OBSERVATIONS ON DIGESTION IN THE RUMINANT

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(With Nine Text-figures.)

PRESENT-DAY knowledge of the physiology of digestion in ruminants is very limited and to a great extent it is based on anatomical deductions. Some of these are doubtless correct; but many of them must be regarded merely as speculations until such time as adequate experimental proof is brought forward. It was with the object of providing this proof that the present work was undertaken. The experiments were concerned chiefly with the progress of the food through the alimentary canal, and, consequently, with the movements of the different sections of the canal itself. The ruminant owes its unique position amongst mammals to the anatomical complexity of the stomachs, and, for this reason, attention was directed particularly to the movements of these viscera. It will be an advantage, before taking up the experimental part of this paper, to consider certain important[1] anatomical features and post-mortem appearances and to discuss the physiological significance which it is believed can be attributed to them.

The ruminant possesses four so-called stomachs—the first or reticulum, the second or rumen, the third or omasum and the fourth or abomasum. Only the abomasum has the characteristics of a stomach, because it alone secretes a digestive fluid, whereas the lining epithelium of the other three viscera is devoid of secreting cells of any kind. Furthermore, the first three pouches arise from the caudal end of the wall of the oesophagus. These pouches are rudimentary at birth and during suckling life; but they develop rapidly after the animal begins to eat coarse fodder. Neither on anatomical nor physiological grounds, therefore, can the first three viscera be classified as stomachs. The term "fore-stomachs" ("Vormägen" of German workers) is more appropriate. They are not secreting organs, and the only digestive juice present normally in them is saliva; this has been shown to contain no ptyalin (Trautmann and Albrecht, 1931), so that the only chemical changes which can occur in the fore-stomachs are those due to fermentation. The contents of the reticulum and rumen are always fluid, and there is no doubt that the organs represent chambers where mixing and fermentation occur. The two pouches communicate freely with each other, and the term "reticulo-rumen" can be correctly applied to

[1] The detailed anatomy of the digestive organs of the ruminant will be found in Sisson's *Anatomy of the Domestic Animals*, 2nd edn., W. B. Saunders and Company, Philadelphia and London.

the combined cavity composed by them. In the living animal, as Schalk and Amadon (1928) have shown by experiments on cows with ruminal fistulae, the contents of these cavities are arranged in accordance with the density of their constituents. Thus, heavy grains are found to lie ventrally, while light materials, such as hay, float on top. The omasum derives its pseudonym, the manyplies, from the fact that its epithelial lining is thrown into numerous folds or laminae of varying length, which almost fill the viscus. The entrance and exit are very close together so that the cavity is essentially a cul-de-sac. The entrance, or reticulo-omasal orifice, is situated at the distal extremity of the oesophageal groove, which is all that remains in the adult of this portion of the original gullet. The oesophageal groove, as Wester (1926) and Schalk and Amadon (1928) have shown, can, by contraction of the lips, form a closed tube which acts as a direct communication from mouth to omasum during the period of suckling; but, in the adult, it rarely if ever functions in this way. Wester (1926) has shown that this rudimentary structure is the starting-point of the peristaltic waves which pass over the reticulum and rumen in one direction and over the omasum in the other; further, when the lips of the groove are contracted, they shut the omasum off from the reticulum. The reticulo-omasal orifice is normally below the level of the contents of the reticulum and rumen; but, although gravity probably plays some part in the onward progress of food, it is apparently a factor of minor importance, as will be seen later. The free borders of the omasal laminae encroach on the groove, the sulcus omasi, which passes obliquely downward and backward from the entrance to the omaso-abomasal orifice. The latter opening is not guarded by a sphincter of any kind, so that the transference of food from omasum to abomasum appears to depend on gravity and on the motive force of the omasal contractions. The muscular wall of the abomasum as compared with that of the omasum is thin and weak, and on this difference in contractile power, as well as on gravity, would appear to depend the absence, normally, of regurgitation from the former into the latter viscus. The pyloric portion of the abomasum is tubular, and at its exit into the duodenum there is a well-developed sphincter.

Post-mortem, the abomasal contents are fluid and the solid matter always finely comminuted. The omasal contents, on the contrary, are always dry and solid in comparison and consist of particles of much larger size. It is obvious, therefore, that the chief function of the omasum is to filter off the coarser pieces from the fluid ingesta transmitted from the reticulo-rumen. The fluid and fine particles pass on to the abomasum, while the coarser material is caught between the laminae, by the movements of which it is ground down to a condition so fine that it is swept into the abomasum by the fluid from the next intake of material from reticulo-rumen. The abomasum is lined with glandular epithelium and is, therefore, the homologue of the stomach in man.

The study of the movements of the stomachs in the present investigation was conducted on goats and sheep of varying ages by means of X-rays. For this purpose a specially designed screening and photographic stand[1] and movable platforms were employed. Side to side transmission with the animal standing was found to be the

[1] Made by Watson and Sons, London, after the design kindly executed for me by Dr A. C. Fowler.

most suitable, but vertical illumination in the standing or lying position was frequently resorted to. The observations were made by screening and by photography. The appearance noted in the former method was either sketched roughly at the time on the screen itself or else immediately afterwards on paper. Photographs were also taken when considered desirable.

Much information concerning the movements of the fore-stomachs was obtained by screening without the aid of opaque meals, as the large collections of gas normally present in the dorsal and posterior sacs of the rumen are easily discernible, and move or change in shape with the contractions of the muscular walls. Observations of the movements of opaque pills of varying specific gravity were found of great assistance in following the contractions of the rumen and reticulum. The basis of these pills was $BaSO_4$ and $CaSO_4$. They were very hard, and if they remained in the reticulum or rumen they were found to resist fermentation changes for periods up to 14 days. The heaviest pills consisted of $BaSO_4$ and $CaSO_4$ only and were about 1 cm. in diameter; the light ones had a core of these salts of about 0·5 cm. in diameter, and, in order to lighten them, they were covered with a layer of paraffin wax of varying thickness.

