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Rumen development in the calf

1. The effect of diets containing different proportions of concentrates to hay on rumen development

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1. Thirty Ayrshire bull calves were used in an experiment to study the effects of diets containing different proportions of concentrates to hay on rumen development at 12 weeks of age. In addition, six milk-fed calves were slaughtered at 3 weeks of age for comparison. 2. Restriction of the maximum daily allowance of concentrates to the lower levels was accompanied by an increase in the voluntary intake of hay, but the performance of calves from 3 to 12 weeks of age was significantly better in calves given the high-concentrate diets. 3. The weight of contents of the reticulo-rumen increased from 0·7 kg at 3 weeks of age in the milk-fed calf to 7·7 kg and 10·9 kg at 12 weeks in calves given the high-concentrate and high-roughage diets respectively. Between 68 and 79% of the total contents of the alimentary tract was contained in the reticulo-rumen of the ruminant calf. The weight of contents of the omasum was significantly greater in calves given 1·36 kg concentrates/day than in those given either 0·45 or 2·27 kg concentrates/day. Equations were developed from the results by which the weight of contents of the various parts of the alimentary tract, and hence empty body weight in the live animal, can be determined from a knowledge of the live weight and daily consumption of concentrates and hay. 4. Volume displacement of the reticulo-rumen tended to increase with increase in the proportion of hay in the diet. The volume displacement of the omasum increased in response to concentrate intake up to a maximum of 1·36 kg/day and thereafter declined, but the nature of the diet had no significant effect on the volume displacement of the abomasum. 5. Calves given the high-concentrate diets had a significantly greater weight of reticulo-rumen tissue at 12 weeks than those given the high-roughage diets. 6. Whereas the thickness of the muscular wall of the rumen did not differ significantly between treatments, there was an increase in the length and density of papillas, particularly in the anterior dorsal and ventral sacs of the rumen, as the intake of concentrates was increased. The results show the marked relationship between the performance of the animal and an advanced stage of development of the rumen papillas.

The practice of weaning calves completely off milk at 5 weeks, or even at an earlier age, from which time they receive only concentrates, hay and water, requires early development of the ruminant stomach. Previous studies on the influence of dietary factors on the anatomical development of the rumen have been made on calves given milk until at least 7 weeks of age (Warner, Flatt & Loosli, 1956) or 12 weeks of age (Brownlee, 1956) and which subsequently received, in the main, diets consisting solely of concentrates or of hay.

The proportion of concentrates to hay in the diet of early-weaned calves is very variable. In view of the considerable differences in development of the ruminant stomach between calves given concentrate or hay diets (Warner *et al.* 1956), the need to study the extent of rumen development in calves weaned at 5 weeks of age, and given concentrates and hay in different proportions, is apparent. An experiment was made, therefore, to examine the effect of diets containing different proportions of concentrates to hay on the development of the digestive system of the calf at 12 weeks of age.

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METHODS

Plan of experiment

The experiment, of randomized block design, was done from April to December 1959, and consisted of five treatments in each of six blocks of Ayrshire bull calves.

Calves

The calves were obtained at 3 weeks of age, having been used in experiments during the first 3 weeks of life to investigate the effect of heat treatment on the nutritive value of milk for the calf (Shillam, 1960). Calves were weighed at the beginning of the experiment and at weekly intervals up to the time of slaughter at 84 days of age.

Table 1. *Composition of the concentrate mixture given to the calves*

Ingredient	Weight (kg)
Flaked maize	40·0
Crushed oats	20·0
Molassine meal*	10·0
Extracted decorticated groundnut meal	15·0
White-fish meal	5·0
Dried skim milk	10·0
Drivite V11†	0·25
Super-mindif‡	1·0

* Contains 75 % molasses and 25 % peat moss (Molassine Co. Ltd, Greenwich, London SE 10).
† Contains 800000 i.u. vitamin A and 200000 i.u. vitamin D_3 per lb (Boots Pure Drug Co. Ltd, Nottingham).
‡ Mineral supplement for cattle (Boots Pure Drug Co. Ltd, Nottingham). Maker's formula: calcium 17·4 %, phosphorus 11·4 %, calcium:phosphorus ratio ($CaO:P_2O_5$) 1:1·07, copper 1800 ppm, cobalt 300 ppm, manganese 510 ppm, iodine 0·025 %, sulphur 0·75 %, iron 0·24 %, sodium + chlorine 30 %.

Table 2. *Chemical composition* (%) *of the foods*

Food	Dry matter	Crude protein	Crude fibre	Ether extract	Ash	Nitrogen-free extract
Concentrates	85·9	19·0	3·3	1·9	4·5	57·2
Hay	87·2	7·5	28·7	1·3	6·8	42·9

Diets

Each calf was given sufficient whole milk, warmed to 37°, in two feeds daily at 07·30 and 17·00 h to supply its requirement for maintenance on the basis of 53 kcal gross energy daily/kg live weight (Roy, Shillam, Hawkins & Lang, 1958). The milk allowance was adjusted when the calves were weighed at 4 weeks, and the calves were weaned abruptly at 5 weeks of age.

From 3 weeks of age hay and water were offered *ad lib.* and a concentrate mixture, designed to contain 20 % crude protein on an air-dry basis, was given to a maximum intake of 0·45, 0·91, 1·36, 1·81 or 2·27 kg/day in treatments 1–5 respectively, up to the age of 83 days. No more food was offered to calves after the morning of the 83rd day of life.

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The composition of the concentrate mixture is given in Table 1 and the chemical composition of the concentrate mixture and hay used during the experiment is given in Table 2.

Post-mortem examination

On reaching 84 days of age, calves were weighed and transported to Reading Abattoir to be slaughtered. Six milk-fed calves were slaughtered at 3 weeks of age for comparison. The calves were killed soon after arrival at the slaughter house and the intact alimentary tract was brought back to the Institute, where it was ligatured and cut into separate parts, care being taken to prevent loss of digesta. The parts comprised the reticulo-rumen, omasum, abomasum and intestine, which were each weighed with their contents.

