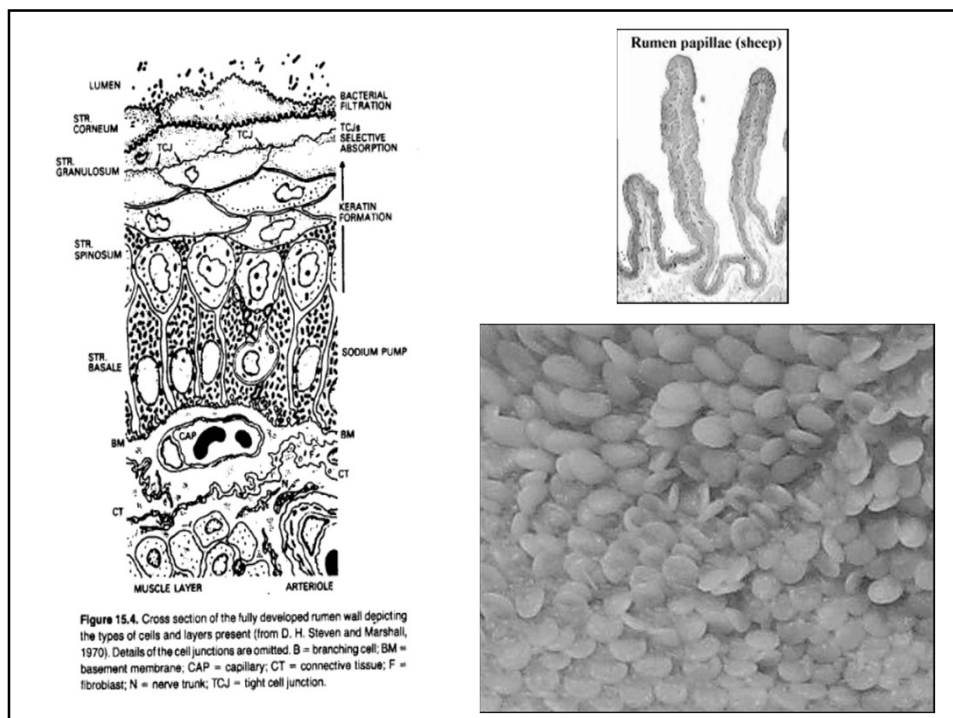
- AA - pouco expressiva (baixas concentrações ruminais)
- Peptideos - alguma

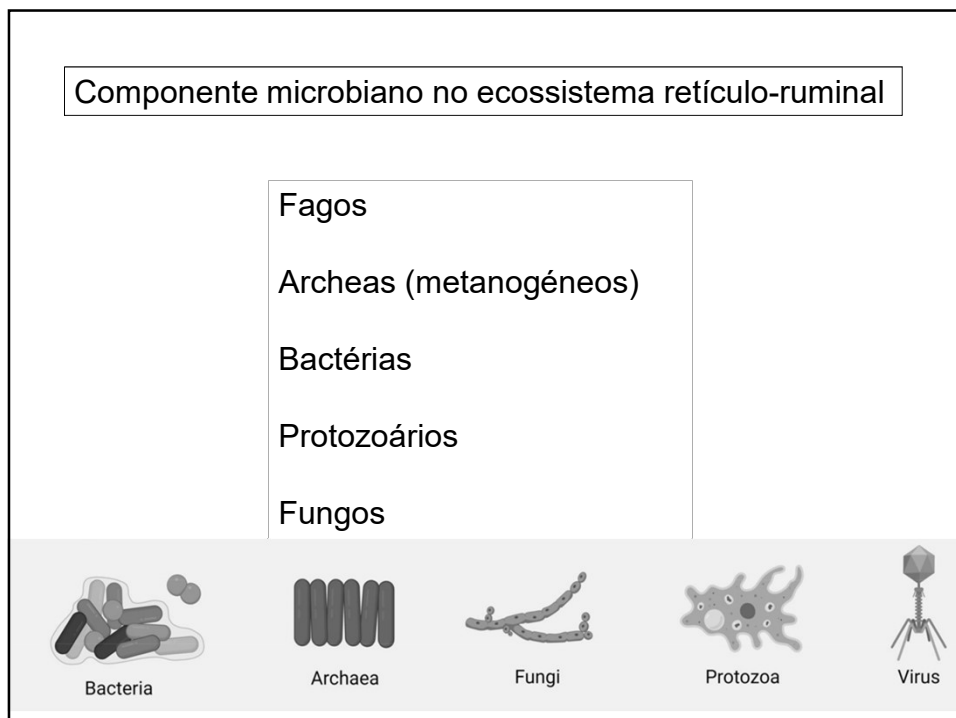
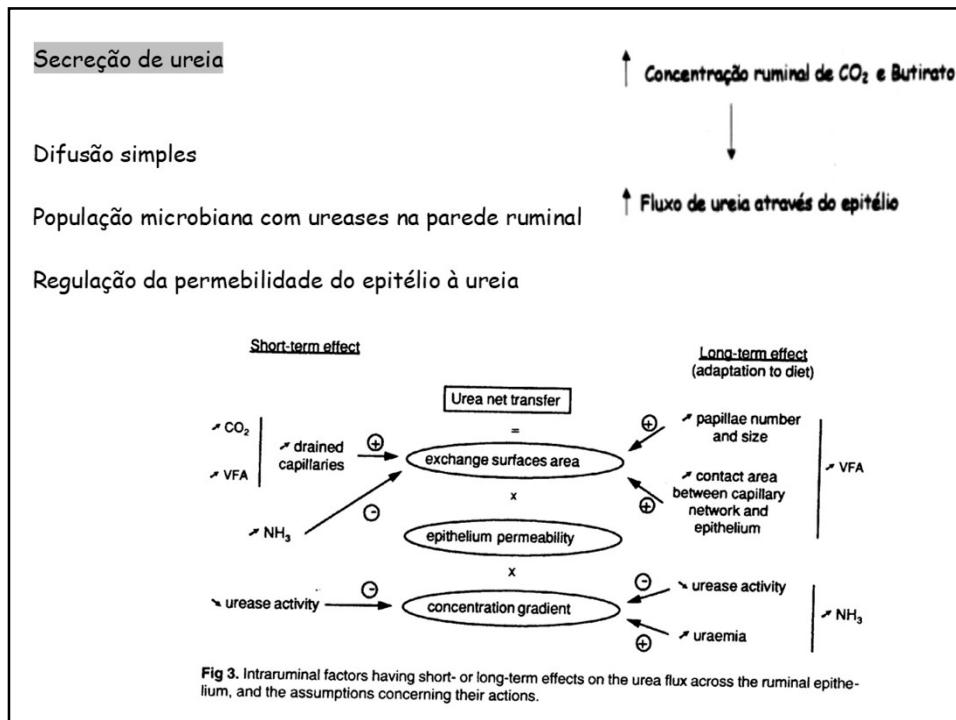
Absorção de vitaminas

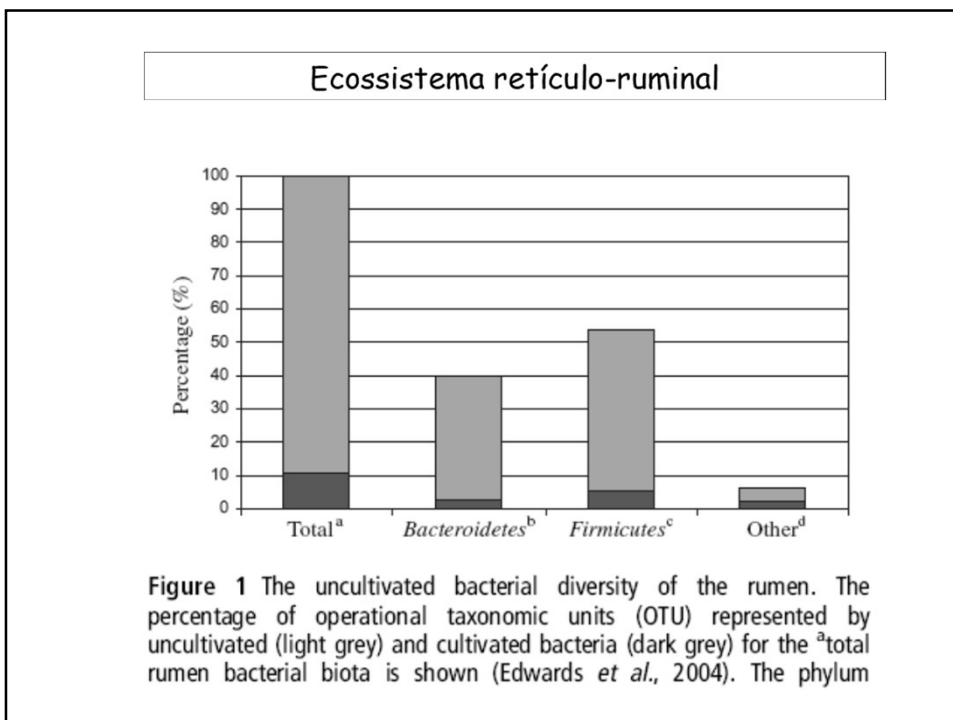
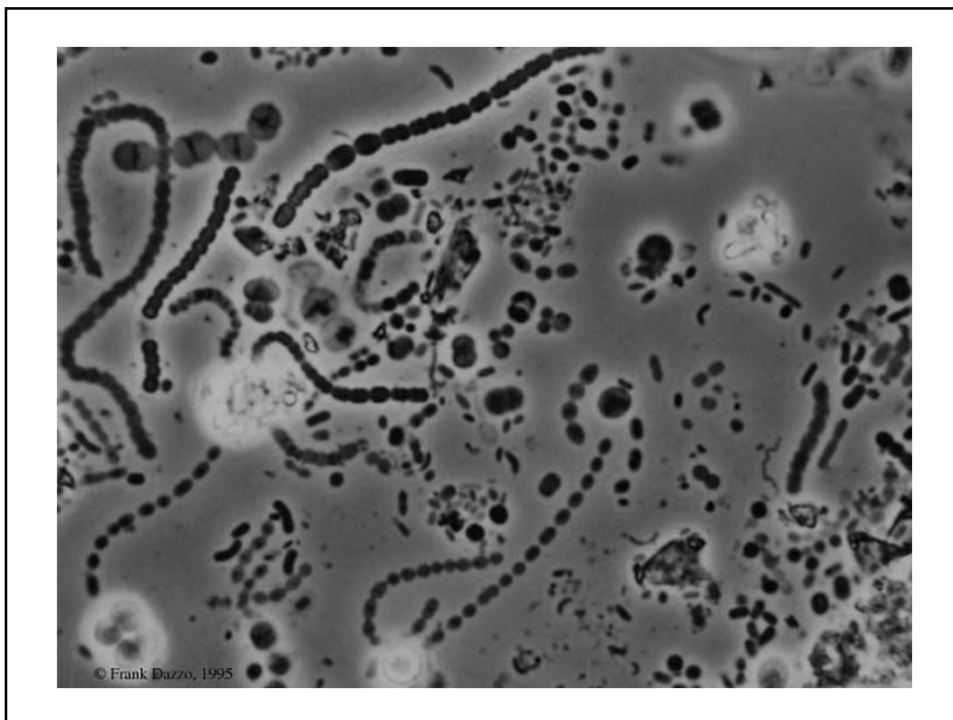
- Pouco expressiva

Absorção de Minerais

- 80% do magnésio é absorvido no rúmen
- Sódio, Cálcio, Enxofre







Examples of Relationships Between Rumen Microorganisms.