The above methods were of great value in determining the rates of contractions of the viscera and the range of movement undergone by the ingesta, but they threw little light on the changes in shape which the different compartments assumed. For this purpose it was necessary to administer opaque meals. It was found impossible to induce goats or sheep voluntarily to eat enough $BaSO_4$ to cast a shadow of sufficient depth to enable one to see the outline and follow the movements of the stomachs. Even when the barium was mixed intimately with ground cereals, chopped grass or other green stuff, the animals could always manage to pick out sufficient food to satisfy their hunger for the time being without swallowing more than a small fraction of the barium. However, the amount ingested in this way made it possible to study deglutition and to determine the destination of the boluses. In order to define the shape and movements of the viscera, fluid barium meals, which cast a dense shadow, had to be administered forcibly. Adult animals and young ones, which had not been trained to suck from feeding bottles, were fed the opaque meals by drenching or by stomach tube. It was considered at first that forcible feeding would give an abnormal direction to the ingested meal; but, as will be pointed out later, this suspicion had little foundation. The meals consisted generally of 100–300 gm. $BaSO_4$ rubbed up with enough gum acacia to form a thick paste and then made up to 1000–1500 c.c. with milk, thin starch paste or water. The administration of contrast meals was usually preceded by a fast of 15 hours or more.

DEGLUTITION AND THE DESTINATION OF THE BOLUS.

Deglutition appeared to be fundamentally the same as in man, except that the boluses were larger. The greater part of a bolus of hay, green stuff or ground cereals invariably passed rapidly into the reticulo-rumen, through the contents of which it darted and twisted at an amazing speed. Separate boluses did not maintain their identity for more than a short time. A few minutes after swallowing they became intimately mixed up with the former contents of the rumen. On account of struggling the forcible administration of pills or of fluid meals was never carried out while the animal was being screened; but it was possible to irradiate the animal in from 5 to 15 min. after doing so. Observed in this way, heavy pills almost invariably lodged in the reticulum, while light pills entered the reticulum or rumen or, less frequently, the omasum. When they passed into the two former sacs they moved in accordance with the contractions of these sacs, as described below. In the omasum they remained almost stationary for a period varying from a few minutes to several hours, and then either disappeared altogether, presumably by being ground down by the movements of the laminae, or descended ventrally and were seen later in the most dependent part of the abomasum. Occasionally, pills were observed in the abomasum 5 to 15 min. after administration. Once a pill entered the omasum it never returned to the rumen or reticulum.

When meals were given, it did not appear to make any difference to the subsequent appearances of the shadow whether they were administered by tube or by drenching, and the path taken by the meal was, therefore, presumably the same with the two modes of feeding. In one especially quiet animal it was possible to make observations with the stomach tube *in situ*, and it was always seen to have passed into the rumen. It is, therefore, evident that the first stopping place of the ingested meal was the reticulo-rumen. Very often the shadow remained entirely in this cavity for from 60 to 90 min. and then began to appear in the omasum and abomasum. But, just as often, it was seen to have passed into all four stomachs as soon as the animal was screened, *i.e.* in from 5 to 15 min. after giving the meal. The cause of this difference was not evident. Both the slow and the rapid onward transit of the food were found on different occasions in the same animal, and it made no difference whether the animal had just been feeding or had fasted for varying periods up to 60 hours. It is probable that the specific gravity of the contents of the reticulo-rumen remaining over from previous meals is a factor which can determine the duration of the stay of the ingested meal in these pouches. When the S.G. was low, a heavier meal would quickly fall towards the ventral wall of the reticulum; heavy particles, as already stated, invariably lodge in this viscus. Meals only slightly denser than the upper levels of the reticulo-ruminal contents would tend to accumulate in the middle of the reticulum, a location which would appear to be the most favourable for early evacuation. This point will be considered later.

MOVEMENTS OF STOMACHS: RETICULUM AND RUMEN.

The clearest outline of reticulum and rumen was observed when evacuation of the barium meal was delayed for 60 to 90 min. A photograph taken soon after feeding gave an appearance as is indicated in Fig. 1, in which reticulum and rumen are depicted in the resting condition, except that the abomasum was not seen until about 90–120 min. later. The contents are fluid, so much so that the upper surface is flat. Fig. 2 shows the reticulum in the contracted state. The contraction is in two stages—the first a sharp movement in a dorsal direction, then a pause for about half a second with the viscus in a half-contracted state, and finally a larger contraction

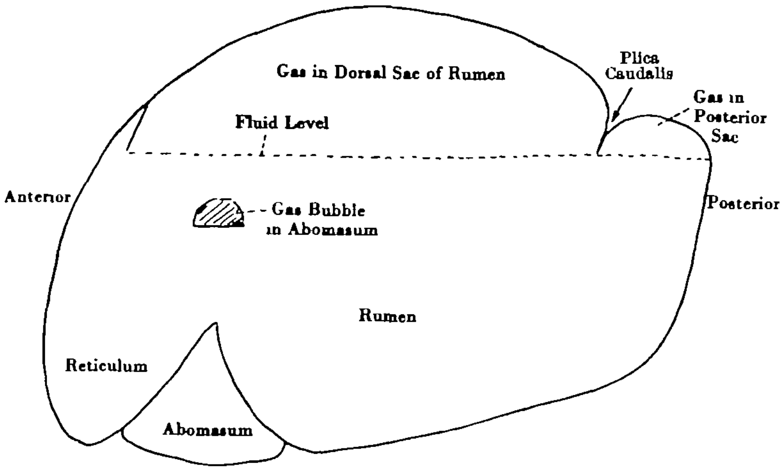

Fig. 1. Appearance of reticulum and rumen in rest after a fluid barium meal. The flat top of the contents is to be noted. The omasum is not shown. The abomasum occupies the triangular area between the reticulum and rumen, and may be seen almost immediately after the meal or about 90–120 min. later.

