

ABSORPTION OF WATER AND ELECTROLYTES FROM THE LARGE INTESTINE OF SHEEP

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Abstract

Rate of passage of digesta, lumen diameter, and rates of absorption of water, sodium, and potassium were calculated from wet weight, dry weight, and sodium and potassium content of digesta in segments of the large intestine of six sheep given 800 g lucerne chaff per day.

Digesta were retained for the longest time in the caecum and the proximal colon. The rate of passage of digesta was comparatively rapid through the spiral colon.

The lumen diameters of the caecum and the proximal colon were much greater than those of other sections of the large intestine.

There was a regular decrease in water per gram of digesta dry matter between the caecum and the rectum. Sodium concentration in this water decreased after the start of the spiral colon. Five of the sheep had low concentrations of potassium in the water of the large intestinal contents but one sheep had higher concentrations. Rates of absorption of water, sodium, and potassium were highest in the centripetal colon and lowest in the rectum. Rates calculated for the caecum and the proximal colon were reduced by mixing of digesta but calculations showed that they were similar to those in the centripetal colon.

I. INTRODUCTION

In the large intestine of the sheep, the consistency of the contents is altered from the liquid digesta that enter from the ileum to the comparatively dry pellets passed as faeces. Inspection of contents in different parts indicates that inspissation occurs along the length of the large intestine. Spörri and Asher (1940) suggested that as pellet formation occurred in the spiral colon, this part was the main site of water absorption. The purpose of the studies presented here was to determine the relative importance of different parts of the large intestine for absorption of water and to relate this to absorption of electrolytes.

II. MATERIALS AND METHODS

(a) Animals and Feeding

Six mature Merino ewes of approximately 40 kg body weight were used. They were given 800 g of lucerne chaff in one feed per day for a period of 3 weeks. For a subsequent 3-4 days before slaughter, they were given approximately 33 g lucerne chaff per hour by an automatic feeding machine (Minson and Cowper 1966).

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(b) Slaughter and Sampling

A polyethylene catheter was inserted into a jugular vein of each sheep several hours before slaughter. Each sheep was anaesthetized with sodium pentobarbitone (30 mg/kg) injected through this catheter and then killed by exsanguination. The intestinal tract was removed from the abdominal cavity after the rectum had been severed in the pelvic cavity. The small intestine was separated from the large intestine and ligatures were placed around the start and the end of the centripetal colon and the point at which the final centrifugal coil departed from its close proximity to the mass of the spiral colon (Smith 1955). The ligatures served later to identify these points which are referred to as the beginning, the apex, and the end of the spiral colon respectively. The large intestine was stripped from its mesentery, care being taken to avoid any stretching. It was divided into segments 15 cm long starting at the apex of the caecum. The digesta in each segment was emptied on to tared 9-cm watch-glasses and weighed to determine the wet weight of digesta in the segment. After heating at 100°C for 2 days, the dry weight of digesta in each segment was determined. Dry matter in ileal digesta was determined by the same method.

(c) Electrolyte Concentrations

Dry digesta were ground and duplicate samples (approx. 0.5 g) were transferred to tared 2-ml plastic syringe barrels (9 mm internal diameter). After weighing, 20 ml of de-ionized distilled water was passed through each syringe barrel. The effluent was collected and evaporated to dryness at 100°C and then dissolved in 4 or 8 ml of de-ionized distilled water. Determinations of sodium and potassium concentrations were made by flame-photometry using a Technicon auto-analyser. Complete recovery of sodium by this technique was checked with radioactive faeces from a sheep injected 24 hr previously with $^{22}\text{NaCl}$. Radioactivity was measured in plastic tubes in a well-type counter with a 2 in. thallium-activated sodium iodide crystal connected to a Packard model 3002 spectrometer. Approximately 90% of the ^{22}Na present was eluted in the first 5 ml of water. After elution with 20 ml, no activity was detected in material remaining in the syringe barrel.

(d) Calculations

Grams of water per gram dry matter (W) was calculated from wet and dry weights of digesta in each segment. The passage rate of digesta was derived as follows. If a grams dry matter and b grams water pass a point per minute, then

$$\text{passage rate (g/min)} = a + b = a(1 + b/a).$$

If c is the wet weight of contents in grams in a segment of length 15 cm, then passage rate R (cm/min) is given by:

$$\begin{aligned} R &= 15a(1 + b/a)/c, \\ &= 15a(1 + W)/c. \end{aligned}$$

Water per gram dry matter W ($= b/a$) and total wet matter (c) were known for each segment. The value for a was the faecal dry matter excretion rate and was calculated from the dry weight of faeces excreted during the 3–4 days before slaughter. It had a mean value of 0.171 g/min.