Based on various papers and review articles, e.g. El-Shazly *et al.*, 1961; Eadie, 1967; Coleman and Laurie, 1974a, b; Jarvis, 1968; Ball, 1969; Pittman and Bryant, 1964; Prins, 1977; Wolin, 1975; Czerkawski, 1978a

Competitive

1. Competition for nitrogen by starch and cellulose digesters.
2. Protozoal antagonisms (e.g. *ophryoscolex* and *epidinium*).
3. Ingestion of protozoa and bacteria by protozoa.
4. Attack of selected bacteria by bacteriophage (e.g. *Fibrisolvans* compared with *S. bovis*).
5. Fungal infection of some protozoa.

Beneficial (to one partner)

1. Utilization of breakdown products of fibre digestion by inhabitants of compartments 1 and 2 (Chapter 5).
2. Utilization of substances known to be produced, but not accumulating (e.g. succinate, formate, lactate).
3. Utilization of tetrapyrroles by microorganisms that possess cytochrome b, but cannot synthesize it.
4. Use of preformed glycolytic intermediates in synthesis (including acetate).
5. Use of branched-chain volatile fatty acids by cellulolytic microorganisms.
6. Use of amino acids and peptides released during fermentation and lysis.

Beneficial (to both partners)

1. Many scavenging reactions, in which the removal of products improves conditions.
2. Known couplets, particularly those that suffer from product inhibition.

Bactérias

- Livres (fase líquida)
- Aderentes às partículas (60 a 90 %)
- Aderentes às paredes ruminais
- Simbióticas com protozoários

Tabla 3.2: Principales bacterias ruminales degradan los polisacáridos de la pared celular.	
Polisacáridos pared celular	Espec
Celulosa	<i>Bacteroides succinogenes</i> <i>Ruminococcus flavefaciens</i> <i>Ruminococcus albus</i> <i>Butyrivibrio fibrisolvens</i> <i>Cillobacterium cellulosum</i> <i>Clostridium lochhea</i> <i>Cellulomonas fi</i> <i>Eubacterium sj</i>
Hemicelulosa	<i>Butyrivibrio fibrisolvens</i> <i>Ruminococcus flavefaciens</i> <i>Ruminococcus albus</i> <i>Bacteroides ruminans</i>
Sustancias péptidas	Todas las especies celulolíticas y hemicelulolíticas m <i>Lachnospira multiplex</i> <i>Streptococcus bo</i> <i>Succinivibrio dextrinosolvens</i>

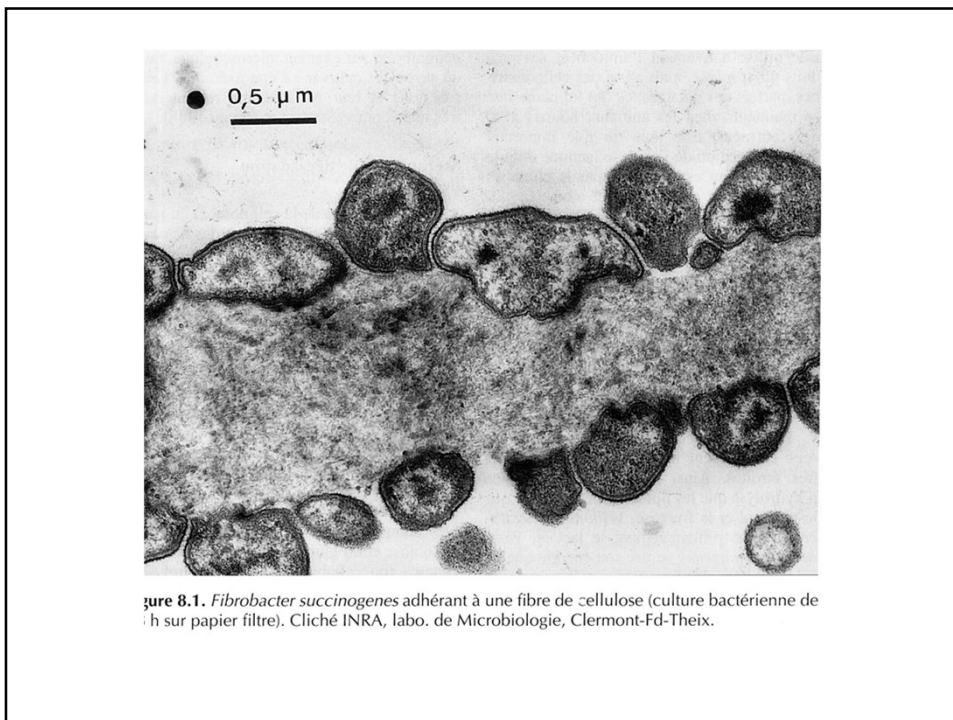
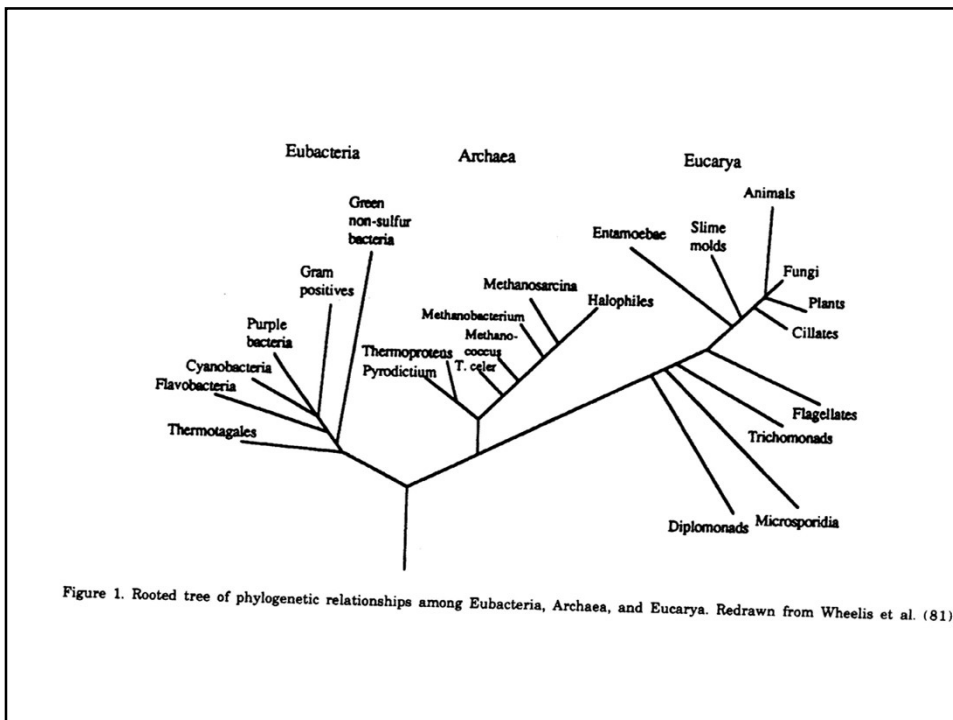
Fuente: Cheng et al (1984)

Table 7-1. Grouping of rumen bacterial species according to the type of substrates which are fermented.

- Major Cellulolytic Species
 - Bacteroides succinogenes*
 - Ruminococcus flavefaciens*
 - Ruminococcus albus*
 - Butyrivibrio fibrisolvens*
- Major Hemicellulolytic Species
 - Butyrivibrio fibrisolvens*
 - Bacteroides ruminicola*
 - Ruminococcus sp.*
- Major Pectinolytic Species
 - Butyrivibrio fibrisolvens*
 - Bacteroides ruminicola*
 - Lachnospira multiplex*
 - Succinivibrio dextrinosolvens*
 - Trigonema bryantii*
 - Streptococcus bovis*
- Major Amylolytic Species
 - Bacteroides amylophilus*
 - Streptococcus bovis*
 - Succinimonas amylolytica*
 - Bacteroides ruminicola*
- Major Ureolytic Species
 - Succinivibrio dextrinosolvens*
 - Selenomonas sp.*
 - Bacteroides ruminicola*
 - Ruminococcus bromii*
 - Butyrivibrio sp.*
 - Trigonema sp.*
- Major Methane Producing Species
 - Methanobrevibacter ruminantium*
 - Methanobacterium formicicum*
 - Methanomicrobium mobile*
- Major Sugar-Utilizing Species
 - Trigonema bryantii*
 - Lactobacillus vitulinus*
 - Lactobacillus ruminus*
- Major Acid-Utilizing Species
 - Megasphaera elsdenii*
 - Selenomonas ruminantium*
- Major Proteolytic Species
 - Bacteroides amylophilus*
 - Bacteroides ruminicola*
 - Butyrivibrio fibrisolvens*
 - Streptococcus bovis*
- Major Ammonia-Producing Species
 - Bacteroides ruminicola*
 - Megasphaera elsdenii*
 - Selenomonas ruminantium*
- Major Lipid-Utilizing Species
 - Anaerovibrio lipolytica*
 - Butyrivibrio fibrisolvens*
 - Trigonema bryantii*
 - Eubacterium sp.*
 - Fusocillus sp.*
 - Micrococcus sp.*

Género	Composición (%)	
	Material de pared celular vegetal	Líquido ruminal
<i>Butyrivibrio</i>	32	7
<i>Selenomonas</i>	14	10
Spirochaete		
sin nombre	8	0
<i>Lachnospira</i>	8	1
<i>Megasphaera</i>	0	11
<i>Streptococcus</i>	3	12
<i>Ruminococcus</i>	16	6
<i>Bacteroides</i>	11	38
Otras	8	15
Número total de cepas aisladas	368	292
Cantidad viable (cfu ml ⁻¹ x 10 ⁷)	230	201

Fuente: Phillips B y Latham MJ, datos sin publicar (citados por Cheng et al 1984)



**Micropopulação aderente ao epitélio
retículo-ruminal**



Figure 8.8. Bacilles adhérant à la muqueuse du rumen chez un jeune agneau (1 barre = 10 μ). Cliché INRA, labo. Microbiologie, Clermont-Fd-Theix.



Figure 8-1. Locations of microbes in the rumen with facultative anaerobes found near the epithelial cells of the rumen wall and anaerobes partially associated with plant cell walls, starch particles or floating free. From Cheng and Costerton (7).



© C.L. Davis, 1995

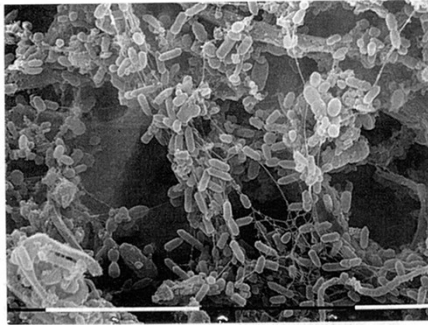


Figure 10.5. Bactéries fixées sur les parois cellulaires de pulpe de betterave (cliché E. Grenet)

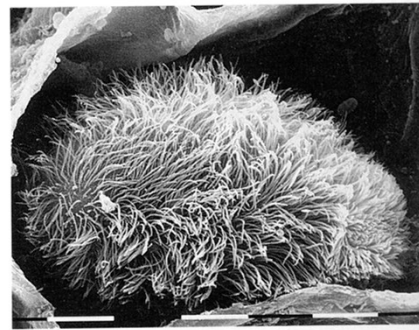


Figure 10.6. Protozoaire cilié (cliché E. Grenet).