The volume displacement of each stomach compartment was determined by a technique based on that of Warner *et al.* (1956). A glass tube was inserted into the reticulo-rumen through a short section of the oesophagus and held in place by a clip. The position of the tube was adjusted to give a clearance of 5 cm between the point of insertion into the organ and a side-limb of the tube, which joined at an angle of 90°. The reticulo-rumen was placed in a tank of water and all air pockets were removed from within the organ, which was filled with water until it became completely submerged. The water level in the tank was raised to the overflow point and the glass tube was held in position with the side-arm extending horizontally 5 cm above the surface of the water. The water level in the stomach was corrected so that it just reached the side-arm of the tube, indicating that there was a pressure in the organ of 5 cm water above atmospheric pressure. The reticulo-rumen was removed from the tank and the volume of water required to restore the water level in the tank to the overflow point was recorded; this gave a measure of the volume displacement of the organ. The volume displacement of the abomasum was measured in a similar manner, with the glass tube inserted through the pyloric sphincter. The omasum was immersed in a vessel filled with water and the displacement measured; no attempt was made to increase the internal pressure of this organ.

In order to obtain information on the structure of the stomach compartments and on their contents, the following procedure was then carried out. The reticulo-rumen was opened by an incision from the reticulo-omasal orifice along the oesophageal groove to the oesophagus, continuing down the right ruminal artery to separate the dorsal and ventral sacs of the rumen. The omasum was opened along the omasal groove and the abomasum along its dorsal length. The organs were washed free of contents, drained of surplus water for approximately 4 h and then weighed. The weight of contents was calculated by subtraction of the weight of tissue forming the organ from the weight of the intact organ plus contents.

The reticulo-rumen was laid out flat and photographed from above to provide a record of the extent of papillary development in the region of the rumino-reticular fold and in the dorsal and ventral sacs near the coronary pillars. A piece of rumen wall, measuring 6 cm square, was cut out from the ventral sac just caudal to the rumino-reticular fold, weighed and photographed in cross-section. The various organs were then dried to constant weight at 100°.

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RESULTS

Performance of the calves

The results are given in Table 3, which shows that there was a positive linear response between treatments of daily live-weight gain, and thus of live weight at 12 weeks, to increasing total concentrate intake. Fig. 1 shows that calves on treatments 1 and 2 were soon ingesting the maximum daily allowance of concentrates, which they did within about 1 h of feeding, whereas calves on treatments 3, 4 and 5 did not eat all the concentrates provided until 8, 9 and 11 weeks of age respectively.

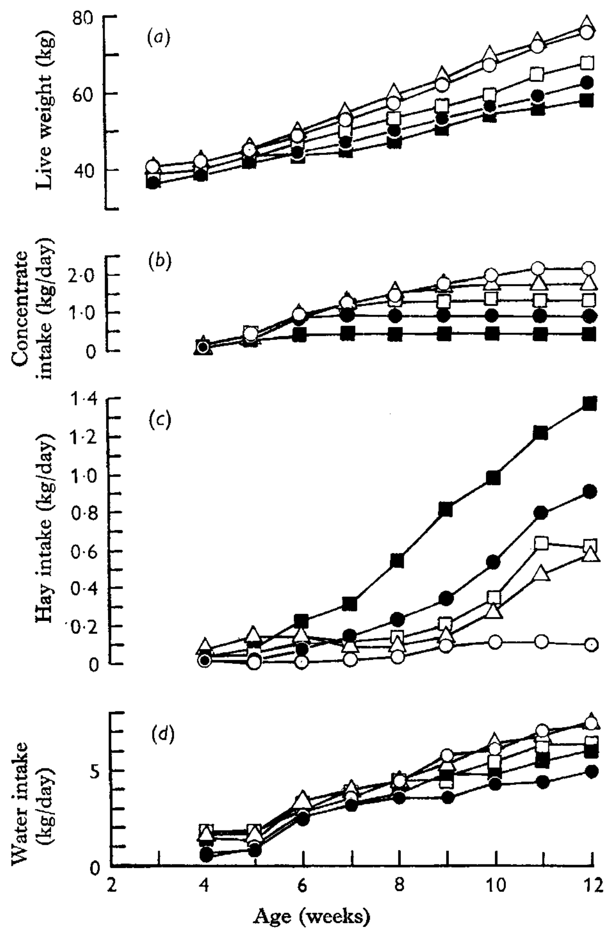

Fig. 1. Mean live weight (*a*) and daily intake of concentrates (*b*), hay (*c*) and water (*d*) of calves weaned at 5 weeks of age and given different allowances of concentrates. ■—■, 0·45 kg concentrates/day; ●—●, 0·91 kg concentrates/day; □—□, 1·36 kg concentrates/day; △—△, 1·81 kg concentrates/day; ○—○, 2·27 kg concentrates/day.

The calves restricted to 0·45 kg concentrates/day consumed considerably more hay than calves on the other four levels of concentrate intake. The total consumption of hay decreased significantly between treatments with increase in total concentrate

Table 3. *Performance (mean values with their standard errors) from 3 to 12 weeks of life of calves weaned at 5 weeks of age and given different allowances of concentrates, with hay offered* ad lib.

	Treatment no. 1	2	3	4	5	Pooled standard error of means	Significance of linear response to increasing concentrate intake
Maximum daily allowance of concentrates (kg)	0·45	0·91	1·36	1·81	2·27	—	—
No. of calves	6	6	6	6	6	—	—
Live weight (kg):							
At 3 weeks	38·6	36·9	38·9	40·8	40·5	±1·6	—
At 12 weeks	58·7	62·7	67·9	77·9	76·6	±2·7	***
Intake of diet (kg):							
Milk (3–5 weeks)	42·5	40·6	40·1	44·0	43·3	±2·0	—
Concentrates	25·1	48·1	65·5	78·7	86·0	±3·1	—
Hay	39·6	21·8	16·3	14·8	3·8	±3·1	***
Water	242	196	265	290	272	±25	—
Live-weight gain/day (kg)	0·32	0·42	0·47	0·60	0·59	±0·030	***

*** Significant at $P < 0·001$.

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Table 4. *Mean values, with their standard errors, for the weight of contents of different parts of the alimentary tract recorded at post-mortem examination of calves given different allowances of concentrates, with hay offered* ad lib.