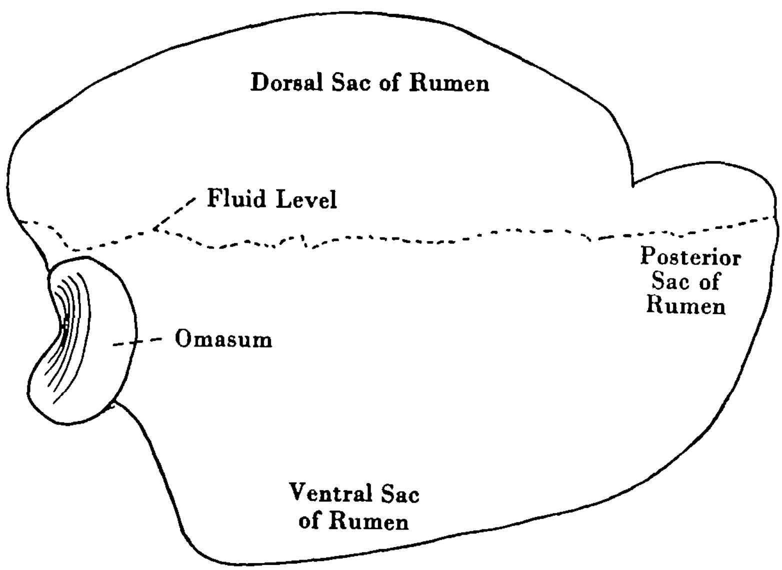

Fig. 2. The reticulum is at the height of contraction and is not seen. The fluid level is irregular. The omasum is shown. For clarity the outline of the abomasum is excluded.

in a dorso-posterior direction, as a result of which the viscus practically disappears from view and its contents are tipped into the rumen. Then follows relaxation. The change in position undergone by a heavy pill in the reticulum gave the best conception of the reticular movements (Fig. 3) and enabled one easily to determine the rate of contraction. In the same adult animal the time interval between the contractions was very constant, often varying by no more than ± 5 sec. during a period of 5 hours. In different animals the interval varied from 40 to 80 sec., and it was not appreciably influenced by periods of fasting up to 48 hours. Fasts of longer duration, however, appeared to affect the frequency (see Table I). These data were obtained from a goat, which was given a meal of cereals and chopped hay after having been deprived of food but not of water for 7 days.

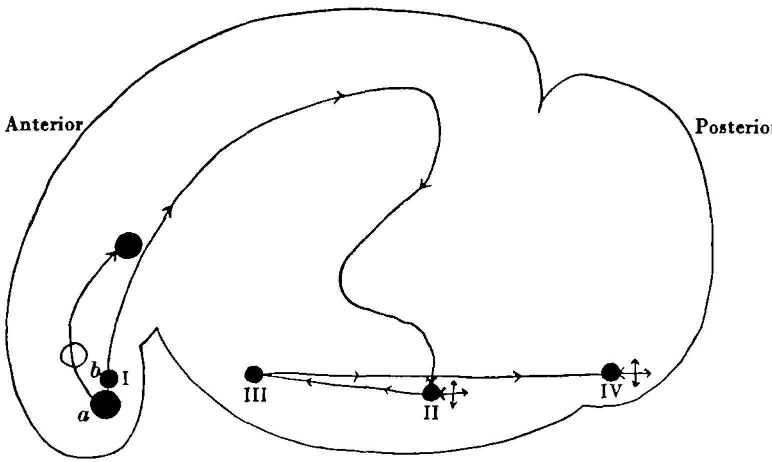

Fig. 3. Movements of (*a*) heavy pill in reticulum and of (*b*) light pill in a 10-min. period. The ✥ indicates that in these positions the pill was relatively stationary, and moved only slightly up and down and to and fro.

Table I.

Minutes after eating began	Before food	4	14	45	255	345
Seconds between reticular contractions	72	47	60	59	81	77

Emotional states slowed the rate. Thus, in animals unaccustomed to the experimental procedure, intervals of several minutes were often observed. In immature animals the contraction rate was slow, but it increased with growth. The following mean intervals at the ages stated were observed in a young goat: 4 months, 90 sec.; 6 months, 75 sec.; 9 months, 40 sec.

The reticular contraction disturbed the flat top of the rumen contents seen in the resting state (Figs. 1 and 2). At the height of the contraction the contents were heaved up and a slight depression occurred during relaxation. Just before relaxation of the reticulum was completed the dorsal ruminal sac contracted, flattened out the large bubble of gas collected in it and pushed the upper layer of contents forwards and slightly downwards. This movement of contents appeared to be due chiefly to the anterior and ventral pull of the plica caudalis, which is the dorsal dividing line between the dorsal and posterior sacs (Fig. 1). The dorsal sac then relaxed and resumed its resting position, and about 2 sec. afterwards the ventral sac contracted and caused a heaving up of contents in an antero-dorsal direction. At the height of contraction the ventral sac was sharply demarcated from the reticulum in front and the posterior sac behind. Within 12 to 30 sec. after the ventral sac relaxed the posterior sac contracted and heaved its contents forwards and slightly upwards, the demarcation between this sac and the ventral one being very clearly seen (Fig. 4).

The contractions always proceeded in this order, and, while the interval between the contraction of the reticulum and that of the dorsal sac was very constant, those between the dorsal and ventral sacs, and also between the ventral and posterior sacs, were much more variable. Often the dorsal and ventral sacs appeared to contract

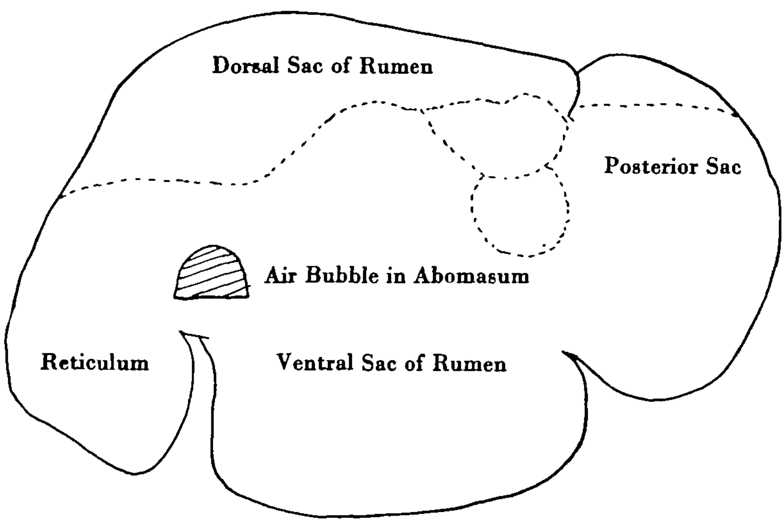

Fig 4. Posterior ruminal sac in contraction. Note the heaving forwards and upwards of the contents and the sharp demarcation between the posterior and ventral sacs. The level of contents is very irregular.

