Further studies on the changing composition of the digesta along the alimentary tract of the sheep

3. Changes in the omasum

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The passage of the digesta through the purse-like omasum is still very much of a mystery. Our colleagues Benzie & Phillipson (1957) have observed by cine-radiography two clear movements of this organ. The first is a downward and forward displacement when the reticulum contracts, the omasum forming a receptacle so that the reticular contents will tend to run into the interlaminal spaces. It is possible that when the organ returns to its upright position the liquid may flow ventrally to the abomasum, leaving the more solid matter trapped in the interlaminal spaces. The second movement is a rotation of the organ on its long axis. A constriction of the lesser curvature occurs at intervals and may persist for short periods in spite of changes in position and can form a marked indentation.

In animals eating solid food Benzie & Phillipson noted from X-ray studies that when barium sulphate is given the whole organ fills with it as time after feeding proceeds. Barium sulphate seemed to pass through the organ initially by the lesser curvature, and was never seen to enter the whole of the upper pole of the organ and slowly work its way to the lower pole. It seemed to permeate the whole organ at once and its amount to increase gradually. This behaviour gives the impression that material flowing through the lesser curvature is drawn between the interlaminal spaces, although it is not possible to detect its course out of these spaces again. Benzie & Phillipson put forward the tentative view that the more solid part of the food enters the interlaminal spaces, and in consequence traverses the organ more slowly than the more liquid fraction which may pass through without remaining in these spaces.

That dehydration of the digesta takes place in the omasum is now well recognized (Garton, 1951; Masson & Phillipson, 1952; Ekman & Sperber, 1952; Gray, Pilgrim & Weller, 1954; Boyne, Campbell, Davidson & Cuthbertson, 1956). Gray *et al.* (1954) have reported that absorption of volatile fatty acids entering the omasum was of the order of 40–69 %. Ekman & Sperber found that the bicarbonate level was lower than that of rumen contents and decreased round the curvature from the ruminal to the abomasal end to below the plasma level. Chloride concentration increased as that of bicarbonate decreased but never fell to the level in plasma. Smiles & Dobson (1956) have described changes in rumen bacteria as the cells pass through the omasum.

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Badawy, Campbell, Cuthbertson, Fell & Mackie (1958) and Badawy, Campbell, Cuthbertson & Mackie (1958) pooled the contents of the omasum, care being taken to remove the partially dehydrated material from between its several laminae as well as to include the much more fluid material found in the sulcus. Although such pooled material represents the contents at the time of death it is unlikely that all the contents are flowing through at the same rate.

This paper describes an attempt to follow the movement of the digesta between the laminae and through the organ, and for this purpose we have used as markers insoluble ash, lignin and chromium sesquioxide, the last being added to the ration.

EXPERIMENTAL

Two similar groups of Blackface ewes, one of seven and one of eight animals, were used. Both groups were fed on hay *ad lib.* at 7 a.m. and 4 p.m. and 225 g concentrate mixture (2 parts linseed meal and 1 part crushed oats) at 11 a.m.

The animals in the groups were divided into the following subgroups, and contents were obtained from the reticulum, omasum and abomasum of all of them.

Group 1 (seven ewes): (*a*) Two with omasal contents examined as a whole and compared with contents of reticulum and abomasum.

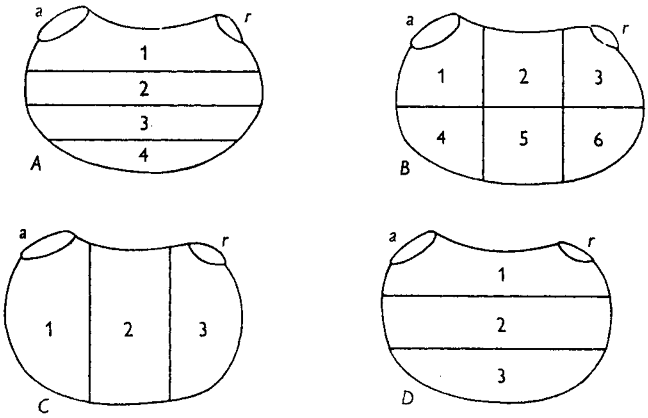

Fig. 1. Way of division of omasum for regional sampling of contents (see this page). In the living animal facing left the omasum as depicted is orientated anti-clockwise some 90°. *a*, abomasal orifice; *r*, reticular orifice.