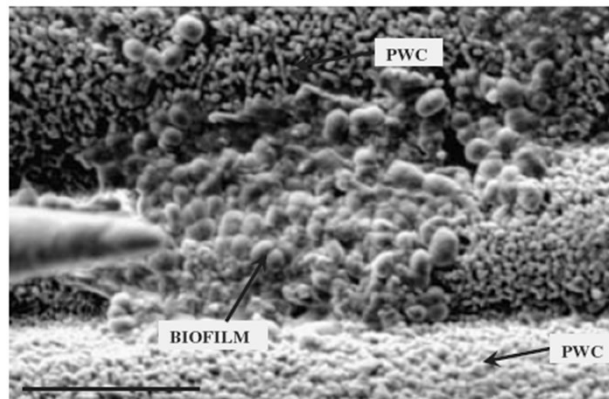


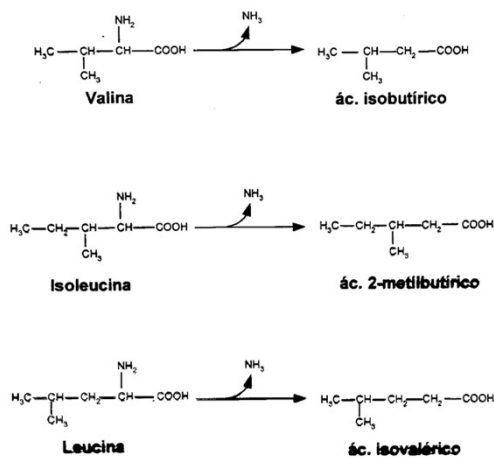
Figure 2 Microbial feed-associated biofilms. Scanning electron microscopy image of a biofilm community present on the adaxial surface of *Lolium perenne* following 2 h of incubation in the presence of rumen fluid and under *in vitro* conditions mimicking the rumen ecosystem (Mayorga *et al.*, 2007). The plant waxy cuticle (PWC) and the scale bar of 10 μm are also indicated on the image.

Bactérias Celulíticas (fibrolíticas):

(*Butyrivibrio fibrosolvens*, *Ruminococcus albus*, *R. flavefaciens*,
Bacteroides succinogenes, *B. ruminicola*)

- Anaeróbias estrictas
- Extremamente sensíveis a pH abaixo de 6
- Necessitam de AGV ramificados para crescer
- Baixas taxas de crescimento
- Aderência às partículas
- Enzimas (glucanases extracelulares: xilanases, celulases,)

Necessidades em AGV ramificados da bactérias celulíticas



Bactérias Amilolíticas e utilizadoras de açúcares

(*Streptococcus bovis*, *Succinimonas amylolytica*, *Bacteroides amylophilus*, *Lactobacillus* spp)

- Mais resistentes ao baixos pH
- Crescimento mais rápido
- Amilase extracelulares

Bactérias Utilizadoras de ácidos intermédios (lactato, succionato, valerato, formato, etc)

(*Megasphaera elsdenii*, *Selenomonas ruminatium*)

Metanogénese no rúmen

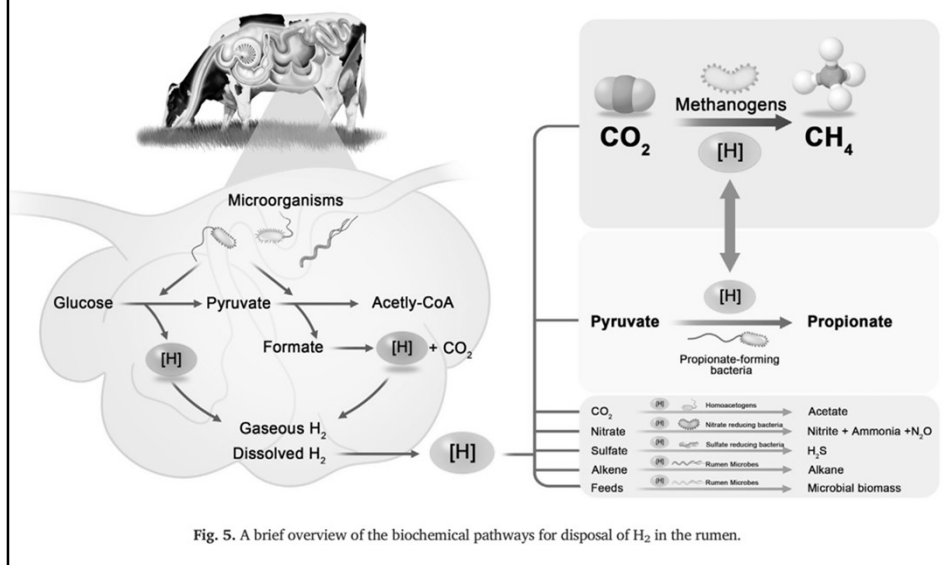
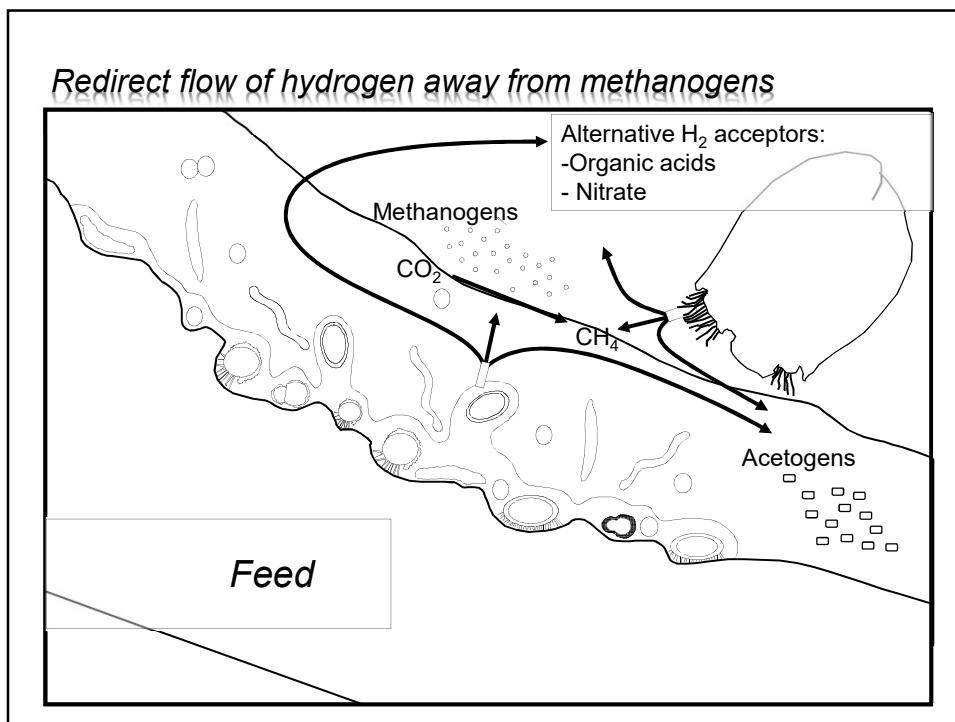
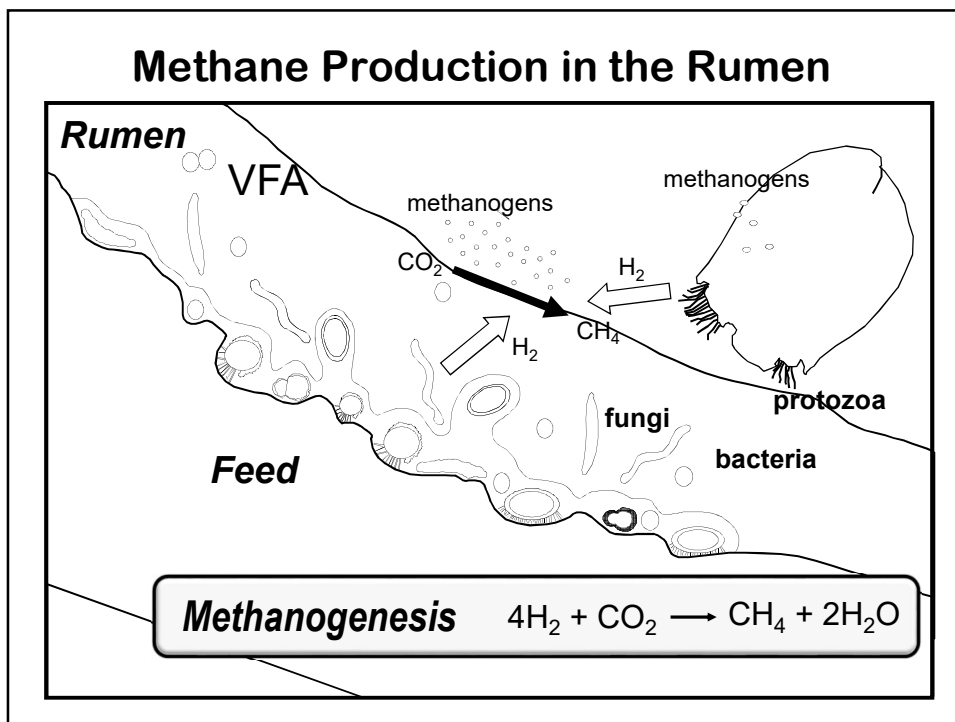
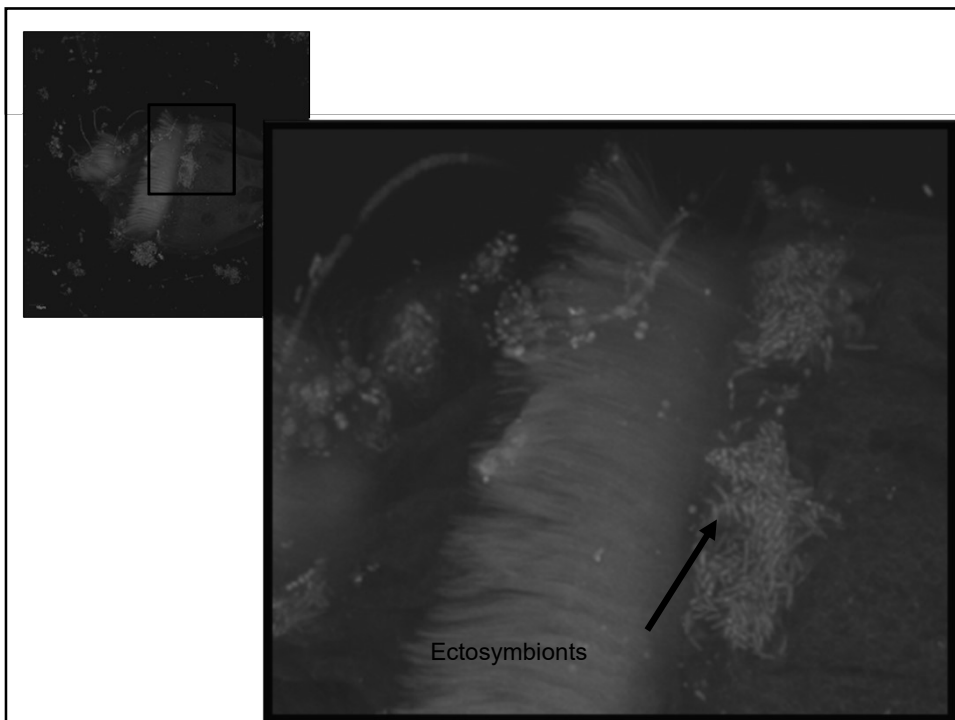
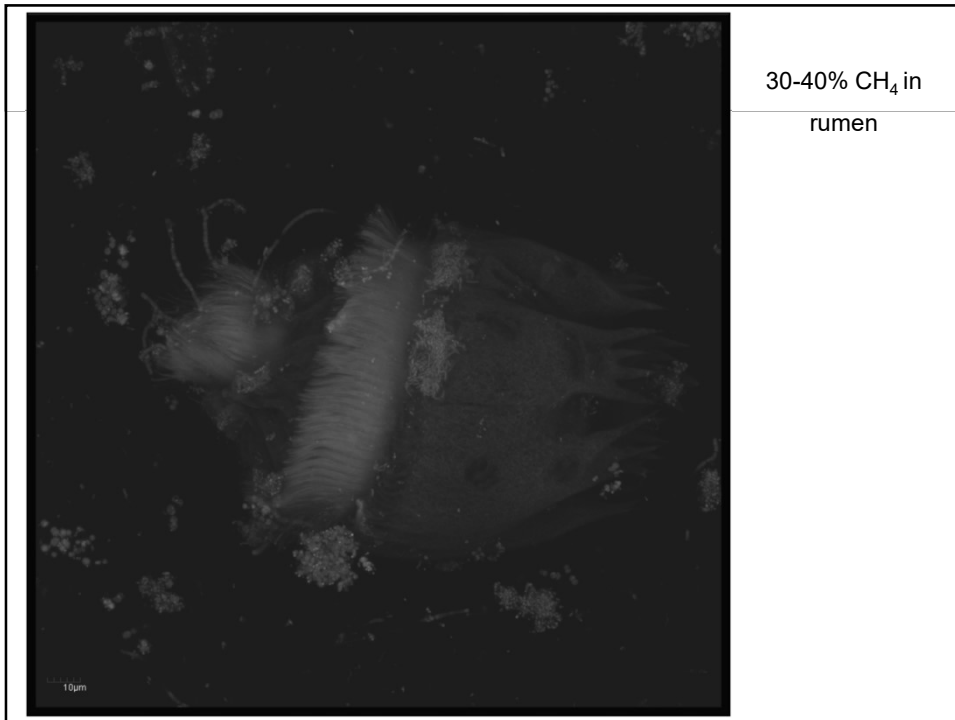
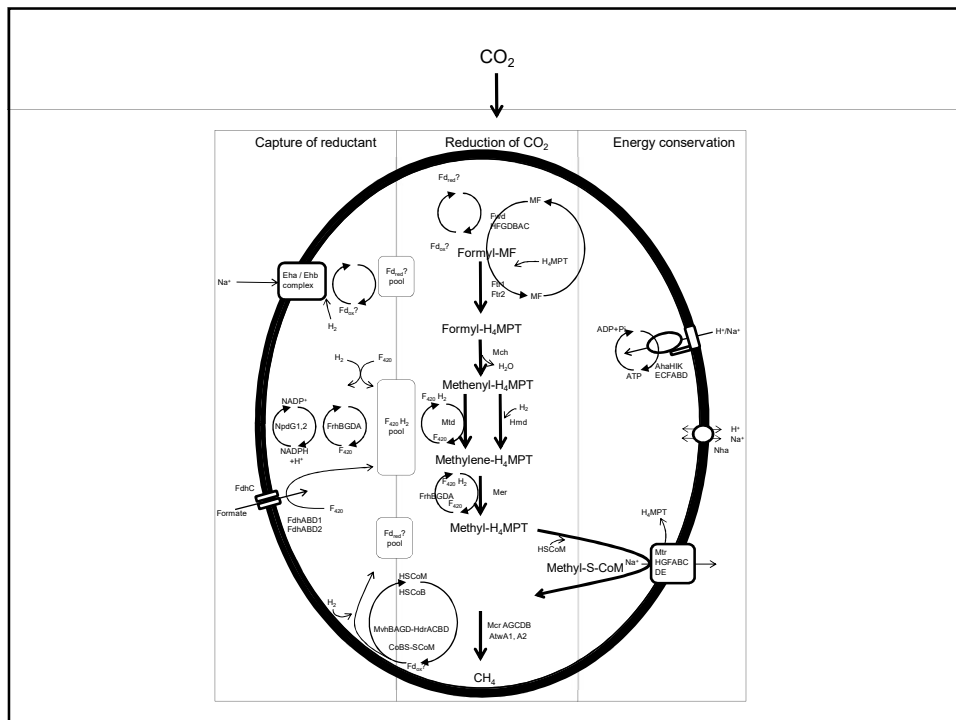
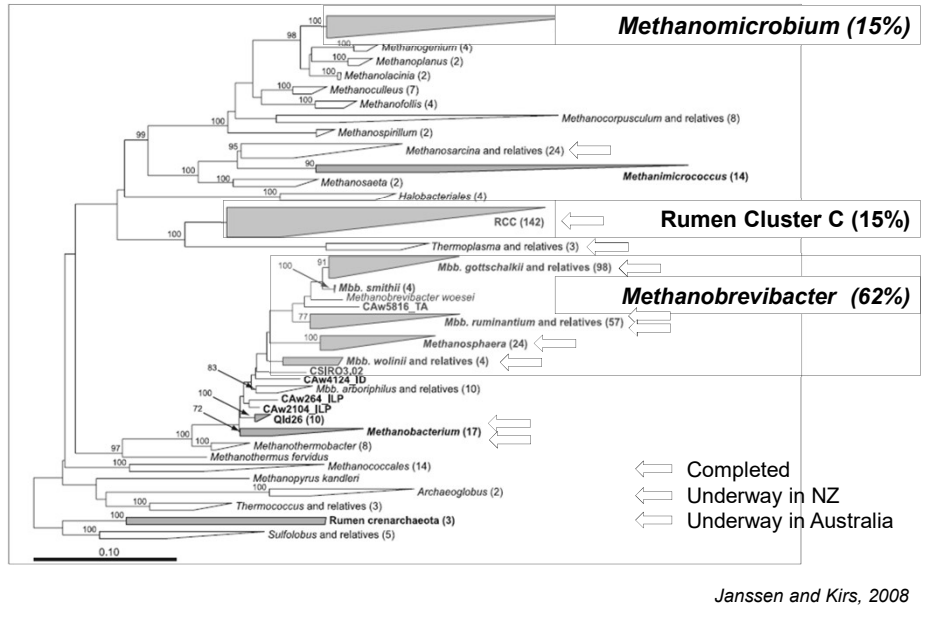