almost simultaneously, and the interval between the movements of the latter and the posterior sac seemed to depend on the emotional state of the animal. In nervous animals the interval was longer than in those which were better trained. The cycle of movements occupied 25 to 40 sec., and a pause of about the same duration intervened between the completion of one cycle and the beginning of the next.

The contractions of the dorsal and posterior sacs were readily identified by observing the changes in shape of the gas bubbles contained in them. These flattened out with the contraction and moved downwards and forwards. Contraction of the posterior sac generally resulted in small bubbles of gas making their way to the large collection of gas in the dorsal sac. The interval between these contractions as thus observed was generally 20 to 25 sec.

Wester (1926) has described, in cows with ruminal fistulae, a double contraction of the posterior sac for every one of the ventral sac or reticulum. He recorded the contractions by means of weighted balloons placed in various divisions of the cavity. Owing to the fact that the compartments communicate freely with one another a contraction in one would conceivably influence a balloon placed in a neighbouring compartment. Results obtained by the graphic method cannot, therefore, be regarded as suitable for interpreting the precise order of contraction of the different pouches. Furthermore, the dorsal ruminal wall is necessarily anchored to the body wall in the making of the fistula, and neither Wester (1926) nor Schalk and Amadon (1928) apparently made any attempt to render the fistula air-tight while their records were being taken. These facts suggest that the conditions which prevailed in the experiments of these observers were not such as would give an accurate picture of the contractile wave as it passed over the reticulum and rumen. The most suitable method for obtaining such a record would be to measure the differences in electrical potential, by means of a string galvanometer connected to different parts of the wall of the reticulum and rumen by leads inserted through a ruminal fistula. As the fore-stomachs are developed from the distal portion of the oesophagus, one would expect that they, as well as this tube itself, would be capable of transmitting a peristaltic contractile wave. For this reason it is believed that Wester is mainly correct in assuming that the contractions are of a peristaltic nature; but, before this view can be taken as an established fact, more satisfactory evidence, such as only the string galvanometer can afford, must be brought forward.

MOVEMENTS OF $BaSO_4$-$CaSO_4$ PILLS IN THE RETICULO-RUMEN.

Heavy $BaSO_4$-$CaSO_4$ pills generally entered the reticulum immediately and remained there for periods up to 9 days. Their manner of disappearance was not

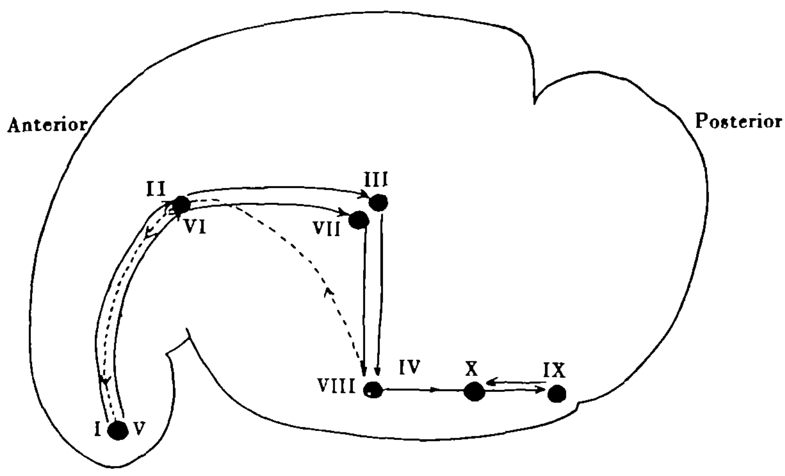

Fig. 5. Path of a light pill during rumination; observed about 10 min.

discovered; presumably, they either disintegrated as a result of maceration and of the friction brought about by the reticular movements, or, less likely, they were shot into the omasum and ground down between its laminae. Light pills, when they entered the reticulum at first, did not remain there for more than about 30 min. The length of their stay in this sac depended on the specific gravity of the pill: the higher the specific gravity the longer they remained. Sooner or later they were shot rapidly into the rumen where they moved about for a variable time. They could be seen in various situations in the rumen moving about with the contractions of the viscus or with the respiratory movements. Pills which settled in the ventral portion of the posterior sac often remained there for several hours and underwent little change in position. Frequently, light pills were shot backwards and forwards repeatedly between rumen and reticulum (see Fig. 3). During rumination the movements were more rapid and more extensive (Fig. 5).

MOVEMENTS OF THE OMASUM AND ABOMASUM.

The outline of the omasum was not clearly discernible until about an hour or more after administering a barium meal, and even then it was usually obscured by the shadow cast by the reticulum and rumen. The clearest picture of this viscus was obtained by washing out the rumen and reticulum about 3 hours after giving a barium meal. Both omasum and abomasum could then generally be seen to be well filled with shadow. No movements of any kind were discerned in the omasum —an observation made also by Czepa and Stigler (1929). Occasionally, a trickle of shadow was observed to pass ventrally in the region occupied by the omasum soon after the meal but before the outline of the viscus became distinct. This trickle always occurred within a few seconds of a reticular contraction.

