FOURTH EDITION

EQUINE NUTRITION & FEEDING

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Equine Nutrition and Feeding

Fourth Edition

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Foreword

This is the fourth edition of *Equine Nutrition and Feeding* and represents a tremendous achievement of scholarship, containing an enormous amount of clearly presented detail, fully referenced and brought up-to-date with all the relevant research published in the last six years – a huge task.

Yet it remains very readable and will be of interest to all horse keepers across the world, for it covers all types of horse, all ages and conditions, in sickness and in health, kept for whatever purpose, sport, work, show or companionship.

David Frape has managed to combine details of all the relevant science with practical advice on the prevention and treatment of disease, the control of pests and parasites, and even the design of facilities, including horse boxes!

The book is well titled 'Nutrition and Feeding' because these are not the same thing and there are important practical issues in translating the one into the other. Thus it is designed to inform and help the whole range of those concerned, from the student to the most practical, from the rider to the breeder and all those involved in the care of the horse.

Such a comprehensive treatment would be a challenge for any author and it is a remarkable achievement to have kept a standard text easily assimilable and up-to-date over some 24 years, during which the science has advanced and the horse world has changed greatly.

The book can be used for easy reference or read as a narrative, helped by clear diagrams and tables.

Above all, the author recognises the individuality of horses: they, like the readers, are all different.

Professor Sir Colin Spedding
Chairman of the UK National Equine Forum

Introduction to the Fourth Edition

During the past six years there has been a surprising amount of work on the dietary requirements and husbandry needs of the horse. This will undoubtedly lead to improvements in equine management in an increasingly competitive world where resources of raw materials, from land space to spices, become scarcer. The mass of work has encouraged me to revise the Third Edition in order to bring the evidence up to date as of September 2009. All chapters and sections of the book have been revised, with, in particular, clarification of the causes and control of several metabolic diseases. In addition, I trust that the principles of equine nutrition, which evolve gradually with time, and are based upon the best experimental evidence, are adequately covered.

The horse plays many roles throughout the world making difficult the determination of improvements in performance by experimental treatment. As Ralston (2007) states: "one of the most difficult problems in equine nutrition research is often the lack of objective and clinically relevant end points". However, adequately controlled experiments are much easier to conduct in equine than in human areas, where the factors and effects to be measured in population studies are confounded by uncontrollable, or only partially controllable, factors.

There have been two major objectives in preparing the Fourth Edition:

(1) to summarize, collate and integrate 647 new research reports and papers not previously reviewed in order to: (a) replace previous speculative evidence by more secure conclusions in several areas of equine husbandry, (b) indicate areas needing further investigation, and (c) inquire about issues not previously investigated by experiment.
(2) to integrate with this text the evidence, conclusions and recommendations published by the NRC in their excellent and comprehensive Sixth Revised Edition, "Nutrient Requirements of Horses" (NRC 2007) and, in particular, to compare their estimates for protein and energy with those of INRA (1984, 1990) at the feed level, where two dissimilar systems of measurement have been used.

David Frape

Acknowledgements

I should like to thank my wife, Margery, for her support and Professor Sir Colin Spedding CBE, for his encouragement and for writing the Foreword.

List of Abbreviations

acetyl-CoA	acetyl coenzyme A
ACTH	adrenocorticotropic hormone
ADAS	Agricultural Development and Advisory Service
ADF	acid detergent fibre
ADG	average daily liveweight gain
ADH	alcohol dehydrogenase
ADP	adenosine diphosphate
a.i.	active ingredient
ALP	alkaline phosphatase
ALT	alanine aminotransferase
AMP	adenosine monophosphate
ANP	atrial natriuretic peptide
AST	aspartate aminotransferase
ATP	adenosine triphosphate
BAL	bronchoalveolar lavage
BCAA	branched chain amino acids
BCS	body condition score (1 extremely emaciated – 9 extremely fat)
BE	base excess
BFGF	basic fibroblast growth factor
BHA	butylated hydroxyanisole
BHT	butylated hydroxytoluene
BMD	bone mineral density
BMR	basal metabolic rate
bpm	beats per minute
BSE	bovine spongiform encephalopathy
BSP	bromsulphalein™ (sulphobromophthalein)
BV	biological value
BW	body weight
CAFO	Concentrated Animal Feeding Operations
CCO	cytochrome c oxidase
CHO-F_R	rapidly fermentable carbohydrate
CF	crude fibre
CFU	colony-forming unit
CK	creatine kinase
COPD	chronic obstructive pulmonary disease
COX-2	cyclo-oxygenase-2
CP	crude protein
CRH	corticotropin-releasing hormone
CT	computed tomography
CTX-1	Type I collagen carboxy-terminal telopeptide
DCAB	dietary cation–anion balance
DCAD	dietary cation–anion difference
DCP	digestible crude protein
DDS	distiller's dark grains
DE	digestible energy
DHA	docosahexanoic acid
DM	dry matter
DMG	*N,N*-dimethylglycine
$DMSO_2$	dimethylsulphone
DNA	deoxyribonucleic acid
DOD	developmental orthopaedic disease
ECF	extracellular fluid
ED	energy digestibility
EDM	equine degenerative myeloencephalopathy
EE	ether extract
EG	ethylene glycol
EIPH	exercise-induced pulmonary haemorrhage
ELF	epithelial lining fluid
ELISA	enzyme-linked immunosorbent assay
EMND	equine motor neuron disease
EPA	Environmental Protection Agency (US)
EPA	eicosapentaenoic acid
EPM	equine protozoal myeloencephalitis

ER	exertional rhabdomyolysis
EU	European Union
EVH-1/4	equine herpesvirus
FAD	flavin adenine dinucleotide
FDA	Food and Drug Agency
FE	fractional electrolyte excretion
FFA	free fatty acid
FMN	flavin mononucleotide
FOS	fructo-oligosaccharide
FSH	follicle-stimulating hormone
FTH	fast twitch, high oxidative
FT	fast twitch, low oxidative
GAG	glycosaminoglycan
GE	gross energy
GGT	gamma-glutamyltransferase
GI	gastrointestinal
Gla	γ-carboxyglutamic acid
GLC	gas-liquid chromatography
GLUT	glucose transporter
GnRH	gonadotropin-releasing hormone
GRAS	generally recognized as safe
GSH-Px	glutathione peroxidase
GSH	glutathione
GSSG	oxidised glutathione
HA	hyaluronic acid
Hb	haemoglobin
HCl	hydrochloric acid
HCN	hydrocyanic acid
HDS	hay dust suspension
HI	heat increment
HP	heat production
HPA	hypothalamo–pituitary–adrenal
HPLC	high performance liquid chromatography
HPP	hyperkalaemic periodic paralysis
HR	heart rate
5-HT	5-hydroxytryptamine (serotonin)
ICF	intracellular fluid
ICTP	telopeptide of type I collagen
IGER	Institute of Grassland and Environmental Research
IGF-1	insulin-like growth factor 1
IL-1	interleukin-1
IL-6	interleukin-6
IMP	inosine monophosphate
INRA	Institut National de la Recherche Agronomique
IR	insulin resistance
iu	international unit
i.v.	intravenous(ly)
LEM	leukoencephalomalacia
LTB_5	leukotriene B_5
LBS	*Lactobacillus* selection
LCT	lower critical temperature
LDH	lactic dehydrogenase
LH	luteinizing hormone
LPL	lipoprotein lipase
LPO	lipid hydroperoxide
LPS	lipopolysaccharide
MAD	modified acid detergent fibre
MADC	matières azotées digestibles corrigées (*or* cheval)
MCV	mean cell volume
MDA	malonyldialdehyde
ME	metabolizable energy
MRT	mean retention time
MRSA	methicillin-resistant *Staphylococcus aureus*
MSG	monosodium glutamate
MSM	methyl sulphonyl methane
NAD	nicotinamide adenine dinucleotide
NADP	nicotinamide adenine dinucleotide phosphate
NDF	neutral detergent fibre
NE	net energy
NEFA	nonesterified fatty acid
NFE	nitrogen-free extractive
NIAB	National Institute of Agricultural Botany, Cambridge
NIS	nutritionally improved straw
NO	nitric oxide
NPN	non-protein nitrogen
NRC	National Research Council
NSAID	non-steroidal anti-inflammatory drug
NSC	non-structural carbohydrate
NSP	non-starch polysaccharides
NSHP	nutritional secondary hyperparathyroidism
OC	osteochondrosis
OCD	osteochondritis dissecans
OM	organic matter
OMD	organic matter digestibility
P_{osm}	plasma osmolality
PABA	*p*-aminobenzoic acid
PAF	platelet-activating factor
PCV	packed cell volume
PCr	phosphocreatine
PDH	pyruvate dehydrogenase
PGE_2	prostaglandin E_2
PICP	propeptide of type I procollagen
PN	parenteral nutrition