Fig. 5. A brief overview of the biochemical pathways for disposal of H₂ in the rumen.

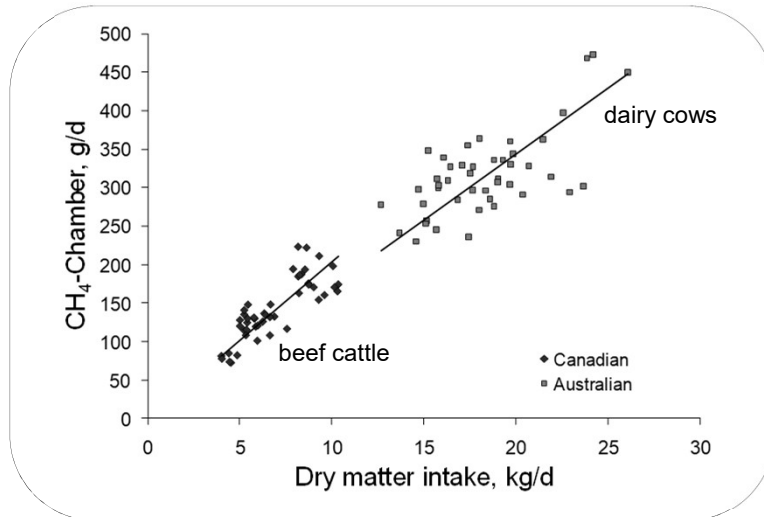




Rumen methanogen diversity



Methane Emission and Dry Matter Intake



Grainger et al. 2007. J. Dairy Sci. 90:2755.

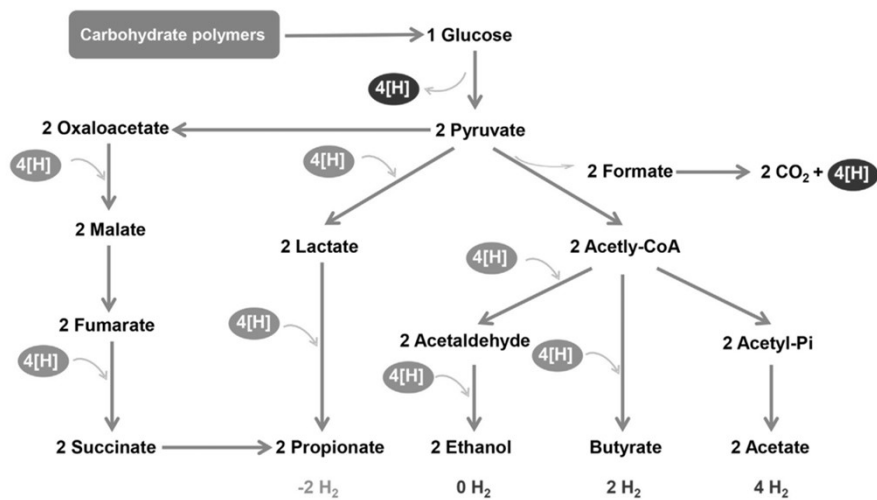
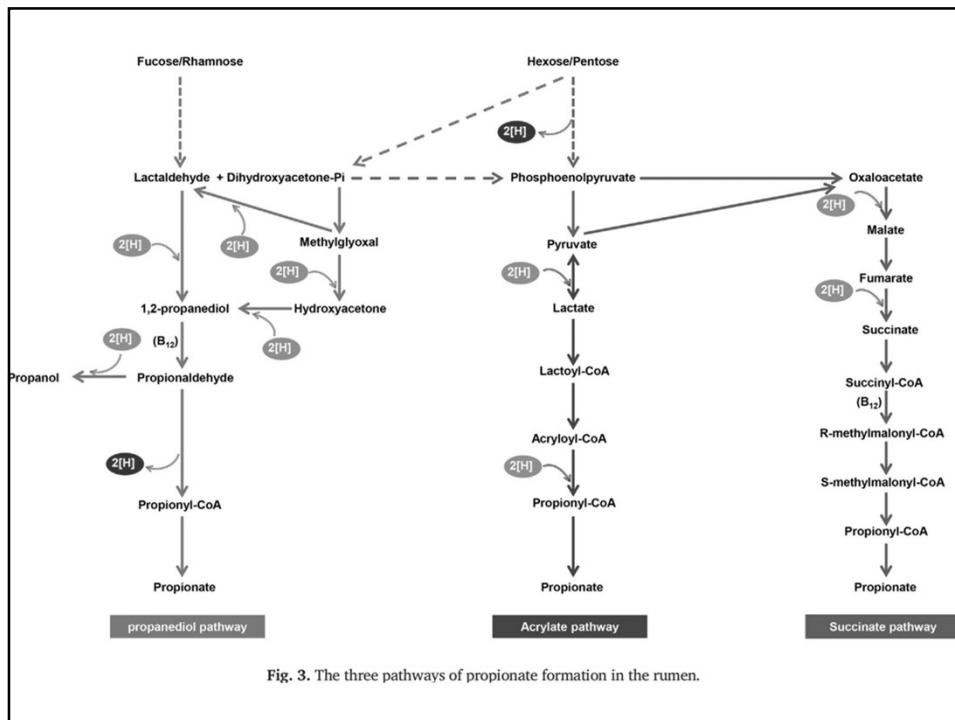


Fig. 2. Production and consumption of metabolic hydrogen ([H]) during rumen volatile fatty acids production.



The characteristics of different strategies that potentially promote propionate formation.

