Pflügers Arch (1983) 399:68–73

Pflügers Archiv
European Journal of Physiology

Regional differences in electrolyte, short-chain fatty acid and water absorption in the hindgut of two species of arboreal marsupilas

K. Rübsamen*, I. D. Hume, W. J. Foley, and U. Rübsamen*

Department of Biochemistry and Nutrition, The University of New England, Armidale, NSW 2351, Australia

Abstract. 1. Short-chain fatty acid, electrolyte and water absorption from the hindgut of two arboreal marsupial species, the greater glider (*Petauroides volans*) and the brushtail possum (*Trichosurus vulpecula*) were studied in vivo using a single perfusion technique.

2. Qualitative and quantitative differences in the net movement of sodium, potassium and chloride were found between the different hindgut segments and between the two species. All transport processes exhibited active characteristics. Net Na^+ transport in all segments was concentration-dependent in the range of $45-135\ mmol \cdot l^{-1} Na^+$. The proximal colon of the greater glider showed a net Na^+, Cl^- and water secretion and K^+ absorption, all electrolyte movements being against the electrochemical gradient.

3. Water followed passively the osmotic gradient generated mainly by the net movement of Na^+.

4. Short-chain fatty acids were absorbed according to their chain length in a constant ratio of 1.0:1.2:1.3 for acetate, propionate and butyrate, respectively.

5. Our data indicate that absorptive and secretory processes in the hindgut of these marsupials are basically similar to those of eutherians, even in epithelia differing significantly in the direction of net solute transport.

Key words: Colon – Marsupials – Solute transport – SCFA absorption

Introduction

The hindgut plays an important role in the water and electrolyte balance of mammals, the driving force being the active transport of sodium (Argenzio and Whipp 1979; Frizzell et al. 1976; Edmonds 1967a; Yorio and Bentley 1977). In herbivores the absorption of short-chain fatty acids (SCFA), which are end products of microbial fermentation of plant structural carbohydrates is another important function of the hindgut epithelium. Because of the high concentrations present in the hindgut lumen, fatty acid absorption can exceed that of any other anion, and may even exceed under physiological conditions the net absorption of sodium (Rübsamen and Engelhardt 1981).

Electrolyte, water and SCFA transport from the large intestine has been studied intensively in a variety of domestic animals (Argenzio and Whipp 1979; Argenzio et al. 1975; Hecker and Grovum 1971), and in the colon of rats (Edmonds 1967b, c), rabbits (Frizzell et al. 1976; Yorio and Bentley 1977) and man (Devroede et al. 1971; Billich and Levitan 1969). Some information is available on the colon function in several highly specialized mammalian species with respect to their ability to absorb water from the colon (Skadhauge and Maloiy 1978; Staaland 1975; Lange and Staaland 1970). All the species studied so far belong to the Eutheria. To our knowledge no studies have been done on absorptive function in either of the other two stems of the class Mammalia, the Prototheria or the Metatheria which separated from the common mammalian stock in the early Creataceous, 70–80 million years ago (Crompton 1980) and which today are represented by the Monotremata and Marsupialia.

Although fermentative processes in herbivorous marsupials appear to be basically similar to those of eutherians, special adaptations seem to have developed among some arboreal marsupial species, particularly in those feeding almost exclusively on *Eucalyptus* leaves such as the koala (*Phascolarctus cinereus*) and the greater glider (*Petauroides volans*) (Hume 1982). The present work was conducted to assess the role of the hindgut of two arboreal marsupial species in electrolyte and water homeostasis.

Methods

Animals

Four mature greater gliders (*Petauroides volans*) and four mature brushtail possums (*Trichosurus vulpecula*) were used in this study. The greater gliders were caught during clear-felling operations in Nowendoc State Forest, 100 km south-east of Armidale, NSW. The brushtail possums were trapped in Armidale on the University of New England campus. The animals were captured and held under the provisions of Licence No. SLF52 from the National Parks and Wildlife Service of New South Wales and Permit No. 079 from the Forestry Commission of NSW. The greater gliders weighed 960–1170 g (mean: 1020 g) and the brushtail possums 1830–2180 g (mean: 1910 g). The animals were kept for an adaptation period of at least three weeks either in an open outdoor enclosure or in separate cages in a temperature-controlled room. The greater gliders were fed a eucalypt diet once a day, between 15.00 and 18.00 h, consisting entirely of *Eucalyptus radiata* foliage. Two of the brushtail possums were fed a mixed diet of fruit and eucalypt leaves, the others exclusively on eucalypt leaves (*E. melliodora*). Water was available ad libitum.

