



Literature Review

Feeding strategy and water homeostasis in equids: the role of the hind gut

J. C. Sneddon* & R. A. Argenzio†

**School of Biological and Earth Sciences, Liverpool John Moores University, Liverpool L3 3AF, U.K.*

†Department of Anatomy, Physiological Sciences and Radiology, College of Veterinary Medicine, North Carolina State University, North Carolina 27606, U.S.A.

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Ungulates are the most abundant and diverse group of mammals in arid areas. Non-ruminants, or hind gut fermenters, constitute only three extant families (horses, rhinos and tapirs); ruminants are far more dominant and form the remainder.

Much of perissodactyl evolution occurred during the Eocene, Oligocene and Miocene eras when arid savannah-type conditions prevailed. Adoption of hind gut fermentation as a digestive strategy early on in their evolution confined equids to feeding on coarse grassland, characterized by high fibre and low protein content. Hind gut fermentation of such vegetation, combined with high rates of voluntary food intake and passage of digesta, gave equids an advantage over ruminants of similar body size in digestive efficiency on high fibre grasses. This digestive strategy explains the present day ecological niche of wild equids. The large volume of water required for microbial fermentation of fibrous vegetation constitutes a fluid reservoir which could act as a potential source of fluid for the remaining body fluid pools during periods of dehydration. Evidence for such a role of the gastrointestinal tract in water homeostasis has recently been reviewed for ruminants. In this review, feeding and digestive strategies of ruminants and hind gut fermenters are compared with respect to body size. Evidence for the existence of a gastrointestinal fluid reservoir in equids is then provided. Finally, an overview of the physiological mechanisms associated with the movement of fluid across the hind gut epithelium in equids is given.

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Introduction

Horses (Equidae) are perissodactyls, which together with artiodactyls, predominantly ruminants, form the Ungulata or hoofed mammals. Ungulates are the most abundant

and diverse group of mammals in arid areas (Van Soest, 1982, 1996; Wilson, 1989). Water homeostasis in ruminants has recently been reviewed by Silanikove (1994). Use of the gastrointestinal tract as a source of water to maintain body water homeostasis is a common strategy employed by desert-adapted ruminants. Use of the same strategy by hind gut fermenters was briefly mentioned (Silanikove, 1994). In a review of water homeostasis in Arab-based horses, this strategy was also mentioned as an important but neglected area of study (Sneddon, 1993).

Fluid homeostasis is inseparable from feeding and digestive strategy, and thus both these areas will be reviewed in some detail. Other topics to be covered include current theories on neural and hormonal mechanisms associated with the movement of fluid across the hind gut.

Evolution of Perissodactyla

Perissodactyla originated as a group in the late Paleocene (65–53 million years B.P.), when they were dominant over Artiodactyla in terms of numbers and diversity in medium- to large-sized herbivore niches. The 'Dawn Horse,' *Eohippus*, evolved 55 million years ago. This animal was the size of a small dog, and from evidence of molar enamel patterns, was thought to be a selective shoot and fruit eater in the then tropical forests of North America (Janis, 1976). Evolution and diversification of perissodactyl species continued throughout the Eocene and early Oligocene (36.6–23 million years B.P.). During the Eocene, the climate in both North America and Eurasia was apparently humid and tropical, but with the start of the Oligocene drier cooler conditions started to prevail. Vegetation was dominated by grassland savannahs (Janis, 1976; Van Soest, 1982), and many perissodactyl species showed an increase in body size (Janis, 1976). By 25 million years ago, the equid genus *Meryhippus* had evolved, characterized by a considerable increase in body size and lengthening of the third metacarpal bone. This animal was adapted to live as a fast-moving grazer in the plains ecosystem. A third and final expansion of evolution of perissodactyls occurred in the Miocene (23.7–5.3 million years B.P.), when similar environmental conditions prevailed. Today, all but three groups of perissodactyls, equids, the rhinos and tapirs, are extinct (Janis, 1976).

The artiodactyls gradually gained superiority in diversity over perissodactyls throughout the Oligocene and continued as the dominant group throughout the Tertiary period, at least in terms of species diversity. A cooler climate produced vegetation dominated by grasslands low in lignin and high in cellulose (Janis, 1976). Reasons for the rise in artiodactyl diversity have thus centred around the differing anatomy of the digestive system. Ruminants do not have to chew their food thoroughly at the site of feeding, and are thus theorized to be better able to avoid predation (Janis, 1976).

A more plausible influence on the successful radiation of artiodactyls in the size range overlapping with that of wild equids is their successful colonization of a range of vegetational niches. These were made available by the concurrent diversification of grassland plants containing cell wall material most suited to the retentive nature of rumination. The Artiodactyla had evolved the optimal body size range for rumination of this material and hence had the opportunity to diversify into a range of new habitats (Janis, 1976; Van Soest, 1982, 1996).

The wear patterns of enamel on molar teeth have suggested that equids were confined to a relatively high fibre diet, i.e. a diet high in polysaccharides and lignin, early in their evolution. This also suggests that equids adopted hind gut fermentation as a digestive strategy early in their evolution (Janis, 1976). This digestive strategy is characterized by high voluntary food intake and rate of passage of feed, together with a low digestive efficiency (Demment & Van Soest, 1985; Van Soest, 1996).