(*b*) Two with contents between the omasal laminae separated into four horizontal strata as in Fig. 1*A*, and corresponding zones pooled.

(*c*) Three with contents between the omasal laminae divided into six divisions as in Fig. 1*B*, and corresponding zones pooled.

Group 2 (eight ewes): (*a*) Four with contents of omasum divided as shown in Fig. 1*C*.

(*b*) Four with contents of omasum divided as in Fig. 1*D*.

In all these corresponding zones were pooled.

It should be noted that in the living animal the omasum is located in a position roughly at 90° to the positions in the diagram shown in Fig. 1, that it fills from above from the reticulum and that the terms 'upper', 'middle' and 'lower' refer to the diagrams.

Group 1. Each sheep from the first group was killed on a separate day at 9 a.m. by humane killer and bled. The organs to be studied were ligatured off and the contents collected as described by Badawy, Campbell, Cuthbertson, Fell & Mackie (1958).

Apart from the last animal in this group analyses of volatile fatty acids (V.F.A.) were not done on the subdivided portions of the omasal contents. In this sheep it was possible to do V.F.A. analyses on the relatively small samples available.

Owing to the very small amount of the moist contents found in the sulcus omasi, only dry matter was estimated in the material in this zone. On the dried material from each of the other portions the dry matter, ash and insoluble ash were estimated. They were then pooled for energy estimation. The concentrations of the different constituents in the omasum as a whole were calculated from the concentrations in the different portions.

Group 2. All the sheep in the second group were killed on a single day 17 h after the last feed. Each sheep was given orally a gelatin capsule containing 4–5 g chromium sesquioxide at 5 p.m. on the day before it was killed. The techniques followed in killing the sheep and ligating, separating and emptying the organs were the same as for the first group. The contents between the individual clefts formed by the laminae of the omasum in the first four sheep were divided into three zones vertically, that is at right angles to the sulcus shown horizontally in Fig. 1 *C*. The three zones were: that nearest the reticulum, the middle portion and the portion nearest the abomasum. In the second four sheep the contents between the individual laminae of the omasum were divided into three zones horizontally (Fig. 1 *D*). The three portions were: upper, middle, and lower. In each of the two groups of four sheep the digesta from the respective omasal zones were pooled in proportion to their wet weight and the results of the analyses of the pooled samples were taken as a mean for the four sheep. Dry matter, total nitrogen and non-protein nitrogen were estimated on the wet contents. V.F.A. were estimated in the different portions of the omasum. The dried material from the reticula and the abomasa of the eight sheep were also pooled in proportion to the dry-matter content of the organ in each sheep, and dry matter, ash, insoluble ash, lignin, chromium sesquioxide and energy were estimated: for the dry matter it was a re-estimation. The concentrations of the different constituents in the omasum as a whole were calculated from the concentrations in the different portions.

Chemical methods. Dry matter, total nitrogen, non-protein nitrogen, V.F.A. and lignin were determined as done by Badawy, Campbell, Cuthbertson, Fell & Mackie (1958), Badawy, Campbell, Cuthbertson & Mackie (1958), or Boyne *et al.* (1956). Chromium sesquioxide was determined by a method recommended by Schürch, Lloyd & Crampton (1950).

RESULTS

Changing composition of the digesta through the reticulum, omasum and abomasum: total contents

Dry matter, ash and insoluble ash. The dry-matter percentage in the omasum of groups 1 and 2 if the omasum is taken as a whole (Table 1) was higher than in the reticulum or the abomasum at the 0·1 % level of significance, but the difference between the reticulum and the abomasum was not significant. Though it is recognized that such findings refer to the contents only at the time of slaughter, nevertheless, since they are the mean for seven and eight sheep the individual differences in content at the moment of death would tend to be minimized, and it is considered reasonable to use them as a basis for tracing what has happened. The losses of water in the omasum calculated from the dry-matter percentages in the reticulum and the omasum were 48 % in group 1 and 55 % in group 2. On the other hand, water added to the abomasal contents amounted to 123 and 197 % in the two groups, respectively.

