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Structure of the ruminant stomach and the movement of its contents

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Through natural development the ruminant stomach has achieved an efficient microbial digestion of plant fibre and also of almost all other plant constituents; synthesis of microbial polysaccharide and protein and of certain vitamins also occurs. The products of microbial digestion are utilized by ruminants, but they are not identical with the products of digestion in non-ruminants. In this Symposium several of the ways in which the peculiarities of the ruminant process influence the behaviour and metabolism of these animals are discussed. As an introduction, this communication is intended to describe some of the more important anatomical features of the ruminant stomach and to consider briefly the manner in which digesta are moved through the various compartments.

Structure

The ruminant stomach has four compartments: rumen, reticulum, omasum and abomasum, although the omasum is virtually absent in camels and llamas. The abomasum has a typical gastric secretory function and corresponds to the stomach in non-ruminants; in very young animals it is as large as the rumen. The other compartments are non-secretory and the saliva contains no enzymes, although produced in large amounts. All four compartments develop from the embryonic stomach (Lewis, 1915). Fig. 1, derived from Schalk & Amadon (1928), serves to illustrate the arrangement of the compartments. The rumen and reticulum occupy most of the left side of the abdomen and are separated by the rumino-reticular fold. The oesophagus enters by the cardia at a point dorsal to the fold and on the right wall. The omasum is reached through the reticulo-omasal orifice in the right wall of the reticulum. Joining this orifice to the cardia are the parallel ridges of the oesophageal groove which during suckling can be stiffened, shortened and raised to form a channel down which milk flows directly to the abomasum. The rumen is buttressed internally by eight muscular pillars and folds.

The oval omasum lies in the right side of the abdomen. Its internal space is largely filled by over one hundred thin leaves of tissue, some extending almost across the

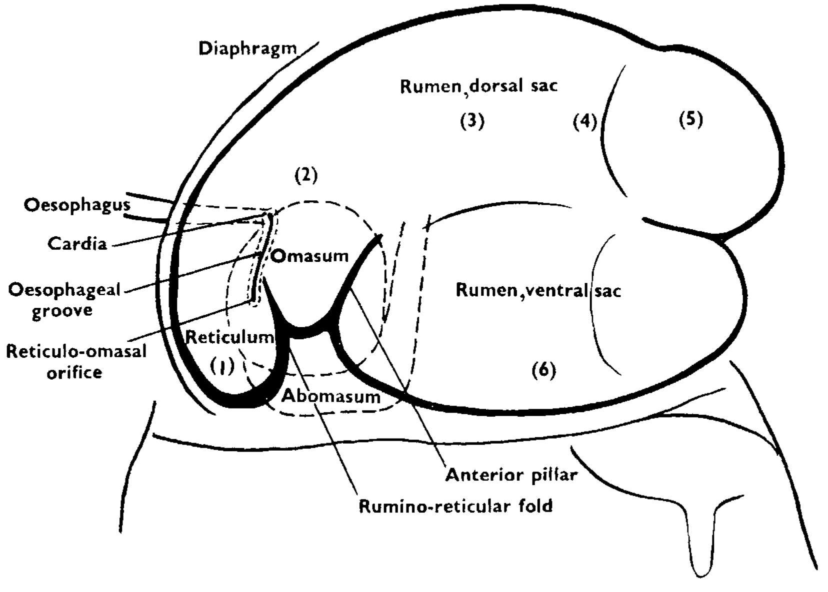

Fig. 1. Diagram showing the approximate position of the reticulo-rumen against the left side, and the omasum and abomasum against the right side, of the cow. The positions of the balloons used to obtain the recordings in Fig. 3 are marked 1–6.

organ and others being merely narrow strips on the periphery (Sisson & Grossman, 1953). The leaves and the walls to which they are attached contain few muscle fibres, but the remaining wall contains a powerful pillar (Wester, 1926).

The internal surfaces of the rumen and omasum are thickly covered with papillae of various kinds; the lining of the reticulum forms the familiar honeycomb-like 'reticulations'.

The abomasum is a tube-like organ, first running backward along the centre of the floor of the abdomen and then bending sharply up the right side, close behind the omasum. The abomasal lining carries a number of loose folds.