* *Permanent address:* Institut für Zoophysiologie, Universität Stuttgart-Hohenheim, D-7000 Stuttgart 70, Federal Republic of Germany

Perfusion technique

The experiments were conducted between 08.00 h and 18.00 h, the resting period of the strictly nocturnal animals. The animals were anaesthetized with halothane, without premedication, and the anaesthesia maintained either with a small face mask or by tracheostomy. The animals were held on a thermostatically controlled plate to maintain a stable body temperature of 36° C, the normal deep body temperature of both species. Heart rate, body temperature, and respiratory frequency were repeatedly measured throughout the experiments to indicate normal body functions of the animal. After opening the peritoneal cavity by midline incision and locating the different hindgut segments, PVC infusion tubes (1 mm I.D.) were positioned at the beginning of the proximal colon, distal to the caecal-colonic junction, and at the beginning of the distal colon. Warmed isotonic saline was then used to rinse out most of the colon contents. After removal of hard fecal pellets from the distal colon another, wider, collection tube (3 mm I.D.) was positioned 15–20 cm aborally from the infusion sites in both the proximal and distal colon, so that the length of each perfused segment was at least 15 cm. The proximal and distal colon were then returned to the abdominal cavity, and both colon sections rinsed with warmed isotonic perfusion solution (Table 1) from an elevated reservoir, until the outflow became clear. Finally, a 15 cm segment of the caecum, which had been kept warm and moist in a small thermostatically controlled glass dish, was prepared in the same way. The abdominal midline incision was then sutured, leaving visible only the infusion and collection tubes. The collection tubes were fixed at a constant level, 1 cm above the animal, in order to keep the fluid pressure inside the caecal and colon segments constant. Care was taken to maintain the blood supply to all parts of the gut, including the perfused sections. Throughout the rinsing procedure the water pressure was never higher than 15 cm H_2O. Before entering the gut segments the saline was warmed to body temperature by passing it through small water perfused heat exchangers.

After 1–2 h when the outflow from all gut segments had become clear, the infusion tubes were connected to a peristaltic pump which maintained a constant perfusion rate of 29.1 ml · h^{-1} in each segment. In preliminary experiments this perfusion rate was found to give large enough concentration differences between in- and outflowing solutions to allow calculation of absorption and secretion rates. The outflow was collected in small vials over a period of 30 min and stored frozen until analysed for Na^+, K^+, Cl^-, SCFA and osmolality. The experiments lasted for up to 8 h, and 2–4 different solutions were tested at random in each animal.

At the end of each experiment, the animal was killed with pentobarbital and the hindgut completely removed. The surface area of each perfused segment was estimated by outlining the slightly stretched gut wall on graph paper. In some experiments the potential difference between colon lumen and the peritoneal cavity was measured using agar-KCl-(3 M) bridges and calomel electrodes connected to a Radiometer millivoltmeter. The luminal electrode was introduced several centimeters into the colon through the collection tube and kept there until a constant reading was obtained.

Table 1. Solute concentration in caecal contents and plasma of four greater gliders and composition of the perfusion solutions mmol · l^{-1}

Solute	Caecal contents	Plasma	Perfusion solution
Na^+	103.2 ± 3.6	127.2 ± 4.5	45–135[a]
K^+	58.1 ± 6.0	4.8 ± 1.1	50
Cl^-	21.5 ± 3.4	108.2 ± 3.8	20
HCO_3^-			20
Acetate	22.8 ± 3.1		25
Propionate	8.4 ± 1.9		10
Butyrate	5.7 ± 1.7		5

[a] Na^+ concentrations varied in the following steps: 45, 80, 100, 135 mmol · l^{-1}. Osmolality and pH of solutions differing in Na^+ concentrations were adjusted with mannitol and H_3PO_4

Movement of water and electrolytes

Net water absorption was measured using either CrEDTA or ^{14}C-polyethylene glycol (PEG) as a marker. Chromium was analysed by atomic absorption spectrometry. The ^{14}C-PEG was used at a concentration of 10 μCi · l^{-1} together with 1 g · l^{-1} unlabelled PEG. Net absorption and secretion rates of water were calculated from the formula: $J_{net}^{H_2O} = [V_i - V_i (M_i/M_o)]/S$, where V_i is the perfusion volume in ml · h^{-1}, M_i and M_o are the marker concentrations before and after perfusion, and S is the surface area of the perfused segments in cm^2.