PSSM	polysaccharide storage myopathy
PTH	parathyroid hormone
PTH-rP	parathyroid hormone-related protein
PUFA	polyunsaturated fatty acid
PV	plasma volume
RAO	recurrent airway obstruction
RBC	red blood cell
RCHV	red cell hypervolaemia
RDR	relative dose response
RER	respiratory exchange ratio
RH	relative humidity
RNA	ribonucleic acid
ROS	reactive oxygen species
RQ	respiratory quotient
RVO	recovered vegetable oil
s.d.	standard deviation
SDH	sorbitol dehydrogenase
SE	standard error
SET	standardized exercise test
SG	specific gravity
SI	insulin sensitivity
SID	strong ion difference
SOD	superoxide dismutase
ST	slow twitch, high oxidative
STP	standard temperature and pressure
T_3	triiodothyronine
T_4	thyroxine
TAG	triacylglycerol
TB	Thoroughbred
TBA	thiobarbituric acid
TBAR	thiobarbituric acid reactive substance
TCA	tricarboxylic acid
TLV	threshold limiting value
TNF-α	tumour necrosis factor-α
TNZ	thermoneutral zone
TPN	total parenteral nutrition
TPP	thiamin pyrophosphate
TRH	thyrotropin-releasing hormone
TSH	thyroid-stimulating hormone (thyrotropin)
TXB_2	thromboxane
UFC	unité fourragère cheval (horse feed units)
UKASTA	UK Agricultural Supply Trade Association
VFA	volatile fatty acid
VLDL	very low density lipoprotein
WBC	white blood cell (leukocyte)

1
The Digestive System

A horse which is kept to dry meat will often slaver at the mouth. If he champs his hay and corn, and puts it out again, it arises from some fault in the grinders … there will sometimes be great holes cut with his grinders in the weaks of his mouth. First file his grinders quite smooth with a file made for the purpose.

Francis Clater, 1786

Horses are ungulates and, according to J.Z. Young (1950), members of the order Perissodactyla. Other extant members include asses, zebras, rhinoceroses and tapirs. Distinctive characteristics of the order are the development of the teeth, the lower limb with the peculiar plan of the carpus and tarsus bones and the evolution of the hind gut into chambers for fermentation of ingesta. Each of these distinctive features will play significant roles in the discussions in this text.

The domesticated horse consumes a variety of feeds, ranging in physical form from forage with a high content of moisture to cereals with large amounts of starch, and from hay in the form of physically long fibrous stems to salt licks and water. In contrast, the wild horse has evolved and adapted to a grazing and browsing existence, in which it selects succulent forages containing relatively large amounts of water, soluble proteins, lipids, sugars and structural carbohydrates, but little starch. Short periods of feeding occur throughout most of the day and night, although generally these are of greater intensity in daylight. In domesticating the horse, man has generally restricted its feeding time and introduced unfamiliar materials, particularly starchy cereals, protein concentrates and dried forages. The art of feeding gained by long experience is to ensure that these materials meet the varied requirements of horses without causing digestive and metabolic upsets. Thus, an understanding of the form and function of the alimentary canal is fundamental to a discussion of feeding and nutrition of the horse.

THE MOUTH

Eating rates of horses, cattle and sheep

The lips, tongue and teeth of the horse are ideally suited for the prehension, ingestion and alteration of the physical form of feed to that suitable for propulsion through the gastrointestinal (GI) tract in a state that facilitates admixture with digestive juices. The upper lip is strong, mobile and sensitive and is used during grazing to place forage between the teeth; in the cow the tongue is used for this purpose. By contrast, the horse's tongue moves ingested material to the cheek teeth for grinding. The lips are also used as a funnel through which water is sucked.

As distinct from cattle, the horse has both upper and lower incisors enabling it to graze closely by shearing off forage. More intensive mastication by the horse means that the ingestion rate of long hay, per kg of metabolic body weight (BW), is three to four times as fast in cattle and sheep than it is in ponies and horses, although the number of chews per minute is similar, according to published observations (73–92 for horses and 73–115 for sheep) for long hays. The dry matter (DM) intake per kg of metabolic BW for each chew is then 2.5 mg in horses (I calculate it to be even less – author) and 5.6–6.9 mg in sheep. Consequently, the horse needs longer daily periods of grazing than do sheep. The lateral and vertical movements of the horse's jaw, accompanied by profuse salivation, enable the cheek teeth to comminute long hay to a large extent and the small particles coated with mucus are suitable for swallowing. Sound teeth generally reduce hay and grass particles to less than 1.6 mm in length. Two-thirds of hay particles in the horse's stomach are less than 1 mm

across, according to work by Meyer and colleagues (Meyer *et al.* 1975b).

The number of chewing movements for roughage is considerably greater than that required for chewing concentrates. Horses make between 800 and 1200 chewing movements per 1 kg concentrates, whereas 1 kg long hay requires between 3000 and 3500 movements. In ponies, chewing is even more protracted – they require 5000–8000 chewing movements per 1 kg concentrates alone, and very many more for hay (Meyer *et al.* 1975b). Horses given a hay diet chewed 40,000 times/day compared with 10,000 times/day for those fed on pellets (Houpt *et al.* 2004). Hay chewing, cf. pellets, by both horses and ponies, is protracted, with a lower chewing-cycle frequency, as the mandibular displacement is greater, both vertically and horizontally with an effect on faecal particle dimensions (Brøkner *et al.* 2009). Clayton *et al*. (2003) concluded that the development of sharp enamel points is more likely with a high concentrate diet.

Mature and young horses have a maximal daily DM intake of 3.0–3.2% of BW, although the average is lower (NRC 2007). Ponies have a higher voluntary DM intake than horses; Pearson *et al.* (2001) found ponies ate 3.9 kg/100 kg BW alfalfa hay while Argo *et al.* (2002) recorded 5.1 kg fresh weight/100 kg BW of a meal of 60% hay and 40% concentrate pellets. Such high intakes might occur with high quality feed after a period of feed restriction, as particle retention time is greater for poor quality feed (Pearson *et al.* 2001). The addition of 35% short chaff (<2 cm) to sweet coarse mix slowed the rate of consumption and doubled the eating time, but increased the eating rate (Harris *et al.* 2005) and the addition of chopped straw, either 2.5 or 4 cm in length at rates of 10–30% of a pelleted diet mixed with chopped alfalfa, increased the time to eat 1 kg wet matter (Ellis *et al.* 2005). These observations are important for an understanding of healthy digestion.

Dentition

As indicated above, teeth are vital to the well-being of horses. Diseased teeth are an encumbrance. Primary disorders of the cheek teeth represented 87% of the dental disorders in 400 horses (Dixon *et al*. 2000a). The disorders included abnormalities of wear, traumatic damage, and fractures from which the response to treatment was good. Dental and head pain have specific behavioural indicators, including altered eating patterns, anorexia, feed refusal and quidding (Ashley *et al.* 2005) and cause digestive disturbances and colic. The prevalence of dental disorders amongst donkeys increases with age, and is especially prominent at 15–20 years of age. Dental disease is associated with poor body condition score (BCS), previous episodes of colic, diastemata (a gap between adjacent teeth) and wave-, smooth- and step-mouth (Du Toit *et al* 2009a,b).

Apparent fibre digestibility, the proportion of faecal short fibre particles and plasma free fatty acids (FFAs) were all increased after dental correction in mares. Consequently, diseased and badly worn teeth, as in the geriatric horse, can limit the horse's ability to handle roughage, that compromises general health. Infections of cheek teeth are not uncommon and Dixon *et al*. (2000b) found that nasal discharge was more frequent with infections of caudal than with rostral maxillary teeth. Hudson *et al* (2006) describe cases of dysphagia in horses caused by a buccal abscess, a lingual abscess, a retropharyngeal foreign body and an oesophageal obstruction. Windley *et al* (2009b) reported that both two- and three-dimensional computed tomography (CT) were valuable as clinical diagnostic tools in detection of dental lesions and in selection of appropriate treatment.