Retention time (T , min) in each segment was calculated from the following equation:

$$T = c/[a(1 + b/a)].$$

For calculation of surface area and lumen diameter of each segment, it was assumed that the contents were contained in a cylinder 15 cm long and that they had a specific gravity of 1. Therefore, the surface area (A , cm^2) and diameter (D , cm) were calculated from the geometrical relations between the volume, diameter, and circumference of a cylinder 15 cm long:

$$A = (188.4 c)^{1/2}.$$

$$D = (0.0849 c)^{1/2}.$$

The estimate of net absorption of water per minute (in grams per 100 cm²) was calculated from the decrease in water per gram dry matter in successive segments. This decrease was multiplied by the mean dry matter content and divided by the mean retention time and the mean surface area of the segments:

$$\text{Water absorption} = \frac{200(d_n + d_{n+1})(W_n - W_{n+1})}{(A_n + A_{n+1})(T_n + T_{n+1})},$$

where n and $n+1$ are successive segments, d is the weight of dry contents in a segment (grams) and other symbols are as defined above.

Concentrations of sodium and potassium in digesta water were calculated by dividing the number of milliequivalents of electrolyte per gram dry matter by the corresponding value of water per gram dry matter for the segment. Net absorption rates of electrolytes were calculated by substituting values of electrolyte per gram dry matter for water per gram dry matter in the above equation for water absorption.

Although the analyses were conducted on digesta from segments 15 cm long, the data were grouped into parts each 5% of the length of the large intestine to overcome problems due to variable lengths of the large intestine.

III. RESULTS

(a) Length of Large Intestine and Weight of Its Contents

The results are summarized in Table 1. The length of the large intestine varied from 360 to 550 cm. The distances from the apex of the caecum to the beginning,

TABLE 1

LENGTH OF LARGE INTESTINE, WET AND DRY MATTER CONTAINED, AND OTHER DATA FOR SHEEP GIVEN 800 G LUCERNE CHAFF PER DAY

Length is the actual length of the sections of the large intestine. For other data, the large intestine was divided into five sections each 20% of the length. Mean values \pm standard deviations are given

Site	Section					Total
	Caecum and Proximal Colon	Centripetal Colon	Centrifugal Colon	Subterminal Colon	Terminal Colon	
Length (cm)	80 \pm 15	80 \pm 18	86 \pm 15	184 \pm 24		430 \pm 58
Length as % of total length	18.5	18.6	20.1	42.9		100
Wet matter (g)	694 \pm 109	70 \pm 6	51 \pm 13	59 \pm 15	122 \pm 43	997 \pm 143
Dry matter (g)	91 \pm 15	12 \pm 1	12 \pm 3	17 \pm 4	47 \pm 21	179 \pm 33
Total retention time (min)	531 \pm 91	70 \pm 5	68 \pm 11	86 \pm 23	295 \pm 114	1050 \pm 192
Surface area (cm ²)	802 \pm 99	272 \pm 21	230 \pm 20	234 \pm 37	238 \pm 73	1921 \pm 243
Water absorbed/min (mg/100 cm ²)	40†	128	95	57	36	
Sodium absorbed/min (μ -equiv/100 cm ²)	2.1	14.3	9.3	5.1	1.7	
Potassium absorbed/min* (μ -equiv/100 cm ²)	-0.6	1.3	0.8	0.6	0.1	

* Data from the sheep with high concentrations of potassium omitted.

† Or 120 (see Section IV).

the apex, and the end of the spiral colon were approximately 20, 40, and 60% of the length of the large intestine respectively. For convenience in presenting results in the succeeding part of this paper, the large intestine has been considered to consist of five sections, each 20% of the total length: caecum and proximal colon, centripetal colon, centrifugal colon, subterminal colon, and terminal colon.

The caecum and proximal colon contained the greatest weights of both wet matter and dry matter (Table 1). Slightly more than a quarter of the dry matter was in the terminal colon. Other sections contained comparatively little digesta.

