Microbiology of the Equine Hindgut

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Summary

Compared with the rumen, only a few studies concerning the microbial population living in the equine large intestine have been done. The objective of this review is to take stock of the present knowledge of the quantitative and qualitative composition and activity of this population. Although an important part of digestion is achieved in the stomach and the small intestine by the digestive enzymes, the microbial digestion remains essential and provides benefits for the equine. Mainly bacteria and protozoa have been studied in the large intestine of horses. Little is known about fungi. Some data reported that the numbers and the specification of bacteria in the equine cecum and colon are similar to those found in the rumen. Some microbial activities in the large intestine are the same too but 30 % less intensive than in the rumen because of the prececal digestion. Cellulolytic and proteolytic bacteria have been studied, hemicellulolytic and pectinolytic bacteria have received less attention. Much work remains to be done on the taxonomy, ecology, physiology and metabolic activities of the cecal and colic microorganisms.

Mikrobiologie des Dickdarms bei Equiden

Im Vergleich zum Pansen wurde die mikrobielle Besiedlung des equinen Dickdarms bislang nur in wenigen Studien untersucht. Ziel der vorliegenden Übersicht ist es, den gegenwärtigen Stand der Kenntnisse zur quantitativen und qualitativen Besiedlung des Dickdarms sowie der Stoffwechselleistungen der Mikroflora zusammenzufassen. Obwohl bereits ein erheblicher Teil der Verdauung durch körpereigene Enzyme in Magen und Dünndarm stattfindet, stellt die mikrobielle Fermentation von Nährstoffen einen essentiellen und für den Organismus nutzbringenden Faktor dar. Überwiegend wurden Bakterien und Protozoen in den bisherigen Untersuchungen zum Dickdarm berücksichtigt. Über den Pilzbesatz ist wenig bekannt. Die bakterielle Besiedlung weist Parallelen zwischen equinem Zäkum und Kolon sowie dem Pansen der Wiederkäuer auf. Auch die mikrobielle Stoffwechselaktivität ist ähnlich, jedoch im Dickdarm aufgrund der präzäkalen Verdauungsabläufe um etwa 30 % im Vergleich zum Pansen reduziert. Zellulolytische und proteolytische Bakterien wurden umfassender, hemizellulolytische und pektinolytische dagegen weniger intensiv untersucht. Künftige Forschungen dürften ausgerichtet sein auf die Taxonomie, Ökologie, Physiologie und die metabolische Aktivität der zäkalen und kolonalen Mikroorganismen.

Introduction

Equidae belong to a large mammals family widespread all over the world. They are largely used for sport, draft power or even food production. Feeding plays an important role in their performances. They are non-ruminant but monogastric herbivores capable of digesting efficiently large amounts of plant fibrous material. Although a large part of digestion is achieved in the stomach and small intestine by the digestive enzymes of the host, the microbial digestion remains essential in their hindgut (combination of a large cecum and even larger colon) and provides benefits for the equines (*Hintz* et *al.*, 1971; *Stevens* et *al.*, 1980; *Maczulak* et *al.*, 1985). The fibrous material of plant is degraded to a more or less extent in the large intestine by the diversified microbial population for which it constitutes the major carbon source. The conditions of the biotope (transit time, pH, humidity, temperature) effect this degradation. The influence of the diet on cecal microorganisms has been studied (*Kern* et *al.*, 1973; *Kern* et *al.*, 1974; *Bellet*, 1982).

The volatile fatty acids produced are absorbed by the intestinal wall and make up a potential energetic source for the animal (*Mac Bee*, 1977; *Prins*, 1977).

Concerning the proteolytic activity of cecal and colonic microflora, and the extent to which this microflora utilize protein and non-protein nitrogen and supply amino-acids to the horse, little is known.

Despite the importance of the hindgut microbial population only a few studies on the microbiology of the large intestine in equines have been done.

The objectives of this review are to take stock of the present knowledge of the quantitive and qualitative composition and activity of this microbial population and to compare it to the knowledge of the rumen microbiology.