	Treatment no.					Pooled standard error of means	Initial value†	Significance of response to daily concentrate intake in 12th week	
	1	2	3	4	5			Linear	Deviation from linear
Maximum daily allowance of concentrates (kg)	0·45	0·91	1·36	1·81	2·27	—	—	—	—
No. of calves	6	6	6	6	6	—	6	—	—
Live weight at slaughter (kg)	59·1	62·9	68·9	77·5	76·7	±2·7	36·9	***	—
Wt of contents of reticulo-rumen:									
kg	10·9	9·6	9·4	8·4	7·7	±0·75	0·75	**	—
kg/100 kg live wt at slaughter	18·4	15·2	13·5	10·8	10·0	±0·81	2·0	***	—
Wt of contents of osmasum (g)	178	273	311	291	157	±42	18	—	*
Wt of contents of abomasum (g)	631	705	811	630	745	±119	578	—	—
Wt of contents of intestine (kg)‡	2·1	2·2	2·3	2·5	2·7	±0·15	0·9	**	—
Wt of contents of alimentary tract:									
kg	13·8	12·8	12·8	11·9	11·3	±0·83	2·3	*	—
kg/100 kg live wt at slaughter	23·3	20·3	18·5	15·2	14·7	±0·90	6·2	***	—
Empty body wt (kg)	45·3	50·1	56·1	65·7	65·4	±2·2	34·6	***	—

* Significant at $P < 0·05$. ** Significant at $P < 0·01$. *** Significant at $P < 0·001$.
† Values obtained from 3-week-old calves given milk diets only.
‡ Values calculated from an estimated 42·4 % of total weight of intestine + contents (see p. 177).

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intake, the response being linear. Although the intake of water tended to increase as the consumption of concentrates rose, the response was not significant. There was a marked difference in the condition of the calves at slaughter, those on treatments 4 and 5 being much healthier in appearance than those on treatments 1, 2 and 3. The latter calves had staring coats and were slightly 'pot-bellied', which could be attributed to the large amount of hay consumed.

Post-mortem findings

Contents of the alimentary tract. The results given in Table 4 show that the weight of contents of the reticulo-rumen declined significantly with increase in the daily intake of concentrates during the week before slaughter. This negative linear response became even more marked when weight of contents was expressed as a percentage of live weight at slaughter.

The contents of the reticulo-rumen of calves given the larger quantities of concentrates (treatments 4 and 5) consisted mainly of a thick gruel, which was brown in colour. When the intake of concentrates was lower (treatments 1, 2 and 3) and hay consumption increased in consequence, a greater proportion of hay was found in the digesta, which were green in colour. There was very little sign of the presence of concentrates in the reticulo-rumen contents of calves on treatment 1, in which concentrate intake was restricted to 0·45 kg/day.

The response of weight of omasal contents to daily concentrate intake in the 12th week was found to deviate from linearity, the highest value being found for calves on treatment 3. The weight of contents of the abomasum did not differ significantly between treatments.

No direct measurements were made of the weight of contents of the intestine, although the weight of intestine plus contents was recorded. Later post-mortem examination of calves receiving concentrates or grass as the sole diet, or hay and concentrates in various proportions (Roy & Stobo, unpublished) indicated that the weight of contents of the intestine was very variable within diets, but did not differ markedly between diets, averaging 42·4% of the total weight of intestine plus contents for eleven calves. The standard deviation was $\pm 8\cdot 1$. This value of 42·4% was used, therefore, in this experiment to make an estimate of total weight of contents of the alimentary tract. A significant linear relationship was found between weight of contents of the intestine and daily concentrate intake during the 12th week of life. On the other hand, the total weight of contents of the alimentary tract declined in response to increase in the daily concentrate intake during the week before slaughter. This response was similar to that occurring in the reticulo-rumen and was to be expected, since between 68% (treatment 5) and 79% (treatment 1) of the total contents of the alimentary tract was contained in the reticulo-rumen.

Empty body weight, determined by deducting the weight of contents of the alimentary tract from the live weight at slaughter, increased significantly as the allowance of concentrates was raised. The results suggest that there was very little deposition of body tissue during the 9-week experimental period in calves restricted to 0·45 or 0·91 kg of concentrates daily, since their mean empty body weights appear to have

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increased by only 10·7 and 15·5 kg respectively, compared with 31·1 and 30·8 kg in calves given 1·81 and 2·27 kg concentrates/day respectively.

The results in Table 5 show that the live-weight gain of calves restricted in concentrate intake to 0·45 kg/day (treatment 1) was 57 % of the live-weight gain of calves given up to 2·27 kg concentrates/day (treatment 5). However, 56·1 % of the live-weight gain in the calves given 0·45 kg concentrates daily was the result of increase in contents of the alimentary tract, compared with only 24·9 % in the calves given 2·27 kg concentrates daily. Most of the difference in increase in contents between calves on treatments 1 and 5 was due to the greater increase in reticulo-rumen contents that occurred in treatment 1 as the result of the greater hay consumption.

Table 5. *Effect of increase in weight of tissue and of contents of the alimentary tract (mean values) on live-weight increase in calves given different allowances of concentrates with hay offered* ad lib.

	Treatment no.				
	1	2	3	4	5
Maximum daily allowance of concentrates (kg)	0·45	0·91	1·36	1·81	2·27
No. of calves	6	6	6	6	6
Live weight of calves (kg):					
At 3 weeks	38·6	36·9	38·9	40·8	40·5
At slaughter	59·1	62·9	68·9	77·5	76·7
Increase	20·5	26·0	30·0	36·7	36·2
Weight of reticulo-rumen tissue (kg):					
At 3 weeks	0·24	0·24	0·24	0·24	0·24
At slaughter	1·68	1·80	1·80	1·89	2·12
Increase	1·43	1·56	1·56	1·64	1·88
% of live-weight increase due to increase in reticulo-rumen tissue	7·0	6·0	5·2	4·5	5·2
Weight of alimentary tract tissue (kg):					
At 3 weeks	1·78	1·78	1·78	1·78	1·78
At slaughter	5·32	5·70	5·84	6·11	6·72
Increase	3·54	3·92	4·06	4·33	4·94
% of live-weight increase due to increase in alimentary tract tissue	17·3	15·1	13·5	11·8	13·7
Weight of contents of reticulo-rumen (kg):					
At 3 weeks	0·75	0·75	0·75	0·75	0·75
At slaughter	10·86	9·60	9·36	8·44	7·71
Increase	10·11	8·85	8·61	7·69	6·96
% of live-weight increase due to reticulo-rumen 'fill'	49·4	34·1	28·7	21·0	19·2
Weight of contents of alimentary tract (kg):					
At 3 weeks	2·26	2·26	2·26	2·26	2·26
At slaughter	13·76	12·76	12·80	11·85	11·29
Increase	11·50	10·50	10·54	9·59	9·03
% of live-weight increase due to 'gut fill'	56·1	40·4	35·1	26·1	24·9
% of live-weight increase due to increase in alimentary tract tissue plus contents	73·4	55·5	48·7	37·9	38·6

Multiple covariance analyses of weight of contents of reticulo-rumen, omasum, abomasum, intestine and total weight of contents were made separately using the variables: live weight at slaughter, daily concentrate consumption and daily hay consumption in the 7-day period before slaughter. The variable (daily concentrate

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Table 6. *Partial regression coefficients of weight of contents of different parts of the alimentary tract on live weight at slaughter and daily concentrate consumption in the week before slaughter in calves given different allowances of concentrates, with hay offered* ad lib.