Table 1. *Mean concentrations of different constituents in the wet contents of the reticulum, omasum and abomasum of two groups of sheep*

Site	Dry matter (%)	Ash (%)	Insoluble ash (%)	Total nitrogen (%)	Non-protein nitrogen (%)	Energy (Cal./100 g)	V.F.A. (m-equiv./100 g)
Group 1 (seven sheep)							
Reticulum	7·86	0·77	0·093	0·234	—	35·0	7·72
Omasum	16·03	1·39	0·282	0·417	—	73·3	5·54*
Abomasum	6·22	0·99	0·238	0·209	—	29·8	1·16
Group 2 (eight sheep)							
Reticulum	10·18	0·90	0·191	0·276	0·035	46·6	—
Omasum	17·84	1·50	0·416	0·437	0·038	86·1	—
Abomasum	8·89	1·57	0·861	0·246	0·061	38·0	—

* Results for three sheep only: the mean percentages of dry matter and of insoluble ash in the wet contents of the omasum for these three animals were 16·01 and 0·295, respectively.

V.F.A., volatile fatty acids.

The concentrations of ash and insoluble ash in the wet contents in the omasum of group 1 (Table 1) were considerably higher than in the abomasum and the reticulum. In group 2, which had received the chromium sesquioxide, however, the ash concentrations in the reticulum and the omasum were relatively similar to those in group 1, but in the second group they were much higher in the abomasum. In both groups the ash as a percentage of the dry matter was much higher in the abomasum than in the reticulum and the omasum, and the reticulum values were slightly greater than those in the omasum (Table 2). Despite the administration of the chromium sesquioxide, the values for group 2 were lower than those for group 1 for the reticulum and the omasum, but the abomasal values for group 2 were higher. The concentration of insoluble ash in the dry matter was at a higher level generally in group 2 and the omasal values were somewhat higher than in the reticulum. The abomasal values were very much higher than the omasal and particularly so in group 2.

Table 2. *Mean concentrations of different constituents in the dry matter and organic matter of the contents of the reticulum, omasum and abomasum of two groups of sheep*

Site	Ash in dry matter (%)	Insoluble ash in dry matter (%)	Total nitrogen (%)		Non-protein nitrogen (%)		Energy (Cal./g)		V.F.A. (m-equiv./100 g)		Lignin (%)	
			In dry matter	In organic matter	In dry matter	In organic matter	In dry matter	In organic matter	In dry matter	In organic matter	In dry matter	In organic matter
						Group 1 (seven sheep)						
Reticulum	9·84	1·18	3·00	3·33	—	—	4·46	4·95	99·8	110·8	—	—
Omasum	8·64	1·76	2·61	2·86	—	—	4·68	5·12	34·7*	38·2*	—	—
Abomasum	15·82	3·82	3·58	4·25	—	—	4·33	5·14	18·6	22·1	—	—
						Group 2 (eight sheep)						
Reticulum	8·80	1·87	2·72	2·98	0·348	0·381	4·58	5·03	—	—	29·9	32·8
Omasum	8·43	2·33	2·45	2·68	0·213	0·233	4·83	5·27	—	—	35·1	38·3
Abomasum	17·64	9·68	2·84	3·45	0·778	0·945	4·27	5·19	—	—	25·5	30·9

* Results for three sheep only: the mean percentages of ash and insoluble ash in the dry matter in the omasum of these animals were 9·68 and 1·84, respectively.
V.F.A., volatile fatty acids.

Total nitrogen and non-protein nitrogen. Total-nitrogen concentration on a wet-material basis (Table 1) was higher in the omasum than in the abomasum or the reticulum at the 0·1 % level of significance. No significant difference existed in this respect between the reticulum and the abomasum. On both a dry-matter and an organic-matter basis (Table 2) the positions were reversed, the concentration in the omasum being significantly lower than in the reticulum and the abomasum at the 5 and 1 % levels, respectively. In both groups 1 and 2, ratios of total nitrogen to insoluble ash (Table 3) indicate a gradual loss of nitrogen from the reticulum through the omasum to the abomasum. On the other hand, whereas ratios of total nitrogen to lignin—only available for group 2 (Table 3)—also indicate a loss from the reticulum to the omasum, they demonstrate an addition in the abomasum. This difference is due to the high percentage of insoluble ash in the abomasum.