The apparent digestibility of the protein and fibre in hay and grain is reduced if the occlusal angle of premolar 307 is greater than 80° relative to the (flattened) vertical angle (Ralston *et al*. 2001). However, no adverse effects were noted by Carmalt & Allen (2008) where normal variation occurs in occlusial characteristics; they found no relationships between cheek tooth occlusal morphology, apparent feed digestibility, and the reduction in particle size of three different hay-based feeds.

The normal horse has two sets of teeth. The first to appear, the deciduous, or temporary milk, teeth erupt soon after birth and are replaced during growth by the permanent teeth. The permanent incisors and cheek teeth erupt continuously to compensate for wear, and their changing form provides a basis for assessing the age of a horse. In the gap along the jaw between the incisors and the cheek teeth the male horse normally has a set of small canine teeth. The gap, by happy chance, securely locates the bit. The dental formulae and configuration of both deciduous and permanent teeth are given in Figure 1.1. The lower cheek teeth are implanted in the mandible in two straight rows that diverge towards the back. The space between the rows of teeth in the lower jaw is less than that separating the upper teeth (Figure 1.1). This accommodates a sideways, or circular, movement of the jaw that effectively shears feed. The action leads to a distinctive pattern of wear of the biting surface of the exposed crown. This pattern results from the differences in hardness which characterize the three materials (cement, enamel and dentine) of which teeth are composed. The enamel, being

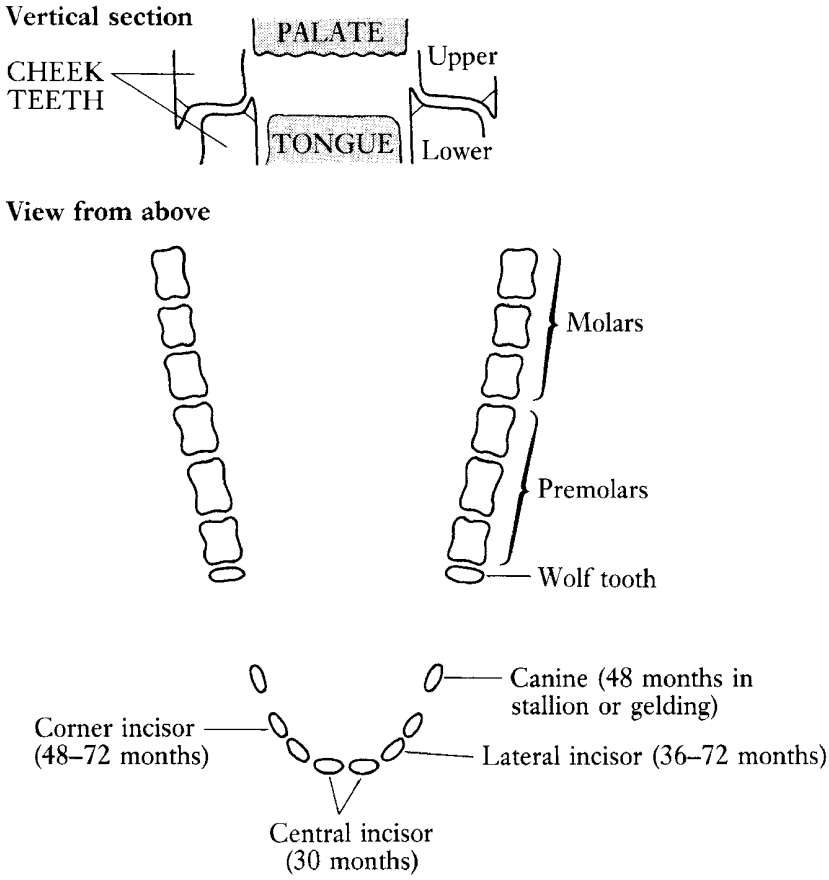

Figure 1.1 Configuration of permanent teeth in the upper or lower jaw (the molars and premolars in the lower jaw are slightly closer to the midline). The deciduous teeth on each side of each jaw consist of three incisors, one canine, and three molars. The deciduous canines are vestigial and do not erupt. The wolf teeth (present in the upper jaw of about 30% of fillies and about 65% of colts) are often extracted, as their sharp tips can injure cheeks when a snaffle bit is used. Months (in parentheses) are approximate ages at which permanent incisors and canines erupt, replacing the deciduous teeth.

the hardest, stands out in the form of sharp prominent ridges. It is estimated that the enamel ridges of an upper cheek tooth in a young adult horse, if straightened out, would form a line more than 30 cm (1 ft) long. This irregular surface provides a very efficient grinding organ.

Horses and ponies rely more on their teeth than we do. The human diet could be said to consist mainly of concentrates, which require much less chewing than does roughage. A dietary regime consisting mainly of concentrate feeds is associated with smaller mandibular excursions during chewing by the horse. This could imply that, during training, more frequent dental prophylactic treatment is needed to avoid development of dental irregularities (Bonin *et al.* 2007). Even among herbivores, horses and ponies depend to a far greater extent on their teeth than do the domesticated ruminants – cattle, sheep and goats.

Ruminants, as discussed in 'Eating rates of horses, cattle and sheep' above, swallow grass and hay with minimal chewing and then depend on the activity of bacteria in the rumen to disrupt the fibre. The fibre is then much more readily fragmented during chewing the cud.

Saliva

The physical presence of feed material in the mouth stimulates the secretion of a copious amount of saliva. Some 10–12 L are secreted daily in a normally fed horse. This fluid seems to have no digestive enzyme activity, but its mucus content enables it to function as an efficient lubricant preventing 'choke'. Its bicarbonate content, amounting to some 50 mEq/L, provides it with a buffering capacity. The production of bicarbonate and sodium chloride in the saliva is directly proportional to the rate of secretion. The continuous secretion of saliva during eating seems to buffer the digesta in the proximal region of the stomach, permitting some microbial fermentation with the production of lactate. This has important implications for the well-being of the horse (see Chapter 11).

Obstruction of the oesophagus by impacted feed or foreign bodies is not uncommon, but attempts to pass a nasogastric tube are not justified, as most cases respond to conservative treatment. For cases of more than 48 h duration a cuffed nasogastric tube is advocated, although the value of oxytocin use is unclear (Duncanson 2006). To facilitate nutritional support during treatment of oesophageal perforation, a cervical oesophagotomy tube is placed and advanced into the stomach (Read *et al.* 2002). An enteral diet includes an electrolyte mixture (partly to compensate for salivary electrolyte losses through the oesophagotomy site), sucrose (1.2 kg/day), casein, canola rapeseed oil (1.1 L/day) and dehydrated alfalfa pellets. A nasogastric tube is subsequently introduced to allow repair of the oesophagotomy site.

THE STOMACH AND SMALL INTESTINE

The first quantitative aspects of digestion were demonstrated by Waldinger in 1808 with the passage of capsulated feedstuff through the intestines. Intensive studies concerning the physiology of digestion were started in Paris around 1850 by Colin, but they were continued predominately from 1880 in Dresden by Ellenberger and Hofmeister who investigated the mouth, stomach and small intestine. Scheunert continued with work on the large intestine in Dresden and Leipzig until the 1920s. Although the apparent digestibility of cellulose was appreciated by 1865 it took another 20 years for the discovery of the process of microbial digestion in the equine large intestine. Until 1950 most routine equine digestibility experiments were conducted in Germany, France and the USA (Klingeberg-Kraus 2001), while comparative studies were conducted by Phillipson, Elsden and colleagues at Cambridge in the 1940s.

Development of the gastrointestinal (GI) tract and associated organs

The GI tract tissue of the neonatal foal weighs only 35 g/kg BW, whereas the liver is large, nearly in the same proportion to BW, acting as a nutrient store for the early critical days. By six months of age the GI tract tissue has proportionately increased to 60 g/kg BW, whereas the liver has proportionately decreased to about 12–14 g/kg BW. By 12 months both these organs have stabilized at 45–50 g/kg BW for the GI tract and 10 g/kg BW for the liver. Organ size is also influenced by the activity of the horse. After a meal, the liver of mammals generally increases rapidly in weight, probably as a result of glycogen storage and blood flow. In the horse the consumption of hay has less impact on liver glycogen, so that following a meal of hay the liver weighs only three-quarters of that following mixed feed. Moreover, during and immediately after exercise the GI tract tissue weighs significantly less than in horses at rest, owing to the shunting of blood away from the mesenteric blood vessels to the muscles. At rest, about 30% of the cardiac output flows through the hepatic portal system. These aspects are discussed further in Chapter 9.