Sodium and potassium concentrations were measured by flame photometry and chloride was estimated by titration. The concentrations of acetate, propionate and butyrate were measured by gas-liquid chromatography. Osmolality of the solutions was estimated with a vapor pressure osmometer. Net absorption and secretion rates of solutes were calculated from changes in solute concentration and net water movement using the equation: $J_{net}^{El} = [E_i V_i - E_o V_i (M_i/M_o)]/S$, where E_i and E_o are the solute concentrations before and after perfusion. The direction of net electrolyte and water movement is indicated by positive and negative signs, (+) being net absorption which is defined as net movement from mucosal to serosal side. According to Edmonds (1967b) the "critical luminal concentration" is that Na^+ concentration where the net movement of Na^+ is zero. The solutions used in both species in our study contained electrolytes and SCFA in concentrations similar to those in the caecal contents measured in four greater gliders (Table 1). Results are given as mean ± standard deviation, and significance of differences was assessed using the paired or unpaired t-test after testing for equality of variances. Differences between regression lines were evaluated by the method of Zerbe et al. (1982).

Results

1. Effect of luminal Na^+ concentration on net Na^+ absorption

In both species net Na^+ transport rates increased linearly with increasing luminal Na^+ concentrations (Fig. 1), except in the distal colon of the greater glider when net Na^+ absorption did not increase at Na^+ concentrations beyond 100 mmol · l^{-1}. The slopes of the regression lines describing this relationship were similar in both species in the caecum and proximal colon, but were greater ($P < 0.001$) in the distal colon of both species. There was no significant difference in the slope of the regression lines between the brushtail possum and the greater glider. The critical Na^+ concentration in the

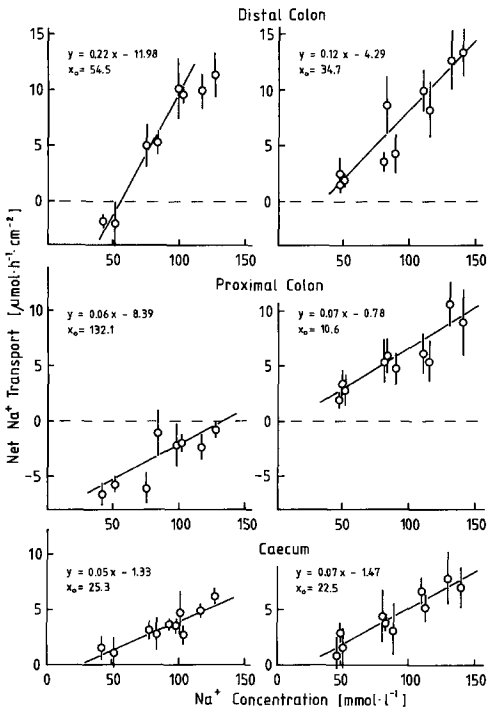

Fig. 1. Effect of luminal Na^+ concentration on net Na^+ transport in the caecum, proximal and distal colon of the greater glider (*left panel*) and the brushtail possum (*right panel*). Each point represents the mean and SD of one experimental period consisting of up to 6 consecutive collection periods of 30 min each