(b) Lumen Diameter

Variations in the diameter of the lumen of the large intestine are shown in Figure 1(a). The lumen was approximately 4 cm in diameter in the caecum and proximal colon. It was narrower in the remainder of the large intestine being approximately 1.5 cm in the rectum and 0.8 cm in other parts.

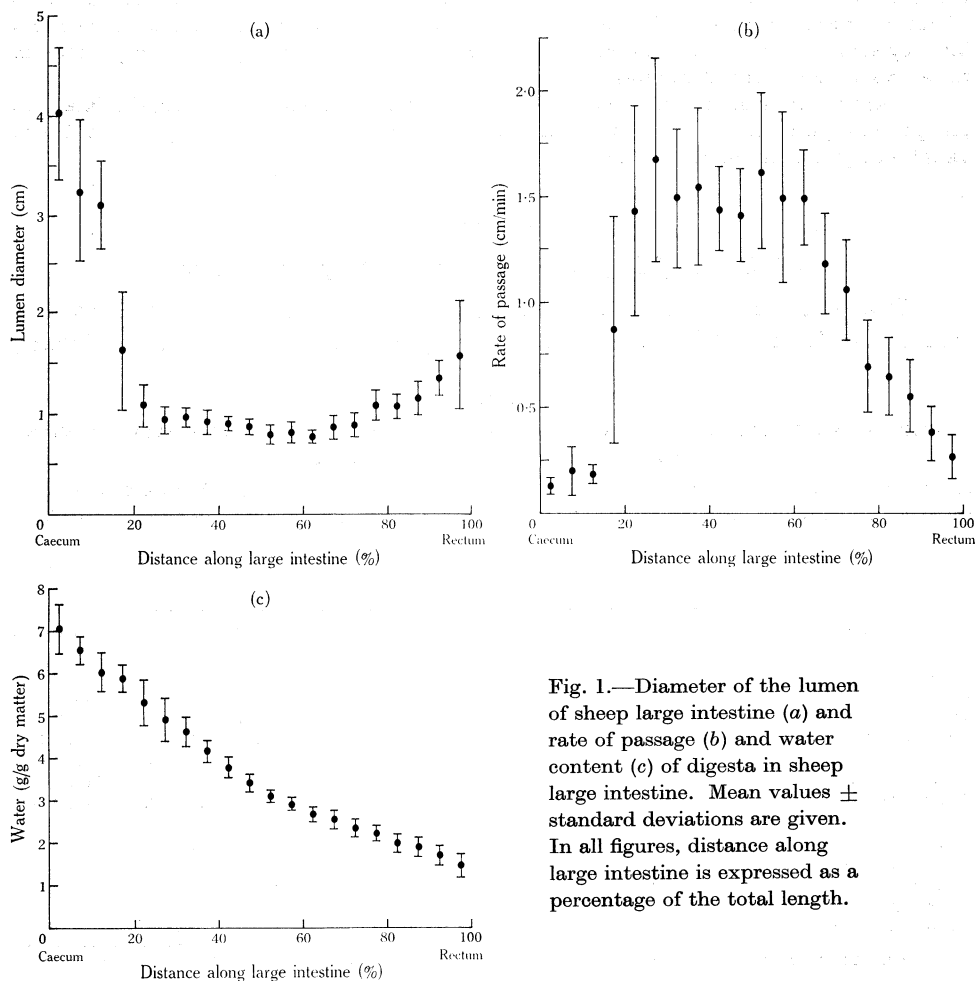


Fig. 1.—Diameter of the lumen of sheep large intestine (a) and rate of passage (b) and water content (c) of digesta in sheep large intestine. Mean values \pm standard deviations are given. In all figures, distance along large intestine is expressed as a percentage of the total length.

(c) Rate of Passage of Digesta

The rate of passage of digesta [Fig. 1(b)] was slowest in the caecum and proximal colon (0.1–0.2 cm/min) and most rapid in the centripetal and centrifugal colon (approx. 1.4 cm/min). The rate decreased from the end of the spiral colon to the rectum.

(d) Water Content

Water per gram dry matter decreased from 7.09 to 1.54 g between the caecum and the rectum [Fig. 1(c)]. Data from individual sheep showed that the decrease was regular with only 10 segments out of a total of 166 in which digesta in a proximal segment contained less water per gram dry matter than did that in an adjacent distal segment. Five of these were in the caecum and proximal colon.

Samples of digesta from the ileum of five of the sheep contained 11.42 ± 1.43 (S.D.) g water per gram dry matter.