	General mean weight of contents	Partial regression coefficient with its standard error†			Residual standard deviation	Significance of regression equation
		Live weight (kg)	Concentrate consumption (kg/day)			
General mean	—	69·0	1·35	2·20‡	—	—
Reticulo-rumen (kg)	9·20	0·194 ± 0·039***	−3·89 ± 0·59***	—	1·33	***
Omasum (g)	242	10·5 ± 3·0**	327 ± 161	−168 ± 57**	103	**
Abomasum (g)	704	2·70 ± 8·0	3·61 ± 122	—	275	ns
Intestine (kg)	2·35	0·0039 ± 0·010	0·288 ± 0·15	—	0·34	**
Total (kg)	12·49	0·212 ± 0·042***	−3·72 ± 0·64***	—	1·44	***

** Significant at $P < 0·01$. *** Significant at $P < 0·001$. ns, non-significant.

† In calculating the partial regression coefficients and their standard errors, arrangement in treatments and blocks has been ignored.

‡ In calculating the partial regression coefficients for the contents of the omasum, the value for (concentrate consumption)^2 was used in addition to concentrate consumption.

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Table 7. *Mean values, with their standard errors, for the volume displacement of the intact organs of the alimentary tract recorded at post-mortem examination of calves given different allowances of concentrates, with hay offered* ad lib.

	Treatment no.					Pooled standard error of means	Initial value†	Significance of response to increasing concentrate intake	
	1	2	3	4	5			Linear	Deviation from linear
Maximum daily allowance of concentrates (kg)	0·45	0·91	1·36	1·81	2·27	—	—	—	—
No. of calves	6	6	6	6	6	—	6	—	—
Empty body weight (kg)	45·3	50·1	56·1	65·7	65·4	—	34·6	***	—
Volume displacement of intact organs (l.):									
Reticulo-rumen	27·3	25·8	25·0	21·1	22·4	±2·0	2·9	*	—
Omasum	0·7	0·9	0·9	0·8	0·7	±0·07	0·1	—	*
Abomasum	3·5	4·1	3·6	3·1	3·5	±0·4	2·5	—	—
Adjusted volume displacement of intact organs‡ (l.):									
Reticulo-rumen	33·1	29·0	25·2	16·5	17·9	±2·3	—	***	—
Omasum	0·9	1·0	0·9	0·7	0·6	±0·09	—	**	*

Regression coefficient of volume displacement of reticulo-rumen on empty body weight = 0·51 ± 0·17**.
Regression coefficient of volume displacement of omasum on empty body weight = 0·015 ± 0·007*.

* Significant at $P < 0·05$. ** Significant at $P < 0·01$. *** Significant at $P < 0·001$.
† Values for 3-week-old calves given milk diets only.
‡ Adjusted for differences between treatment groups in mean empty body weight.

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consumption)[2] was also used in the covariance analysis of weight of contents of the omasum, in an attempt to fit a linear regression to the response curve of weight of omasal contents to concentrate intake. Hay consumption did not have a significant effect on weight of contents of any of the sections of the alimentary tract and the partial regression coefficients were therefore recalculated after exclusion of this variable. The values given in Table 6 may be used to estimate weight of contents of the alimentary tract and hence empty body weight in the live animal. Alternatively the equation given below, which includes the effect of hay intake, may be used for this purpose:

$$y = 12{\cdot}49 + 0{\cdot}200(x_1 - 69{\cdot}0) - 3{\cdot}33(x_2 - 1{\cdot}35) + 0{\cdot}40(x_3 - 0{\cdot}72),$$

where y = total contents of the alimentary tract (kg),
x_1 = live weight (kg),
x_2 = daily intake of concentrates in previous week (kg),
x_3 = daily intake of hay in previous week (kg).

Volume displacement of the stomach compartments. The results given in Table 7 show that the volume displacement of the reticulo-rumen was largest in treatment 1 and decreased gradually with increase in concentrate consumption, to reach its lowest level in treatment 4. The simple regression coefficient of volume displacement on total hay consumption from 3 to 12 weeks of age ($0{\cdot}165 \pm 0{\cdot}075$) was significant at $P < 0{\cdot}05$. The response to total concentrate intake deviated significantly from linearity in the case of the volume displacement of the omasum, but there was no significant response of volume displacement of the abomasum to increasing concentrate intake.

Multiple covariance analyses of volume displacement of the three organs were made using the variables: empty body weight, total concentrate consumption and total hay consumption during the period 3–12 weeks of age. Since only the partial regression coefficient of volume displacement on empty body weight was significant for the reticulo-rumen and the omasum, the treatment means were adjusted by using the respective simple regression coefficients of volume displacement on empty body weight shown in Table 7. The adjusted mean volume displacement of the reticulo-rumen declined steadily from 33·1 l. in treatment 1 to about half this value in treatment 4. After adjustment the mean volume displacement of the omasum rose from 0·9 l. in treatment 1 to 1·0 l. in treatment 2 and then declined steadily to 0·6 l. in treatment 5, both the linear response and deviation from linearity being significant.

Weight of tissue forming the organs of the alimentary tract. The results are presented in Table 8, which shows that the weight of fresh tissue forming the organs of the alimentary tract, with the exception of the omasum, increased as the level of concentrate intake increased. The weight of intestine tissue was assumed to be 57·6% of the measured weight of intestine plus contents (see p. 177). Differences between treatments in weight of tissue forming the omasum were non-significant, but followed a similar pattern to that found in weight of contents and volume displacement of this organ.

The weight of tissue of the reticulo-rumen and omasum of 12-week-old calves increased to about eight times that found in the corresponding organs of 3-week-old

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Table 8. *Mean values, with their standard errors, for the weight of tissue forming the organs of the alimentary tract recorded at post-mortem examination of calves, given different allowances of concentrates, with hay offered* ad lib.