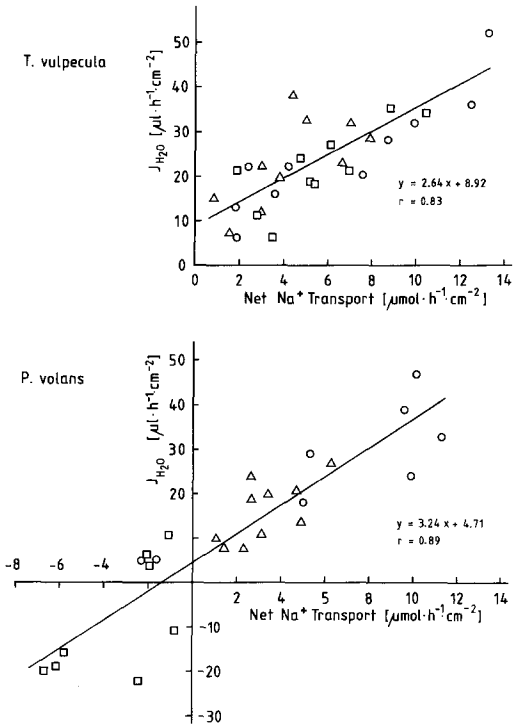

Fig. 2. Interrelationship between net Na^+ transport and net water movement in the colon of the greater glider and the brushtail possum. Each point represents the mean of one experiment, consisting of up to 6 consecutive collection periods. The regression lines were calculated from the combined values for caecum, proximal and distal colon (△ caecum; □ proximal colon; ○ distal colon)

caecum was 22.5 mmol · l^{-1} in the brushtail possum and 25.3 mmol · l^{-1} in the greater glider. The most striking difference between the species was found in the proximal colon. In both species net Na^+ transport and luminal Na^+ concentration showed a linear relationship as in the caecum. In the proximal colon of the greater glider, however, Na^+ was secreted while Na^+ was absorbed from the proximal colon of the brushtail possum at a rate comparable to that in the caecum (Fig. 1). The difference between the intercepts of the regression lines was highly significant ($P < 0.001$). The extrapolated values for the critical Na^+ concentrations were 11 mmol · l^{-1} for the brushtail possum, but 132 mmol · l^{-1} for the greater glider, which means that at the mean Na^+ concentration of 103 mmol · l^{-1}, measured in the caecal contents of four animals, 2.2 μmol · h^{-1} · cm^{-2} Na^+ would be secreted into the proximal colon. The extrapolated critical Na^+ concentration in the distal colon was also higher ($P < 0.001$) in the greater glider than in the brushtail possum. Moreover, net Na^+ transport in the distal colon of the brushtail possum was higher than in the greater glider at luminal Na^+ concentrations below 50 mmol · l^{-1} ($P < 0.005$), but was similar at Na^+ concentrations above 50 mmol · l^{-1}.

2. *Net water movement*

The net absorption and secretion of water in the different sections of the hindgut of both species was closely related to the net movement of Na^+ (Fig. 2). Since neither the slopes of the regression lines nor their intercepts differed significantly between the caecum, proximal colon and distal colon the regression lines shown in Fig. 2 are based on combined data from the three hindgut regions. The net Na^+

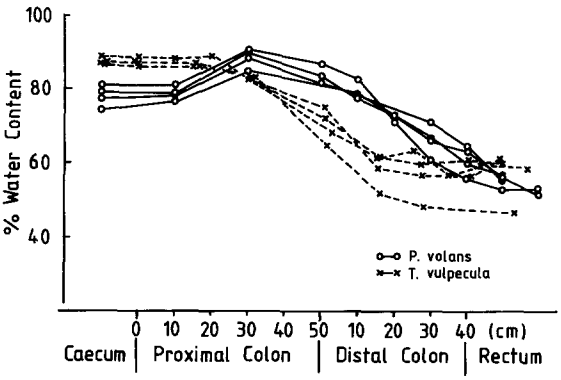

Fig. 3. Water content in % in different sections of the hindgut of the greater glider and the brushtail possum

secretion into the proximal colon of the greater glider was accompanied by a concomitant net water secretion. In the brushtail possum there was no water secretion even at low net Na^+ transport rates. The slope and the y-intercept of this regression line were similar to those of the greater glider. The osmolality of transport, which relates the net water movement to the net movement of all osmotically active solutes, was 513 ± 120 μosm · ml^{-1} in the greater glider and 416 + 83 μosm · ml^{-1} in the brushtail possum, which was not statistically different. The difference in the net water absorption rates between the different colon sections and between the two species are confirmed by the measurement of the water content along the hindgut (Fig. 3). The highest water content (90 %) was measured in the proximal colon of the