It is, however, clear from the work of Wester and of Schalk and Amadon that the above-mentioned absence of signs of contraction in the omasum itself was apparent only and not real, and that the ventral trickle of shadow was due to the movements which they found to occur in this viscus. These workers were able to obtain tracings of the omasal movements by inserting balloons into the vestibule. They showed that the omasum relaxes at the height of the reticular contraction, so that a fall in pressure from the reticulo-rumen to the omasum is produced. In this manner a passage is open for the transference of food from the reticulo-rumen into the omasum. It would appear from these results that the ingesta in the neighbourhood of the oesophageal groove, *i.e.* from about the middle and lower levels of the reticulo-rumen, are thus aspirated with each omasal relaxation. This is followed by a slow but powerful contraction of the omasum, which doubtless squeezes the fluid into the vestibule and thence into the abomasum, the solid material being at the same time trapped between the laminae. In Wester's opinion these, in the relaxed state of the viscus, hang loosely and so hinder the progress of the larger pieces of food. But his conception that the leaves play a passive rôle in the grinding of the food does not appear to be in conformity with anatomical facts. Each lamina possesses three layers of smooth muscle. The middle one runs radially and the two outer layers are arranged at right angles to it. In addition there is a well-marked circular band of muscle which runs just inside the free border. It is probable that these layers of muscle stand in the same relation to the muscular wall of the omasum as the muscularis mucosae and villous musculature do to the muscular coats of the intestine, and that the laminae can be retracted or relaxed, made tense or loose independently of the movements of the viscus as a whole. Alternating movements of the laminae would obviously cause neighbouring ones to rub against each other; so that the coarser matter would be ground down sufficiently to permit of its being washed away by the succeeding inrush of ingesta from the reticulo-rumen.

In the abomasum a gas bubble of variable size was always seen in its most dorsal portion (see Figs. 1 and 4). It moved slightly to and fro in an antero-ventral direction at about the same rate as the reticulum contracted. As no such extensive movements were ever seen in the ventral part of the fundus, the movement of the bubble must have been due to displacement by the contractions of the reticulum or omasum. As soon as a sufficient amount of barium had entered the abomasum typical peristaltic contractions were seen in the pyloric portion.

If, as occasionally happened, a $BaSO_4$-$CaSO_4$ pill lodged in the abomasum soon after administration it was often observed to remain in the same situation for periods up to 2 days. The manner of its final disappearance was not discovered. For periods up to 9 days after feeding contrast meals, small areas of shadow were often seen, apparently spread out along the ventral wall of the abomasum. These were obviously cast by $BaSO_4$ which had silted out from suspension; they diminished gradually in size. Neither they nor pills situated in the abomasum showed any significant change of position, other than could be attributed to the movements of the fore-stomachs or of respiration.

It would appear from these observations that the movements executed by the fundus of the abomasum are much feebler than those of the other stomachs. It is also probable that, as in the case of the human stomach, the chief objective of the fundic movements is to maintain a more or less constant pressure on the ingesta so that the pyloric portion is kept full. The absence of a sphincter at the omaso-abomasal orifice suggests the existence of some other mechanism which protects the abomasum against overfilling. In the absence of such a provision, it is conceivable that the powerful contractions of the omasum plus the effect of gravity would cause the abomasum to be overfilled. Wester has shown that pressure in the omasal vestibule inhibits the contractions of the other fore-stomachs, and it is likely, as Wheeldon and Thomas (1922) found in man, that duodenal distension inhibits the pyloric contractions. It is conceivable, then, that intestinal distension would induce in turn a decrease in the contractile force of the abomasum, omasum and reticulo-rumen, so that the *vis a tergo* tending to drive the food onward would be diminished. The variations in the rate of contraction of the reticulum and rumen are probably to be accounted for by impulses of different intensity emanating from the intestine and abomasum.

RUMINATION.

Only two of the animals used ruminated while on the platform. The observations made during the performance of the act are stated briefly below.

(1) The reticulum contracts. (2) The diaphragm descends sharply. (3) The breath is held. (4) A clear space appears in the region of the oesophageal opening,

apparently almost synchronous with the contraction of the dorsal ruminal sac. (5) The clear space disappears and a mass of food shoots up the gullet and enters the mouth. (6) A trickle of apparently fluid material is swallowed, which has obviously drained off from the rejected mass in the course of its ascent to the mouth. (7) The animal chews for a time, the length of which evidently depends, to some extent, on the rate of reticular contraction, because a reticular contraction was always found to precede the rejection of a food mass. Usually chewing ceases and the animal swallows just before a reticular contraction. Very often the rate of chewing increased rapidly towards the end, and the impression was formed that the animal at these times had voluntarily speeded up mastication in order to be in a position to receive the next food mass. The events numbered (1) to (5), above, took place within such a short space of time that it was very difficult to determine precisely the order in which they occurred. This was especially the case with (2), (3) and (4). Wester has brought forward evidence which goes to show that the reticulum is not indispensable for regurgitation. From the observations made in this research it would seem that the contraction of the forepart of the rumen rather than of the reticulum plays an important rôle in the rejection. It should also be mentioned that Czepa and Stigler (1929) noticed food masses ascending the gullet without a preceding reticular contraction.

The most plausible explanation of the formation of the clear space at the lower end of the oesophagus is that given by Wester. He attributes it to relaxation of the oesophageal circular muscle and of the muscular ring formed by diaphragmatic muscle, which surrounds the cardiac opening and acts as a sphincter. Simultaneously, the longitudinal oesophageal musculature contracts and the head is suddenly extended slightly. The combined effect of this co-ordination of muscular activity is to produce a funnel-shaped dilatation of the oesophageal opening. The respiratory apparatus apparently plays a dominant rôle at this stage. The sudden descent of the diaphragm and the closure of the glottis produces a negative pressure in the gullet which may, according to Wester, amount to 25 to 50 mm. Hg in the ox. Wester has also shown that the pressure in the cow's rumen is generally positive. A difference in pressure of the above magnitude is, doubtless, adequate to cause some of the contents of the reticulo-rumen to ascend the oesophagus for some distance. The act could presumably be completed by an oesophageal anti-peristaltic wave.