	Treatment no.					Pooled standard error of means	Initial value†	Significance of response to increasing concentrate intake	
	1	2	3	4	5			Linear	Deviation from linear
Maximum daily allowance of concentrates (kg)	0·45	0·91	1·36	1·81	2·27	—	—	—	—
No. of calves	6	6	6	6	6	—	6	—	—
Empty body weight (kg)	45·3	50·1	56·1	65·7	65·4	—	34·6	***	—
Weight of fresh organ tissue (g):									
Reticulo-rumen	1678	1804	1803	1885	2120	±103	244	*	—
Omasum	397	498	475	428	410	±47	54	—	—
Abomasum	405	444	414	421	555	±26	239	*	*
Intestine‡	2835	2952	3148	3375	3636	±207	1241	**	—
Total	5315	5698	5840	6109	6722	±265	1778	**	—
Weight of oven-dried tissues (g):									
Reticulo-rumen	196	242	265	272	313	±17	40	***	—
Omasum	53	75	77	70	72	±9	9	—	—
Abomasum	56	90	101	101	109	±7·1	41	***	—

* Significant at $P < 0·05$. ** Significant at $P < 0·01$. *** Significant at $P < 0·001$.
† Values for 3-week-old calves given milk diets only.
‡ Values estimated as 57·6% of total weight of intestine + contents (see p. 177).

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calves given milk diets only, whereas the abomasum and intestine tissue increased in weight to only two or three times the initial value. Reference to Table 5 shows that the increase in weight of the tissue of the alimentary tract amounted to between 12 and 17 % of the total live-weight increase from 3 to 12 weeks. The weight of tissue of the alimentary tract, expressed as a percentage of empty body weight increased therefore from 5·1 % in the 3-week-old calf to 9·3 % (treatment 4) and 11·7 % (treatment 1) in the 12-week-old calf.

The weight of the stomach compartments, after drying to constant weight, showed trends similar to those of the corresponding weight of tissue on a fresh basis (see Table 9).

Multiple covariance analyses were attempted on the fresh and dried weight of tissues using the variables: empty body weight, total concentrate consumption and total hay consumption in the period 3–12 weeks of age. There was no relationship between weight of tissue of any of the stomach compartments and empty body weight.

Development of the rumen. Examples of the extent of development of the reticulo-rumen in the ventral sac and in the anterior dorsal sac in the region of the rumino-reticular fold are shown in Pls. 1–3. The muscular pillars were much thicker and better developed in the 12-week-old calves given solid food than in the 3-week-old milk-fed animals, but there was no apparent difference between treatments in the size and thickness of the muscular pillars in calves that had been weaned on to solid food at 5 weeks of age.

In the 3-week-old calf given only milk, virtually no development of papillas had taken place, but in calves which received a diet consisting mainly of hay (treatment 1) papillas were fairly numerous in the ventral sac and anterior dorsal sac of the rumen, although practically absent from the main part of the dorsal sac and in the region of the muscular pillars. As the amount of concentrates in the diet increased, the papillas tended to be of greater length and formed a dense covering over the ventral and anterior dorsal sacs of the rumen, often occurring in dense clumps in calves on treatments 4 and 5. In those calves given high levels of concentrates, there was also a tendency for papillary development to occur in the dorsal sac of the rumen.

The thickness of the rumen wall and length of papillas in the region just caudal to the rumino-reticular fold were measured from the photographs of the reticulo-rumen of each individual calf and the mean values are presented in Table 9. Although the muscular wall of the rumen of the 3-week-old milk-fed calf was reasonably thick, papillas were decidedly small and undeveloped. The thickness of the muscular wall increased from 2·2 mm in treatment 1 to 2·8 mm in treatment 4, but differences were not significant. The average length of papillas for each of the thirty calves ranged from 3·5 to 8·7 mm, significant increases occurring between treatments as the concentrate allowance rose from 0·45 to 1·81 kg/day.

The mean weight of the pieces of rumen tissue that were used for the cross-section photographs, and which measured 6 × 6 cm, are given in Table 9. The weight of rumen tissue in this small area increased significantly as the daily intake of concentrates rose and was significantly correlated to total thickness of rumen wall ($r = +0·75$), length of papillas ($r = +0·73$), dried rumen tissue weight ($r = +0·68$) at $P < 0·001$, fresh rumen tissue weight ($r = +0·56$) at $P < 0·01$ and muscle thickness ($r = +0·46$) and volume displacement of the reticulo-rumen ($r = -0·40$) at $P < 0·05$.

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Table 9. *Mean values, with their standard errors, for the thickness of muscle and papillas in a 6 cm square section of the rumen wall from the region of the rumino-reticular fold, together with the weight of the section, recorded at post-mortem examination of calves given different allowances of concentrates, with hay offered* ad lib.

	Treatment no.					Pooled standard error of means	Initial value†	Significance of response to increasing concentrate intake	
	1	2	3	4	5			Linear	Deviation from linear
Maximum daily allowance of concentrates (kg)	0·45	0·91	1·36	1·81	2·27	—	—	—	—
No. of calves	6	6	6	6	6	—	6	—	—
Cross-section of rumen wall:									
Thickness of muscle (mm)	2·2	2·2	2·3	2·8	2·6	±0·23	1·4	—	—
Length of papillas (mm)	4·2	5·2	5·5	7·4	7·4	±0·27	2·1	***	*
Total thickness of muscle and papillas (mm)	6·4	7·4	5·7	10·2	10·0	±0·40	3·5	***	—
Weight of 6 × 6 cm section of rumen wall (g)	23·3	24·3	29·2	33·9	39·2	±1·4	—	***	*

* Significant at $P < 0·05$. *** Significant at $P < 0·001$.
† Values for 3-week-old calves given milk diets only.

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DISCUSSION

The intake of concentrates had a marked effect on the performance and well-being of calves weaned at 5 weeks of age. Low intakes of concentrates were accompanied by corresponding increases in the voluntary intake of hay, which resulted in the weight of contents of the reticulo-rumen being up to 41 % greater than that with high intakes of concentrates.

The mean daily live-weight gain during the period 3–12 weeks of age of calves given 1·81 and 2·27 kg concentrates/day was similar to the results obtained by Preston (1956*a*, *b*) from 32 to 87 days of age in calves weaned at 3 weeks of age. At lower levels of concentrate intake (treatments 1, 2 and 3) the increase in hay consumption was insufficient to supply the nutrient requirement for an adequate rate of growth, thus confirming similar observations by Warner *et al.* (1956).