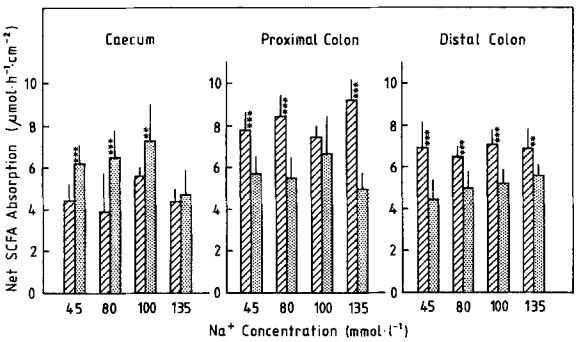

Fig. 4. Net SCFA absorption rates in the colon of the greater glider (*left columns*) and of the brushtail possum (*right columns*) at different luminal Na^+ concentrations. Means ± SD. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

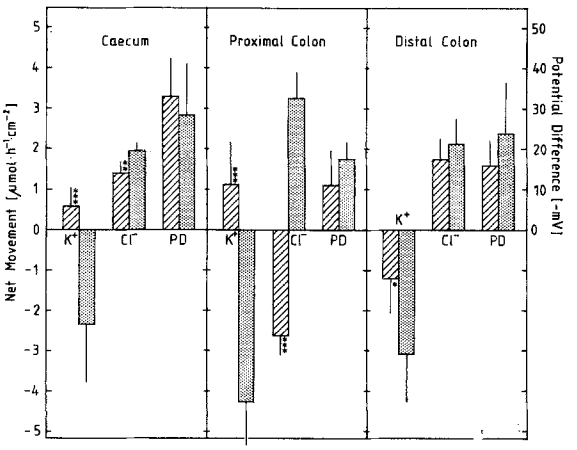

Fig. 5. Net movement of K^+ and Cl^- and potential difference in the colon of the greater glider (*left column*) and the brushtail possum (*right column*). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Means ± SD

greater glider whereas the brushtail possum kept a constant water content of 87% in the caecum and the proximal colon.

3. Absorption of short-chain fatty acids

Short-chain fatty acids (SCFA) were rapidly absorbed from all sections of the hindgut of both the greater glider and the brushtail possum (Fig. 4). The luminal Na^+ concentration did not affect net SCFA absorption rates, and therefore there was no significant correlation between net SCFA and net Na^+ transport. Net SCFA absorption rates in the proximal colon of the greater glider were nearly twice those measured in the caecum of the same species (Fig. 4). Net SCFA absorption in the brushtail possum was similar in all three sections. However, it was lower than that of the greater glider in the proximal and distal colon. SCFA showed differences in the rate of absorption according to their chain length. When the absorption rates were divided by the mean concentration differences between plasma and lumen, which gives a relative measure of the permeability, acetate, propionate and butyrate were absorbed in the ratio 1:1.16:1.29. There was no significant difference in this ratio between the different sections of the hindgut or between the two species.

4. Net potassium and chloride absorption

The net movements of K^+ showed considerable variations in both species studied, as indicated by the large SD in Fig. 5. The most obvious difference between the species was that K^+ was secreted in all colon sections of the brushtail possum, whereas in the greater glider K^+ was absorbed in the caecum and the proximal colon and secreted only in the distal colon. Net K^+ movements were not affected by luminal Na^+ concentration thus there was no correlation between net Na^+ and net K^+ movement.

Chloride was absorbed from all hindgut sections of the brushtail possum, the highest rates being measured in the proximal colon. However, Cl^- was secreted into the proximal colon of the greater glider, independent of the luminal Na^+ concentration (Fig. 5). Except in the proximal colon, net absorption rates did not differ significantly between species.

5. Potential difference

The colon lumen was always negative against the serosal side, with differences ranging from 5 mV in the proximal colon to 48 mV in the caecum. Measurements were only made occasionally, and so the significance of differences between the segments could not be established. There was no significant difference in potential difference using solutions differing in Na^+ concentration.

Discussion

The present study on solute and water transport in the hindgut of two arboreal marsupial species revealed that there are significant qualitative and quantitative differences in solute transport between the different hindgut segments, and also between the species. In general, the distal colon showed the highest capacity for Na^+ and water absorption, whereas net transport rates in the caecum and proximal colon of both species were lower. It must be borne in mind, however, that the following comparison of our data with those of other workers is based mainly on the expression of flux rates per unit of surface area, tissue weight, or segment length. Only a few other studies include similar morphometric data and some comparisons are therefore based on assumptions. Even with such information, differences in transport rates between hindgut segments may reflect artefacts caused by the use of inadequate references which do not consider differences in surface structure (Argenzio and Whipp 1979; Yau and Makhlouf (1975).