The next point for consideration is the nature of the contents driven into the gullet. The cardiac opening lies some distance below the general fluid level in the reticulum and rumen, and, if the aspiratory action occurred when these viscera were in the resting state, material from the middle layers of the contents would make their way to the mouth. As already stated the solid matter in this region is relatively fine, whereas that floating on the top is coarse and therefore in need of remastication. That it is this coarse material which is regurgitated is apparent from the fact that the clear space at the cardia occurs almost simultaneously with the contraction of the dorsal ruminal sac. By the contraction of this pouch the supernatant coarse material is moved towards the funnel-shaped oesophageal opening into which it is, presumably, sucked by the negative pressure.

There has been much argument as to whether rumination is the result of a reflex or a voluntary act. But, as no data that might throw any light on the matter were obtained in this study, discussion of it would be out of place.

DEVELOPMENT OF THE FORE-STOMACHS.

In order to follow the stages in the growth of the fore-stomachs, observations were made on a lamb and young goat at intervals from the age of 3 weeks until the viscera attained adult form. The lamb had been nourished artificially almost from

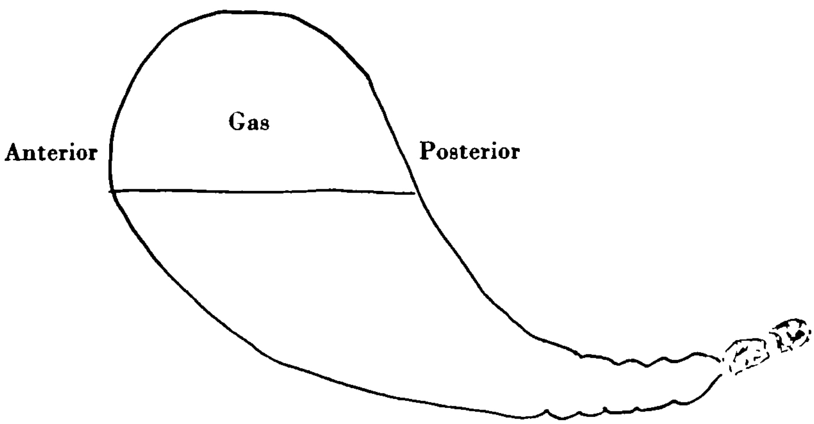

Fig. 6. Outline of sheep's abomasum, at 3 weeks of age, after a barium meal, showing peristalsis in pylorus.

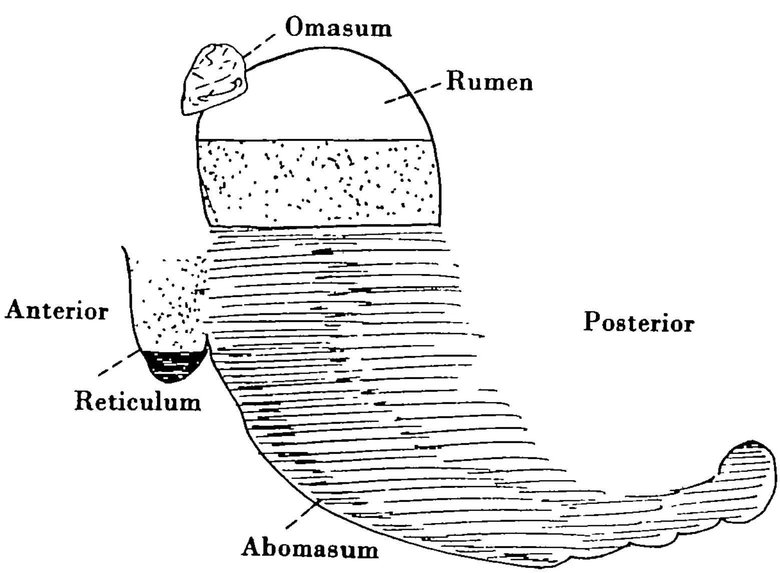

Fig. 7. Appearance of sheep's stomachs at 3 months of age after a barium meal, showing gas bubble in rumen and peristalsis in pylorus.

birth on cow's milk suckled from a bottle and the barium meals were given suspended in the milk. The goat was fed the contrast meal by drenching. Between the X-ray examinations the animals were allowed to graze in the company of others.

The shadows cast in the case of animals 3 weeks old were those of simple stomachs showing distinct peristalsis in the pyloric region (Fig. 6). At 1 month a small amount of shadow appeared near the oesophageal opening and anterior to the abomasum. This was taken to be the reticulum. This pouch was easily discernible at 2 months; and a month later a further fluid level was distinguished with a gas bubble on top situated dorsal to the abomasum. This sac was taken to be the rumen (Fig. 7). As age advanced the reticulum and rumen became more and more obvious, until at about 7 months the adult form appeared.

NERVOUS CONTROL OF THE FORE-STOMACHS.

The nature of the nervous control of the fore-stomachs was studied indirectly by noting the effects on the reticular contractions produced by drugs having an influence on the autonomic nervous system. The procedure adopted was to screen an animal after administering a few heavy $BaSO_4$-$CaSO_4$ pills. The interval between the reticular contractions was then determined a sufficient number of times to obtain a mean. The drug was then injected, and the mean contraction interval ascertained for as long as the effect of the drug was observed. Examples of results are given below (Table II). The figures give the intervals between reticular contractions in seconds, the average of each series being in brackets. All drugs except amytal were injected subcutaneously.

Table II.

16. ix. 31. *Goat fasted* 24 *hours.*

Time	Intervals in seconds
2.30	60, 65, 70, 80, 60, 60 = (66)
3	Atropine $\frac{1}{30}$ grain.
3.25	65, 75, 75, 70, 80, 80 = (74)
4	110, 105, 145, 180, 165 = (141)
4.50	325, 340 = (332)

29. ix. 31. *Sheep fasted* 15 *hours.*

Time	Intervals in seconds
3.4	50, 70, 70, 80, 60, 70 = (67)
3.12	0·75 c.c. 1 % pilocarpine.
3.30	55, 65, 65, 65 = (62)
3.59	Tetany
4.2	0·5 c.c. pilocarpine.
4.42	55, 55, 30, 75, 80 = (59)
5.5	Tetany

20. x. 31. *Sheep not fasted.*

Time	Intervals in seconds	
11 55	65, 60, 55, 50 = (57)	
12.5	1 c.c. liquor adrenaline 0·1 %	
12.15	65, 55, 60 = (60)	Contractions very sluggish
12.20	75, 55, 70, 75 = (69)	
12.30	80, 70, 62, 60 = (68)	
12.40	90, 70, 65, 62, 70, 55 = (69)	

Table II (*contd*).