The weight of contents of the alimentary tract increased from 6·2 % of the live weight at 3 weeks of age to 14·7 % in treatment 5 and 23·3 % in treatment 1, the largest proportion of the increase relative to live weight being due to increase in contents of the reticulo-rumen and omasum. In contrast to these results, Roy, Gaston, Shillam, Thompson, Stobo & Greatorex (1964) found, in 15-week-old calves given large volumes of whole milk, that the weight of contents of the alimentary tract was 3·6 % of the live weight 16 h after the last feed, and Kesler, Ronning & Knodt (1951) found, on slaughtering 8-day-old milk-fed calves 8 h after feeding, that the weight of alimentary tract contents was 4·1 % of the live weight. It seems likely that the value of 6·2 % obtained in this experiment was high because the 3-week-old milk-fed calves were slaughtered within 2 h of feeding.

The observations of Marshall, Arnold & Becker (1950) that the weight of rumen contents increased from birth and exceeded that of the abomasum contents between 7 and 30 days of age is confirmed by our values for the 3-week-old calf, in which the weight of rumen contents was greater than that of the abomasum contents and represented 33 % of the total contents. At 12 weeks of age, 68 % of the total contents was contained in the reticulo-rumen in treatment 5 and 79 % in treatment 1. The considerable increase in weight of reticulo-rumen contents that resulted from the introduction of solid food is in close agreement with the findings of Kesler *et al.* (1951) in the 12-week-old calf weaned at 5 weeks of age and given a diet similar to that received by calves on treatment 5. The greater weight of contents of the reticulo-rumen of calves consuming large quantities of hay is to be expected, in view of similar observations by Freer & Campling (1963) on cows given either hay or concentrate diets. The apparent absence of concentrates in the reticulo-rumen contents of calves on treatment 1, 24 h after concentrates were last eaten, may have been due to the fact that the mean retention time of concentrates in the reticulo-rumen is much less than that of hay (Paloheimo & Mäkelä, 1959; Freer & Campling, 1963).

The observation that the weight of contents of the omasum was significantly greater in treatment 3 than in either treatment 1 or 5 suggests that the weight of contents was determined by two interacting factors. The explanation offered below is based on the assumption that the weight of contents of the omasum was dependent

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on the relative rates at which the different diets were digested in the reticulo-rumen, with a resultant effect on the mean retention time of food particles in the omasum and on rate flow of digesta through this organ.

It would seem likely that in treatment 5, the retention time of the high-concentrate diet was low, whereas in treatment 3 the greater intake of hay would result in the digesta remaining in the reticulo-rumen for a considerable time. It is known that concentrates may have a depressing effect on the digestibility of hay in the reticulo-rumen (Balch, 1957), and this condition could lead to the mean retention time of hay being increased further. In treatment 1 the concentrate part of the diet was invariably eaten immediately it was offered, and it is likely that the digesta from this part of the diet were soon passed on to the abomasum. If this occurred, there would be no depressing effect on the digestibility of hay, which would then pass to the omasum, where it would not be retained for any great length of time.

The method used by us to obtain a measurement of volume displacement is open to criticism on the grounds that, as muscle tonus is soon lost, the walls of the organ may be capable of considerable stretching, particularly if time elapses between slaughtering the animals and measuring the volume displacement. Although it is realized that the in vivo technique of Flatt, Warner & Loosli (1959) is likely to give a more accurate measurement of reticulo-rumen volume, Harrison & Warner (1961) found that the volume of water required to fill the reticulo-rumen in vivo was, on average, 1·6 times the volume displacement of the digesta removed through the fistula. Flatt *et al.* (1959) obtained an increase of about 27% in volume capacity measured *post mortem* compared with that obtained 1 h before slaughter, but part of the increase was attributed to the presence of an airpocket in the rumen during the determinations in vivo. Since these workers reported that the performance of fistulated calves given dry diets was inferior to that of intact animals, because of leakage at the cannula, it would appear that the method employed in our study to determine volume displacement was the most satisfactory, bearing in mind that values so obtained were used for comparative purposes only.

Inclusion of solid food in the diet of the milk-fed calf has been shown to result in an increase in the capacity of the forestomach compartments of the calf. Blaxter, Hutcheson, Robertson & Wilson (1952) suggested that, when hay was given, this increase occurred merely by stretching the walls, but Warner *et al.* (1956) found that the weight of tissue forming the reticulo-rumen and omasum also increased. The results of our investigation support the observations of Warner *et al.* (1956), since a comparison of results for the 3-week-old milk-fed calf with those for the 12-week-old calf showed that dry feeding resulted in a considerable increase in weight of the reticulo-rumen and omasum per unit of empty body weight, whereas the abomasum and intestine increased only slightly.

The considerable increase in size of the reticulo-rumen that occurred when solid food was given was accompanied by a relatively small increase in thickness of the muscular wall, suggesting that the musculature of the reticulo-rumen is sufficiently developed for movements to begin at an early age, as was shown by Roy (1956) and Benzie & Phillipson (1957). On the other hand, there was a considerable increase in

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thickness of the mucosa, particularly in the reticulum and the ventral and anterior dorsal sacs of the rumen, showing that the major part of the increase in weight of tissue took place in the mucosal layer.

Brownlee (1956) reported that the weight of mucosa was not related to the weight of muscle in the rumen wall, calves given concentrates having less muscle and considerably more mucosa in their rumens than hay-fed animals. Despite the fact that the rumen mucosa was not separated from the muscle layer in our experiment, the greater length and density of papillas that occurred in treatments 4 and 5 tend to confirm Brownlee's results.

Brownlee (1956) first suggested that the extent of development of the rumen papillas was not predetermined, but depended on the energy value of the food or the rapidity with which it was broken down into absorbable fractions. It is now known that papillary development is stimulated by the presence of volatile fatty acids (VFA) in the rumen (Flatt, Warner & Loosli, 1958; Tamate, McGilliard, Jacobson & Getty, 1962), butyrate and, to a lesser extent, propionate having a considerably greater effect than acetate (Sander, Warner, Harrison & Loosli, 1959). Since the production of propionic, butryic and higher acids has been shown to rise with increase in the proportion of concentrates in the diet (Carroll & Hungate, 1954; Balch & Rowland, 1957) and with increase in the protein content of the diet (Balch & Rowland, 1957), it is clear that conditions favourable to rumen papillary development existed with treatments 4 and 5 of our study, whereas with treatments 1 and 2 in which there was likely to have been produced a greater proportion of acetic acid, papillary development did not occur to such a marked extent.