Strategies	Mechanism of mitigation	Effects on propionate	Effects on CH ₄	Potential problems
Ionophores	Inhibition of microbes that produce H ₂ or formate	Medium	Medium	<ul style="list-style-type: none"> • Bacterial resistance • Residues
Halogenated compounds	Inhibition of methanogens	Low	High	<ul style="list-style-type: none"> ◊ Toxicity ◊ Residues ◊ Bacterial resistance
Plant secondary compounds	A broad spectrum of antimicrobial activity	Medium	Medium	<ul style="list-style-type: none"> • Costs • Bacterial resistance • Negative effects on performance
Lipids	Inhibition of methanogens and protozoa	Medium	Medium	<ul style="list-style-type: none"> ◊ Costs ◊ Negative effects on performance
Nitrooxy compounds	Inhibition of methanogens	Low	High	<ul style="list-style-type: none"> • Costs • Potential bacterial resistance
Propionate precursors	Competing with methanogenesis for [H]	High	Low	<ul style="list-style-type: none"> ◊ Costs ◊ Inefficiency
Concentrates	Competing with methanogenesis for [H]	High	Medium	<ul style="list-style-type: none"> • Costs
Forages	Lowing CH ₄ emission per unit of meat and milk	Non	Non	<ul style="list-style-type: none"> • The risk of ruminal acidosis
Non-forage fiber sources	Competing with methanogenesis for [H]	Low	Low	<ul style="list-style-type: none"> • Inefficiency

Metanogénese

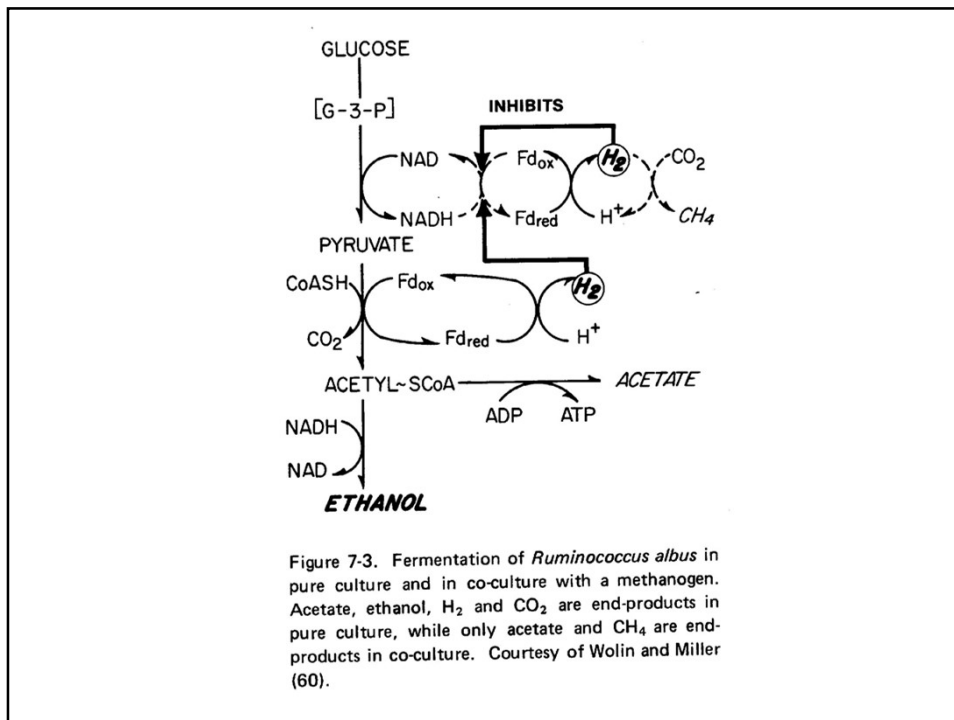
Permite que os microorganismos produtores de H_2 utilizem vias metabólicas com maior rendimento em ATP

- Aumenta o rendimento microbiano (proteína microbiana)
- Aumenta a actividade fibrolítica (maior digestão da fibra)

Por outro lado representa uma perda de energia disponível para o metabolismo do animal

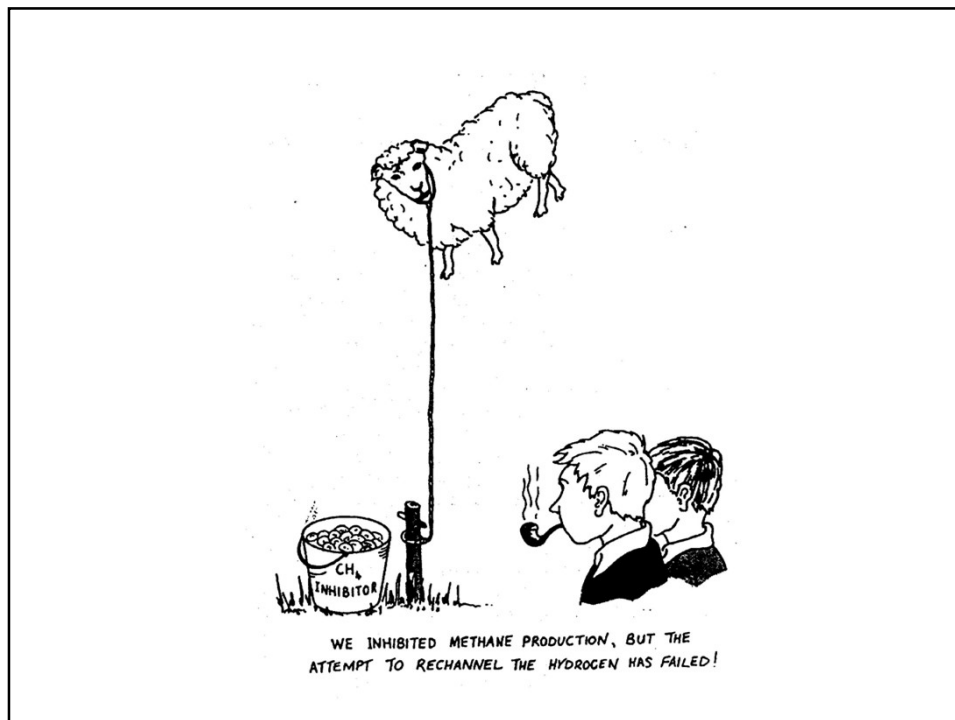
Stoichiometry of Fermentation of Glucose by Two Rumen Organisms Grown in Continuous Culture (Based on the Values Given by Iannotti *et al.*, 1973)

Products	Amounts (mol/100 mol glucose)	
	<i>R. albus</i> alone	<i>R. albus</i> with <i>V. succinogenes</i>
Ethanol	69	0
Acetate	74	147
H_2	237	0
Succinate	0	384



Balanco da Produção de ATP (~P) e de equivalentes redutores (2H) nas diversas vias de fermentação

	Lactato	Acetato	Propionato	Butirato	Etanol	Valerato
Total (~P)	2	4	4	3	2	2
Total (2H)	0	4	-2	2	0	-1



Protozoários ciliados

- Entodinomorfos
- Holotricos

Predadores: Aumentam a reciclagem de N no rúmen

Ingestão de partículas

Digestão de celulose !?!

Simbiose com bactérias metanogénicas

Não são indispensáveis

Table 16.4. Classification and characteristics of rumen protozoa

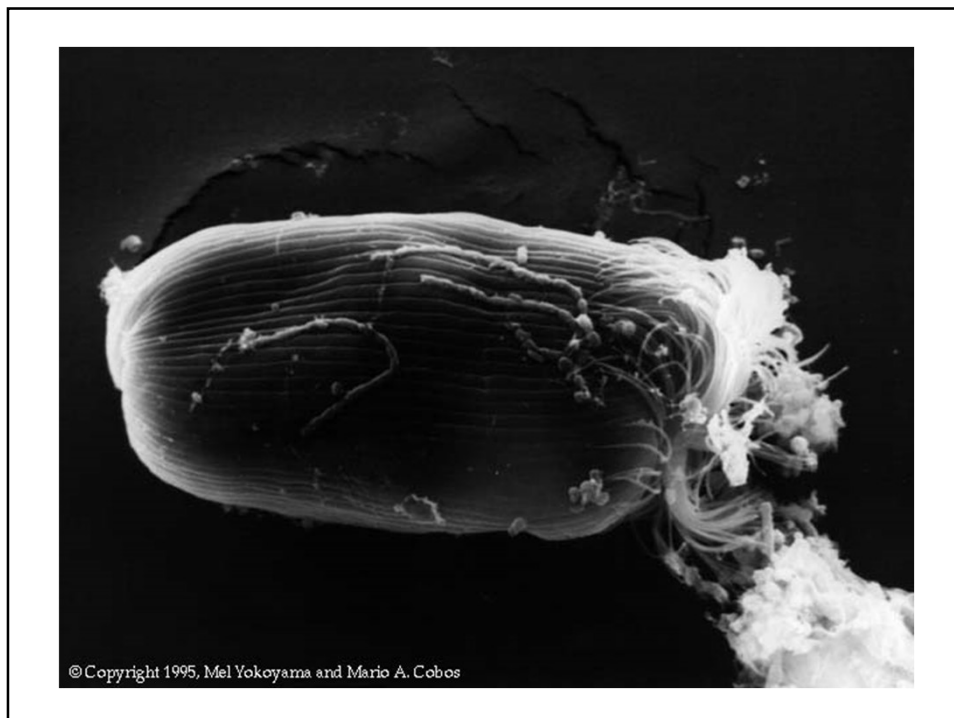
<i>Genus</i>	Probable main carbohydrate substrate	Cellulose digestion	Products ^a	Approximate generation time (h)
Holotrichs				
<i>Isotricha</i>	Starch and sugars ^b	0	2,3,La,H ₂	48
<i>Dasytricha</i>	Starch and sugars	0	2,3,La,H ₂	24
Entodiniomorphs				
<i>Entodina</i>	Starch	0(+)	1,2,3,4,(La)	6-15
<i>Epidinium</i>	Starch, hemicellulose	0	2,3,H ₂ ,(1,3,La)	
<i>Ophryoscolex</i>	Starch ^b	0	2,3,H ₂ ,(3)	24-48
<i>Diplodinium</i>		+		
<i>Eudiplodinium</i>		+	H ₂ ,fatty acids	
<i>Polyplastron</i>		+		48

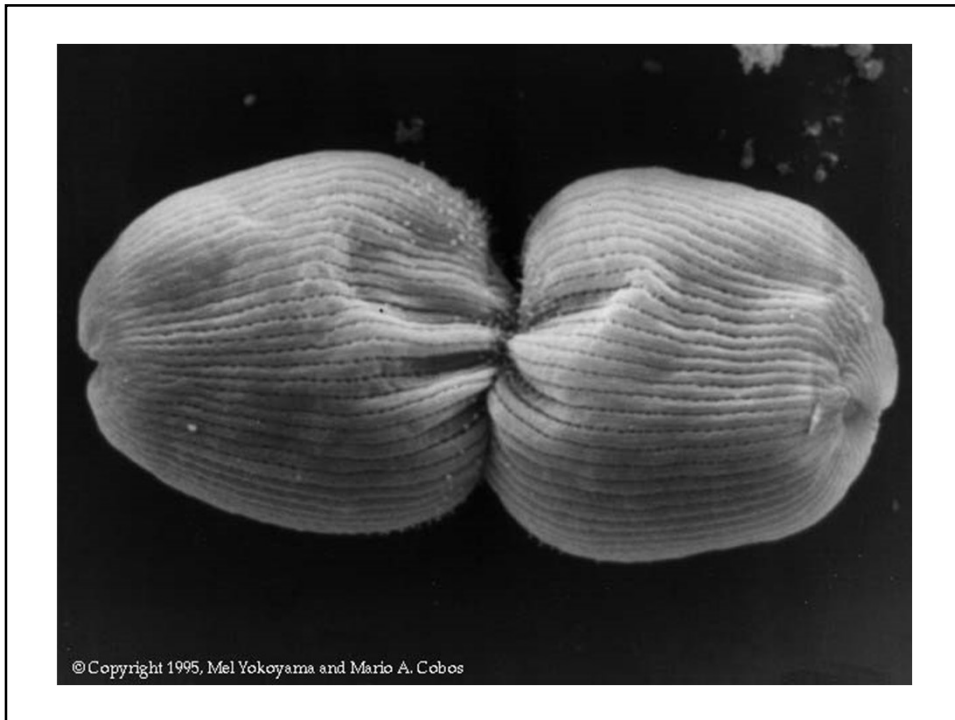
Source: Hungate, 1966.