Table 3. *Ratios of the amounts of the different constituents to the amounts of insoluble ash and lignin in the contents of the reticulum, omasum and abomasum of two groups of sheep*

(Values derived from Table 2)

	Total nitrogen		Non-protein nitrogen		Energy		
Site	Ratio to insoluble ash (g/g)	Ratio to lignin (g/g)	Ratio to insoluble ash (g/g)	Ratio to lignin (g/g)	Ratio to insoluble ash (100 Cal./g)	Ratio to lignin (Cal./g)	Ratio, V.F.A.: insoluble ash (m-equiv./g)
			Group 1 (seven sheep)				
Reticulum	2·54	—	—	—	3·78	—	84·5
Omasum	1·48	—	—	—	2·65	—	18·7
Abomasum	0·94	—	—	—	1·13	—	4·9
			Group 2 (eight sheep)				
Reticulum	1·45	0·091	0·19	0·012	2·45	15·4	—
Omasum	1·05	0·070	0·09	0·006	2·07	13·8	—
Abomasum	0·29	0·112	0·08	0·031	0·44	16·8	—

V.F.A., volatile fatty acids.

Non-protein nitrogen concentration, available only for group 2 in the wet contents (Table 1), did not reflect the changes in total nitrogen, the level in the abomasum being much higher than in the reticulum and the omasum. When expressed as a percentage of the dry matter or organic matter, non-protein nitrogen was considerably higher in the abomasum than in the reticulum, and the value in the latter was somewhat higher than for the omasum. Non-protein nitrogen values as percentages of total nitrogen in the reticulum, omasum and abomasum, respectively, were 13, 9 and 28.

Volatile fatty acids and energy. V.F.A. concentrations in the wet contents (Table 1) and on the dry-matter and organic-matter bases (Table 2) were considerably higher in the reticulum than in the omasum, and higher in the latter than in the abomasum, in agreement with the findings of Badawy, Campbell, Cuthbertson & Mackie (1958). Insoluble-ash ratios (Table 3) indicated a loss of 77 % from the reticulum to the omasum, and a loss from the omasum to the abomasum of about 74 %, which confirms that the omasum is a site for the absorption of V.F.A. as well as for dehydration of the digesta. Owing to this dehydration, energy values of the contents on a wet-material basis (Table 1) were markedly higher in the omasum than in the reticulum. In the reticulum the values were slightly higher than in the abomasum. On a dry-matter, and more particularly on an organic-matter basis (Table 2), there were only slight differences in the results for the three organs, as would be expected. Ratios of energy to insoluble ash (Table 3) indicated a loss—presumably due to absorption—of about 16% from the reticulum to the omasum in group 2 and 30% in group 1. Because of the higher insoluble-ash content of the abomasum, the fall in value from the omasum to the abomasum is more difficult to interpret without reference to the ratio to lignin. Energy:lignin ratios (Table 3, group 2) indicate a loss of only about 10% from the reticulum to the omasum and an increase of about 20% from the latter to the abomasum—changes of a much smaller order than those derived by reference to insoluble ash.

Distribution of the various constituents in the different portions of the omasum

Dry matter, ash, insoluble ash, chromium sesquioxide and lignin. For the purpose of this study the omasal contents in the groups of sheep were divided into three, four or six different portions or zones as shown in Fig. 1 *A–D* and the results are shown in Tables 4 and 5.

Table 4. *Mean concentrations of dry matter, ash and insoluble ash in the contents of the omasum of sheep, divided into four portions as shown in Fig.* 1 *A for group* 1 *b and six portions as shown in Fig.* 1 *B for group* 1 *c*

Portion (or zone)	Dry matter (%)	Ash (%) In wet contents	Ash (%) In dry matter	Insoluble ash (%) In wet contents	Insoluble ash (%) In dry matter
	Group 1 *b* (two sheep)				
Sulcus fluid	10·22	—	—	—	—
Upper	14·24	1·24	8·71	0·224	1·57
Middle	15·37	1·34	8·73	0·255	1·66
Lower	17·35	1·37	7·89	0·267	1·54
	Group 1 *c* (three sheep)				
Upper near reticulum	15·30	1·29	8·46	0·381	2·49
Upper middle	15·19	1·31	8·64	0·366	2·41
Upper near abomasum	14·94	1·34	8·98	0·300	2·01
Lower near reticulum	16·53	1·35	8·18	0·404	2·45
Lower middle	17·44	1·49	8·56	0·417	2·39
Lower near abomasum	16·44	1·29	7·85	0·307	1·87