Given the small body size of equid ancestors, it is doubtful whether hind gut fermentation evolved as a digestive strategy whose prime function was to provide energy after digestive processes in the small intestine were complete (Demment & Van Soest, 1985). Extant small herbivores employing hind gut fermentation commonly practise coprophagy, which increases digestive efficiency, particularly by exposing partially fermented material to digestive processes in the small intestine. Coprophagy also extends the range of digestible plant species available to small herbivores — an important advantage when the common availability of plants high in fibre and low in digestibility is considered. Equids evolved from small animals, adapted to feed selectively on rapidly digested (low fibre) vegetation. This digestive strategy presumably incorporated a large component of small intestinal absorption/coprophagy, as small animals require a high rate of passage of nutritious food to meet their high metabolic needs (Kleiber, 1961; Demment & Van Soest, 1985; Van Soest, 1996).

The evolution of equids has been characterized by an increase in body size and a move from tropical forest to an arid plains ecosystem as a feeding habitat. It is probable that the hind gut only assumed a nutritional role of any significance, in the absence of coprophagy, when body size had become large enough to require significant energy input from the fermentation of dietary fibre. As water is required for fermentation processes, and given that fibre has a high water-holding capacity (Van Soest, 1996), it is probable that physiological mechanisms linking the gut to water homeostasis evolved as these larger animals became adapted to function in the aridity of the plains ecosystem.

In summary, it appears that body size at the time of adopting a fibrous diet is the critical factor in determining the type of digestive system that will be evolved (Van Soest, 1982, 1996). Hind gut digestion is superior to rumen digestion for dealing with high fibre herbage, provided intake is not limited by the quantity of herbage available, i.e. voluntary food intake and rate of passage of digesta are not limited by availability of fodder. The equidae continued to be successful in the face of artiodactyl radiation because they could maintain themselves on a herbage more fibrous than could be tolerated by a ruminant of similar body size (Janis, 1976; Van Soest, 1996).

Gross anatomy of the gastrointestinal tract in relation to digestive function

Retentive mechanisms have been described as the most important factor determining intake and digestion of feed (Demment & Van Soest, 1985). The hind gut of equids has evolved primarily as a storage organ for digesta for further fermentation and for the retrieval of water and inorganic ions secreted into the upper digestive tract (Argenzio, 1975). To this end, the hind gut constitutes about 75% of total gastrointestinal volume (Argenzio, 1975; Maloiy & Clemens, 1980). The caecum and large intestine are voluminous, sacculated and lined with columnar epithelium. Longitudinal muscle bands known as haustra or 'taeniae' delay the rate of passage of digesta, through convergence towards valves and sphincters (Burns & Cummings, 1993).

In terms of nomenclature, the ventral and dorsal colons are often termed the proximal colon, and the small colon (transverse colon to rectum) the distal colon. The proximal colon, correctly termed the ascending colon, contains by far the greatest volume (Fig. 1).

Up to half the energy requirements can be met by nutrients absorbed by the caecum and colon, as only 25% of basal energy is supplied by glucose on a high grain diet (Argenzio & Hintz, 1972). The rate of passage of digesta must therefore be limited so as to provide optimal conditions for fermentation. The ventral and dorsal colon are the primary sites of retention. Apart from the above-mentioned taeniae, barriers are the ileo-caecal, the caecal-ventral colonic, the ventro-dorsal colonic and the dorso-small

colonic junctions. In the small (distal or transverse) colon, there are definitive faecal nodules; this is where 'fine tuning' of water and electrolyte absorption occurs, as in the distal convoluted tubule and collecting duct of the kidney (Argenzio, 1975). All these barriers act to decrease aboral flow of digesta.

The gross nature of the retentive mechanisms in the equid hind gut has been recently reviewed by Björnhag (1989). In brief, they allow coarse feed residues of low digestibility to pass rapidly through the gastrointestinal tract, while passage of the smaller more easily digestible particles is delayed. This enhances digestive efficiency as well as guaranteeing minimal loss of micro-organisms with faeces. The dorsal part of the proximal colon holds more fluid contents than the ventral part. The fluid contents of the right dorsal component of the proximal colon move dorsally to the distal or small colon, where muscular contraction forces fluid back in a retrograde direction, into the right dorsal colon. Water soluble substances and micro-organisms accumulate in the right dorsal colon, and remain at much higher concentrations than are found in the ventral colon, caecum or distal colon (Björnhag, 1989). In addition, flow of digesta is of course slowed at several narrowed segments of the colon mentioned previously, particularly at the junction between the ventral and dorsal components of the proximal colon, and at the pelvic flexure. In the case of the pelvic flexure, complex motility patterns have been recorded with a distinct regional distribution, involving vasoactive intestinal polypeptide reactive neurones.