It was suggested by Armstrong, Blaxter & Graham (1957) that an actively metabolizing rumen epithelium was necessary for the absorption of VFA. Sander *et al.* (1959) showed that the increase in metabolic activity, in combination with the greater blood flow to the mucosal region that had been shown to occur (Dobson & Phillipson, 1956) could account for the development of rumen epithelium in the presence of VFA. This could lead to the stimulation of the absorptive ability of the mature rumen (Sutton, McGilliard & Jacobson, 1963). It has been reported (Phillipson, 1959, quoted by Sander *et al.* 1959) that the relative increase in blood flow from the rumen was dependent on the acid present, butyrate giving rise to a greater flow than propionate, which in turn gave rise to a greater flow than acetate. The combination of increased metabolic activity and the resultant increase in blood flow, which occurs in the presence of butyrate, could well be responsible for the greater development of rumen papillas in calves given large quantities of concentrates. Thus, the growth rate of the animal as a whole is related to and might even be dependent upon, an advanced stage of development of the rumen papillas.

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EXPLANATION OF PLATES

Rumen development in the ventral sac (top) and the anterior dorsal sac in the region of the rumino-reticular fold (middle) in calves given different allowances of concentrates with hay offered *ad lib.* (scale graduated to 0·1 in). The cross-section photograph (bottom) shows muscle thickness and papilla length in the anterior dorsal sac just caudal to the rumino-reticular fold (scale graduated to 0·5 mm).

PLATE 1

F 33. Rumen development in a 12-week-old calf given concentrates up to a maximum intake of 0·45 kg/day with hay offered *ad lib.* (treatment 1).

F 42. Rumen development in a 12-week-old calf given concentrates up to a maximum intake of 0·91 kg/day with hay offered *ad lib.* (treatment 2).

PLATE 2

F 34. Rumen development in a 12-week-old calf given concentrates up to a maximum intake of 1·36 kg/day with hay offered *ad lib.* (treatment 3).

F 28. Rumen development in a 12-week-old calf given concentrates up to a maximum intake of 1·81 kg/day with hay offered *ad lib.* (treatment 4).

PLATE 3

F 30. Rumen development in a 12-week-old calf given concentrates up to a maximum intake of 2·27 kg/day with hay offered *ad lib.* (treatment 5).

C 79. Rumen development in a calf that received only milk between birth and slaughter at 3 weeks of age (control).

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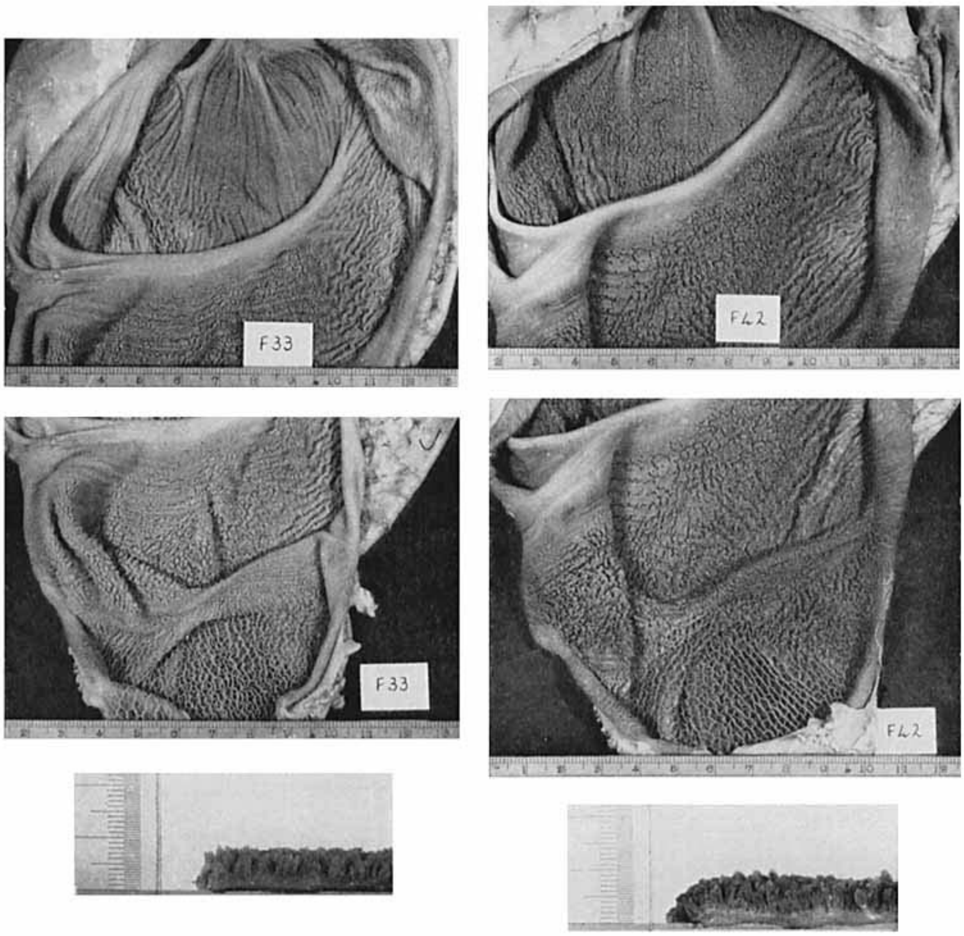