I – Microbial Population of the Equine Hindgut

Information about the microbial population of the equine hindgut is scare whether it concerns its quantification, characterization or activity. Some bacteria, protozoa, and, recently, fungi have been described in cecal or colon contents.

I-1 – *Protozoa and fungi in the equine hindgut*

Protozoa

Protozoa of the equine digestive tract have been counted and characterised by different authors (*Bonhomme-Florentin*, 1969; *Kern* et *al.*, 1973; *Bellet*, 1982).

They are ciliate oligotrichs. Two typical equine cecal and colic genera have been described: Cycloposthium spp. and Blepharocorys spp. Both of these genera possess β-galactosidasic and lipolytic activities (*Bonhomme*, 1986 a), but the genus Cycloposthium has only a slight cellulolytic activity (*Bonhomme-Florentin*, 1969).

In the cecum, protozoa colonize the plant fragments to which they are attached (*Bonhomme-Florentin*, 1985). In vitro, Cycloposthium attach preferentially to partially degraded plant tissues (epiderm and mesophyll). Attachment is followed by the ingestion of plant tissue. This ingestion of plant material suggests a possible degradation of

cellulose and non-cellulolytic polysaccharides in vivo (*Fonty* and *Gouet*, 1989).
An endosymbiotic microbial population made up with protozoa and bacteria of the equine hindgut digest cell-wall polysaccharides (hemicellulose and pectin) in vitro (*Bonhomme-Florentin*, 1988). Both bacteria and protozoa have two enzymatic activities involved in the degradation of pectic substances: depolymerase and esterase; Cycloposthium spp. but also Blepharocorys spp. degrade actively pectic substances by means of a polygalacturonase, a pectin lyase and a pectinesterase. Both bacteria and protozoa have also an enzymatic activity involved in the degradation of hemicellulosic substrates; the xylan endo-1,3-β-xylosidase activity is significant, but the β-mannosidase activity is weak. The actual enzyme activities in the equine hindgut are probably higher than the activities observed in vitro (*Bonhomme-Florentin*, 1988).

Fungi
Fungi are also present in the digestive tract of the horse (*Orpin*, 1981). 3 morphologically distinct isolates of strictly anaerobic phycomycete fungi from cecum contents have been watched. In vitro, 2 of the isolates were capable of entensive degradation of milled-grass particles including degradation of the major structural polysaccharides, cellulose and hemi-cellulose. They also digested pectin (*Orpin*, 1981). Recently, we succeeded in counting and isolating strictly anaerobic phycomycetes from the intestinal contents of horses, ponies and donkeys (unpublished results). In horses, the fungi were less than 10^3 per ml of cecal content and the fungal strains appeared to be similar to pyromayes communis and to Caecomyces communis.

I-2 – *Bacteria in the equine hindgut*
In the equines, the cecum and the colon are densily populated by bacteria (*Kern* et *al.*, 1974; *Mackie* and *Wilkins*, 1988). Forty to forty-five percent of cecal microorganisms are strictly anaerobic (*McCreery* et *al.*, 1971; *Kern* et *al.*, 1973).
Microbial population seems particularly abundant in the cecum (Mackie and *Wilkins*, 1988).
Data about the total cecal population vary with the authors and with experimental conditions. *Baruc* et *al.* (1983) found from 4.4 to 5.0 · 10^8 and *Maczulak* et *al.* (1985) from 2.62 to 4.12 · 10^8 CFU/ml of cecal content from fistulated horses maintained on pasture. *Mackie* and *Wilkins* (1988) found 25.8 · 10^8 CFU/ml cecal content collected from slaughtered anglo-arab horses previously maintained on pasture. In cecal samples collected from ponies killed after feeding a 7 percent crude protein, long timothy hay at 2 percent of body weight for 30 days. *Kern* et *al.* (1974) counted 4.92 · 10^8 CFU/g. In our laboratory, *de Vaux* (1992) found from 1.21 to 9.97 · 10^8 CFU/ml of cecal content from fistulated ponies fed with 15 percent crude protein pellets.