Dense networks of Auerbach's plexus are found at the pelvic flexure — this point has been shown to be the site for a pacemaker whose electrical activity initiates propagations in both directions, and where the circular and longitudinal muscle coats of equid 'midcolon' were found to be directly electrically coupled and act in concert

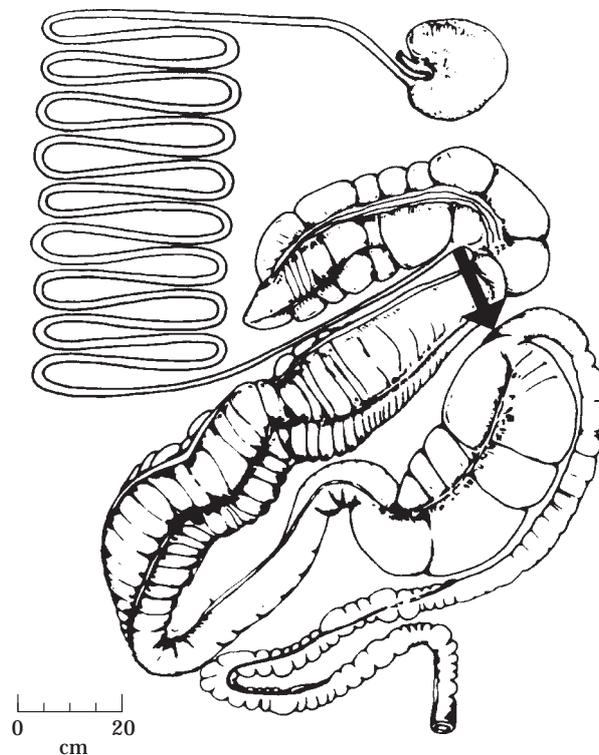


Figure 1. Schematic representation of digestive tract of a pony. Large (ascending) colon is arranged in right and left ventral colons, and left and right dorsal colons, which terminate at the origin of the small colon. Arrow indicates termination of ascending colon (Stevens, 1996).

(Sellers *et al.*, 1982; Ross *et al.*, 1986). The retropulsive contractions keep the caecum, the right ventral and left ventral divisions of the colon filled, imposing a time delay for fermentation of cellulose and bacterial protein synthesis. In the proximal (ascending) colon, fluid content is similar to that of the caecum and motor activity is dominated by antiperistaltic movements. In the distal colon, faecal nodules first appear and peristaltic contraction predominates (Sellers *et al.*, 1979, 1982).

In more recent studies the neurons of the pacemaker have been found to exhibit vasoactive intestinal polypeptide-like activity, and are thought to participate in the initiation of the propulsive/retropulsive contraction waves which emanate from the location of the pacemaker. These events are believed to lend a sphincter-like capacity to the pelvic flexure (Burns *et al.*, 1996). In addition, it has been shown that the taeniae of the colon are involved in the propagation of myoelectrical signals involved in peristalsis (Burns & Cummings, 1993).

In summary, the gastrointestinal anatomy of equids has evolved to achieve a balancing act between a high rate of passage of digesta, and sufficiently efficient rates of energy extraction from food of low digestibility. Retentive mechanisms required for this balance evolved early in equid evolution when small body size (high metabolic rate) was a driving force for enhancing digestive efficiency (Björnhag, 1989). These retentive mechanisms, collectively known as colonic separation mechanisms, were a prerequisite for caecal hypertrophy (Björnhag, 1989).

Feeding strategies and digestive processes — legacies of arid ecosystems

As stated above, a considerable amount of the evolution of ruminants and hind gut fermenters occurred in dry climates when grassland savannas were the dominant form of vegetation (Janis, 1976; Van Soest, 1982, 1996; Demment & Van Soest, 1985). Consequently, wild and domestic ungulates are the most abundant and widely distributed large mammals in tropical and arid areas today, where similar ecosystems prevail (Van Soest, 1982; Wilson, 1989; Silanikove, 1994). Semi-arid and arid regions of the world are characterized by low and erratic rainfall and vegetation having a high fibre content, a low protein content, and low digestibility for much of the year (Demment & Van Soest, 1985; Wilson, 1989; Louw, 1993). The successful adaptation of ungulates to arid regions is thus largely due to their ability to digest this vegetation, with the assistance of microbial fermentation. The gastrointestinal function of ungulates has thus evolved to ferment fodder containing high amounts of cellulosic carbohydrates and lignin for much of the year (Janis, 1976; Parra, 1978; Demment & Van Soest, 1985; Louw, 1993). In addition, the relatively high water content of the gastrointestinal tract which is required for fermentation purposes (Silanikove, 1994; Meyer, 1996*a,b*) serves as a water reservoir during frequent bouts of dehydration while animals are ranging for fodder. This phenomenon has been thoroughly reviewed in ruminants (Silanikove, 1994) and forms the emphasis of this review for hind gut fermenters.

An understanding of feeding strategy and digestive processes is a prerequisite for understanding the role of the gastrointestinal tract in water homeostasis.

In terms of feeding strategy, limitations to the adaptations of ungulate grazers within a given ecological niche are set by availability of forage of requisite cell wall quality (Van Soest, 1982, 1996). In addition, differences in digestive efficiency between and within ruminants and non-ruminants are due to *gastrointestinal capacity* for fermentation and *proportion of the diet catabolized* in the fermentation process.

Fermentation contents in kg (X) are related to body size in kg (Y) by the following equation:

$$\log Y = 1.032 \log X - 0.936 \quad (r = 0.99, N = 59)$$

Regression slopes for ruminants and non-ruminants are not significantly different. The slope for ruminants is 1.04 (Van Soest, 1982; Demment & Van Soest, 1985).