The percentage of dry matter tended to increase progressively from the sulcus through the greater curvature—a progressive dehydration, but there was no constant change in its concentration from the reticulum towards the abomasum. The concentration of ash and insoluble ash in the dry matter showed little differentiation between the different parts. If anything, the insoluble ash tended to decrease slightly in the dry matter in the deeper parts of the omasum and to decrease progressively from the reticular end to the abomasal end. On the other hand, the ingested chromium sesquioxide tended to remain fairly constant, with a slight tendency to concentration in the deeper zones. The percentage of lignin in the dry matter showed a slight progressive fall from the level in the material near to the reticulum through the mid-zone to that nearest the abomasum, and the lignin and the chromium sesquioxide tended to show increased concentration from the sulcus to the greater curvature, but the change was hardly significant. It may be said from these analyses that, apart from the progressive dehydration down through the laminae to their points of attachment to the wall of the omasum, no significant change has been noted so far in the composition of the dry matter in the different parts. The various fractions seemed to behave in the same way, with lignin forming rather more than a third of the dry matter.

Table 5. *Mean concentrations of dry matter, ash, insoluble ash, lignin and chromium sesquioxide in the omasum of sheep, divided into three portions as shown in Fig.* 1 *C for group* 2*a and in Fig.* 1 *D for group* 2*b*

Portion (or zone)	Dry matter (%)	Ash (%)		Insoluble ash (%)		Lignin (%)		Chromium sesquioxide (%)	
		In wet contents	In dry matter	In wet contents	In dry matter	In wet contents	In dry matter	In wet contents	In dry matter
				Group 2*a* (four sheep)					
Near reticulum	17·80	1·50	8·44	0·470	2·643	6·58	37·0	0·104	0·584
Middle	17·96	1·46	8·15	0·393	2·187	6·02	33·5	0·113	0·630
Near abomasum	18·10	1·60	8·82	0·338	1·867	5·90	32·6	0·115	0·636
				Group 2*b* (four sheep)					
Upper	17·68	1·49	8·43	0·468	2·646	6·04	34·2	0·111	0·630
Middle	16·96	1·42	8·38	0·402	2·372	6·13	36·1	0·119	0·700
Lower	18·69	1·56	8·36	0·437	2·338	6·94	37·1	0·133	0·709

Total nitrogen. The total-nitrogen percentage in the wet contents of the two sheep of group 1*b* (Table 6) with the omasum divided as in Fig. 1*A*, increased towards the greater curvature. When the results were expressed as a percentage of the dry matter or organic matter, the percentages of total nitrogen in the middle and lower portions were only about 50% higher than in the upper one. Ratios of total nitrogen to insoluble ash indicated an increase of about 8% in the concentration of total nitrogen in the lower portion over the middle and upper portions. Such differences are scarcely significant.

In group 1*c* (Table 6) the percentage of total nitrogen on a dry-matter basis, or in terms of organic matter, increased slightly towards the abomasum, and in the lower portions it was almost the same as in the respective upper portions. From the same table it can be seen that ratios of total nitrogen to insoluble ash indicated the same trend.

In the ewes of group 2 (Table 7) the highest concentration of total nitrogen in the dry matter and the highest ratios to insoluble ash, lignin and chromium sesquioxide were to be found in the middle horizontal portions of the omasum (Fig. 1*D*). For the vertical divisions (Fig. 1*C*) no significant differences were found.

There was little, if any, significant difference in the percentage of the total nitrogen present as non-protein nitrogen in the contents of the different portions of the omasum

(Table 7) when the omasum was divided either horizontally or vertically; if anything, it was highest near the reticulum and in the uppermost zone.

Energy. There were no marked differences in energy values in the different zones of the omasum (Table 8). Ratios, energy:lignin and energy:chromium sesquioxide, indicated a very slight decrease towards the lowermost zones within the omasum when it was divided horizontally (Fig. 1 *D*).