Table 1: Mean counts of protozoa in the equine hindgut

Kern et *al.* (73)	*Bellet* (82)	
cecum $5.7 \cdot 10^3$/ml	cecum $5.1 \cdot 10^4$/ml	colon $5.6 \cdot 10^4$/ml

Table 2: Mean counts of bacteria in the equine digestive tract

	Kern et *al.* (1974)		*Mackie* and *Wilkins* (1988)	
stomach	fundic	200	CFU* · 10^6/ml	–
stomach	pyloric	10		–
duodenum		–		3
jejunum		–		29
ileon		36		38
cecum		492		2585
colon		363		607

*CFU = Colony Forming Unit

Table 3: Quantification of anaerobic cecal microflora in Equidae

Authors	Animals	Diets	Anaerobic flora	
			total	viable
Kern et *al.* (1973)	slaughtered ponies	timothy hay alone (7 % C.P.)	$48.1 \cdot 10^8$CFU/g	$3.5 \cdot 10^8$CFU/g
		+ oats	$70.2 \cdot 10^8$CFU/g	$16.7 \cdot 10^8$CFU/g
		clover hay alone (12 % C.P.)	$45.8 \cdot 10^8$CFU/g	$3.9 \cdot 10^8$CFU/g
		+ oats	$65.2 \cdot 10^8$CFU/g	$18.1 \cdot 10^8$CFU/g
Kern et *al.* (1974)	slaughtered ponies	timothy hay (7 % C.P.)	$64.2 \cdot 10^8$CFU/g	$4.9 \cdot 10^8$CFU/g
Bellet (1982)	ponies	hay		$36 \cdot 10^8$CFU/g
Maczulak et *al.* (1985)	horses	pasture	2.4 to $4.5 \cdot 10^9$CFU/ml	2.5 to $3.7 \cdot 10^8$CFU/ml
Mackie and *Wilkins* (1988)	slaughtered horses	pasture		$25.9 \cdot 10^8$CFU/g
de Vaux (1992)	ponies	pellets (15 % C.P.)		1.2 to $9.9 \cdot 10^8$CFU/ml

Table 4: Characteristics of cecal microflora of the equine

	Kern et *al.* (1973)	*Kern* et *al.* (1974)	*Baruc* et *al.* (1983)	*Maczulak* et *al.* (1985)
Rods %				
Gram-negative	61.1	63.8	52.0	50.9
Gram-positive	7.4	6.4	34.0	22.8
Cocci %				
Gram-negative	20.0	33.1	8.0	21.9
Gram-positive	11.0	5.6	6.0	4.4

I-2.1 – *Bacterial characterisation*
Characteristics of the total cecal microflora of the equines are shown in table 4 (*Kern* et *al.,* 1973; 1974; *Baruc* et *al.,* 1983; *Maczulak* et *al.,* 1985).

Streptococci were isolated from the large colon of fistulated ponies (*Alexander* et *al.,* 1952). They were differenciated serologically from other types of streptococci. The gram-negative coccus Veillonella gazogenes were also found in the colon. Later, the major groups of bacteria were identified from cecal contents of ponies (*Kern* et *al.,* 1973) and of horses (*Baruc* et *al.,* 1983; *Maczulak* et *al.,* 1985). Results are shown in table 5.

I-2.2 – *Bacterial activities*
The streptococci isolated by *Alexander* et *al.* (1952) were capable of fermenting lactose and starch, and Veillonella gazogenes was an anaerobic fermenter of lactate. *Davies* (1964) showed that some types of bacteria found in the large intestine of horses can digest cellulose. Some physiological characteristics of the bacteria from pony cecal fluid are given in table 6.

More recently, the different functional groups of bacteria in the cecum and colon of the horse have been enumerated (*Mackie* and *Wilkins,* 1988): glycolytic, amylolytic, lactate utilizers, proteolytic, hemicellulolytic and cellulolytic bacteria were found.
It appears clearly that equine cecal bacteria have diversified numerous activities. The proteolytic activity since protein digestion is dependant on microorganisms and the fibre degrading activity since the digestion of cellulose and other plant fibrous material are essential in the horse nutrition, are the two main acitivities.