Grooves in the digesta indicating commencement of pellet formation were observed first approximately half-way along the centripetal colon while the first distinct pellets were present in the middle of the centrifugal colon.

(e) Electrolytes

The sodium concentration in the caecum and the proximal colon was 80–85 m-equiv/kg water. The concentration decreased from the start of the spiral colon to approximately 15 m-equiv/kg in the rectum [Fig. 2(a)]. Data for sodium concentration per gram dry matter for the individual sheep showed a regular but more accentuated decrease between the caecum and rectum than did the sodium concentration per kilogram water.

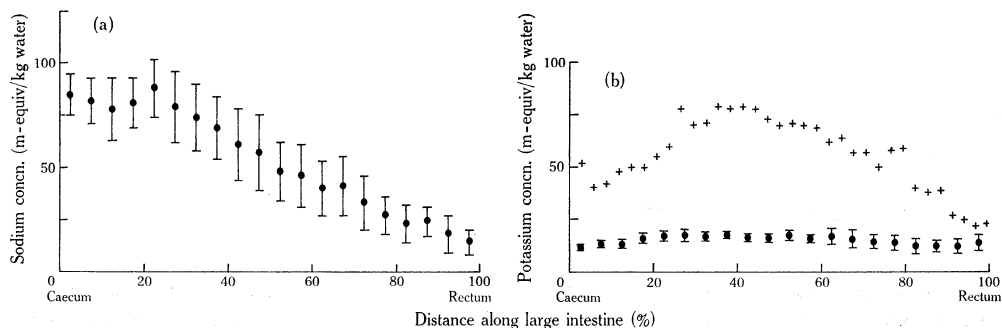


Fig. 2.—Sodium (a) and potassium (b) concentrations in digesta water in sheep large intestine. In (a) mean values \pm standard deviations are given for six sheep. In (b) these values are given for five sheep. Plus symbols indicate values for one sheep with higher concentrations.

The concentrations of potassium are shown in Figure 2(b). Five of the sheep had a concentration of potassium of approximately 15 m-equiv/kg in water of large intestinal contents. The concentration in the other sheep was much higher. It increased from between 40 and 50 m-equiv/kg in the caecum and proximal colon to approximately 80 m-equiv/kg at the apex of the spiral colon, after which it decreased to 20 m-equiv/kg in the rectum.

(f) Rates of Absorption of Water and Electrolytes

Rates of absorption of water and sodium in the six sheep and of potassium in the five sheep with low concentrations of potassium are shown in Figures 3(a)–3(c).

The rates were low in the caecum and proximal colon and highest in the centripetal colon. The rates tended to decrease between the apex of the spiral colon and the rectum.