Several studies point to similarities in gastrointestinal capacity between hind gut fermenters and ruminants. Determination of gut capacity using evacuation of total gut contents (kg) has revealed no major differences between fore and hind gut fermenters in terms of gut capacity as a proportion of body weight (Parra, 1978). In addition, a number of studies have revealed that the fermentation contents (% body weight) of hind gut fermenters compared with those of fore gut fermenters of comparable size ranged between 10–12% of body weight (Adolph, 1949; Parra, 1978; Van Soest, 1982; Demment & Van Soest, 1985). In a recent large study on horses a value of $13.5 \pm 4.0\%$ was obtained (Meyer, 1996a).

The evolutionary influences of body size, gut architecture and ecological niche on the adoption of a cellulose-based diet have already been mentioned (Janis, 1976; Van Soest, 1982; Demment & Van Soest, 1985). The influence of such phenomena on digestive efficiency now needs consideration.

The proportion of diet catabolized differs between ruminant species (Van Soest, 1982, 1996; Demment & Van Soest, 1985), and between ruminants and hind gut fermenters (Parra, 1978; Van Soest, 1982; Demment & Van Soest, 1985). Optimum digestion of cellulosic carbohydrates by ruminants depends on selective retention of fodder by the fermentation chamber—failure of retention promotes faecal loss of nutrients (Van Soest, 1982). Small ruminants and hind gut fermenters can counteract this by practising coprophagy on low fibre diets. Outwith coprophagy, their limited gastrointestinal and thus fermentation capacity limits their capacity for expanding their ecological niche to feed on more common low quality feeds (Van Soest, 1996). With increased body size, all herbivores have developed the capacity for increasing digestibility of the slowly digestible fraction of forage: ruminants have achieved retentive mechanisms at smaller body sizes than hind gut fermenters, and in so doing have limited feed intake (Demment & Van Soest, 1985; Van Soest, 1996). This has put them at a disadvantage to hind gut fermenters of similar body size in grazing situations where the availability of high fibre feed is not limiting. In other words, equids have responded to competition with ruminants by increasing their body size to a point where they could eat high fibre diets at a higher rate. This was possible as feed intake was not influenced by the rate of particle size breakdown (Demment & Van Soest, 1985; Van Soest, 1996).

Equids are in turn confined to this niche; indeed, all perissodactyls are still largely confined to continual and selective grazing of non-fruiting high fibre parts of grasses because they developed their digestive strategy early in their evolution (Janis, 1976; Demment & Van Soest, 1985; Van Soest, 1996). In addition, the small diversity of body size in wild equid species may also be explained by the differing digestive strategies of equids and ruminants. In a competitive situation within a grazing community there may be room for large numbers of individuals in a specialized niche involving digestion of high fibre vegetation, but there would be little room for diversification into numerous species filling other ecological roles within this niche (Janis, 1976).

It has been found that ruminants and equids are equally effective in digesting low fibre feeds. As the fibre concentration of the ration increases, digestion of organic matter decreases in both species, but relatively more so in equids due to increased rate of passage (Olsson & Ruudvere, 1955).

Moving from gross digestive strategy issues to fermentation chemistry, there appears to be no essential difference between hind gut and ruminal digestion of celluloses or protein in biochemical terms. Short chain volatile fatty acids (SCFA) are produced from the fermentation of celluloses in a similar manner to those produced in ruminants on similar diets (Parra, 1978; Argenzio, 1991; Julliand, 1992; Stevens, 1996).

Amino acid absorption is confined to the small intestine in both ruminants (McDonald *et al.*, 1973) and hind gut fermenters (Argenzio, 1975; Stevens, 1996). Nitrogen absorption across both the rumen and hind gut is thus confined to ammonia absorption (McDonald *et al.*, 1973; Argenzio, 1975; Stevens, 1996), with recycling of ammonia occurring in both cases (McDonald *et al.*, 1973; Izraely *et al.*, 1989; Pearson *et al.*, 1992). In the case of the hind gut fermenter, ammonia is derived from microbial protein and additionally from nitrogenous compounds from the small intestine (Argenzio, 1975; Drochner & Meyer, 1991; Stevens, 1996). This additional source of protein from the small intestine has been linked to greater efficiency in the degradation (50 vs. 20%) and absorption (0.2 vs. $0.1 \text{ mg N kg}^{-0.75} \text{ day}^{-1}$) of nitrogen in horses over ruminants (Prior *et al.*, 1974; Drochner & Meyer, 1991).

The reasons for similar digestive efficiency between ruminants and hind gut fermenters under *ad libitum* feeding conditions are thus associated with greater voluntary feed intake and rate of gastrointestinal passage on high fibre diets by the latter, with more efficient use of low protein content (Janis, 1976; Pearson *et al.*, 1992).

In terms of adaptation to arid environments, donkeys appear to be in a league of their own in that both dry matter intake per unit body mass and digestive efficiency on high fibre diets are superior to that of other equids, under dry grazing conditions (Izraely *et al.*, 1989; Suhartanto *et al.*, 1992). This enhanced digestive efficiency has been attributed to higher dry matter intake, slower gastrointestinal transit time, and longer retention times of food residues on high fibre diets, and enhanced recycling of urea (Pearson & Merritt, 1991; Tisserand *et al.*, 1991; Pearson *et al.*, 1992; Mueller *et al.*, 1994; Cuddeford *et al.*, 1995). Although donkeys were observed to spend the bulk of total feeding time grazing grasses under range conditions, during dry periods they were superior to cattle at increasing intake of more nutritious dicotyledonous plants. There was also evidence of increased dry matter intake during dry periods, when output of faecal dry matter was increased by 35% (Rutagwenda *et al.*, 1990). Under conditions where the gastrointestinal tract is full of poor quality fodder, the proportion of total body weight occupied by the gut can double. The gastrointestinal tract of donkeys under extensive grazing situations in southern Africa accounts for up to 21% of body weight (pers. obs.; $N = 11$). This could be attributed to the poor quality of the diet, which required prolonged retention time for fermentation. Similar feeding strategies have been observed in camels (Rutagwenda *et al.*, 1990).