Fibre degrading bacterial activity
In 1964, *Davies* showed that the number of cellulolytic bacteria in the large intestine of different horses varied from 7×10^3 to 1×10^6 g^{-1} of intestinal contents. Isolates included 2 non-motile, gram-negative and pleomorphic rods resembling some members of the genus Bacteroides, a gram-negative spore-forming organism resembling Bacillus cellulosae dissolvens and several other unidentified bacteria.
In ponies, *Kern* et *al.* (1974) found that the number of viable cellulolytic bacteria g^{-1} ingesta was 6 times greater in the cecum than in the terminal colon. However, the cecal ingesta weight was only one sixth of the entire colon. If it is assumed that the different regions of the colon had similar numbers of cellulolytic bacteria g^{-1} ingesta, then the total number of fibre-digesting bacteria in the cecum and the

Table 5: Identification of cecal bacteria in Equidae

	Kern et *al.* (1973)		*Baruc* et *al.* (1983)		*Maczulak* et *al.* (1985)	
Rods % G-negative	Bacteroides spp	5.8 %	Bacteroides	7.4 %	Bacteroides	10.2 %
			Butyrivibrio	16.6 %	Butyrivibrio	22.2 %
			Selenomonas	14.8 %	Selenomonas	6.5 %
	unknown	30.6 %	unknown	12.9 %	unknown	12.0 %
Rods % G-positive	Lactobacillus		Lactobacillus	5.6 %	Lactobacillus	10.2 %
	anaerobic	1.8 %				
	facultative	2.8 %				
	Propionibacterium	0.9 %	Propionibacterium	3.7 %	Propionibacterium	3.7 %
			Eubacteria	14.8 %	Eubacteria	6.5 %
			Clostridium	5.6 %		
	unknown	21.7 %			unknown	4.6 %
Cocci % G-negative			Megaspheara Ruminococcus and Veillonella	8 %		
	unknown	3.9 %			unknown	3.7 %
Cocci % G-positive	Streptococcus		Streptococci	6 %	Streptococci	16.7 %
	bovis	12.2 %				
	equinus	5.4 %				
					Staphylococci	1.8 %
	unknown	11.6 %			unknown	1.8 %

Table 6: Physiological characteristics of cecal bacteria (*Kern* et *al*, 1973)

Physiological characteristics	Mean % of isolated strains
H_2S producers	7.5
gas producers	2.2
amylolytic	46.9
proteolytic	24.2
acid producers from glucose	18.7

entire colon would be the same. This suggests that both the cecum and the colon have the potential to be important sites of intestinal fibre digestion in the horse. Cellulolytic bacteria were also found in the stomach and the small intestine of ponies, but in very low numbers (*Kern* et *al.*, 1974). No significant effects of the diet on the number of cellulolytic bacteria in the cecal equine ingesta were observed (*Kern* et *al.*, 1973).

More recently, *Bonhomme* (1986 b) showed that, as in the rumen, a large bacterial population is attached to forage on grass cell walls in the cecum of the horse. With the transmission electron microscope, she observed 13 forms of bacterial attachment: (1) cocci appeared to be attached via capsule-like material; (2) many cocci and bacilli appeared to be attached by a diffuse fibrous extracellular electron-dense material; (3) some other bacilli appeared to be adhering by conforming their bacterial shape to the shape of plant cell walls and by a slime material. In vitro, the cecal bacteria degraded leaves of Trifolium or Agropirum. Bacteria extensively colonized mesophyll cell and intracellular spaces between the cells. The bacteria were also attached to lignified thick walls of sclerenchyma cells and of the vascular tissue of xylem. Location of bacteria attached near to the degradation areas suggested the action of extracellular enzymes. The presence of cecal bacteria with the capability of degrading lignified tissues represents an important biochemical function previously unknown in the cecal ecosystem.
Cellulolytic bacteria represent no more than one per cent of the total cecal flora (*Kern* et *al.*, 1974; *Mackie* and *Wilkins,* 1988) although the cellulolytic activity is intensive in the cecum (*Kern* et *al.*, 1973).