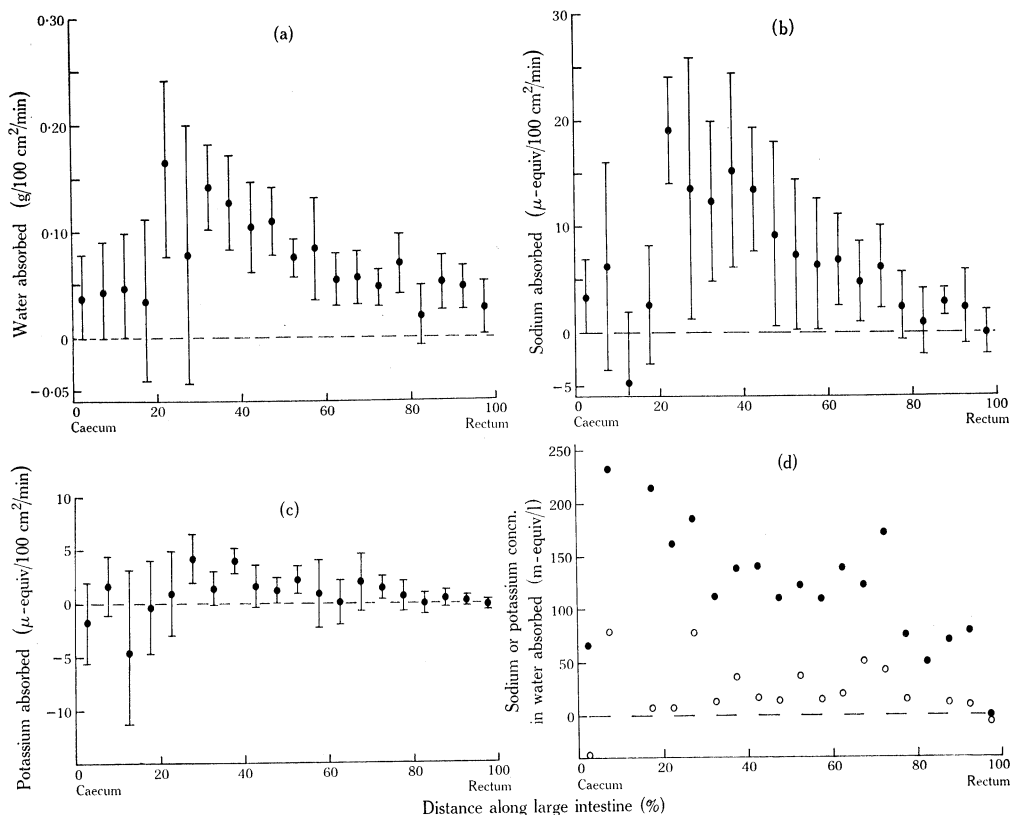


Fig. 3.—Rates of absorption of water (a), sodium (b), and potassium (c) across the wall of the sheep large intestine. Mean values \pm standard deviations are given. (d) Sodium (●) and potassium (○) in water absorbed from sheep large intestine. Data from the sheep with high potassium concentrations omitted from calculations.

The calculated concentrations in the absorbed water of sodium for the six sheep and of potassium for the five sheep with low concentrations are shown in Figure 3(d). The sodium concentration showed a decrease between the anterior part of the large intestine (about 200 m-equiv/kg) and the terminal colon (about 50 m-equiv/kg). The potassium concentration was lower than that for sodium and showed no decrease along the large intestine. The mean potassium concentration (16 m-equiv/kg) was similar to the potassium concentration in the digesta water.

IV. DISCUSSION

The calculations assume that there was negligible digestion of dry matter in the large intestine. Other experiments have shown that from 16 to 25% of the dry matter entering the large intestine is digested and absorbed there (Hogan and Phillipson 1960; Goodall and Kay 1965a; Bruce *et al.* 1966). Thus our assumption was not

valid. However, since most parameters that were calculated varied by factors of two or more along the length of the large intestine, any errors caused by digestion of dry matter would be small. Errors due to digestion of dry matter would cause underestimation of the rate of passage of digesta and overestimation of the rates of absorption of water and electrolytes. The errors would be least in the rectum and would become greater nearer to the caecum. It is likely that most digestion of dry matter occurred in the caecum and proximal colon as the digesta were retained in this section for longer than in the rest of the large intestine. Hence, errors due to digestion of dry matter in sections other than the caecum and proximal colon would be negligible.

The retention times measured in this experiment were approximately 9 hr in the caecum and proximal colon, 8.5 hr in the remainder of the large intestine, and 17.5 hr in the total organ. These values are comparable with estimates of 6–11 hr in the caecum and 10–11 hr in the colon and rectum (Hydén 1961) and 19 hr for the entire large intestine (Coombe and Kay 1965).

Mixing of digesta between segments would reduce the gradients of water or electrolytes along the large intestine and thus reduce the estimates of absorption rates. It is unlikely that much mixing occurred once the digesta entered the spiral colon as the lumen diameter was narrow and the digesta was of firm consistency. Peristalsis and antiperistaltic movements which would cause mixing have been reported in the ovine caecum and proximal colon (Spörri and Asher 1940) but not in the remainder of the large intestine of the sheep. Mixing appears to have occurred in the caecum and proximal colon of the sheep in this experiment as there was a marked difference between values for water per gram dry matter in ileal and caecal digesta. If the caecum and proximal colon are considered as one large segment containing 91 g dry matter, with a surface area of 802 cm² and a retention time of 536 min (Table 1), then the difference in water per gram dry matter between ileal digesta and digesta at the start of the spiral colon corresponds to an absorption rate of 0.12 g water per 100 cm² per minute. This is greater than the estimate for this section of the large intestine and is similar to the rate in the first section of the spiral colon [Fig. 3(a)]. As the digesta were retained in the caecum and proximal colon for a relatively long time, this must be the most important section of the large intestine for absorption of water.