In summary, given the broad similarities in digestive biochemistry between hind gut fermenters and ruminants (Stevens *et al.*, 1979; Stevens, 1996), rate of passage does seem to have a major influence on digestive efficiency on high fibre diets. It appears that the ruminant gut architecture imposes more restrictions on passage of digesta than is seen in the non-ruminant herbivore. Ruminants thus display more selective retention of solids than is seen in the equid lower tract, and their ability to consume large quantities of fibrous feeds is lessened (Uden *et al.*, 1982; Demment & Van Soest, 1985).

The great enlargement of the caecum and colon, characteristic of hind gut fermenters, appears to provide an adequate surface area for the absorption of fermentation products. In addition, unlike ruminants, hind gut fermenters are not limited by a need to reduce particle size for passage out of the reticulo-rumen (Uden *et al.*, 1982). It seems that the strategy of hind gut fermenters is to maintain the same absorption per unit time as a ruminant by having a greater intake and a shorter passage time at the expense of a reduced efficiency of fibre digestion. This strategy may be essential for the use of herbage above a given fibre content level (Van Soest, 1982, 1996).

The role of gastrointestinal tract as a fluid reservoir during dehydration and rehydration in hind gut fermenters

Water homeostasis is inseparably linked with gastrointestinal function in ruminants and hind gut fermenters, as water is required for the operation of the digestive processes mentioned above. To this end, water constitutes up to 85–90% of total gastrointestinal fill in ruminants and hind gut fermenters (Silanikove, 1994; Meyer, 1996*a,b*). In studies on equids *post mortem*, the water content of the gastrointestinal tract has been found to constitute a sizeable fluid reservoir: about 20% of the total body water pool, in fully hydrated animals (Kasirer-Izraely *et al.*, 1994; Meyer, 1996*a,b*).

The contribution of this sizeable gastrointestinal fluid reservoir to maintenance of the body fluid pool during periods of dehydration is well documented for ruminants (Silanikove, 1994). It has been estimated from fluid pool marker studies that the fluid from the gut can bolster declines in the plasma, interstitial and intracellular fluid pools by decreasing by between 20–80% of its original volume, depending on the species and the severity of dehydration (Macfarlane *et al.*, 1963; Denny & Dawson, 1975; Silanikove, 1994).

A similar function of the gastrointestinal tract has been postulated for horses (Tasker, 1967; Sneddon *et al.*, 1993*a*). There are a few direct observations in the literature which support this hypothesis.

Experimental observations have established that a sizeable fluid reservoir is retained in the gastrointestinal tract during periods of dehydration in donkeys (Maloiy *et al.*, 1978; Kasirer-Izraely *et al.*, 1994) and in horses involved in a study on reduced feed intake (Meyer, 1996*b*). In the latter study, fasting for up to 4 days did not significantly reduce gastrointestinal fill. In addition, horses have been observed to behave normally throughout 8 days of water and feed restriction, when it was assumed that the gastrointestinal fluid was drawn upon to maintain plasma volume (Tasker, 1967). The enigma of water retention in the gastrointestinal tract during periods of dehydration in equids may be explained by a significant reduction in SCFA in the digesta, with water reduction, as SCFAs are involved in sodium and water reabsorption, as well as being the main energy supply for colonocytes (Meyer, 1996*b*).

Fluid movement across the gastrointestinal wall during dehydration has been described in a few studies.

In studies where donkeys were subjected to 4 days or 20% dehydration, followed by investigation *post mortem*, the gastrointestinal fluid pool was estimated to drop by up to 40% of its original volume (Maloiy *et al.*, 1978; Kasirer-Izraely *et al.*, 1994). Similarly, in a 12% (72 h) dehydration study on horses *in vivo*, the gastrointestinal fluid pool was estimated to diminish by between 40–50% while other body fluid pools are maintained (Sneddon *et al.*, 1993*a*). In this study, there was also hormonal evidence for controlled release of gastrointestinal water from the hind gut during the dehydration process (Sneddon *et al.*, 1993*b*). There was evidence of aldosterone-mediated absorption of fluid from the gut (Clarke *et al.*, 1988) when plasma aldosterone concentrations showed a significant upsurge between 48–72 h dehydration. This implied that the hind gut constituted a sizeable aldosterone-mediated fluid reservoir in dehydrating horses (Sneddon *et al.*, 1993*a*). When these dehydrated horses were allowed access to water, there was continued evidence for aldosterone-mediated controlled release of fluid from the gastrointestinal tract so as to maintain plasma volume, and prevent water toxicity and osmolysis of erythrocytes (Sneddon *et al.*, 1992). These physiological mechanisms are similar to those displayed by arid-adapted ruminants (Silanikove, 1994).