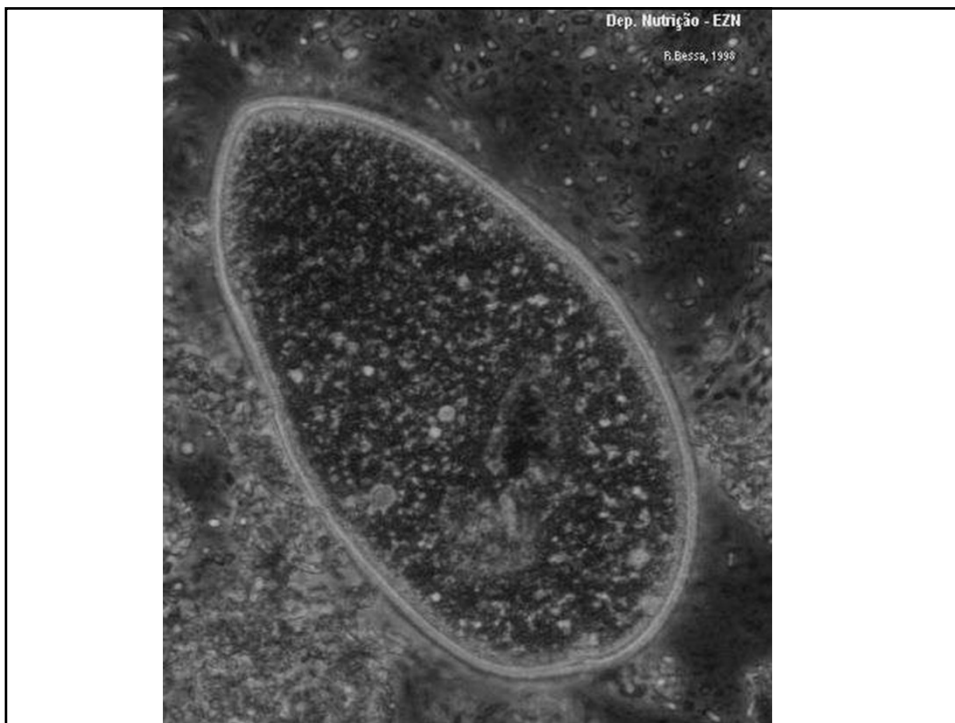
Note: Morphological features of the rumen protozoa are described in Hungate, 1966, and Church, 1975.

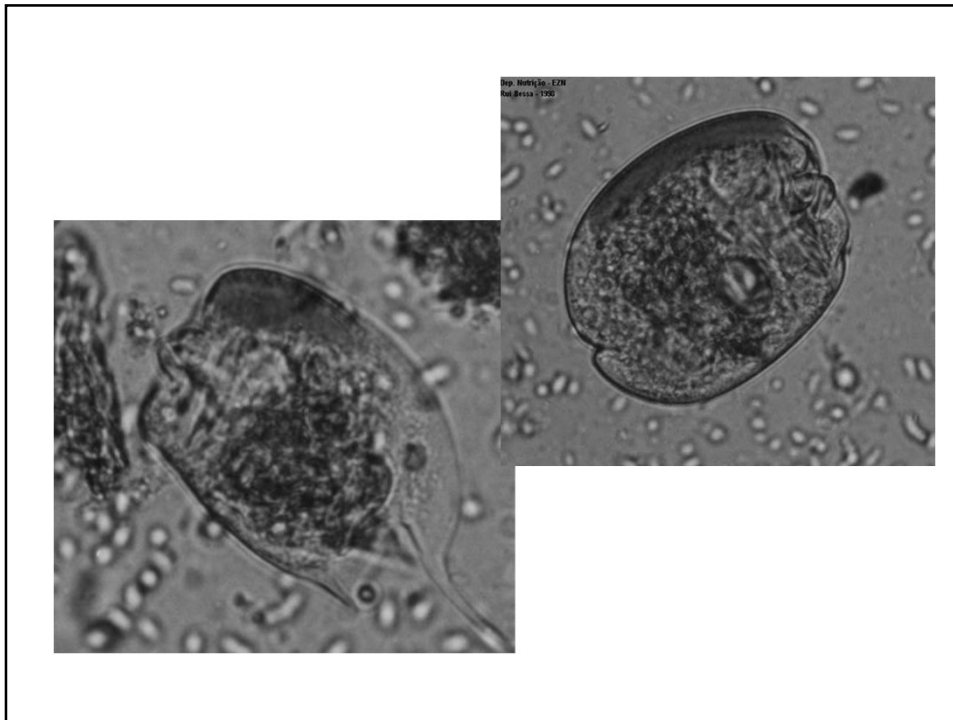
^aAbbreviations are from Table 16.2; parentheses indicate a minor product.

^bPectinolytic, but do not seem to utilize products.









Fungi

Anaeróbios

Presentes em maior número em dietas pobres

- Zoosporos
- germinação
- rizóide

<http://www.goatbiology.com/animations/funguslc.html>

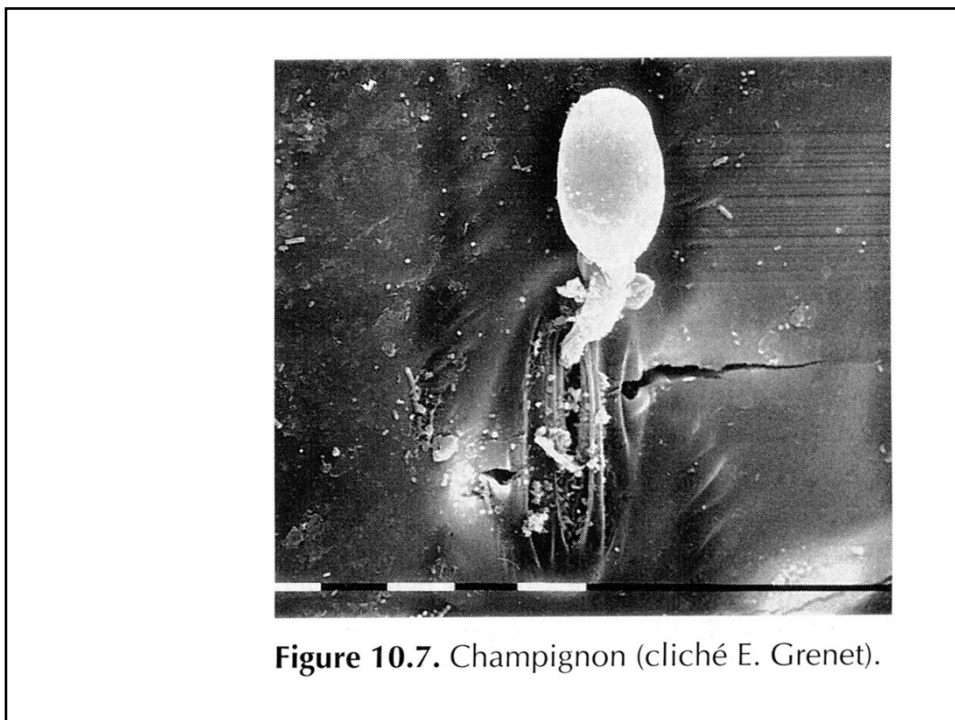
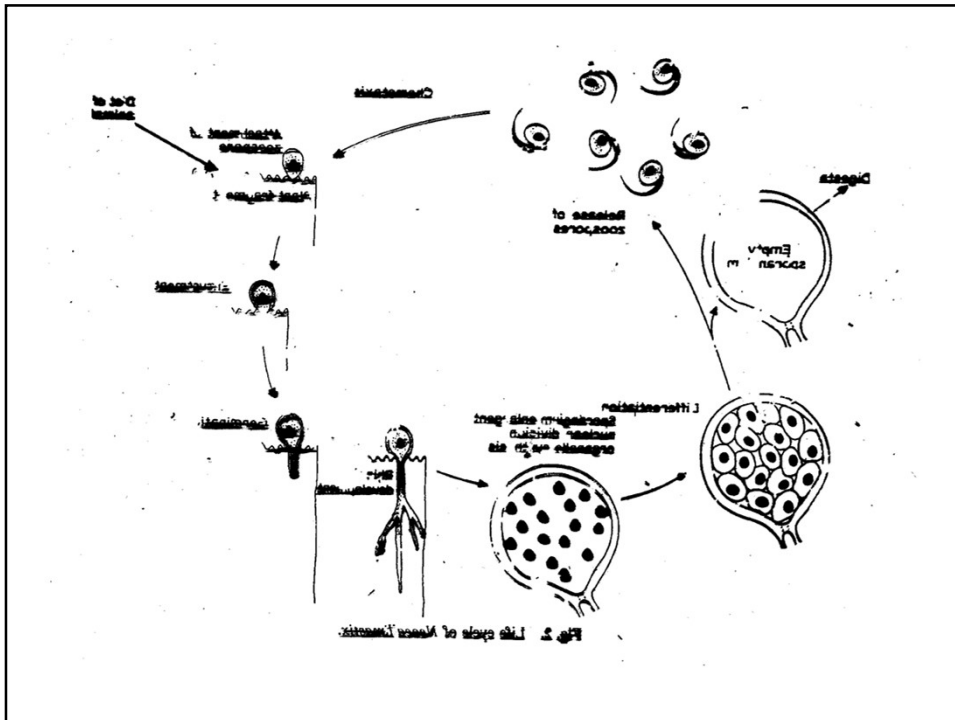


Figure 10.7. Champignon (cliché E. Grenet).

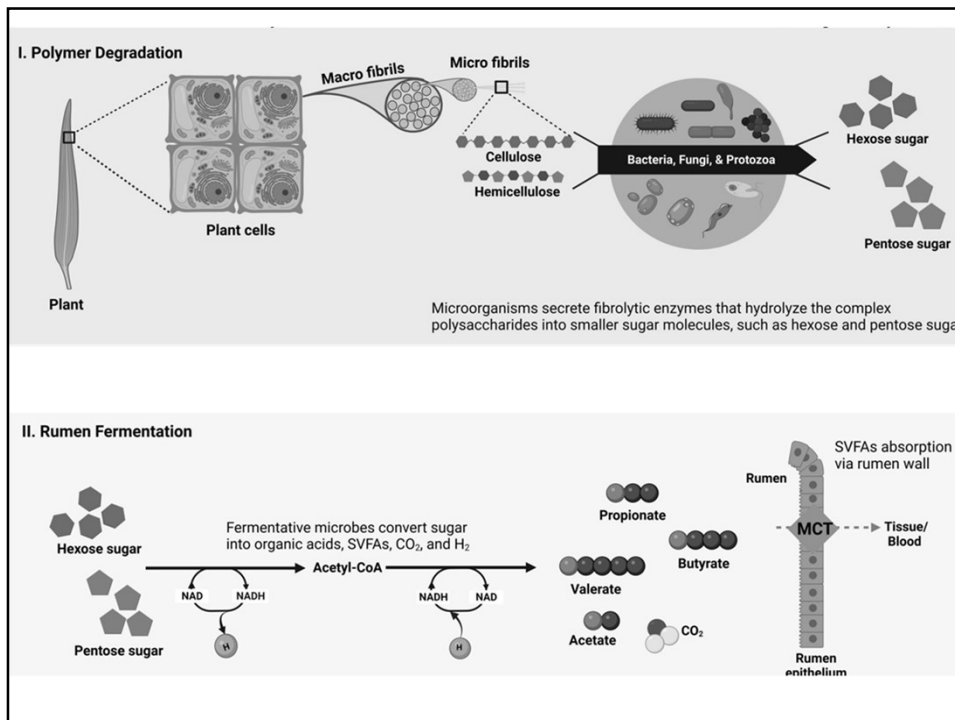
Micropopulação aderente ao epitélio retículo-ruminal