Surprisingly, the small intestine does not materially increase in length from 4 weeks of age, whereas the large intestine increases with age, the colon doing so until 20 years at least. The distal regions of the large intestine continue extension to a greater age than do the proximal regions. This development reflects the increasing reliance of the older animal on roughage. In an adult horse of 500 kg BW the small intestine is approximately 16 m in length, the caecum has a maximum length of about 0.8 m, the ascending colon 3 m and the descending colon 2.8 m.

Transit of digesta through the GI tract

The residence time for ingesta in each section of the GI tract allows for its adequate admixture with GI secretions, for hydrolysis by digestive enzymes, for absorption of the resulting products, for fermentation of resistant material by bacteria and for the absorption of the products of that fermentation. Transit time through the GI tract is normally considered in three phases, owing to their entirely different characteristics. These phases are:

(1) expulsion rate from the stomach into the duodenum after a meal;
(2) rate of passage through the small intestine to the ileocaecal orifice;
(3) retention time in the large intestine.

The first of these will be considered below in relation to gastric disorders. Rate of passage of digesta through the small intestine varies with feed type. On pasture this rate is accelerated, although a previous feed of hay causes a decrease in the rate of the succeeding meal, with implications for exercise (see Chapter 9). Roughage is held in the large intestine for a considerable period that allows microbial fermentation time to break down structural carbohydrates. However, equine GI transit time of the residue of high fibre diets is less than that of low fibre diets of the same particle size, in common with the relationship found in other monogastric animals.

Digestive function of the stomach

The stomach of the adult horse is a small organ, its volume comprising about 10% of the GI tract (Figure 1.2, Plate 1.1; Meyer *et al.* 1993a). In the suckling foal, however, the stomach capacity represents a larger proportion of the total alimentary tract. Most digesta are held in the stomach for a comparatively short time, but this organ is rarely completely empty and a significant portion of the digesta remain in it for 2 to 6 h. Some digesta pass into the duodenum shortly after eating starts, when fresh ingesta enter the stomach. Expulsion into the duodenum is arrested as soon as feeding stops. When a horse drinks, a high proportion of the water passes along the curvature of the stomach wall so that mixing with digesta and dilution of the digestive juices it contains are avoided. This process is particularly noticeable when digesta fill the stomach.

The entrance to the stomach is guarded by a powerful muscular valve called the cardiac sphincter. Although a horse might feel nauseated, it rarely vomits, partly because of the way this valve functions. This too has important consequences. Despite extreme abdominal pressure the cardiac sphincter is reluctant to relax in order to permit the regurgitation of feed or gas. On the rare occasions when vomiting does occur, ingesta usually rush out through the nostrils, owing to the existence of a long soft palate. Such an event could indicate a ruptured stomach.

Gastric anatomy differentiates the equine stomach from that of other monogastrics. Apart from the considerable strengths of the cardiac and pyloric sphincters, almost half the mucosal surface is lined with squamous, instead of glandular, epithelium. The glandular mucosa is divided into fundic and pyloric regions (Figure 1.2). The fundic mucosa contains both parietal cells that secrete hydrochloric acid (HCl) and zymogen cells which secrete pepsin, while the polypeptide hormone gastrin is secreted into the blood by the pyloric region. The hormone's secretion is triggered by food, and equine studies in Sweden have shown that the gastric phase of release is triggered by distension of the stomach wall, rather than the sight of feed. The greatest and most prolonged gastrin secretion occurs when horses eat hay freely (A. Sandin, personal communication). In the horse, gastrin does not act as a stress hormone. The hormone strongly stimulates secretion of gastric acid and the daily secretion and release of gastric juice into the stomach amounts to some 10–30 L. Secretion of gastric juice continues even during fasting, although the rate seems to vary from hour to hour (see Chapter 11, Laminitis).

HCl secretion continues, but declines gradually at a variable rate when the stomach is nearly empty and hence at that time the pH is around 1.5–2.0. The pH rises rapidly during a subsequent meal, especially that of grain only, partly as a consequence of a delay in gastrin secretion, compared with the more rapid gastrin response to hay. The act of eating stimulates the flow of saliva – a source of sodium, potassium, bicarbonate and chloride ions. Saliva's buffering power retards the rate at which the pH of the stomach contents decreases. This action, combined with a stratification of the ingesta, brings about marked differences in the pH of different regions (about 5.4 in the fundic region and 2.6 in the pyloric region).

Fermentation, primarily yielding lactic acid, occurs in the oesophageal and fundic regions of the stomach, but particularly in the part known as the *saccus caecus*, which is lined by squamous cells. As digesta approach the pylorus at the distal end of the stomach, the gastric pH falls, owing to the secretion of HCl, which potentiates the proteolytic activity of pepsin and arrests that of fermentation. The activity of pepsin in the pyloric region is some 15–20 times greater than in the fundic region. Because of the stomach's small size and the consequentially relatively short dwelling time, the degree of protein digestion is low.

Gastric malfunction

Meyer and his colleagues in Hanover (Meyer *et al.* 1975a) have made detailed investigations of the flow of ingesta and digesta through the GI tract of horses. Their thesis is that abnormal gastric fermentation occurs when the postprandial dry matter content of the stomach is particularly high and a low pH is not achieved. There is, nevertheless,

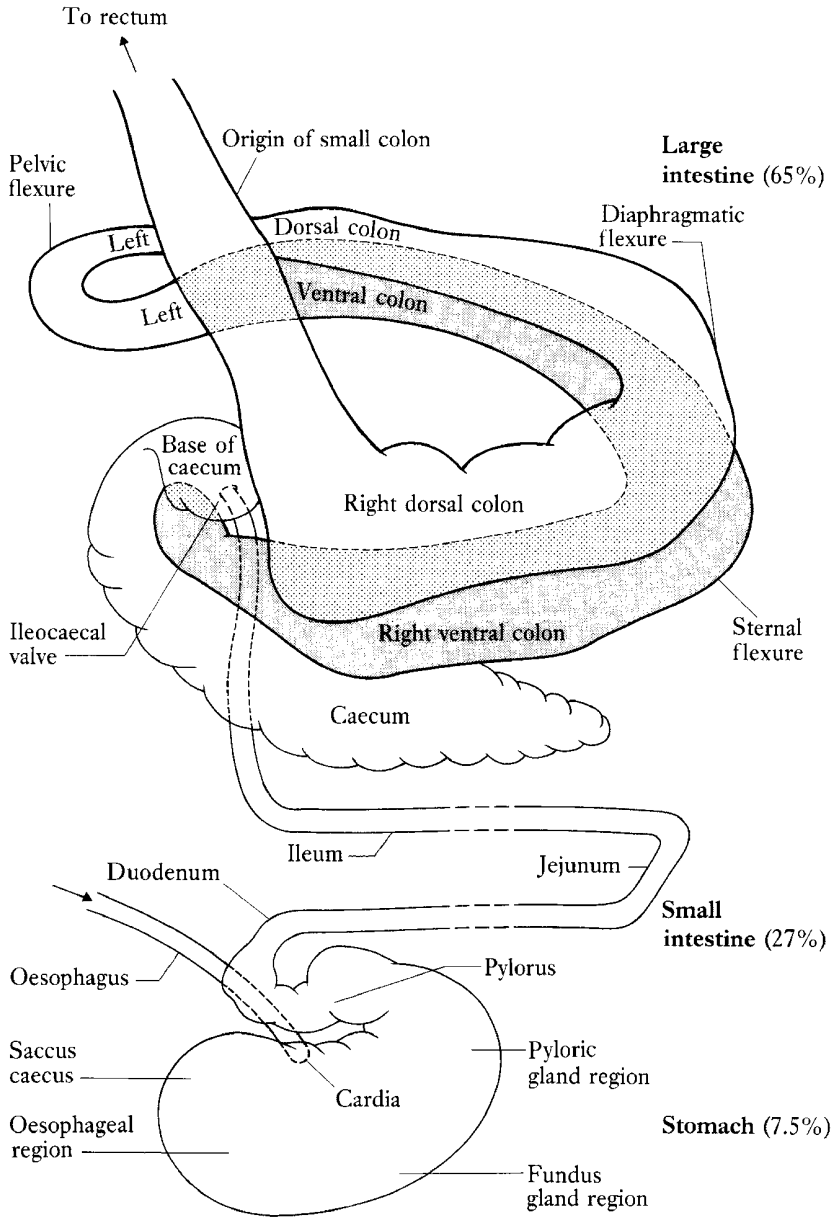

Figure 1.2 GI tract of adult horse (relative volumes are given in parentheses).

considerable layering and a differentiation in pH between the *saccus caecus* and pyloric region. Fermentation is therefore a normal characteristic of regions with a higher pH, in which the larger roughage particles tend to float. However, the dry-matter content is lower following a meal of roughage than it is following one of cereals. After meals of 1 kg loose hay and 1 kg pelleted cereals the resulting gastric dry matters were 211 and 291 g/kg contents, respectively.