Studies on the gastrointestinal fluid reservoir in donkeys *post mortem* have also revealed sensitive regulation of fluid movement across the hind gut wall during periods of rehydration, after water deprivation (Kasirer-Izraely *et al.*, 1994). These authors compared the hind gut to the rumen of the Bedouin goat in terms of its capacity to store and gradually release water.

Mechanism of ion and water absorption in the hind gut

Assignment of the historical role of the hind gut to the reabsorption of water and electrolytes escaping from the small intestine is an oversimplification. The primary role is microbial digestion of soluble and insoluble carbohydrate and rapid absorption of SCFAs and other end products of fermentation (Argenzio *et al.*, 1974; Argenzio, 1975; Maloij & Clemens, 1979, 1980). SCFAs in turn exert a primary influence on colonic ion transport. The capacity of the hind gut in perissodactyls places considerable fluid and electrolyte homeostatic problems on the cardiovascular system as well as on the gastrointestinal tract. It has been estimated that the large intestine receives a volume equivalent to the extracellular fluid volume from the small intestine per 24 h, and that 95% of ileal outflow plus net fluid secretion is absorbed under conditions of euhydration (Argenzio *et al.*, 1974).

A considerable volume of fluid is selectively absorbed from the large intestine. However, it should be remembered that the small intestine constitutes a much more permeable barrier to ion and water absorption, and is a major site of both secretion and absorption of water and ions in mammals. Fine tuning of water homeostasis is carried out by the kidney, where there appears to be considerable convergent evolution in specialization of renal epithelial function.

In the pony, control of transmucosal fluid movement is critical because of a need to provide a fluid buffered environment for microbial growth while maintaining systemic fluid homeostasis for the animal (Argenzio, 1975). It thus follows that an important function of the equid large intestine is its capacity for storage and absorption of large volumes of fluid.

Figure 2 represents the gastrointestinal volumes and daily movement of water through the large intestine of a 160 kg pony (Argenzio *et al.*, 1974). On a conventional diet, large cyclic exchanges of water between digesta and plasma were observed, associated with meal-induced osmotic gradients. Interestingly, these observations are absent in frequently fed animals, as were diurnal variations in the renin-angiotensin-aldosterone system associated with enhanced sodium and fluid movement from the gut to the plasma (Clarke *et al.*, 1988).

Cellular mechanisms of colonic ion and short chain fatty acid absorption

In the non-ruminant herbivore the caecum and proximal colon are the chief sites of microbial digestion and operate under conditions similar to those of the ruminant forestomach: delayed transit of digesta, neutralization or removal of the end products of fermentation, dilution of accumulating end products to prevent feedback inhibition on their production. The last two phenomena depend on ion transport mechanisms.

Mechanisms of Na^+ transport differ in the equid proximal and distal colon and are related to the respective functions of SCFA production and absorption, and Na^+ and water conservation. In the proximal colon, Na^+ is absorbed by an electroneutral Na^+-H^+ exchange process located on the apical membrane of the absorptive cells. This process is indirectly coupled to a neutral $\text{Cl}^--\text{HCO}_3^-$ exchanger; however, these mechanisms can operate independently, thereby adjusting the luminal pH. Both electroneutral exchangers are driven by the hydration of intracellular metabolic CO_2 , as mammalian colonocytes contain high levels of carbonic anhydrase (Berne & Levy, 1992). More importantly, the operation of the Na^+-H^+ exchanger contributes to SCFA absorption by protonating the ionized form of the weak acid thereby conferring lipid solubility and rapid absorption across the apical membrane. Hydrogen ions are also provided by hydration of CO_2 in the luminal contents, which ensures a source of rapidly absorbable undissociated SCFA (Fig. 3). Thus, even in the absence of net Na^+ absorption, this latter process allows SCFA to be absorbed independently of Na^+ , and

was proposed as a mechanism for SCFA absorption by the rumen epithelium nearly 40 years ago by Ash & Dobson (1963).

The uncoupling of SCFA absorption from Na^+ absorption has important functional consequences. As shown in Fig. 3, hydration of CO_2 provides both a HCO_3^- and H^+ ion; the protonated SCFA is absorbed, leaving the HCO_3^- behind. The process therefore behaves functionally as an SCFA-HCO_3^- exchanger and as such does not contribute to osmotic water absorption. Consequently, the SCFA can be absorbed in the absence of net water absorption, which intuitively prevents the dehydration and impaction of colonic contents during periods of rapid fermentation. It is interesting to note that, when extrapolated to the surface area of the entire colon, net ion flux accounts for $\pm 25\%$ of net water flux (Clarke, 1989). In the horse, this mechanism is of fundamental importance because the junction between the ventral and dorsal colons is the most common site of impaction in this species.

As discussed below, the Na^+-H^+ exchanger is controlled both by aldosterone and by local paracrine mediators. The latter respond to local environmental conditions and can therefore adjust the luminal pH and fluidity of digesta. In euvoletic animals, this paracrine control can even override aldosterone action thereby preventing excess fluid absorption in response to the systemic hormone.