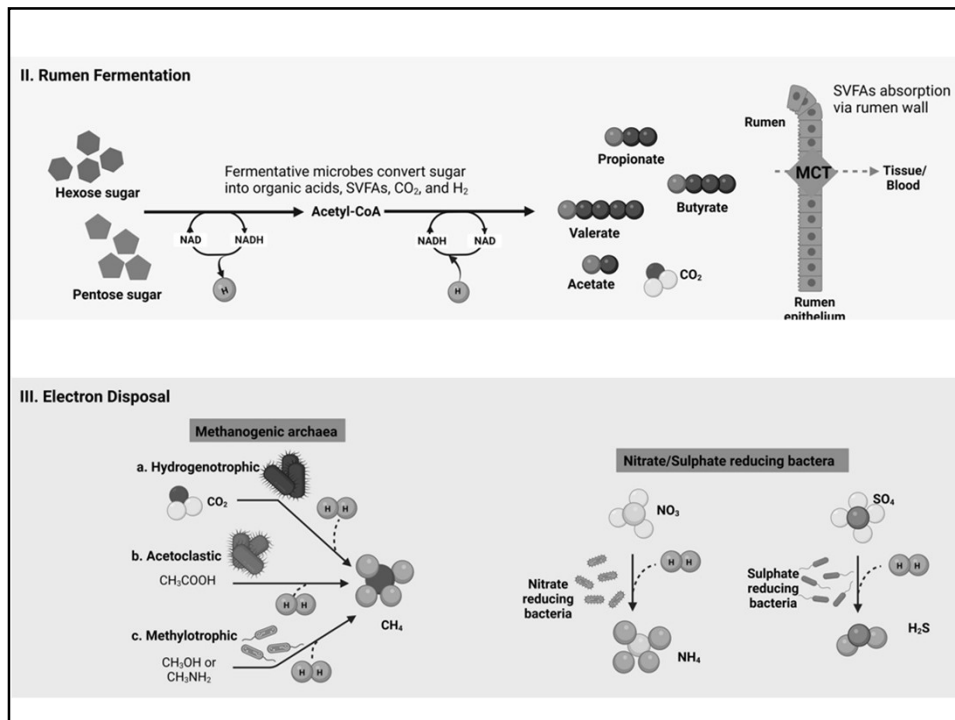


Figure 8.8. Bacilles adhérant à la muqueuse du rumen chez un jeune agneau (1 barre = 10 μ). Cliché INRA, labo. Microbiologie, Clermont-Fd-Theix.



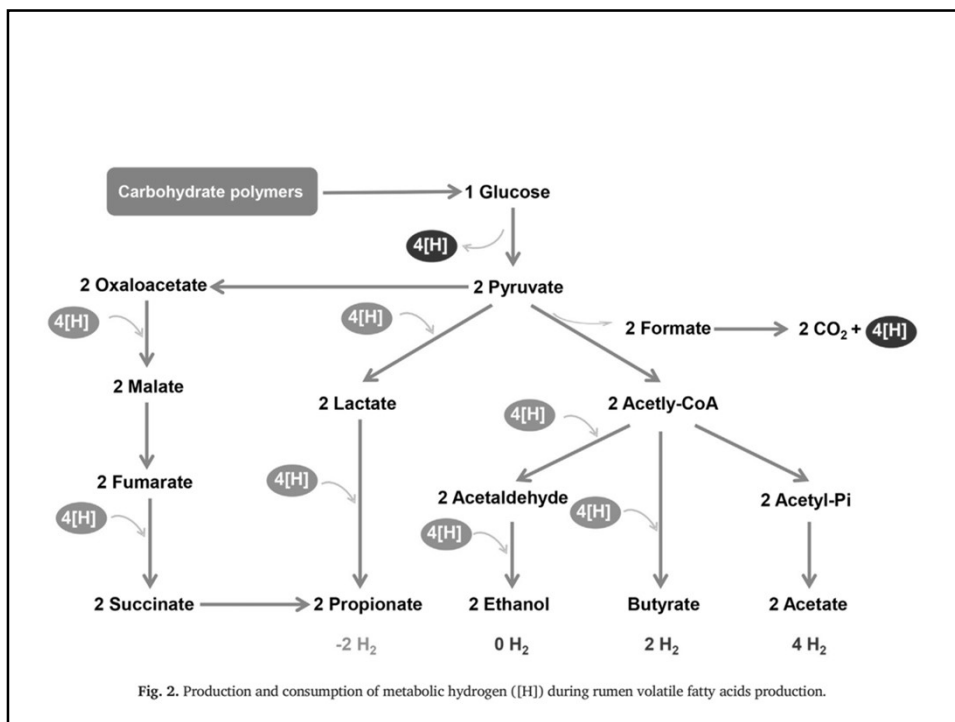
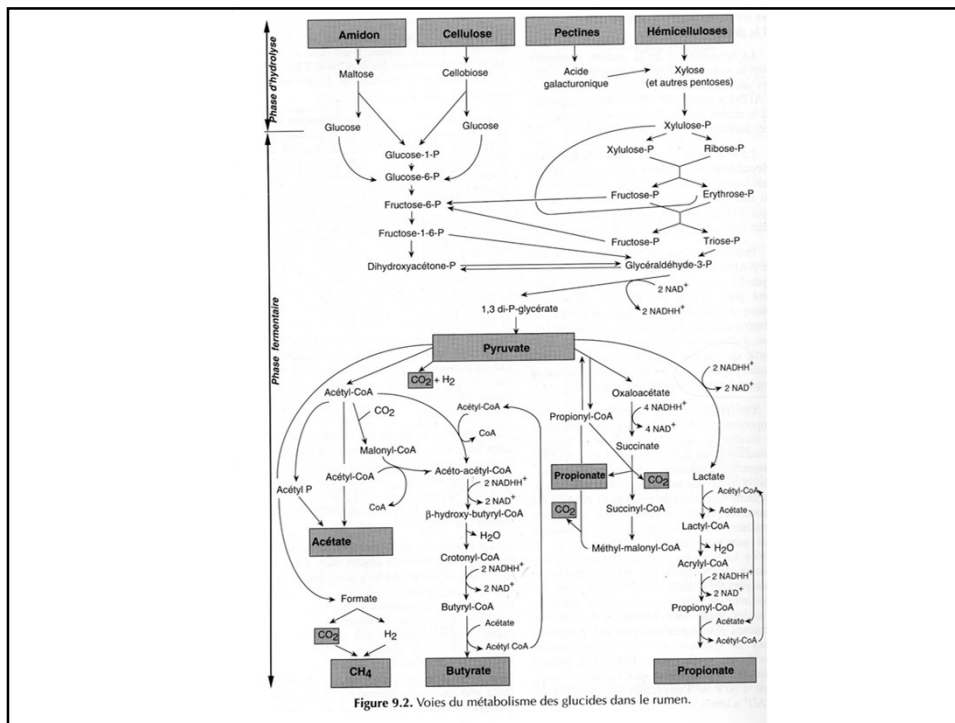
Figure 8-1. Locations of microbes in the rumen with facultative anaerobes found near the epithelial cells of the rumen wall and anaerobes partially associated with plant cell walls, starch particles or floating free. From Cheng and Costerton (7).

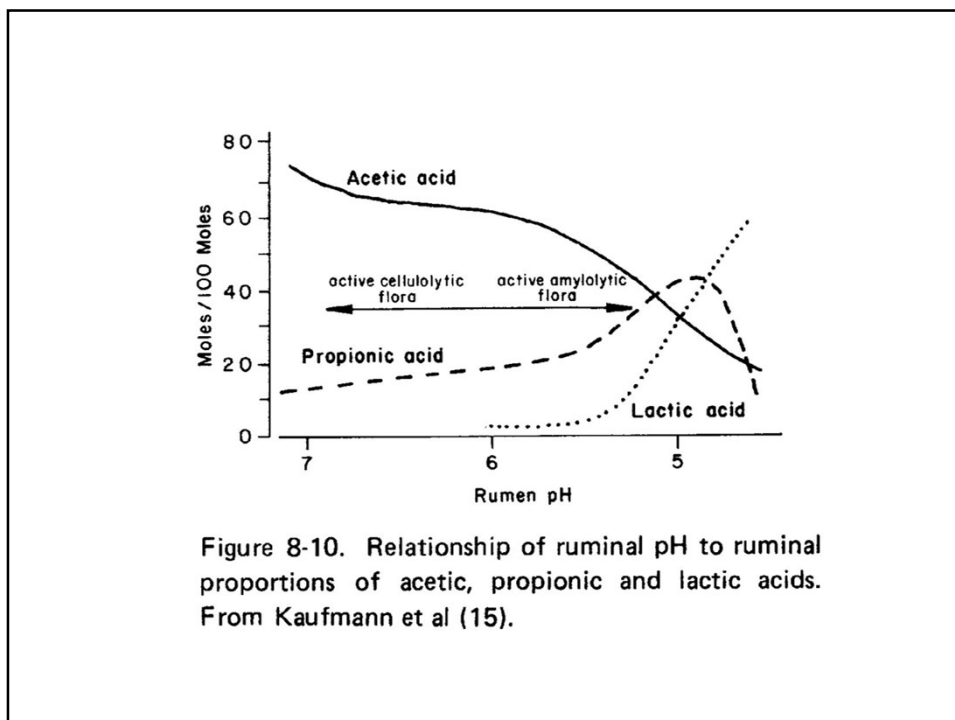
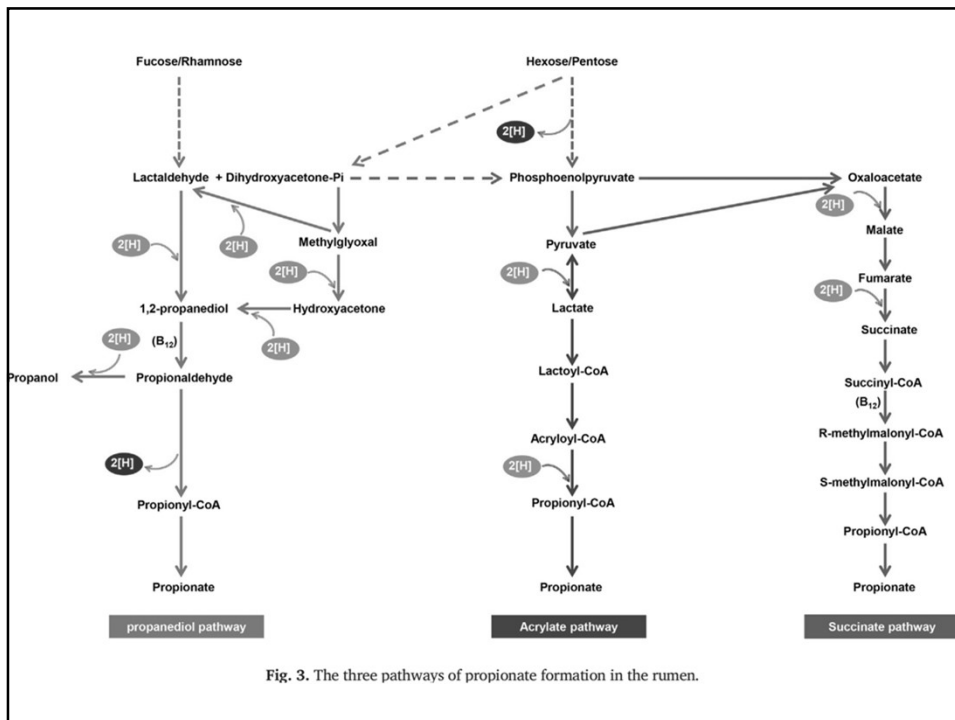




Degradação da MO e produção de AGV

- Extensa degradação dos polissacarídeos e outro material orgânico
- Colonização das partículas vegetais por biofilmes microbianos
- AGV, CO₂ e CH₄ são os produtos finais do metabolismo anaeróbico ruminal
- Síntese de biomassa microbiana (proteína; vitaminas e lípidos)





Relação entre a digestibilidade da MO e a proporção de AGV no rúmen.