The Hanover group compared long roughage with that which was chopped, ground or pelleted and observed that, as particle size of roughage decreased, the gastric dry matter contents decreased from 186 to 132 g/kg contents and the rate of passage of ingesta through the stomach

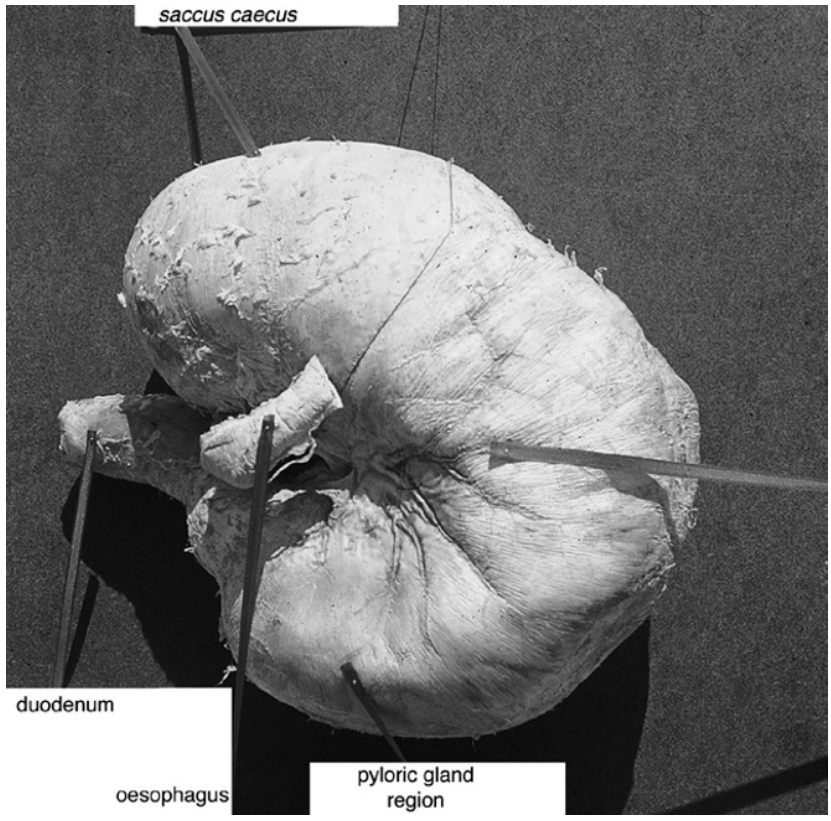

Plate 1.1 Stomach of a 550 kg TB mare, capacity 8.4 l, measuring about 20 × 30 × 15 cm. Acid fermentation of stomach contents takes place in the *saccus caecus* (*top*).

increased. The reason for this is probably that it is the finely divided material in a gastric slurry which passes first to the intestines. The slurry is forced into the duodenum by contractions termed *antral systole* at the rate of about 3 g/min. Nevertheless, particle size is generally small as a result of comminution by the molars. With larger meals of pelleted cereal, up to 2.5 kg/meal, the gastric dry matter content increased to 400 g/kg, and the pH to 5.6–5.8, for as long as 2–3 h after consumption. The dry matter accumulated faster than it was ejected into the duodenum and, as cereals could be consumed more rapidly than hay with a lower secretion of saliva, the dry matter of the stomach was higher following large meals of cereals. As much as 10–20% of a relatively small meal of concentrates (given at the rate of 0.4% BW) remains in the stomach 6 h after feeding ponies. A high dry-matter content acts as a potent buffer of the HCl in gastric juice and the glutinous nature of cereal ingesta inhibits the penetration of cereal ingesta by gastric juices.

Together with the delay in gastrin release during a cereal meal, these factors could account for the failure of the postprandial pH to fall to levels that inhibit further microbial growth and fermentation. Lactic-acid producing bacteria (*Lactobacilli* and *Streptococci*) thrive (see Chapter 5, Probiotics). Whereas *Streptococci* do not produce gas, some *Lactobacillus* species produce carbon dioxide, thrive at a pH of 5.5–6.0 and even grow in the pH range 4.0–6.8, with some strains growing in conditions as acid as pH 3.5. During the first hour after a starchy concentrate meal there was a linear increase in total gastric anaerobes, the concentrations of *Lactobacilli*, *Streptococci* and lactate-utilizing bacteria were, respectively, 5.52, 4.82 and 6.95 $\log_{10}$ colony-forming units (cfu)/mL. Lactate (mostly L-lactate) and volatile fatty acid (VFA) concentrations increased linearly over a period of up to 210 min (Varloud *et al.* 2007). The pH of the gastric contents will even increase to levels that permit non-lactic-acid-producing, gas-producing bacteria to survive, producing large amounts

of VFAs. Gas production at a rate greater than that at which it can be absorbed into the bloodstream causes gastric tympany, and even gastric rupture, and hence it is desirable that the postprandial gastric pH falls sufficiently to arrest most bacterial growth and to kill potential pathogens.

Gastric ulceration

Ulceration and erosion occur in the gastric stratified squamous mucosa, particularly that adjacent to the *margo plicatus*, as the squamous epithelial mucosa lacks the protective processes, especially the mucus–bicarbonate barrier, possessed by the glandular mucosa (see Chapter 11 for a discussion of aetiology). This squamous mucosa exists in a potentially acidic environment and is susceptible to damage by HCl and pepsin. Bile, which is found in significant amounts in the stomach during long fasts, increases the risk of damage (Berschneider *et al.* 1999). Routine post-mortem examination of 195 Thoroughbreds (TBs) in Hong Kong (Hammond *et al.* 1986) revealed that 66% had suffered gastric ulceration. In TBs in training, the frequency was 80%, whereas it was only 52% among those that had been retired for a month or more. The lesions seem to be progressive during training, but to regress during retirement. Husted *et al.* (2008) gave horses coastal Bermuda hay *ad libitum* and commercial coarse mix under two housing schemes: a box stall bedded with wood shavings and a grassed paddock. The proximal and ventral gastric pH values were similar in both groups. Ventral pH was uniform throughout the study, while the proximal pH demonstrated a 24 h circadian pattern in both treatments. The authors concluded that housing alone during training does not explain the increased risk of squamous ulcer development. There was a low prevalence of gastric lesions in Caspian horses that had received anthelmintic drugs in Iran (Moghaddam *et al.* 2008). The prevalence was found to increase with increasing exercise and to occur in the glandular region in those having long-term treatment with nonsteroidal anti-inflammatory drugs (NSAIDs; NSAIDs reduce prostaglandin secretion, thus inhibiting mucus production. author). Observations by the research group in Hanover showed that clinical signs of periprandial colic and bruxism (grinding of teeth) were more pronounced in horses with more severe gastric lesions from diffuse ulcerative gastritis.

Concretions

Soluble tannins present in the persimmon fruit bind proteins, such as digestive enzymes. In the presence of gastric HCl the tannic acid polymerises to form a coagulum, described as a phytobezoar, that includes persimmon seeds and dietary fibre. This concretion can cause mechanical damage and abrasion to the mucosal lining of the stomach (Hurtado *et al.* 2007, Johnson & Kellam, 2007)

Foals

Lesions are not restricted to adult horses. Neonatal foals of 2 days of age are able to produce highly acidic gastric secretions; the mean pH of the glandular mucosal surface and fluid contents of 18 foals at 20 days of age were 2.1 and 1.8, respectively (Murray & Mahaffey 1993). Lesions in suckling foals include neonatal gastro-duodenal ulceration, gastric glandular ulceration and squamous mucosal ulceration (Lester 2004). Gastric mucosal inflammation and ulceration of foals post-weaning has been associated with cribbing, treated and reduced by antacids, and resolves on ulcer healing (Nicol *et al.* 2002). The intragastric pH was raised from a mean of 3.19 ± 1.5 to 6.20 ± 0.93 in eight clinically ill, full term, neonatal foals by one dose of omeprazole (4 mg/kg BW orally; Javsicas & Sanchez 2008).