The position of these organs during life can be observed in small ruminants by radiographic methods (Benzie & Phillipson, 1957) and in cattle from sections of frozen cadavers (cf. Lagerlöf, 1929) as shown in Fig. 2. The very great extent to which the rumen fills the abdominal cavity, displacing the left kidney and restricting the other viscera to a small area against the right side, is clear from Fig. 2. Lagerlöf also reconstructed valuable lateral and ventral views from his sections. Amongst many interesting points they demonstrate is the considerable extent to which the uterus encroaches on the ventral rumen during late pregnancy and presses the abomasum in an anterior direction. During the movements of the various parts there are marked changes in their relative positions (Benzie & Phillipson, 1957), which cannot be appreciated in frozen sections.

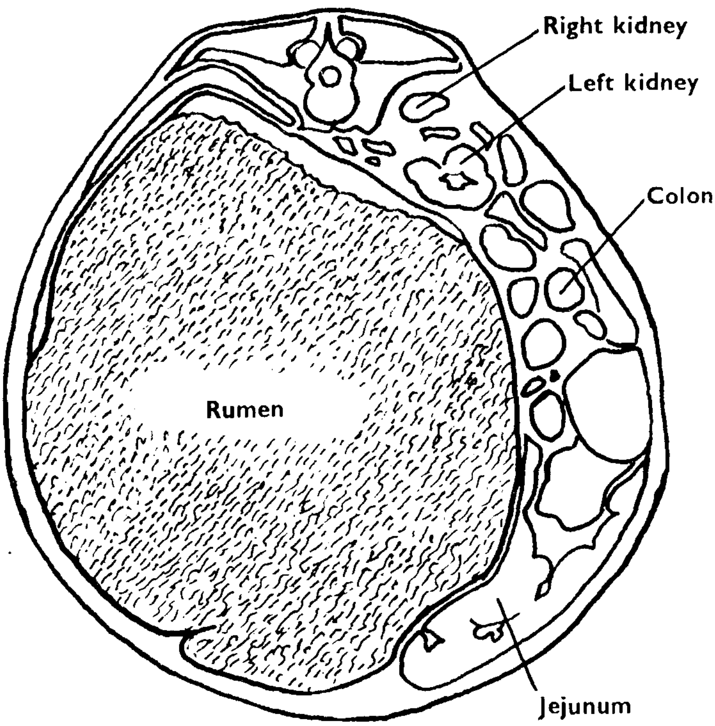

Fig. 2. Transverse section through the third lumbar vertebra of a 9-month-old heifer. (From Lagerlöf, 1929.)

Movements

Co-ordinated movements of the omasum, reticulo-omasal orifice, reticulum and rumen can be recorded pneumatically or shown radiographically. The cycles of movement in the reticulo-rumen were described by Wester (1926), Czepa & Stigler (1926) and Schalk & Amadon (1928).

I have made recordings in animals with large rumen fistulas, by means of small balloons on special holders operating pens leaving a tracing on paper charts (Balch, Kelly & Heim, 1951). Balloons were maintained by weights in the reticulum and in the ventral sac of the rumen, and at four positions in the dorsal sac by a flexible rod attached to the weight in the reticulum and to the rumen cannula. The positions of the balloons are shown in Fig. 1 and an example of the recording in Fig. 3.

The reticulum has a regular double contraction, not well shown in Fig. 3, averaging about one/min over the 24 h, but the rate of contraction varies according to the activity of the animal and is most rapid during eating (Schalk & Amadon, 1928; Balch, 1952). During rumination another contraction precedes this double movement and the regurgitation of the bolus is brought about by a complicated reflex of which the extra contraction is part (Wester, 1926). The second stage of the reticulum