Mixing of digesta in the caecum and proximal colon would reduce also the estimates of rate of sodium absorption in this section. The true rate of sodium absorption was probably similar to the rate in the centripetal colon. The rate of absorption of sodium decreased distal to the apex of the spiral colon. This may have been due to the decreased concentration of sodium in the lumen between this part and the rectum as Curran and Schwartz (1960) demonstrated that efflux from the rat colon was dependent on the concentration of sodium in the lumen. The same authors showed that the rate of water transport was dependent on the rate of sodium transport across the wall. This may account for the decreased rate of water absorption observed in these experiments in the distal large intestine.

The present technique appears to be the only one that has been used to determine actual rates of absorption of water and sodium from contents of the large intestine. Other estimates of rates of absorption from the colon of the rat (Curran and Schwartz 1960), dog (Cooperstein and Brockman 1959), and human (Levitan *et al.*

1962) are not directly comparable as the lumens during these experiments were perfused under anaesthesia with saline solutions and as no estimates of mucosal surface area were given by the authors. However, comparison of these data with the data of Curran and Schwartz (1960) suggests that absorption of sodium across the colonic mucosa of the sheep may be greater than that for the rat when the lumen sodium concentration is low.

A decrease in sodium concentration in digesta water occurs between the caecum and the rectum in many mammals (van Weerden 1961; Alexander 1962, 1965; Edmonds 1967). Potassium concentration appears to be more variable. In this experiment, all of the sheep except one had low concentrations of potassium and the concentration of potassium in water of rectal contents was lower than in other published results for sheep (Goodall and Kay 1965*a*, 1965*b*; Bruce *et al.* 1966; English 1966) and lower than in several penned sheep at this establishment sampled at random. This may have been due to a relatively constant rate of secretion of hormones in the body associated with the hourly feeding of the sheep in this experiment. There is evidence that concentrations of sodium and potassium in the small intestine are influenced by the hormone aldosterone (Smith 1969) and that this hormone may influence electrolyte absorption from the large intestine (Edmonds and Marriott 1967). A change in the rate of secretion of aldosterone several hours before slaughter may be an explanation for the different concentrations of potassium in one of the sheep.

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VI. REFERENCES

- ALEXANDER, F. (1962).—*Res. vet. Sci.* **3**, 78.
 ALEXANDER, F. (1965).—*Res. vet. Sci.* **6**, 239.
 BRUCE, J., GOODALL, E. D., KAY, R. N. B., PHILLIPSON, A. T., and VOWLES, L. E. (1966).—*Proc. R. Soc. B* **166**, 46.
 COOMBE, J. B., and KAY, R. N. B. (1965).—*Br. J. Nutr.* **19**, 325.
 COOPERSTEIN, I. L., and BROCKMAN, S. K. (1959).—*J. clin. Invest.* **38**, 435.
 CURRAN, P. F., and SCHWARTZ, G. F. (1960).—*J. gen. Physiol.* **43**, 555.
 EDMONDS, C. J. (1967).—*J. Physiol., Lond.* **193**, 589.
 EDMONDS, C. J., and MARRIOTT, J. C. (1967).—*J. Endocr.* **39**, 517.
 ENGLISH, P. B. (1966).—*Res. vet. Sci.* **7**, 233.
 GOODALL, E. D., and KAY, R. N. B. (1965*a*).—*J. Physiol., Lond.* **176**, 12.
 GOODALL, E. D., and KAY, R. N. B. (1965*b*).—*J. Physiol., Lond.* **176**, 18P.
 HOGAN, J. P., and PHILLIPSON, A. T. (1960).—*Br. J. Nutr.* **14**, 147.
 HYDÉN, S. (1961).—In "Digestive Physiology and Nutrition of the Ruminant". (Ed. D. Lewis.) pp. 35–47. (Butterworths Scientific Publications: London.)
 LEVITAN, R., FORDTRAN, J. S., BURROWS, B. A., and INGELFINGER, F. J. (1962).—*J. clin. Invest.* **41**, 1754.
 MINSON, D. J., and COWPER, J. L. (1966).—*Br. J. Nutr.* **20**, 757.
 SMITH, R. H. (1969).—*Proc. Nutr. Soc.* **28**, 151.
 SMITH, R. N. (1955).—*J. Anat.* **89**, 246.
 SPÖRRI, H. VON, and ASHER, T. (1940).—*Schweizer Arch. Tierheilk.* **82**, 204.
 WEERDEN, E. J. VAN (1961).—*J. agric. Sci., Camb.* **56**, 317.