Table 6. *Mean concentrations of total nitrogen in the omasum of sheep, divided into four portions as shown in Fig.* 1 *A for group* 1 *b and into six portions as shown in Fig.* 1 *B for group* 1 *c, and ratios to insoluble ash*

Portion (or zone)	Total nitrogen: In wet contents (%)	In dry matter (%)	In organic matter (%)	Ratio to insoluble ash (g/g)
	Group 1 *b* (two sheep)			
Upper	0·368	2·58	2·82	1·64
Middle	0·416	2·71	2·97	1·63
Lower	0·477	2·74	2·97	1·78
	Group 1 *c* (three sheep)			
Upper near reticulum	0·371	2·41	2·63	0·97
Upper middle	0·410	2·54	2·78	1·05
Upper near abomasum	0·406	2·69	2·96	1·34
Lower near reticulum	0·438	2·47	2·69	1·01
Lower middle	0·468	2·60	2·84	1·09
Lower near abomasum	0·459	2·73	2·96	1·46

Table 7. *Mean concentrations of total nitrogen and non-protein nitrogen in the omasum of sheep, divided into three portions as shown in Fig.* 1 *C for group* 2 *a and in Fig.* 1 *D for group* 2 *b, and ratios of total nitrogen to insoluble ash, lignin and chromium sesquioxide*

Portion (or zone)	Total nitrogen: In dry matter (%)	Non-protein nitrogen as percentage of total nitrogen	Ratio to insoluble ash (g/g)	Ratio to lignin (g/g)	Ratio to chromium sesquioxide (g/g)
		Group 2 *a* (four sheep)			
Near reticulum	2·40	9·1	0·91	0·07	4·11
Middle	2·52	8·2	1·15	0·08	3·99
Near abomasum	2·46	8·1	1·31	0·08	3·87
		Group 2 *b* (four sheep)			
Upper	2·28	10·2	0·86	0·07	3·62
Middle	2·63	9·3	1·11	0·07	3·75
Lower	2·37	8·3	1·01	0·06	3·34

Volatile fatty acids. V.F.A. concentration within the omasum showed a wider range of difference throughout than did that of any of the other individual constituents. For the sheep of group 2, in which the omasal contents were divided into three horizontal or three vertical portions (Fig. 1 *C* and 1 *D*), the V.F.A. concentration (Table 8) decreased both towards the abomasum and downwards through the organ.

The ratios to insoluble ash, lignin and to chromium sesquioxide all indicated losses in V.F.A. in these directions. These changes pointed to absorption of the V.F.A. as the digesta passed through the omasum. The V.F.A. concentrations in six different portions of the omasum of one sheep (Fig. 1 *B*) are given in Table 9 and they tend to show the same type of change, though in this instance the ratios to insoluble ash did not suggest a loss towards the abomasum. The concentrations in the three upper portions were higher than in the respective lower portions and the ratios to insoluble ash followed the same trend.

Table 8. *Mean concentrations of energy and volatile fatty acids in the omasum of sheep, divided into six portions as shown in Fig.* 1 *C for group* 2*a and in Fig.* 1 *D for group* 2*b, and ratios to insoluble ash, lignin and chromium sesquioxide*

	Energy				V.F.A.			
Portion (or zone)	Cal./g dry matter	Ratio to insoluble ash (100 Cal./g)	Ratio to lignin (Cal./g)	Ratio to chromium sesquioxide (100 Cal./g)	m-equiv./100 g dry matter	Ratio to insoluble ash (m-equiv./g)	Ratio to lignin (m-equiv./g)	Ratio to chromium sesquioxide (m-equiv./g)
			Group 2*a* (four sheep)					
Near reticulum	4·78	1·81	12·9	8·18	33·6	12·7	0·91	57·5
Middle	4·74	2·17	14·1	7·52	22·8	10·4	0·68	36·2
Near abomasum	4·92	2·64	15·1	7·74	19·7	10·5	0·60	30·9
			Group 2*b* (four sheep)					
Upper	4·76	1·80	13·9	7·56	23·0	8·7	0·67	36·4
Middle	4·93	2·08	13·6	7·05	24·0	10·1	0·66	34·3
Lower	4·82	2·06	13·0	6·80	18·9	8·1	0·51	26·7