Sodium transport and net water movement

The hindgut epithelium of both marsupial species transported sodium against an electrochemical gradient, as does that of other mammalian species (Yorio and Bentley 1977; Argenzio et al. 1975; Devroede et al. 1971; Edmonds 1967a; Argenzio and Whipp 1979; Fromm and Hegel 1978). Restrictions have to be made for the proximal colon of the greater glider, a species that has developed a highly specialized digestive system according to its nutritive habits (Hume 1982).

Net sodium transport in all sections of both species was highly dependent on the luminal Na^+ concentration (Fig. 1), a finding consistent with those in rat colon using a similar in vivo perfusion technique (Edmonds 1967b; Umesaki et al. 1979). Similar concentration dependency was reported for the

intact human colon (Billich and Levitan 1969) the rectum of the dikdik (Skadhauge and Maloiy 1978) and the temporarily isolated colon of conscious sheep (Rübsamen and Engelhardt 1981). From the data of Edmonds (1967b) it can be calculated that net Na^+ transport in the distal colon is limited at a luminal Na^+ concentration of 150 mmol $\cdot$ l^{-1}. In our study saturation in net Na^+ transport in the distal colon of the greater glider occurred at 100 mmol $\cdot$ l^{-1} but not in the brushtail possum. There is also good agreement with net Na^+ transport rates measured in the rectum of the dikdik, with a critical Na^+ concentration of 28 mmol $\cdot$ l^{-1} in normally hydrated animals (Skadhauge and Maloiy 1978).

Reports indicating different Na^+ transport rates in the ascending and descending colon in other mammal species are conflicting. In some instances net Na^+ absorption in the ascending colon was higher than in the distal colon (Bentley and Smith 1975; Yau and Makhlouf 1975; Devroede et al. 1971; Fromm and Hegel 1978). Argenzio and Whipp (1979) found no difference, while the results of Edmonds (1967b) and of the present study clearly indicate that, at least at higher luminal Na^+ concentrations, the distal colon transports Na^+ faster than the proximal colon. In our study net Na^+ transport rates were identical in the proximal and distal colon at luminal Na^+ concentrations below 80 mmol $\cdot$ l^{-1}. This suggests that at least some of the conflicts in the literature can be attributed to the use of different luminal Na^+ concentrations in different studies. Another source of conflict may be in the use of different techniques, and the use of animals in different hormonal states, especially with regard to plasma levels of aldosterone (Fromm and Hegel 1978).

The most significant interspecific difference in net Na^+ transport was found in the proximal colon (Fig. 1). In contrast to net Na^+ absorption in the brushtail possum Na^+ was secreted at all luminal Na^+ concentrations in the greater glider. Notwithstanding this difference, the relationship between net Na^+ transport and luminal Na^+ concentration in the proximal colon was of similar slope in the two species. Sodium concentrations in the lumen of both species at equilibrium clearly indicate that an active absorption process must be involved. Net Na^+ secretion in the greater glider proximal colon can therefore only be explained by a high passive permeability to Na^+. Although this hypothesis cannot be proved on the basis of our data, it is strongly supported by the results of Edmonds (1967b) who found that although ascending and descending rat colon transported Na^+ actively and to a similar extent, the descending colon showed a substantially lower passive permeability to Na^+ ions than did the ascending colon.

Our data on net water movement indicate that water followed passively the osmotic gradient generated mainly by the net absorption or secretion of Na^+. The osmolality of transport was 513 $\pm$ 120 µosm $\cdot$ ml^{-1} in the glider and 416 $\pm$ 83 µosm $\cdot$ ml^{-1} in the brushtail possum, neither of which are significantly different from values for the rat colon (Powell and Malawer 1968) with 544 $\pm$ 24 µosm $\cdot$ ml^{-1}. This confirms their suggestion that fluid transport in the large intestine is hypertonic and related to the movement of total solute rather than the net flux of Na^+ alone.