Nitrogen degrading activity
Proteolytic bacteria are numerous in the equine hindgut (*Mackie* and *Wilkins,* 1988; *de Vaux,* 1992). They represent from 19.7 % of the total cecal microflora, ie 11 x 10^8 CFU/g of cecal content (*Kern* et *al.*, 1973) to 41 %, ie

Table 7: Quantification of cellulolytic bacteria in the pony digestive tract (*Kern* et *al.*, 1974)

		Cellulolytic bacteria – CFU/g
stomach	fundic	10^2
	pyloric	$3 \cdot 10^2$
small intestine		7
cecum		$43 \cdot 10^6$
colon		$7 \cdot 10^6$

Table 8: Total culturable bacteria and proteolytic bacteria in the gastro-intestinal tract of the horse (*Mackie* and *Wilkins,* 1988)

	total bacteria CFU/g	proteolytic bacteria CFU/g
duodenum	$2.9 \cdot 10^6$	$3.0 \cdot 10^6$
jejunum	$29.0 \cdot 10^6$	$15.5 \cdot 10^6$
ileum	$38.3 \cdot 10^6$	$22.0 \cdot 10^6$
cecum	$25.8 \cdot 10^8$	$15.7 \cdot 10^8$
colon	$6.0 \cdot 10^8$	$3.0 \cdot 10^8$

2.0 x 10^8 CFU/ml (*Baruc* et *al.*, 1983) or even more than a half of the total cecal or colic flora (*Mackie* and *Wilkins,* 1988; *de Vaux,* 1992). These quantifications are somewhat higher than those of *Reitnour* and *Mitchell* (1979) who observed that the proteolytic bacterial population varies from 2 to 8 – 10^5 CFU/ml.

Some cecal proteolytic bacteria isolated from pony cecal contents were characterised by *Kern* et *al.* (1973) (table 9).

Baruc et *al.* (1983) showed that 34 % of cecal bacteria exhibited a proteolytic activity degrading gelatin and 27 % were capable of degrading casein. The authors suggested that cecal bacteria may be capable of contributing to the amino-acid metabolism of the horse. Urea can be degraded by some few bacteria (*Baruc* et *al.*, 1983).
Therefore, urea may not be used as a non-protein nitrogen feed source. *Maczulak* et *al.* (1985) showed that the growth of most of the isolates was supported by peptones and amino acids and that 20.5 % of the organisms were able to grow with ammonia as the sole nitrogen source. Only 18 % were able to use urea for growth and urease activity was detected in only 2 of the 114 isolates tested.
Nitrogen degrading bacterial activity in vivo remains to be studied.

II – A Comparison of Knowledges on Hindgut Microbiology and Rumen Microbiology

In the equines, data about the enumeration or description of bacteria, protozoa and fungi in the gastro-intestinal tract

Table 9: Characteristics of proteolytic cecal bacteria (*Kern* et *al.*, 1973)

Strains	% of total proteolytic strains (159 strains were proteolytic)
Rods	
gram-negative	43.4
gram-positive or variable	19.5
Cocci	
gram-negative	3.8
gram-positive or variable	12.6
Streptococcus bovis	5.7
Bacteroides spe	5.0
Bacteroides amylophilus	3.1
Streptococcus equinus	2.5
Bacteroides ruminicola	1.3
Lactobacilles (anaerobic)	1.3
Lactobacilles (facultatively anaerobic)	0.6
Propionibacterium	0.6
Borrelia	0.6

are very scare compared to the ruminants. The rumen which is a complicated ecosystem has been indeed studied extensively and is now wellknown (cf. table 10).
It appears that the hindgut has remarkable similarities with the rumen regarding some anatomo-physiological aspects: in ruminants, the forestomach makes up the largest part of the intestinal tract, whereas in equines, the hindgut holds this largest part (*Johnson*, 1969).