In contrast to the proximal colon, Na^+ absorption in the distal (small) colon is entirely electrogenic and amiloride-sensitive. Therefore, this process is not coupled to SCFA absorption, nor to acid/base adjustments. It is solely concerned with Na^+ and water conservation and is controlled exclusively by aldosterone. Thus, it is a powerful mechanism for Na^+ and water retrieval, and is placed in a position distal to the major site of fermentation. The electrogenic Na^+ absorptive process also results in an

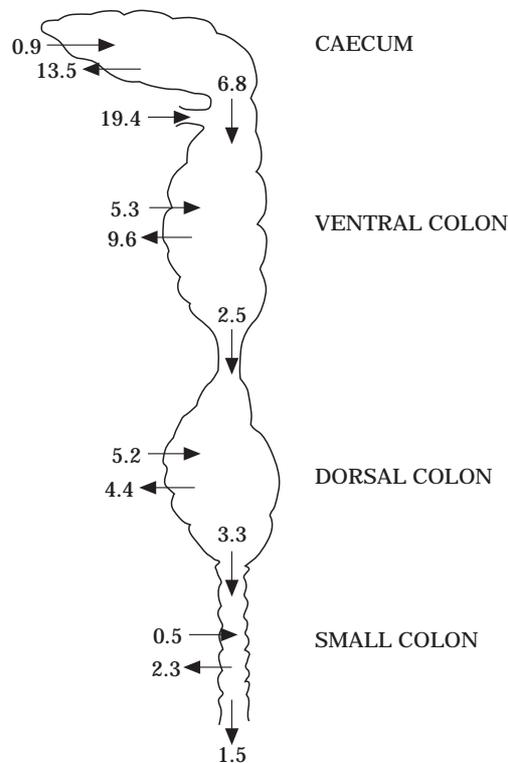


Figure 2. Net movement of water (l day⁻¹) through the large intestine of a 160kg pony (Argenzio *et al.*, 1974).

The enteric nervous system can also provide control independent from the central nervous system. Integrated local circuits can drive such fundamental functions as peristalsis and secretory activity without extrinsic command. Thus, intrinsic sensory neurones, responding to the local environment, control much of the activity during a feeding cycle. For example, cholinergic and VIPergic motor neurons inhibit the action of the neutral $\text{Na}^+ - \text{H}^+$ exchanger on the absorptive cells and induce Cl^- secretion in the crypt cells. Neurones containing opioid peptides, somatostatin or neuropeptide Y have the opposite effect (Cooke & Reddix, 1994).

Paracrine/immune control

In addition to the nervous systems and systemic hormones (see below), entero-endocrine cells in the gut release potent mediators of ion and water transport. These include serotonin, a mediator of increased net secretion, and somatostatin and peptide YY, which induce net absorption. These agents either occupy receptors on epithelial cells, thereby controlling ion transport directly, or connect with enteric neurones of the plexus, thereby altering ion and water transport indirectly (Brown & O'Grady, 1997).

Mesenchymal and immune cells in the lamina propria also are important in the overall control of absorption. For example, the fibroblastic sheath positioned just beneath the epithelium releases prostaglandins, which are potent inhibitors of absorption and inducers of secretion (Berschneider & Powell, 1992). Thus, these agents act as paracrine mediators of transport. In the equine proximal colon, such paracrine control by prostaglandins seems to dominate secretory patterns, as treatment with prostaglandin synthesis inhibitors, such as indomethacin and ibuprofen, increases basal rates of absorption in this tissue (Clarke & Argenzio, 1990). In fact prostaglandin production must be suppressed before aldosterone influence in this tissue is possible. Such mediators become even more important in inflammation. Inflammatory mediators released from mast cells and phagocytic cells are capable of stimulating fibroblasts and other mesenchymal cells (e.g. endothelium) to release prostaglandins (Powell, 1991). Certain prostaglandins, such as prostacyclin, are in turn capable of stimulating enteric neurones, as well as epithelial cells directly. Thus, the immune and mesenchymal cell system can act to amplify signals released from phagocytes and mast cells, resulting in massive intestinal secretion. Although not yet proven in the equid, such synergism in signalling pathways undoubtedly provides important control under physiological conditions and is a point for further study, especially in this family, in which colonic fluid transport must be so rigidly controlled.

Hormonal control of absorption

Aldosterone

The primary effect of aldosterone is to increase sodium and water movement into target tissues. It increases sodium permeability of the lumen-facing (apical) membrane by activation of pre-existing quiescent channels at short-term exposure, and by the incorporation of newly synthesized channels after more long-term exposure. Other effects might involve an increase in the energy supply and synthesis of $\text{Na}^+ - \text{K}^+$ ATPase which is responsible for the extrusion of Na from the cytoplasm to the blood (Lewis, 1983).

There is a large degree of aldosterone sensitivity in the proximal colon, but only after prostanoid blockade. Aldosterone has been proven to significantly increase electro-neutral sodium chloride absorption in the proximal colon, and electrogenic Na^+

absorption in the distal colon. Chloride absorption in the distal colon appears to be independent of sodium absorption (Argenzio, 1991).

In vivo, in the euvolaemic animal, aldosterone stimulation of Na^+ absorption is only expressed in the distal colon (Clarke *et al.*, 1992). This may relate to the high level of endogenous inhibitory 'tone' by local prostanoids in the proximal colon, as discussed above.