Table 9. *Concentrations of volatile fatty acids in the omasum of one sheep, divided into six portions as shown in Fig.* 1 *B, and ratios to insoluble ash*

Portion (or zone)	On wet-material basis (m-equiv./100 g)	On dry-matter basis (m-equiv./100 g)	On organic-matter basis (m-equiv./100 g)	Ratio to insoluble ash (m-equiv./g)
Upper near reticulum	5·99	34·6	37·8	13·9
Upper middle	5·84	34·2	37·4	14·2
Upper near abomasum	4·91	30·9	34·0	15·4
Lower near reticulum	5·68	30·1	32·8	12·3
Lower middle	5·54	30·4	33·3	12·7
Lower near abomasum	4·86	27·4	29·7	14·6

DISCUSSION

The amount of water lost in the omasum was found to be 48 and 55% in the two groups of sheep studied, and the significance to be attached to this finding has already been discussed. Both figures are within the range found by Gray *et al.* (1954), who reported that dehydration taking place in the omasum is mainly through absorption, but they are slightly higher than the figure of 43% calculated by Boyne *et al.* (1956). This water may be removed by the mechanism suggested by Balch, Kelly & Heim (1951), who consider that the movements of the omasum are likely to press the digesta entering the neck of the omasum against the omasal leaves and as a result of this pressure water, and the smaller solid particles carried with the water, are more likely than larger solid particles to enter the spaces between the leaves. Their view is that most of the solid digesta pass through the neck without passing between the leaves. Alternatively, the dehydration might be the result of the movement of the digesta described by Benzie & Phillipson (1957), who interpret their radiological findings as compatible with the more solid part of the food entering the interlaminal spaces and traversing the organ more slowly than the more liquid fraction, which may pass through without remaining in these spaces. The change in disposition of the omasum, which they noted when the reticulum contracts, means that the organ forms a receptacle at this time so that the reticular contents flowing into it would tend to run into the interlaminal spaces. When the organ returns to its upright position the liquid may then flow ventrally to the abomasum leaving the more solid matter trapped in the interlaminal spaces. The observations of Gray *et al.* (1954) indicate that only very small amounts of reticular contents would appear to pass directly to the abomasum through the sulcus and that little, if any, liquid is squeezed away mechanically from the solids in the omasum. Acceptance of the radiological evidence means that at least part of the reduction in moisture content would be due to the onward passage of the more fluid part of the digesta rather than absorption, but as this differential movement also would mean a build-up of the more solid matter between the leaves, a situation which obviously cannot continue, there must be some part of the movements of the omasum which effects a periodic turnover. Our results would not be incompatible with this explanation and would also indicate considerable absorption.

The decrease in dry-matter percentage in the abomasum can be attributed to the more dilute nature of the added gastric juice. The amount of water calculated as added to the omasal contents on their entering the abomasum, to bring the dry-matter percentage down to the level existing in the abomasum in the two groups of sheep studied, is 123 and 197%, that is without reference to the solids of the gastric juice. Masson & Phillipson (1952) have reported that gastric juice is added to the omasal contents in the abomasum in the ratio of 2:1 or more, which supports the finding concerning the dilution of omasal contents in the abomasum.

In the abomasum the concentration of ash was higher than in the omasum. It was assumed that the chloride of the gastric juice would be one of the main sources contributing to this rise. Insoluble ash is another main source of the rise of total ash in the abomasum, since its concentration in the dry matter of the abomasum—a relatively immobile organ—has been found to increase to a considerable extent. The explanation for this rise in insoluble ash is possibly to be sought in the absorption of acid-soluble salts from the abomasum leaving the dry matter relatively richer in terms of the insoluble material.

On a dry-matter and an organic-matter basis the concentration of total nitrogen in the omasum was less than in the reticulum, presumably owing to the absorption of degradation products of microbial activity, e.g. ammonia. On the same basis total nitrogen was considerably higher in the abomasum than in the omasum, which can be attributed to the addition of nitrogen through the gastric juice and to absorption of acid-soluble material. Ratios of total nitrogen to insoluble ash and to lignin indicated a loss of nitrogen from the reticulum to the omasum. A further loss from the omasum to the abomasum was indicated by the ratio to insoluble ash but not by the ratio to lignin (Table 3), though this latter was only available in one group. Owing to its relative immobility the abomasum may have a variable concentration of insoluble ash and in consequence too much reliance should not be placed on this ash as a marker. As already mentioned, ratios of total-nitrogen to lignin indicate an addition of nitrogen in the abomasum, which would be expected, since there would be a small addition of nitrogen to the digesta in the abomasum through the gastric juice.