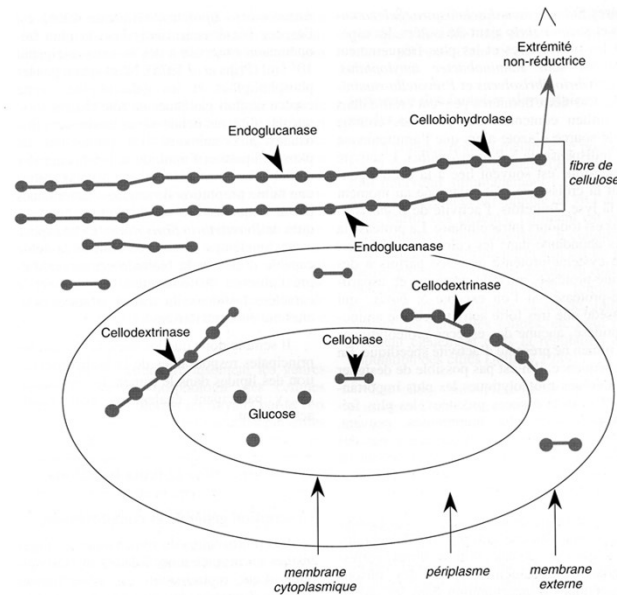
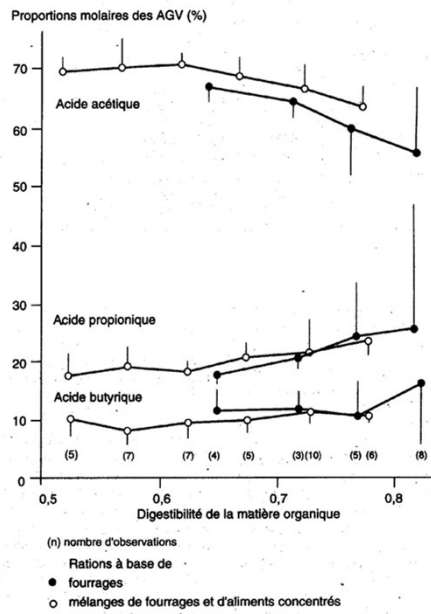
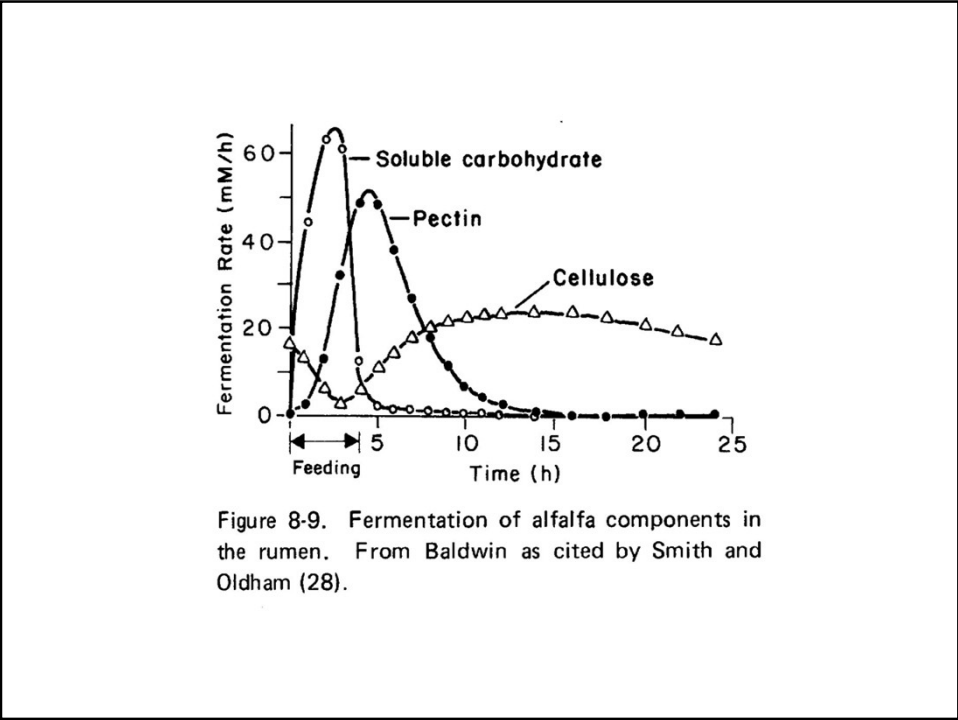
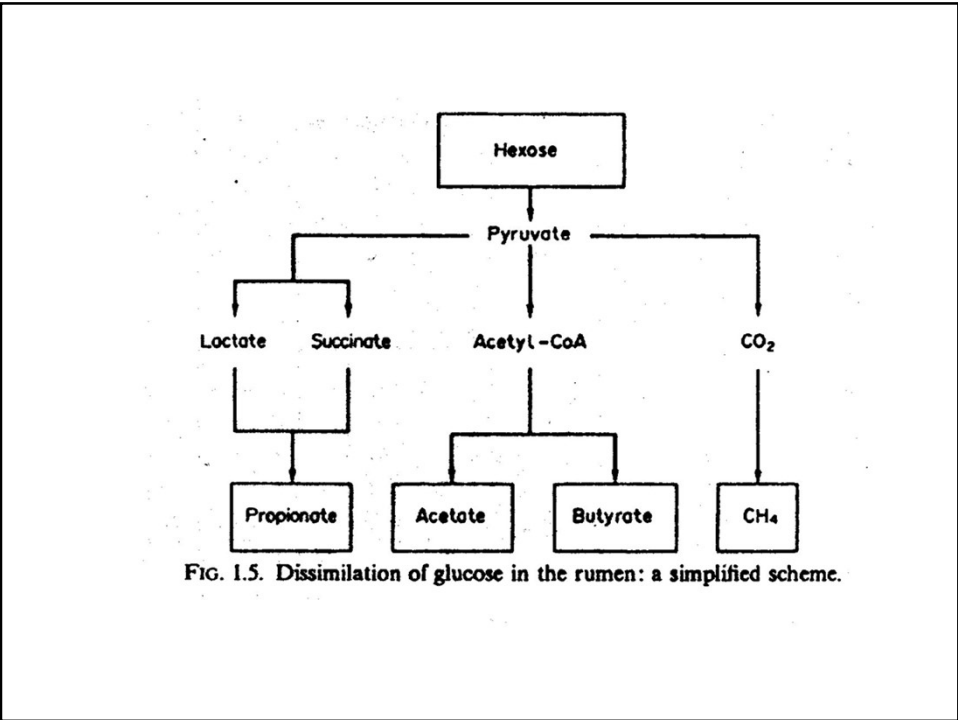
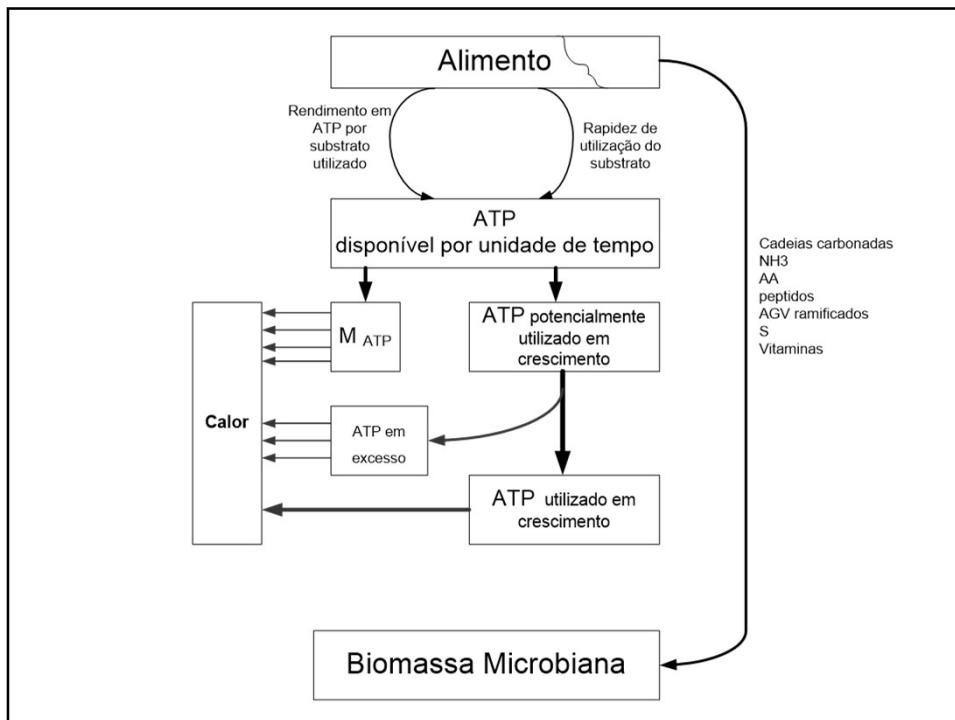
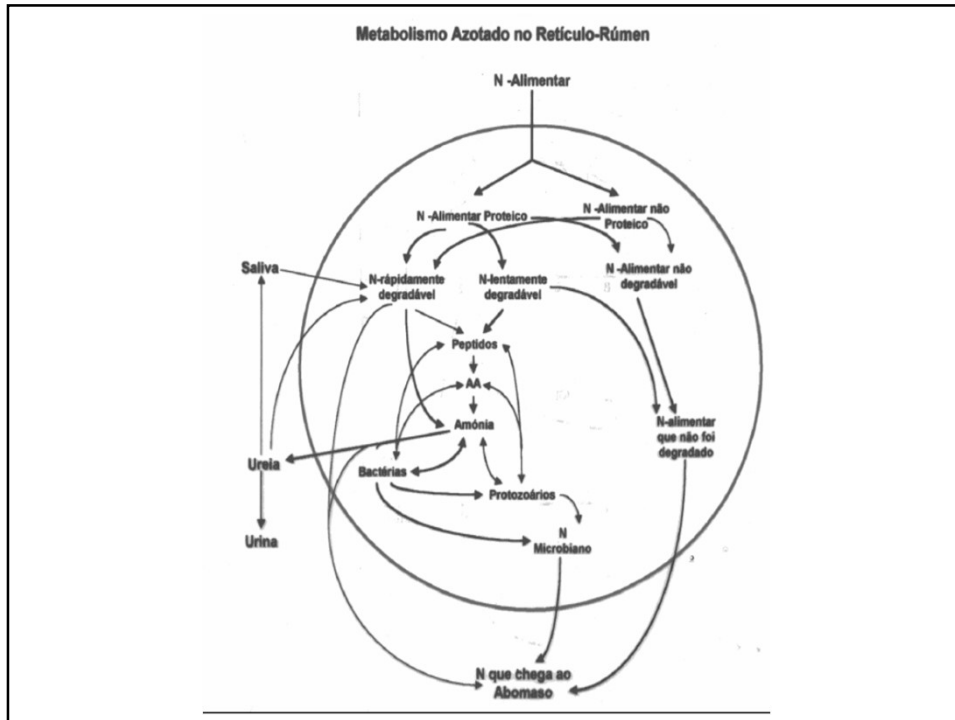


Figure 8.4. Modèle actuel de la dégradation de la cellulose par les enzymes caractérisées de *Fibrobacter succinogenes*.





Obrigado pela atenção