Although treatment with omeprazole (Franklin *et al.* 2008), cimetidine or ranitidine, is effective, *Helicobacter* infection plays no part in the equine syndrome (as *H. pylori* frequently does in man, where the organisms shrewdly protect themselves from acid by urease secretion with an acid pH optimum). *H. equorum* is able to colonize the equine lower bowel without apparent GI disease or other pathology (Moyaert *et al.* 2007). Despite the greater risk to concentrate-fed horses, both periprandial microbial activity and the pH of gastric contents are higher in concentrate-fed than in hay-fed animals. Moreover, the pH is lowest during a fast. Horses are continuous secretors of gastric acid and feed deprivation for repeated 24-h periods, alternating with 24-h periods of *ad libitum* access to hay, induces gastric squamous tissue ulceration, associated with an intragastric pH of 1.6 during deprivation, cf. 3.1 during hay feeding (Murray & Schusser 1993).

Digestion in the small intestine

The 450 kg horse has a relatively short small intestine, 21–25 m in length, through which transit of digesta is quite rapid, some appearing in the caecum within 45 min after a meal. Much of the digesta moves through the small intestine at a rate of nearly 30 cm/min. and its motility is under both neural and hormonal control. When a liquid marker was instilled into the stomach of a pony, 50% reached the distal ileum in 1 h, and by 1.5 h after instillation 25% was present in the caecum (Merritt 1992, personal. communi-

cation); transit of feed from stomach to caecum is much more rapid following a fast.

To estimate transit time monofilament polyester bags with a pore size of 41 µm containing 200 or 130 mg feed can be introduced into the stomach via a nasogastric tube and recovered in the faeces after transit times of 10–154 h. Transit times and digestibility in the small intestine are estimated following capture of the bags from near the ileocaecal valve with a magnet (Hyslop *et al*. 1998d). Caution should, however, be exercised in the interpretation of precaecal N-digestibility values, which can be considerably higher from the mobile bag cf. the ileal-fistula technique (Macheboeuf *et al*. 2003).

In consequence of the rapid transit of ingesta through the small intestine, it is surprising how much digestion and absorption occur there. Mechanisms of absorption have been studied by Cehak *et al.* (2009). Although differences in the composition of digesta entering the large intestine can be detected with a change in diet, it is a considerably more uniform material than that entering the rumen of the cow. This fact has notable practical and physiological significance in the nutrition and well-being of the horse. The material leaving the small intestine consists of fibrous feed residues, undigested feed starch and protein, microorganisms, intestinal secretions and cell debris.

Digestive secretions

Large quantities of pancreatic juice are secreted as a result of the presence of food in the stomach in response to stimuli mediated by vagal nerve fibres, and by gastric HCl in the duodenum stimulating the release of the polypeptide hormone secretin into the blood. In fact, although secretion is continuous, the rate of pancreatic juice secretion increases four- to five-fold when feed is first given. This secretion, which enters the duodenum, has a low order of enzymatic activity, although some active trypsin is present, but provides large quantities of fluid and sodium, potassium, chloride and bicarbonate ions. There is conflicting evidence for the presence of lipase in pancreatic secretions, and bile, secreted by the liver, probably has a greater, although different, influence on fat digestion. The stimulation of pancreatic juice secretion does not increase its bicarbonate content, as in other species. The bicarbonate content of digesta increases in the ileum, where it is secreted in exchange for chloride, so providing a buffer to large intestinal VFAs (see 'Products of fermentation', this chapter).

The horse lacks a gall bladder, but stimulation of bile is also caused by the presence of gastric HCl in the duodenum. Secretion of pancreatic juice and bile ceases after a fast of 48 h. Bile is both an excretion and a digestive secretion. As a reservoir of alkali it helps preserve an optimal reaction in the intestine for the functioning of digestive enzymes secreted there. In the horse, the pH of the digesta leaving the stomach rapidly rises to slightly over 7.0.

Carbohydrates

The ability of the horse to digest soluble carbohydrates and the efficiency of the mucosal monosaccharide transport systems of the small intestine have been established in a series of oral disaccharide and monosaccharide tolerance tests (Roberts 1975b). This ability is important to an understanding of certain digestive upsets to which the horse is subject.

A high proportion of the energy sources consumed by the working horse contain cereal starches. These have relatively long branched chains, the links of which are α-D-glucose molecules joined as shown in Figure 1.3. Absorption into the bloodstream depends on the disruption of the bonds linking the glucose molecules. This is contingent entirely upon enzymes secreted in the small intestine. These are held on the brush border of the villi in the form of α-amylase (secreted by the pancreas) and as α-glucosidases (secreted by the intestinal mucosa) (see Table 1.1).

The secretions of the pancreatic juice release sufficient oligosaccharides for further hydrolysis by the brush border enzymes at the intestinal cell surface (Roberts 1975a). Active carrier-mediated mechanisms then transport the final hexose products across the intestinal cell for uptake in the hepatic portal system. The digestive system can, however, be overloaded. Ponies weighing 266 kg BW were given 4 kg feed/day, as oat hulls : naked oats 2 : 1 (i.e. 1.33 kg naked oats). This led to changes in intracaecal fermentation, indicating that oat starch was reaching that organ, although the intracaecal pH did not decrease below 6.5. A comparison of unmolassed sugar beet pulp, hay cubes, soya hulls, or a 2 : 1 mixture of oat hulls : naked oats, indicate that beet pulp is subject to greater hind-gut fermentation than the other feeds (Moore-Colyer *et al*. 1997, Table 1.2). Starch fermentation in the hind-gut and its consequences are discussed below and in Chapters 2 and 11.

The concentration of α-amylase in the pancreatic juice of the horse is only 5–6% of that in the pig, whereas the concentration of α-glucosidase is comparable with that in many other domestic mammals. Thus, the addition of supplemental amylase from bacterial sources increases the digestion of ground maize (Meyer *et al.* 1993b) and

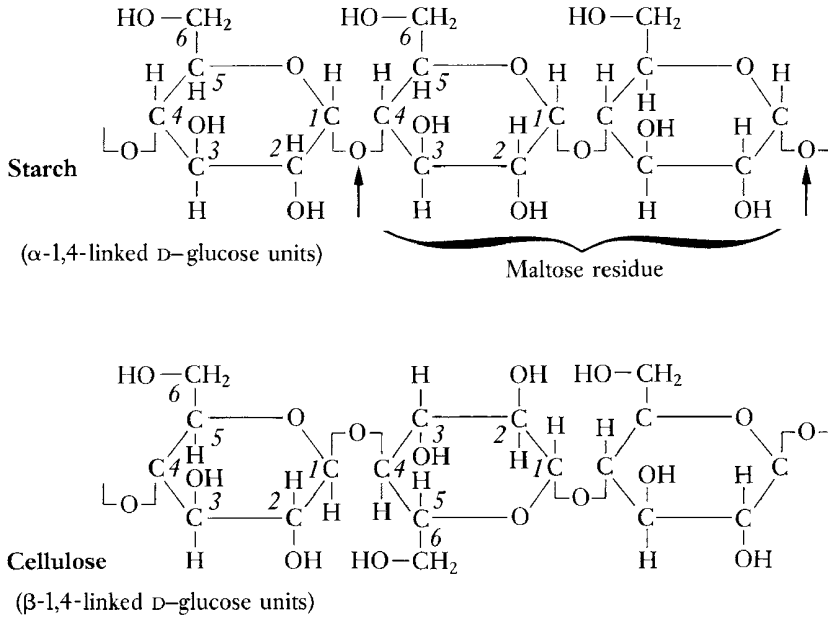

Figure 1.3 Diagrammatic representation of three glucose units in two carbohydrate chains (the starch granule also contains amylopectin, which has both 1–4 linkages and 1–6 linkages). *Arrows* indicate site of intermediate digestion.

Table 1.1 Carbohydrate digestion in the small intestine.

Substrate	Enzyme	Product
Starch	α-Amylase	Limiting dextrins (about 34 glucose units)
Limit dextrins	α-Glucosidases (glucoamylase, maltase and isomaltase)	Glucose
Sucrose	Sucrase	Fructose and glucose
Lactose	Neutral-β-galactosidase (lactase)	Glucose and galactose

Table 1.2 *In sacco* organic matter and crude protein (CP) disappearance from the DM or from the CP, in polyester bags during passage from the stomach to the caecum of Welsh cross ponies (Moore-Colyer *et al.* 1997).