The increase in the concentration of non-protein nitrogen in the abomasum can be attributed mainly to the proteolytic activity of the gastric juice. The fact that loss of non-protein nitrogen occurs in the omasum is indicated by reference to the results for insoluble ash and lignin. On the other hand, the apparent marked decrease in the abomasum of non-protein nitrogen, as indicated by insoluble-ash ratios compared with the relatively large addition as indicated by lignin ratios, could be attributed to relative enrichment of the dry matter in insoluble ash for the reason given above.

The concentration of total nitrogen in the different portions of the omasum differed but slightly from one part to another. Non-protein nitrogen concentration remained a fairly constant but small proportion of the total. This relative constancy in ratios of total-nitrogen to lignin throughout, might be held to indicate that little fluid is expressed into the abomasum or reticulum, as would be likely to result if the dehydration were due to contraction of this organ. This finding supports the view expressed by Gray *et al.* (1954) that separation of liquid from the solids by squeezing of the digesta in the omasum cannot be extensive, and is not at variance with the radiological picture (Benzie & Phillipson, 1957). Expressed either as a percentage of the organic dry matter or as a ratio to lignin, the concentration of nitrogen was highest in the abomasum. It is also of interest to note that Gray *et al.* (1954) found that the starch: lignin ratios were greater for the reticulum (and also for the rumen) than those for the omasum and abomasum, which were similar. They concluded that only very small amounts of reticular contents may pass directly to the abomasum through the omasal groove and that little, if any, liquid is squeezed away mechanically from the solids in the omasum.

The highest concentration of V.F.A. was found in the reticulum, followed by the omasum and then the abomasum. These observations are in agreement with the findings of Barcroft, McAnally & Phillipson (1944), Elsden, Hitchcock, Marshall & Phillipson (1946), Masson & Phillipson (1952), Boyne *et al.* (1956) and Badawy, Campbell, Cuthbertson, Fell & Mackie (1958). Ratios of V.F.A. to insoluble ash indicated a loss of 77 % from the reticulum to the omasum and a loss from the omasum to the abomasum of 74 %. Gray *et al.* (1954) found from their V.F.A.: lignin ratios an absorption of 40–69 % of the acids entering the omasum.

Slight variations can be observed between the different portions of the omasum in respect of ash concentration in the dry matter. We have already referred to the findings of Ekman & Sperber (1952) who considered that the absorption of bicarbonate may be part of the function of the omasum and would prevent unnecessary neutralization of the gastric juice.

Of the other constituents examined, only the V.F.A. showed definite trends through the omasum, trends generally supported by reference to the markers employed. These changes in concentration could fit into a description of movement of digesta through the omasum, whereby the material not only passed through the sulcus omasi but spread also through the laminae and moved through them towards the abomasal orifice. Absorption of water and V.F.A. would occur to the greatest extent wherever the digesta involved spent longest time. The observations of Ekman & Sperber (1952) on the absorption of bicarbonate in the omasum would also fit in with these findings.

SUMMARY

1. Fifteen sheep were killed to study the changing composition of the digesta in the reticulum, omasum and abomasum. The estimations which were conducted as rapidly as possible were: dry matter, ash, insoluble ash, chromium sesquioxide (in those sheep that received it), lignin, total nitrogen, non-protein nitrogen, volatile fatty acids, and energy.

2. That dehydration takes place in the omasum was confirmed. It appeared to occur to the greatest extent in the digesta between the laminae at the deepest point within the greater curvature with a tendency to further dehydration towards the abomasal orifice. The concentration of nitrogen in terms of the markers used was less in the omasum than in the reticulum, indicating that absorption occurred in the omasum.

3. The concentration of V.F.A. decreased progressively through the deeper zones of the omasum and from the reticulum to the abomasum, indicating absorption during the time spent in the omasum. It was calculated to be of the order of 77% of that entering the organ.

4. The concentration of energy-yielding material in the different zones of the omasum showed only a slight variation.

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