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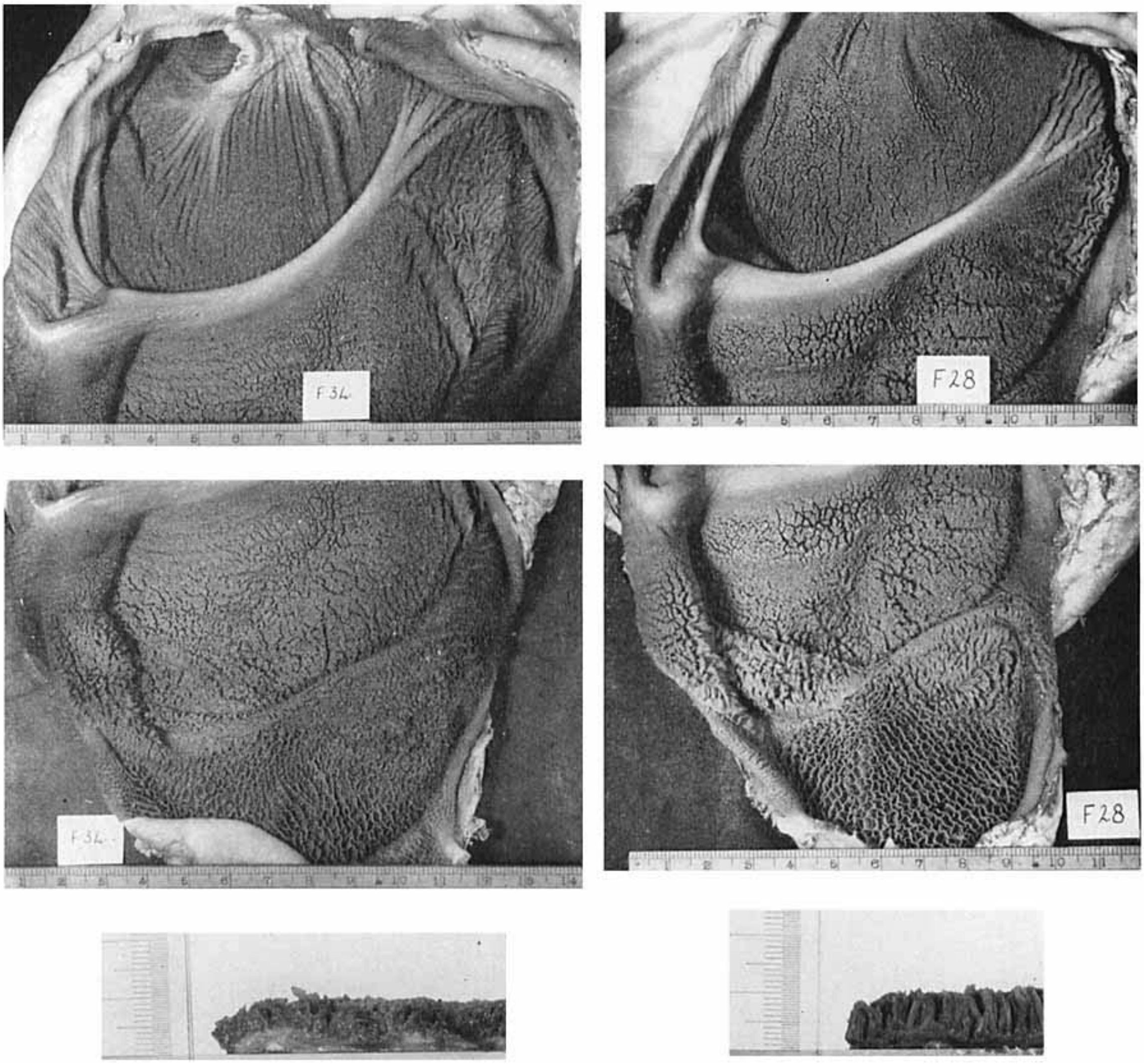

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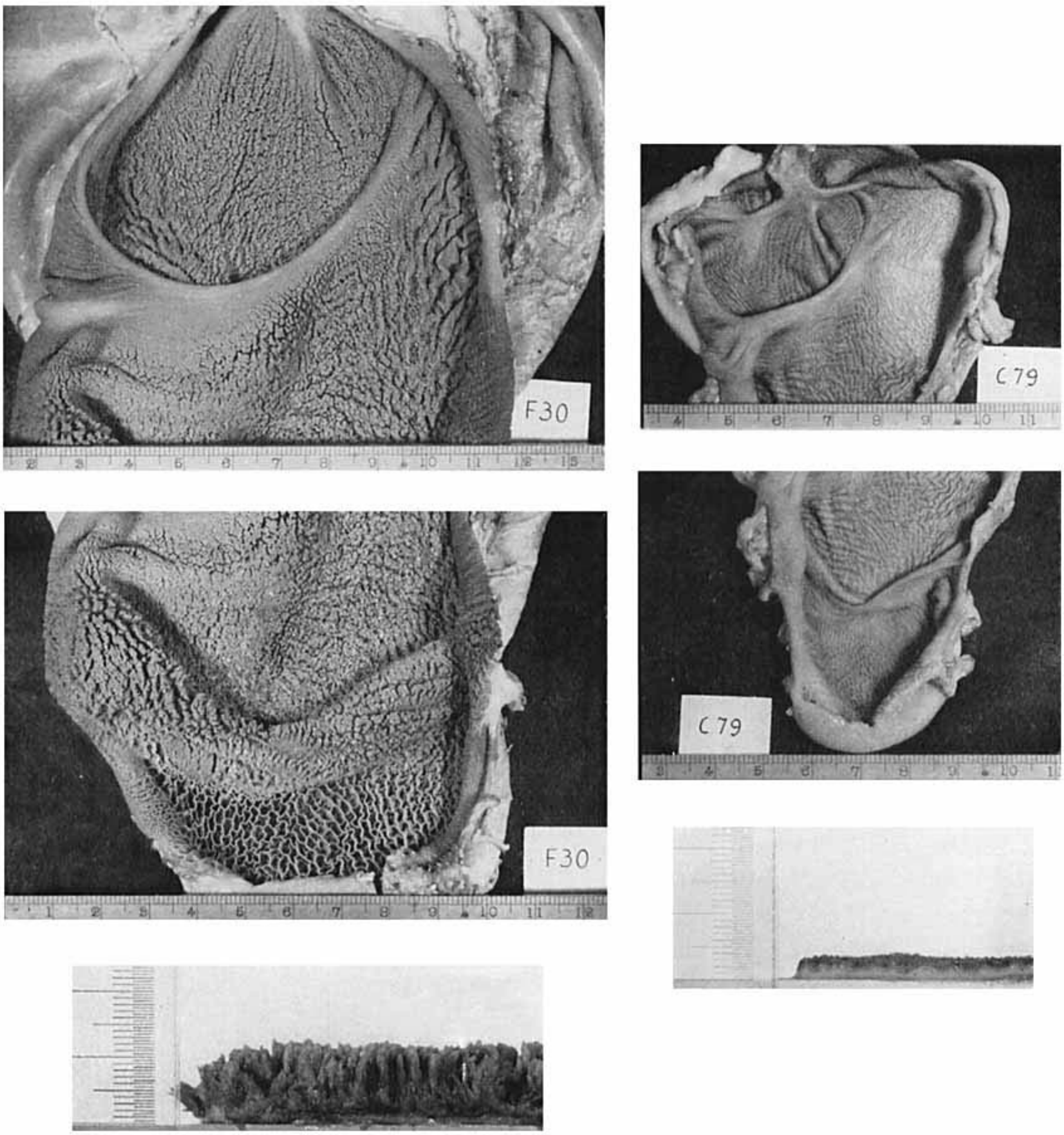

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