27. x. 31. *Sheep not fasted.*

Time	Intervals in seconds
3.3	50, 40, 40, 45 = (44)
3.20	0·04 gm. amytal into jugular
3.24	60, 60, 55, 50, 50 = (55)
3.34	70, 65, 60, 55, 55 = (61)
3.46	85, 80, 80, 85 = (83)
3.55	70, 80, 60, 60, 65 = (67)

These results show that (1) atropine and amytal, which block impulses via the vagus, slowed the contractions, (2) pilocarpine, which intensifies vagal activity, caused tetany of the reticulum, and (3) adrenalin, which induces sympathetic effects, slowed the contractions. There can be no doubt, therefore, that, as in animals with simple stomachs, the vagus in general carries motor and the splanchnics inhibitory impulses to the fore-stomachs.

THE BLOOD SUGAR IN STARVATION.

It was thought that a study of the blood sugar in relation to ingestion of food would give information of value for the interpretation of the X-ray findings. Before taking up this question it was considered desirable to determine how the blood-sugar level was affected by starvation. Two goats were given water only for 7 days and the blood sugar was estimated daily. The results (Fig. 8) agree in that a general upward trend set in after 40 hours' starvation and continued until the end of the experiments. It is very probable that the rising blood sugar was a consequence of a metabolic change. To indicate the nature of the change the course of the R.Q. and of the nitrogen excretion or of the blood non-protein nitrogen would be of great assistance. Regarding the two latter particulars, there are no data available, so far as is known, and for the R.Q. during starvation there is only one set of observations which can be considered of value, viz. those of Magee and Orr (1924). Benedict and Ritzman (1927, 1931) have, it is true, made determinations of the R.Q. in fasting cattle and sheep. They found, for cattle, a steady value of 0·71–0·70 from the 3rd until the 7th fasting day, and for sheep one of 0·72–0·71 on the 3rd and 4th days. Unfortunately, in these studies no account was taken of the CO_2 arising from fermentation in the rumen, and the values are, therefore, too high. In the experiments of Magee and Orr, the fermentation CO_2 was allowed for, so that the R.Q. found by them cannot be far from the truth. But, unfortunately, their experiment was stopped when the animal had fasted 84 hours. They found that the R.Q. in the starving goat remained steady at a value of 0·67 from the 40th until the 84th hour, and suggested that the low R.Q. might result from the oxidation of substances, with a low combustion R.Q., which may have been set free from the ingesta present in the rumen. Magee (1924) has also pointed out that the R.Q. of lactates is 0·67. In the present investigation, the rumens of the two animals contained fairly large amounts of food at the end of the 7 days' fast; so that fermentation must have been going on throughout the period of starvation. It must also be assumed that the water which the animals consumed carried away soluble fermentation products, from the rumen into the intestine, which were absorbed along with the water. If lactates formed the bulk of the absorbed fermentation products, and if they were oxidised as such, a low R.Q. must have prevailed. On the other hand lactates may not be oxidised as such but may instead, as the work of Cori and Cori (1929) suggests, be condensed to form liver glycogen, and this, on mobilisation, might account for the rising blood sugar. A study of the blood lactic acid in relation to the ingestion of food would throw some light on this perplexity.

Another possible explanation of the increase in the blood sugar is that it is due to the conversion of fat into sugar, a process which would also give rise to a low R.Q. Although this might seem the more plausible explanation the fate of the fermentation products has also to be considered. It is also interesting to note that the blood sugar of fowls shows a sharp rise of about 40 mg. on the 3rd or 4th day of starvation (MacOwan and Magee, 1931).

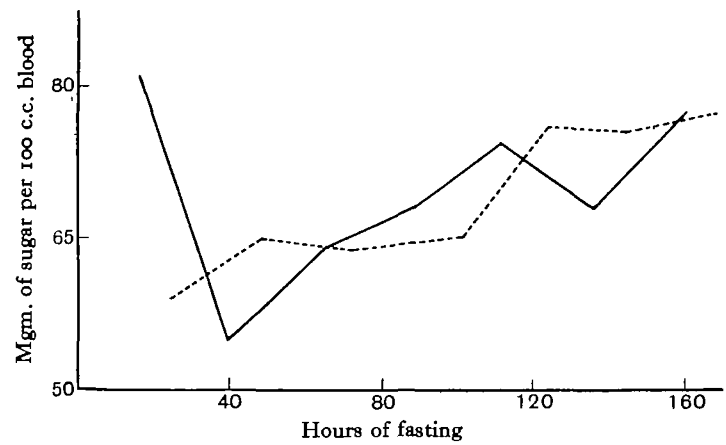

Fig. 8. Blood sugar of two fasting goats.

THE INFLUENCE OF FOOD ON THE BLOOD SUGAR.

In Fig. 9 are shown a number of curves depicting the effect of carbohydrate food on the blood sugar of goats after various periods of fasting. It will be seen from these curves that (*a*) the fasting level is lower than in most other mammals, (*b*) the post-prandial curves do not conform to any general type and (*c*) the amount of increase is small compared with what would be expected in other mammals after administration of correspondingly large amounts of carbohydrate. It will be noticed also that the level in the non-fasting animals was scarcely affected by the meals fed.