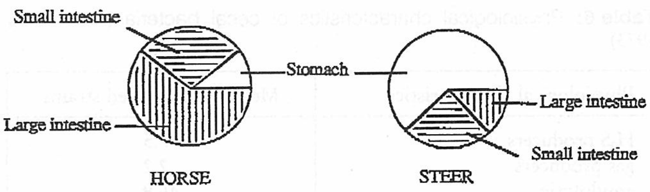

Figure 1: Relative capacity of the digestive tract (*Johnson*, 1969).

The data on the rumen are based on the reviews of *Hungate*, 1966; *Orpin* and *Joblin*, 1988; *Steward* and *Bryant*, 1988; *Williams* and *Colemar*, 1988; *Dehority* and *Orpin*, 1988; *Fonty* and *Joblin*, 1991.

Table 10: Comparison between present knowledges on rumen microflora in ruminant and hindgut microflora in equine

	Rumen	Hindgut
MICROFLORA		
– Quantitative composition		
total microflora	+ + +	+ +
cellulolytic microflora	+ + +	+
– Qualitative composition		
total microflora	+ + +	+
cellulolytic microflora	+ + +	–
– Factors of variation, Ecology of:		
total microflora	+ +	±
cellulolytic microflora	+ +	–
– Physiology of main species	+ + +	+
– nutritional requirements	+ +	–
– enzymatic activities of:		
total microflora	+ +	–
cellulolytic microflora in vitro	+ +	–
total cellulolytic microflora in vivo	+ +	+
main cellulolytic species in vivo	+	–
– cellulases	+ +	–
– Endproducts of fermentation		
total microflora	+ + +	±
cellulolytic species	+ + +	±
– Genetics and molecular biology	±	–
cellulolytic microflora	+	–
– Interactions between bacterial species	+ +	–
– Activity of detoxification	+ +	–
PROTOZOA		
– Quantification	+ + +	+ +
– Qualification	+ + +	+ +
– Factors of variation	+ +	+
– Activity in vitro	+ +	±
– Enzymatic equipment	+ +	–
– Activity in vivo		
– total population	+ +	–
– main species	+ +	–
– Endproducts of fermentation	+	–
– Interactions between species	+	–
FUNGI		
– Quantification	+	–
– Qualification	+ +	±
– Factors of variation	+	–
– Activity in vitro	+ +	±
– Enzymatic equipment	+ +	–
– Activity in vivo	±	–
– Endproducts of fermentation	+ + +	–
– Interactions between species	–	–
MICROBIAL INTERACTIONS		
– Bacteria/Protozoa	+	–
– Bacteria/Fungi	+	–
– Fungi/Protozoa	±	–

Physiologically, the construction and motor activity of both the forestomach and the hindgut allow for prolonged retention of microbes and digesta (*Stevens* et *al.*, 1980). They both are large fermentative bowls whose physical and chemical characteristics offer a suitable environment for the local anaerobic microbial population. Secretion, absorption and microbial digestion are similar (*Stevens* et *al.*, 1980; *Argenzio* and *Stevens*, 1984). However, the contribution of the hindgut to the host's nutrition is less efficient than that of the rumen; *Kern* et *al.*, 1974; *Van Soest*, 1982). The rumio-reticulum and the large intestine possess several similar functions. Therefore, informations and procedures developped from studies on the ruminant digestion might be applied to studies of horse digestion.

Conclusion

The hindgut of the equidae and the rumen of the ruminant are similar ecosystems. However, compared to the microbiology of the rumen, a lot is still ignored about the microbiology of the hindgut. But the main anaerobic species of the cecum and colon, their quantification and characterisation, their ecology and physiology, probably are similar to that of the rumen. To develop the knowledge on the anaerobic microflora and microfauna living in the large intestine of horses, it appears then possible to adapt studies made on the rumen. Horse nutrition will make new advances with a better knowledge on the hindgut microbiology.

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