Potassium and chloride movement

Our data on net K^+ flux in the colon of the brushtail possum indicating a net serosal to mucosal K^+ movement, are in agreement with previous studies (Edmonds 1967b, c; Powell and Malawer 1968; Fromm and Hegel 1978; Yorio and Bentley 1977). However, we did not find differences in net K^+ secretion between the proximal and distal colon, which can be significant in other species (Yau and Makhlouf 1975; Fromm and Hegel 1978). This may be due to the fact that K^+ intake in our animals was not controlled and luminal K^+ concentration was high, which can result in adaptive changes in K^+ secretion according to the K^+ requirements of the animal (Fisher et al. 1976; McCabe et al. 1982; Hayslett and Binder 1982).

The most important observation was that in the greater glider the proximal colon absorbed K^+ at quite high rates. So far net K^+ absorption has only been demonstrated in the distal colon under certain conditions and is ascribed to active transcellular transport (Hayslett et al. 1982; Wills and Biagi 1982) and not, as suggested earlier, to a nonselective paracellular pathway (Frizzell et al. 1976). On the other hand the proximal colon of the greater glider is characterized by a low potential difference of 9 – 15 mV, lumen negative to blood. Under equilibrium conditions the observed K^+ activity in the luminal fluid significantly exceeded the value predicted from the Nernst equation, which indicates an active secretion mechanism. Absorption therefore must have occurred passively via paracellular pathways along the concentration gradient; this coincides with our observation that the proximal colon of the greater glider has a high passive permeability for Na^+ as well. Hayslett and Binder (1982) suggested that the entry of potassium from the cell into the lumen fluid may involve an electrically neutral exchange with other ions, which in our case could be Na^+ moving in the opposite direction.

In the brushtail possum Cl^- was transported against its electrochemical gradient in all hindgut segments. There was no evidence for different transport rates or transport mechanisms in the three different segments, which is in agreement with the findings of Yau and Makhlouf (1975) and Fromm and Hegel (1978). Further, there was no evidence for coupled Na^+-Cl^- transport (Binder and Rawlins 1973), which can presumably be attributed to the use of low luminal Cl^- concentrations and the presence of SCFA which interfere with the transport of other anions (Umesaki et al. 1979; Argenzio et al. 1975) and affect Na^+ absorption as well (Rübsamen and Engelhardt 1981). As in the case of Na^+, the high rate of net Cl^- secretion in the proximal colon of the glider does not necessarily indicate an active transport mechanism; it is more likely that its passive permeability is high, which leads to a net flow of Cl^- along the concentration gradient.

Absorption of SCFA

SCFA absorption varied significantly between the different hindgut segments and between the two species. The transport mechanism seems to be basically identical, because in all cases SCFA were absorbed according to their chain length; this is also the case in isolated rumen epithelium (Stevens and Stettler 1966). An interrelationship between net Na^+ and net SCFA absorption, as demonstrated in the colon of pigs, goats and rats (Argenzio and Whipp 1979; Argenzio et al. 1975; Umesaki et al. 1979) was not found in our study; this may have been due to the fact that our perfusion solutions were significantly different from each other in their buffering capacity. This presumably clouded the role of SCFA anions as proton acceptors (Rübsamen and Engelhardt 1981).

Differences in transport rates were not correlated with the role of the different hindgut sections in SCFA production. For instance, SCFA were rapidly absorbed from the distal colon of both species although there is no evidence for significant SCFA production in the distal colon of these two marsupial species or of any other mammal. On the other hand, the highest SCFA absorption rates were measured in the proximal colon of the glider, where Na^+ and water were secreted. As discussed earlier, this may indicate a high passive permeability of the proximal colon due to a low paracellular resistance. It may also reflect its role as an additional fermentation chamber, a suggestion supported by its highly distensible nature. The net inflow of water into this segment may facilitate mixing within the lumen contents. Although net secretion of water into the proximal colon has also been shown in the lemming (Staaland 1975), further studies on fermentation and absorption characteristics of this section are necessary for a convincing explanation.

Acknowledgement. K. Rübsamen was supported by a Feodor Lynen fellowship from the Alexander von Humboldt-Stiftung.