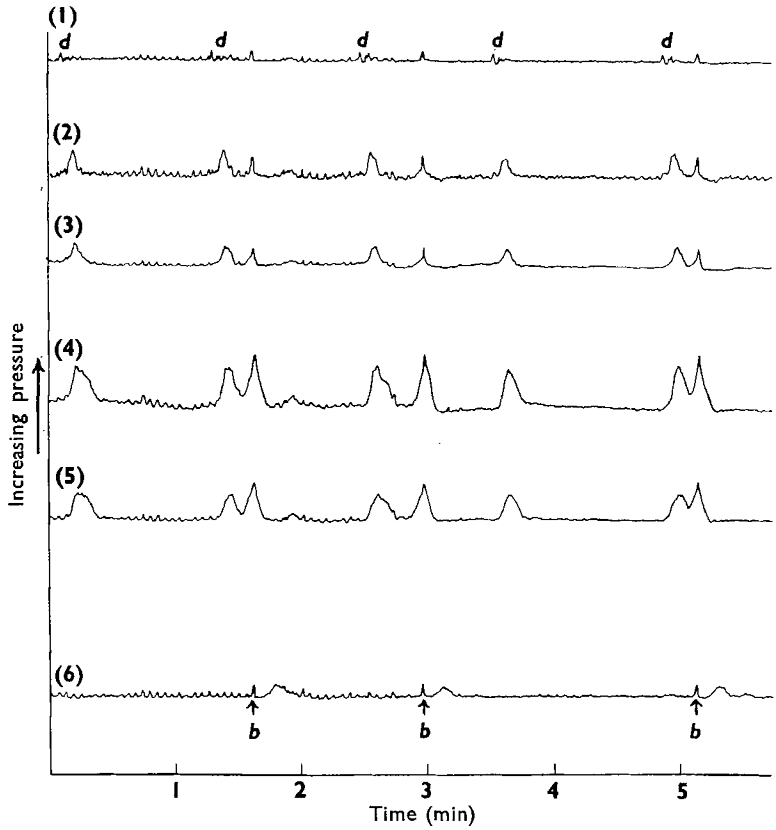

Fig. 3. Pressure changes in the reticulum (1) and in the dorsal (2–5) and ventral (6) sacs of the rumen. The double contraction of the reticulum (*d*) and three belches (*b*) are indicated.

contraction continues into the dorsal sac of the rumen as a powerful movement involving the anterior rumen and anterior pillar, and then the more posterior regions of the dorsal sac, the pressure waves taking 3–4 sec to pass from the reticulum to the posterior dorsal blind sac (Fig. 3). This movement was called the peristaltic wave by Wester (1926) and the primary peristaltic wave by Schalk & Amadon (1928). Fig. 3 does not show well the periods of relaxation which are an important part of the wave; the most critical of these is probably a relaxation of the reticulum during the later stages of the wave.

As Fig. 3 shows, there may be no further major movement between two consecutive primary movements, but it has long been recognized that there is regularly an additional secondary, extra-ruminal or anti-peristaltic, movement, manifest in the dorsal sac of the rumen, but which does not include the reticulum. Some examples of this movement are shown in Fig. 3. Benzie & Phillipson (1957) could find no evidence to support the contention of Weiss (1953) that this contraction moves in a caudal–oral direction, although their radiographs confirmed Weiss's observation that, aided by a simultaneous dilation of the reticulum, this movement brings about a forward movement of gas in the anterior rumen and reticulum. Wester (1926) and Weiss (1953) have drawn attention to the fact that belching, the reflex necessary to remove gasses which have accumulated in the dorsal sac, occurs at the time of the secondary movement. In our recordings the initiation of the movement appeared to be later in the anterior than in the posterior regions, although the peak of contraction was reached simultaneously in all parts, including small pressure rises in the reticulum and ventral sac, possibly due to a general abdominal movement. There was usually, but not necessarily, a belch during each secondary movement.

The main contraction recorded in the ventral sac of the rumen usually follows the secondary movement of the dorsal sac. In our recordings pressure rises were rarely recorded in the ventral sac after the primary movements, except during eating when they were usual. Because of the increased motility in general during eating, it follows that the movements of the ventral region are then especially frequent.

Movement of digesta

During eating, the food boluses are deposited in the anterior rumen where they rapidly merge. By the end of a meal of hay most of the new food will be found tightly packed in the dorsal sac as a relatively dry, fibrous layer (dry matter 14–16%), whereas the ventral regions will contain a layer of more fluid digesta, those in the reticulum typically containing only 5–8% dry matter.

Aided by the stiffened anterior pillar, the primary movement raises the fluid contents of the reticulum and anterior rumen into the dorsal sac (Wester, 1926; Schalk & Amadon, 1928). Through the rumen fistula, fluid can be seen passing through and over the fibrous mass in the dorsal sac; at the end of this movement a marked flow of digesta back into the reticulum, evidently largely from the ventral regions, can be felt by palpation. The dilation of the reticulum occurring at this time is thought to be implicated in this flow (Weiss, 1953; Dougherty & Meredith, 1955; Benzie & Phillipson, 1957).

At the end of a meal the contents of the reticulo-rumen of stall-fed Shorthorn cows frequently amount to 150–180 lb, and may exceed 200 lb, although the rumen never empties and in fact rarely contains as little as half its capacity (Balch & Line, 1959). The contents of the reticulo-rumen normally make up over 70% of the total gut contents and about 14% of the live weight of the animal; they are not greatly influenced by even severe reductions in the amount of hay given (Mäkelä, 1956). The contents of the reticulo-rumen are considerably less in grazing than in stall-fed animals (Balch & Line, 1957).