	Component disappearance from the small intestine		
	Organic matter g/kg (DM)	Crude protein g/kg (CP)	Digestible crude protein g/kg (DM)
Sugar beet pulp	185	296	30
Hay cubes	294	521	52
Soya hulls	239	597	60
Oat hulls : naked oats, 2 : 1	337	771	54

elevates the glycaemic response to a triticale diet (Richards *et al.* 2004).

The α-glucosidases (disaccharidases) include sucrase, a disaccharidase present in concentrations five times that of glucoamylase and capable of digesting sucrose. Sucrase activity is highest in the proximal small intestine where its activity is similar to that reported for other non-ruminant species; by contrast, maltase activity is extremely high in comparison with that reported for other species. Maltase activity is expressed similarly in proximal, mid- and distal regions. D-glucose and D-galactose are transported across the equine intestinal brush border membrane by a high-affinity, low-capacity, Na^+/glucose cotransporter type 1 isoform, with rates of transport in the order: duodenum > jejunum > ileum (Dyer *et al*. 2002).

Another important disaccharidase in the intestinal juice is the β-glucosidase, neutral β-galactosidase (neutral or brush-border lactase), which is necessary for the digestion of milk sugar in the foal. This enzyme has a pH optimum of around 6.0. Whereas functional lactase is expressed all along the small intestine of the adult horse, the activity is less than that in the immature horse (Dyer *et al*. 2002), thus large quantities of dietary lactose may cause digestive upsets and adult horses are relatively lactose intolerant. Healthy horses of all ages can absorb a glucose : galactose mixture without any change in the faeces. The relative intolerance is due to reduced lactose hydrolysis and does not normally involve the monosaccharide transport systems or malabsorption. If a suckling foal, or one given cow's milk, lacks an active form of the enzyme, it suffers from diarrhoea. An oral lactose tolerance test (1 g/kg BW as a 20% solution) may be of clinical value to determine small intestinal mucosal damage in diarrhoeic foals, when the continued ingestion of lactose might be detrimental. The deficient digestion or malabsorption of carbohydrate, whether primary or secondary, can almost always be localized to a defect in the enzymic, or transport, capacity of the small intestinal surface cell (see Chapter 11).

Lindemann *et al*. (1983) gave adult horses lactose or maize starch at 2 g/kg BW daily before a feed of wheat straw, or mixed with a diet of concentrate. Apparent precaecal digestibility of lactose was 38% and 71% in the straw and concentrate periods, respectively, while the digestibility of starch in the same periods was 88% and 93%, respectively. For straw about 1.2 g and for concentrate 0.6 g lactose per kg BW flowed into the caecum daily, leading to higher caecal VFA concentrations and a lower caecal pH with lactose than with starch in the straw period. Ileocaecal water flow reached 16.5 and 8.2 kg/kg feed DM with lactose in the straw and concentrate periods, respectively, compared with 15.2 and 7.0 kg/kg with starch. The 38% and 71% apparent precaecal digestibility of lactose is partly a reflection of microbial fermentation in the ileum. Faecal looseness with the feeding of lactose is therefore explicable.

Proteins

The amount of protein hydrolyzed in the small intestine is about three times that in the stomach. Proteins are in the form of long folded chains, linked by amino acid residues. For proteins to be digested and utilized by the horse these amino acids must usually be free, although the gut mucosal cells can absorb dipeptides. The enzymes responsible are amino- and carboxy-peptidases secreted by the wall of the small intestine.

Fats

The horse differs from the ruminant in that the composition of its body fat is influenced by the composition of dietary fat. This suggests that fats are digested and absorbed from the small intestine before they can be altered by the bacteria of the large intestine. The small intestine is the primary site for the absorption of dietary fat and long-chain fatty acids. Bile, continuously draining from the liver, facilitates this by promoting emulsification of fat, chiefly through the agency of bile salts. Emulsification increases the fat–water interface so that the enzyme lipase more readily hydrolyses neutral fats to fatty acids and glycerol, which are readily absorbed, although a proportion of dietary fat is absorbed into the lymphatic system as finely emulsified particles of neutral fat – triacylglycerols (TAGs) – and transported as lipoprotein in chylomicrons. The horse digests fat quite efficiently and the addition of edible fat to the diet has merit, particularly when endurance work is concerned (see Chapters 5 and 9).

Medium-chain TAGs (carbon chain length of 6–12) are readily absorbed as such by horses, followed by portal transport to the liver, where they are metabolized to ketones (Jackson *et al.* 2001).

Feed modification to improve digestion

The extent of precaecal breakdown of cereal starch from pelleted diets is in the sequence: oats > barley > maize (Meyer *et al*. 1995; de Fombelle *et al*. 2003a,b). Varloud *et al*. (2003) and de Fombelle *et al*. (2003b) found that, although much starch disappeared (but was not absorbed) in the stomach, the amount escaping precaecal digestion increased with starch intake: by 20% from barley and 30% from maize when horses received 281 g starch/100 kg BW in a meal. Thus, in order to increase digestibility and

Table 1.3 Precaecal digestion of various sources of starch and digestion in the total GI tract of horses (Kienzle *et al.* 1992), (Rosenfeld & Austbø 2009)* and ponies (Potter *et al.* 1992a) (digested, g/kg intake).

	Starch intake, g/100 kg BW	Precaecal maize	Precaecal oats, barley*	Total oats	Total barley*	Precaecal sorghum	Total sorghum, maize*	Reference
Whole	200	289	835	—	—	—	—	Kienzle *et al.* 1992[1]
Rolled	200	299	852	—	—	—	—	Kienzle *et al.* 1992
Ground	200	706	980	—	—	—	—	Kienzle *et al.* 1992
""	—	663	949 705*	990	960*	—	910*	Rosenfeld & Austbø 2009
Crimped[2]	264^{CO} 295^{CS}	—	480	944	—	360	940	Potter *et al.* 1992a
Micronized	237MO 283^{MS}	—	623	938	—	590	945	Potter *et al.* 1992a

[1]Maize and oat digestibilities measured by these workers refer to preileal measurements.

[2]Dry rolled with corrugated rollers to crack the kernels. ^{CO}, crimped oats; ^{CS}, crimped sorghum; ^{MO}, micronized oats; ^{MS}, micronized sorghum.

*Refer to barley and maize data in their respective columns.

avoid fermentation of starch in the equine large gut, commercial cooking of cereals is of economic interest. The processes used include infrared micronization of cereals and expansion or extrusion of products – the resulting starch gelatinization enhances small intestinal digestion at moderate, or high, rates of intake. The extent of cooking by the extrusion process varies considerably amongst the cookers used. Nevertheless, while small-intestinal digestibility is influenced, even in adult horses, *total* digestibility is not improved. The digestibility of raw and cooked cereals is similar when the comparison is between carbohydrate consumed and loss in faeces. Thus, the extent of precaecal and pre-ileal digestion influences the proportions of carbohydrate absorbed as glucose, VFAs, and lactic acid. Oat starch generally has greater small-intestinal digestibility than starch from either maize or barley (Kienzle *et al*. 1992; Meyer *et al.* 1993b; de Fombelle *et al.* 2004; Rosenfeld & Austbø 2009; Table 1.3).

The proportion of starch digested is influenced not only by cereal processing, but also by the amount fed. When starch intake per meal is only 2 g/kg BW the pre-ileal starch digestibility of ground oats is over 95%, whereas at the other extreme, that of whole or broken maize is less than 30%. The grinding of cereals increases pre-ileal digestibility compared with whole, rolled or cracked grain, although the keeping quality, or shelf-life, of ground grain is relatively short (Meyer *et al*. 1995). Workers in Hanover found that there is a much greater increase in the postprandial concentration of organic acids, including lactate, and in acidity, in jejunal chyme when oats are fed rather than maize. Whether this is related to the putative 'heating' effect of oats, compared with other cereals, has not been established. Lactate and other organic acid production is increased, and the pH is decreased in the ileum and caecum when undigested starch reaches those regions. In order to avoid starch 'overload', and therefore excessive starch fermentation, especially in the large intestine, starch intake in horses given two to three meals daily, should be limited to 4 g/kg BW per meal (Potter *et al.* 1992a; see also Chapter 11, Laminitis). This limit is too liberal where there is risk of laminitis. The Texas group (Gibbs *et al*. 1996) have found that when N intake is less than 125 mg/kg BW, 75–80% of the truly digestible protein of soya-bean meal is digested precaecally, 20% is digested in the large intestine, and 10% is indigestible. Physical state also influences protein digestibility. Extruded and micronized oats, barley and maize have a higher total tract protein digestibility than ground and pelleted forms, while pelleted and micron-

Table 1.4 Effect of diet on the pH, production of VFAs and lactate and on microbial growth in the caecum and ventral colon of the horse 7 h after a meal.