References

Argenzio RA, Miller N, Engelhardt W von (1975) Effect of volatile fatty acids on water and ion absorption from the goat colon. Am J Physiol 229:997–1002

Argenzio RA, Whipp SC (1979) Interrelationship of sodium, chloride, bicarbonate and acetate transport by the colon of the pig. J Physiol 295:365–381

Bentley PJ, Smith MW (1975) Transport of electrolytes across the helicoidal colon of newborn pigs. J Physiol Lond 249:103–117

Billich CO, Levitan R (1969) Effects of sodium concentration and osmolality on water and electrolyte absorption from the intact human colon. J Clin Invest 48:1336–1347

Binder JJ, Rawlins CL (1973) Electrolyte transport across isolated large intestinal mucosa. Am J Physiol 225:1232–1239

Crompton AW (1980) Biology of the earliest mammals. In: Schmidt-Nielsen K, Bolis L, Taylor CR (eds) Comparative physiology: Primitive mammals. University Press, Cambridge, pp 1–22

Devroede GJ, Phillips SF, Code CF, Lind JF (1971) Regional differences in rates of insorption of sodium and water from the human large intestine. Can J Physiol Pharmacol 49:1023–1029

Edmonds CJ (1967a) The gradient of electrical potential difference and of sodium and potassium of the gut contents along the caecum and colon of normal and sodium-depleted rats. J Physiol 193:571–588

Edmonds CJ (1967b) Transport of sodium and secretion of potassium and bicarbonate by the colon of normal and sodium-depleted rats. J Physiol 193:589–602

Edmonds CJ (1967c) Transport of potassium by the colon of normal and sodium-depleted rats. J Physiol 193:603–617

Fisher KA, Binder HJ, Hayslett JP (1976) Potassium secretion by colonic mucosal cells after potassium adaptation. Am J Physiol 231:987–994

Frizzell RA, Koch MJ, Schultz SG (1976) Ion transport by rabbit colon. I. Active and passive components. J Membr Biol 27:297–316

Fromm M, Hegel U (1978) Segmental heterogeneity of epithelial transport in rat large intestine. Pflügers Arch 378:71–83

Hayslett JP, Binder HJ (1982) Mechanism of potassium adaptation. Am J Physiol 243: F103–F112

Hayslett JP, Halevy J, Pace PE, Binder HJ (1982) Demonstration of net potassium absorption in mammalian colon. Am J Physiol 242:G209–G214

Hecker JF, Grovum WL (1971) Absorption of water and electrolytes from the large intestine of sheep. Aust J Biol Sci 24:365–372

Hume ID (1982) The digestive physiology of marsupials. Comp Biochem Physiol 71:1–10

Lange R, Staaland H (1970) Adaptations of the caecum colon structure of rodents. Comp Biochem Physiol 35:905–919

McCabe R, Cooke HJ, Sullivan LP (1982) Potassium transport by rabbit descending colon. Am J Physiol 242:C81–C86

Powell DW, Malawer SJ (1968) Relationship between water and solute transport from isoosmotic solutions by rat intestine in vivo. Am J Physiol 215:49–55

Rübsamen K, Engelhardt W von (1981) Absorption of Na, H ions and short chain fatty acids from the sheep colon. Pflügers Arch 391:

Skadhauge E, Maloiy GMO (1978) The intestine and osmoregulation. Alfred Benzon Symposium XI. Munksgaard, Copenhagen, pp 325–337

Staaland H (1975) Absorption of sodium, potassium and water in the colon of the Norway lemming *Lemmus lemmus* (L). Comp Biochem Physiol 52:77–80

Stevens CE, Stettler BK (1966) Transport of fatty acid mixtures across rumen epithelium. Am J Physiol 211:264–271

Umesaki Y, Yajima T, Yokokura T, Mutai M (1979) Effect of organic acid absorption on bicarbonate transport in rat colon. Pflügers Arch 379:43–47

Wills N, Biagi B (1982) Active potassium transport by rabbit descending colon epithelium. J Membr Biol 64:195–203

Yau WM, Makhlouf GM (1975) Comparison of transport mechanisms in isolated ascending and descending rat colon. Am J Physiol 228:191–195

Yorio T, Bentley PJ (1977) Permeability of the rabbit colon in vitro. Am J Physiol 232:F5–F9

Zerbe GO, Archer PG, Banchero N, Lechner AJ (1982) On comparing regression lines with unequal slopes. Am J Physiol 242:178–180

Received February 8/Accepted June 17, 1983