Hay particles remain for many hours in the rumen of the cow (Balch, 1950) goat (Castle, 1956) and sheep (Blaxter, Graham & Wainman, 1956). Faecal-excretion curves for undigested residues from small meals of stained hay eaten normally have a sigmoid shape and often show that 90% is not excreted for about 100 h. In contrast, 90% of the residue from ground hay placed in the abomasum has been found to be excreted in about 20 h (Balch, 1950). The amount of food given, and probably especially the amount of hay, is a major factor influencing the time residues remain in the rumen (Blaxter *et al.* 1956; Balch, Balch, Bartlett, Johnson, Rowland &

Turner, 1954). In general the rate of passage increases as intake increases. When swallowed, all types of food enter the rumen, but there is some slight tendency (Balch, 1950) for concentrates and succulents to sink into the ventral regions and pass out of the rumen more rapidly than roughages.

After rumination the bolus is returned to the rumen, but the chances of any given particle then passing to the omasum are increased by the reduction in particle size achieved during the chewing. Gordon (1955) found that the onward passage of particles of hay was greatest during rumination. The transfer of digesta through the reticulo-omasal orifice is, however, a continuous process probably occurring mainly at the time of the second reticulum contraction when the orifice is open and pressure is low in the omasum (Wester, 1926; Balch *et al.* 1951). Wester (1926) also thought that the transfer was most rapid during rumination, but Balch (1958), studying diets mainly containing concentrates or succulents in addition to hay, found emptying to be most rapid during eating. The material passing to the omasum has a low content of dry matter, water being a most important vehicle for the transport of solid digesta within and from the reticulo-rumen. The omasum appears to have an absorptive function (Trautman, 1933; Ekman & Sperber, 1953) and appears to be ideally situated to absorb much of this water when the transporting role is accomplished. There is little agreement on the precise mode of omasal functioning, especially on the proportion of the food solids passing between the leaves. Passage through the abomasum appears to result from a normal peristaltic movement.

When the complexity of the ruminant stomach and the large amounts of varied materials it is called on to digest are considered, it is perhaps surprising that the organ works so efficiently and fails so rarely.

REFERENCES

Balch, C. C. (1950). *Brit. J. Nutr.* **4**, 361.
Balch, C. C. (1952). *Brit. J. Nutr.* **6**, 366.
Balch, C. C. (1958). *Brit. J. Nutr.* **12**, 330.
Balch, C. C., Balch, D. A., Bartlett, S., Johnson, V. W., Rowland, S. J. & Turner, J. (1954). *J. Dairy Res.* **21**, 305.
Balch, C. C., Kelly, A. & Heim, G. (1951). *Brit. J. Nutr.* **5**, 207.
Balch, C. C. & Line, C. (1957). *J. Dairy Res.* **24**, 11.
Benzie, D. & Phillipson, A. T. (1957). *The Alimentary Tract of the Ruminant.* London: Oliver & Boyd.
Blaxter, K. L., Graham, N. McC. & Wainman, F. W. (1956). *Brit. J. Nutr.* **10**, 69.
Castle, E. J. (1956). *Brit. J. Nutr.* **10**, 15.
Czepa, A. & Stigler, R. (1926). *Pflüg. Arch. Ges. Physiol.* **212**, 300.
Dougherty, R. W. & Meredith, C. D. (1955). *Amer. J. vet. Res.* **16**, 96.
Ekman, J. & Sperber, I. (1953). *LantbrHögsk. Ann.* **19**, 227.
Gordon, J. G. (1955). Rumination in the sheep. Thesis, University of Aberdeen.
Lagerlöf, N. (1929). *Skand. VetTidskr.* **19**, 253.
Lewis, F. T. (1915). *Anat. Rec.* **9**, 102.
Mäkelä, A. (1956). *Suom. Maataloust. Seur. Julk.* no. 85.
Schalk, A. F. & Amadon, R. S. (1928). *Bull. N. Dak. agric. Exp. Sta.* no. 216.
Sisson, S. & Grossman, J. D. (1953). *The Anatomy of the Domestic Animals.* 4th ed. London: Saunders.
Trautman, A. (1933). *Arch. Tierernähr. Tierz.* **9**, 178.
Weiss, K. E. (1953). *Onderstepoort J. vet. Res.* **26**, 251.
Wester, J. (1926). *Die Physiologie und Pathologie der Vormagen beim Rinde.* Berlin: R. Scheotz.

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