Diet	pH	FA (mmol/L)				Total bacteria per (mL × 10^{-7})
		Acetate	Propionate	Butyrate	Lactate	
Hay	6.90	43	10	3	1	500
Concentrate plus minimal hay	6.25	54	15	5	21	800
Fasted	7.15	10	1	0.5	0.1	5

Note: Values given are typical, but all except the pH show large variations.

ized forms were shown to have the highest precaecal protein digestibility (Rosenfeld & Austbø 2009).

Nitrogen utilization

At high rates of protein intake more non-protein N (NPN) enters the GI tract in the form of urea. The N entering the caecum from the ileum is 25–40% NPN, varying with the feed type. Meyer (1983b) calculated that, in a 500 kg horse, 6–12 g urea N pass daily through the ileocaecal valve. The amount of N passing into the large intestine also varies with protein digestibility. At high intake rates of protein of low digestibility more N in total will flow into the large intestine, where it will be degraded to NH_3. From Meyer's evidence, about 10–20% of this total is urea N, as the daily range of total N flowing into the caecum is:

$$0.3\text{–}0.9 \text{ g N/kg BW}^{0.75}$$

N also enters the large intestine by local secretion, although the amount seems to be less than that entering through the ileocaecal valve and net absorption nearly always takes place. Nevertheless, net secretion can occur with low-protein, high-fibre diets.

Utilization of the derived NH_3 by gut bacteria is between 80% and 100%. Excessive protein intake must increase the burden of unusable N, either in the form of inorganic N, or as relatively unusable bacterial protein. This burden is influenced by feeding sequence. The provision of a concentrate feed 2 h after roughage, compared with simultaneous feeding, caused higher levels of free, particularly essential, amino acids in plasma 6–9 h later (Cabrera *et al.* 1992; Frape 1994). Plasma urea did not rise with dissociated, or separate, feeding, but rose continuously for 9 h after simultaneous feeding of roughage and concentrate. This indicates that mixed feeding led to a large flow of digesta N to the caecum, with much poorer dietary protein economy; interestingly, the separate feeding was in the reverse order to the standard practice of giving concentrates before roughage. More recently, Vervuert *et al.* (2009a,c) concluded that adding a fibre source to a cereal meal, or giving it before or after the cereal, prolonged precaecal digestion of starch, but did not influence precaecal starch digestibility or glucose and insulin responses.

THE LARGE INTESTINE

Grazing herbivores have a wide variety of mechanisms and anatomical arrangements for making use of the chemical energy locked up in the structural carbohydrates of plants. A characteristic of all grazing and browsing animals is the enlargement of some part of the GI tract to accommodate fermentation of digesta by microorganisms, producing steam-volatile FAs and lactate (Table 1.4).

More than half the dry weight of faeces is bacteria and the bacterial cells in the digestive tract of the horse number more than 10 times all the tissue cells in the body. No domestic mammal secretes enzymes capable of breaking down the complex molecules of cellulose, hemicellulose, pectin, fructo- and galacto oligosaccharides and lignin into their component parts, suitable for absorption, but, with the exception of lignin, intestinal bacteria do achieve this. The process is relatively slow in comparison with the digestion of starch and protein. This means that the flow of digesta has to be arrested for sufficient time to enable the process to reach a satisfactory conclusion from the point of view of the energy economy of the host animal. Physiochemical changes in the caecal contents over 24 h were reported by Tisserand *et al.* (1977a, b).

During the weaning and postweaning periods of the foal and yearling, the large intestine grows faster than the remainder of the alimentary canal to accommodate a more fibrous and bulky diet, hence energy digestibility of a mixed concentrate and forage diet increases at 5–8 months of age (Turcott *et al.* 2003).

At the distal end of the ileum, the large blind sack known as the caecum is about 1 m long in the adult horse and has a capacity of 25–35 L. At one end there are two

muscular valves in relatively close proximity, one through which digesta enter from the ileum and the other through which it passes from the caecum to the right ventral colon. The right and left segments of the ventral colon and the left and right segments of the dorsal colon constitute the great colon, which is some 3–4 m long in the adult horse, having a capacity more than double that of the caecum. The four parts of the great colon are connected by bends known as flexures. In sequence, these are the sternal, pelvic and diaphragmatic flexures (Figure 1.2). Their significance probably lies in changes in function and microbial population from region to region and they probably act as foci of intestinal impactions.

Digestion in the caecum and ventral colon depends almost entirely on the activity of their constituent bacteria and ciliate protozoa. In contrast to the small intestine, the walls of the large intestine contain only mucus-secreting glands, that is, they provide no digestive enzymes. However, high levels of alkaline phosphatase activity, known to be associated with high digestive and absorptive action, are found in the large intestine of the horse, in contrast to the large intestinal environment in the cat, dog and man.

The diameter of the great colon varies considerably from region to region but reaches a maximum in the right dorsal colon where it forms a large sacculation with a diameter of up to 500 mm. This structure is succeeded by a funnel-shaped part below the left kidney where the bore narrows to 70–100 mm as the digesta enter the small colon. The latter continues dorsally in the abdominal cavity for 3 m before the rectum, which is some 300 mm long, terminates in the anus (Figure 1.2).

Contractions of the small and large intestine

The walls of the small and large intestine contain longitudinal and circular muscle fibres which are essential:

- for the contractions necessary to move the digesta, by the process of peristalsis, in the direction of the anus;
- for allowing thorough admixture with digestive juices; and
- for bathing the absorptive surfaces of the walls with the products of digestion.

During abdominal pain these movements stop so that the gases of fermentation accumulate.

Passage of digesta through the large intestine

Many digestive upsets are focused in the large intestine and therefore its function deserves discussion. The extent of intestinal contractions increases during feeding – large contractions of the caecum expel digesta into the ventral colon, but separate contractions expel gas, which is hurried through much of the colon. The reflux of digesta back into the caecum is largely prevented by the sigmoid configuration of the junction. Passage of digesta through the large intestine depends on gut motility, but is mainly a function of movement from one of the compartments to the next through a separating barrier. Considerable mixing occurs within each compartment, but there seems to be little retrograde flow between them. The barriers are:

- the ileocaecal valve already referred to;
- the caecoventral colonic valve;
- the ventrodorsal colonic flexure (pelvic flexure), which separates the ventral from the dorsal colon; and
- the dorsal small colonic junction at which the digesta enter the small colon.

Resistance to flow tends to increase in the same order, that is, the last of these barriers provides the greatest resistance (see Chapter 11). This resistance is much greater for large food particles than for small particles. In fact, the delay in passage for particles of 2 cm length can be more than a week. Normally the time taken for waste material to be voided after a meal is such that, in ponies receiving a grain diet, 10% is voided after 24 h, 50% after 36 h and 95% after 65 h. Mean retention time (MRT) in 18-month-old horses given a hay and concentrate diet was shown to be 42.7 and 33.8 h, respectively, for the solid and liquid phases of digesta (Chiara *et al*. 2003), while for a hay-based diet in mature heavy horses it was 21–40 h, decreasing within this range as intake increased (Miraglia *et al*. 2003). Within moderate variations of intake the digestibility of the diet was constant. A large decrease in MRT was associated with a lower digestibility coefficient.

Most digesta reach the caecum and ventral colon within 3 h of a meal, so that it is in the large intestine that unabsorbed material spends the greater proportion of time. The rate of passage in domestic ruminants is somewhat slower, and this partly explains their greater efficiency in digesting fibre. Nevertheless, the horse utilizes the energy of soluble carbohydrates more efficiently by absorbing a greater proportion of sugars in the small intestine.

In the horse, passage time is influenced by the physical form of the diet; for example, pelleted diets have a faster rate of passage than chopped or long hay, and fresh grass moves more rapidly than hay. Work at Edinburgh (Cuddeford *et al*. 1992) showed that fibre was digested more completely by the donkey than by the pony, which in turn digested it more effectively than the TB. These differences are probably due, in large measure, to the rela-