It was hoped that these experiments would throw some light on the significance of the X-ray observations and on the results of previous work in which the influence of different kinds of foodstuffs on the metabolic rate was determined (Magee, 1924). In regard to the first point this expectation has been partially fulfilled, for the degree and rate of increase in the blood sugar were, like the rate of progress of barium meals from the rumen into the intestine, very variable. The reason for this inconstancy is not clear; but two possible complicating factors occur to one. The first depends on the peculiar formation of the fore-stomachs, a consequence of which is that they, as these experiments have shown, do not empty themselves after prolonged fasting. Accordingly, when a meal is ingested it is only discharged into the abomasum after being mixed more or less completely with the former contents of the reticulo-rumen. Obviously, the response of the blood sugar to a carbohydrate meal would depend on the extent to which it had been diluted before it reached the intestine. The greater the amount of dilution the smaller would be the increase in blood sugar and *vice versa*. The curves obtained from the non-fasting

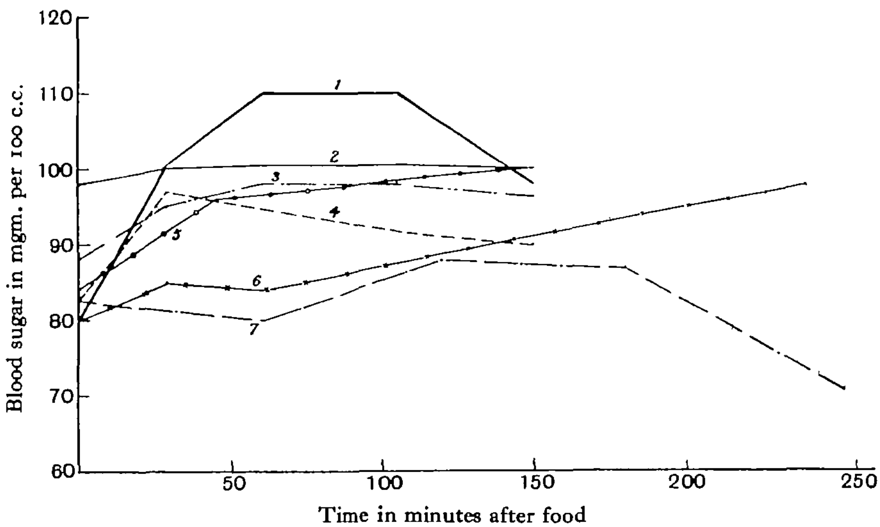

Fig. 9. Effect of food on blood sugar of goats.

Curve 1. Fasted 48 hours and given 150 gm. starch and 50 gm. sucrose in 300 c.c. water.
Curve 4. Fasted 72 ,, ,, ,, ,, ,, ,,
Curve 6. Fasted 48 ,, ,, ,, ,, ,, ,,
Curve 2. Not fasted ,, ,, ,, ,, ,, ,,
Curve 3. Not fasted ,, ,, ,, ,, ,, ,,
Curve 5. Fasted 18 hours and given 250 gm. starch and 100 gm. sucrose in 500 c.c. water.
Curve 7. Fasted 88 hours and given oats and then grass *ad libitum*.

Curves 1 and 3; 2, 4 and 6; 5 and 7, from three animals respectively.

animals (Fig. 9) support this argument. The second factor that has to be considered follows from the first. It is that the degree of dilution and the rate of discharge of the ingested carbohydrates into the intestine probably depend on the specific gravity of the former reticulo-ruminal contents. It has been suggested above that the ingesta in the region of the oesophageal groove are aspirated into the omasum each time this viscus relaxes. Assuming this conception to be correct, it is clear that ingesta sufficiently dense to take up their position at this level would pass into the omasum and abomasum soon after being swallowed; whereas meals lighter than the former contents of the reticulo-rumen would tend to remain in the upper levels. The study of the metabolic rate (Magee, 1924) showed that at $2\frac{1}{2}$ hours after ingestion of carbohydrate diets a well-marked secondary increase regularly took place. Neither the blood-sugar curves nor the X-ray observations suggest any reason for this acceleration in the rate of metabolism.

SUMMARY.

The results of experiments conducted on goats and sheep by X-rays and by blood-sugar analyses have been considered with the data of other observers and the deductions outlined below have been made.

Ingesta, whether liquid or solid, first enter the reticulum and rumen. Heavy matter lodges in the former and light material may enter the same cavity or the rumen. Heavy particles remain in the reticulum for several days until they are broken down, probably by maceration. Light particles move all through the reticulo-rumen at a rapid rate, but the range of movement is least in the posterior ruminal sac. The reticulo-rumen is a mixing and fermentation cavity. Mixing is caused by rhythmical waves of contraction which pass over the reticulum, dorsal sac, ventral sac and posterior sac of the rumen in this order at intervals of 40 to 80 sec., the whole cycle requiring 25 to 40 sec. Onward passage of ingesta from reticulo-rumen is probably due, chiefly to an aspiratory act on the part of the omasum, the leaves of which filter off coarse materials and, by alternating contractions, grind them, while the contraction of the viscus as a whole squeezes the fluid and fine materials into the abomasum. The fundus of the abomasum shows no gross movements, but maintains a steady pressure on its contents, and thus drives them into the pylorus which expels them by peristalsis into the duodenum. Distension of the abomasum probably prevents its overfilling by reflexly inhibiting the movements of the fore-stomachs.

The essential factors causing the rejection of the food mass in rumination are (1) thoracic negative pressure produced by sudden descent of the diaphragm and closure of the glottis, (2) relaxation of the circular muscle of the cardia and its dragging forwards by extension of the head and contraction of the longitudinal oesophageal muscle, (3) contraction of the dorsal ruminal sac. A reticular contraction precedes rejection, and swallowing of the remasticated bolus just precedes the succeeding reticular contraction. The fore-stomachs attain adult form at about the 7th month.

The vagus is motor and the splanchnics inhibitory to the fore-stomachs.

The fore-stomachs contain food after 7 days' starvation.

The fasting blood sugar varies from 63 to 86 mg. per 100 c.c., and it rises steadily from the 40th to the 169th hour of fasting.

The blood sugar rises slightly but very variably after carbohydrate meals. The inconstancy is related to the X-ray findings, which showed that barium meals may remain in the reticulo-rumen for 60 min. or more, or may pass into the omasum and abomasum within 5 min. after ingestion.

The percentage increase in blood sugar after carbohydrate meals is greater in fasted than in non-fasted animals.

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