The dorsal proximal colon appears to possess transitional properties between those of the ventral proximal and small colons. Both aldosterone-mediated electrogenic and electroneutral sodium absorption have been observed, and hence this segment shows the greatest sodium absorption of the three gut segments (Clarke *et al.*, 1992). Therefore it is a transitional zone from fermentation to the formation of faecal matter.

Further studies are required to assess the quantitative contribution of aldosterone to post-fermentation fluid retrieval (Clarke, 1989; Clarke *et al.*, 1992). Aldosterone in high physiological concentrations (six times basal) doubled the rate of electroneutral Na^+ absorption in the ventral and dorsal colon and there was a small amiloride-sensitive current in the dorsal colon. Pre-treatment with a prostaglandin inhibitor was necessary to observe the aldosterone-mediated NaCl absorption in the ventral colon. In the small colon, the Na^+ current was entirely electrogenic and amiloride-sensitive. Aldosterone increased the rate of Na^+ absorption three times. Hyperaldosteronism can significantly increase colonic Na^+ absorption and thereby facilitate colonic fluid absorption during the concluding period of meal induced fermentation. However, in the ventral colon (the prime site of fermentation), mineralocorticoid action does not dominate control of electroneutral Na^+ transport because accelerated absorption is abolished by the antiabsorptive effect of local prostanoids (Clarke *et al.*, 1992). It must be stressed that these equid studies were conducted in euvolaemic animals. It is quite possible that in hypovolaemic states, the combined activation of sympathetic nerve activity and the renin-angiotensin system may suppress the prostanoid inhibitory action and allow aldosterone access to this potential fluid reservoir.

Escape from aldosterone suppression due to hypernatraemia imposed by hypertonic dehydration has been observed in horses undergoing a 72-h dehydration period (Sneddon *et al.*, 1993a). Spontaneous circadian activity of the renin-aldosterone-angiotensin system (RAAS) cannot be demonstrated in the horse during a steady state feeding regime. As mentioned before, single feeds do cause significant diurnal variations in the RAAS (15% drop in plasma volume) associated with transient hypovolaemia when fluid was secreted into the gastrointestinal tract for fermentation purposes (Clarke *et al.*, 1988).

The quantitative contribution of mineralocorticoid action to total fluid uptake during the fermentation cycle is difficult to estimate. The distal colon contributes relatively little to colonic fluid retrieval. Primary volume changes occur in the fermentation chambers of the proximal colon where mucosal Na^+ transport is electroneutral and may be modulated by other controlling influences like net effects of prostaglandins and adrenaline. Indeed, active Na^+ transport in these segments may only have a moderate influence on fluid absorption compared with bulk water flow that accompanies osmotic pressure changes in fermenting digesta.

Rates of active ion transfer across the proximal colon suggest these processes play a secondary role in fluid movement during the colonic fermentation cycle. When extrapolated to the surface area of the ventral colon, net ion flux *in vitro* is accountable for less than 25% of fluid movement *in vivo*. Thus, as in the rumen, much proximal colonic fluid movement *in situ* may be passively driven by osmotic gradients (Clarke, 1989).

On the other hand, electroneutral Na absorption in the proximal colon is a high capacity transport system, and doubling it through mineralocorticoid action may provide a potent synergism with other absorbed substances (Argenzio, 1991).

Angiotensin II

In vivo, angiotensin II exerts a dose-dependant dual action on intestinal absorption from all intestinal areas (Levens, 1985). Low doses stimulate water and sodium absorption. High doses potentiate net secretion. Stimulation of jejunal absorption of sodium and water in relation to angiotensin II is secondary to the release of noradrenaline by sympathetic nerves. In addition, angiotensin is a potent pressor and can alter intestinal haemodynamics to favour absorption. The inhibitory (high dose) effect of angiotensin II is due to prostaglandin secretion in the enteric plexus.

Angiotensin II also exerts a dose-dependant dual action on intestinal ion and water absorption *in vitro*, in the absence of haemodynamic influences. The mechanism for this is unknown. The enteric nerves are severed from their ganglia and thus the involvement of noradrenaline is unlikely. Angiotensin II exerts a major control over intestinal absorption following volume depletion via the RAAS axis.

Atrial natriuretic peptide

Recent evidence in the pig suggests that the atrial natriuretic peptide system may play an important role in colonic secretion. This peptide acts through the cyclic guanosine monophosphate and Ca^{2+} second messenger systems and promotes an inhibition of neutral NaCl absorption and electrogenic Cl^- secretion in the proximal colon (Argenzio & Armstrong, 1993). In pig distal colon, it inhibits Na^+ absorption and promotes active K^+ secretion (Traynor & O'Grady, 1991). The physiological stimulus for release of this peptide from the right atrium is an increase in right atrial pressure resulting from extracellular fluid volume expansion. Thus, it is a systemic hormone system responding to increases in blood volume and pressure, which acts on both kidney and colon to promote ECF volume decrease. Inasmuch as ion transport mechanisms in pig and equid proximal colon are identical, and both organs support a high level of microbial fermentation, it is likely that this peptide may also play an important role in equid colonic transport.

In summary, the mechanisms controlling transmural fluid movements during the fermentation cycle are only partially known. Much has yet to be learned about endo and paracrine mediators and their effects on the gastrointestinal nervous system. Epithelia have evolved specialized water transport mechanisms, unlike the majority of cells where water transport is incidental to the transport of other substances.

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