A RADIOLOGICAL STUDY OF THE PATTERNS OF CONTRACTION AND DIGESTA MOVEMENT IN THE ALIMENTARY TRACT OF THE SHEEP.

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ABSTRACT

A radiological study of the motility of the stomach and small intestine and the movement of their contents was undertaken to define, in detail, the forms of contractions and their effect on digesta.

A variety of radiographic techniques were employed depending on the information sought. For continuous observation over extended time periods fluoroscopy was used which combined image intensification with a closed circuit television chain and video-tape recorder. For detailed analysis of contractions or movements radiographic cine-film, serial spot-films or plain radiographs were used. The radiographic contrast of digesta was enhanced by the addition of barium sulphate which was either administered orally or introduced to a particular site through a fistula or cannula. Stainless steel wire loops sutured into particular structures formed radio-opaque markers of sites of specific interest. In the study of the small intestine the electrical activity of the intestinal wall was recorded in conjunction with the radiographic techniques.

The sequential contractions of the compartments, folds and pillars of the reticulo-rumen that comprise A and B sequences were found to be the result of waves of contraction migrating across reticulo-rumen caudally from the reticulum and cranially from the caudal ventral blind sac. The different character of A and B sequences in the fasted and replete animal reflected waves of contraction that migrated at different speeds over varying distances.

The pattern of digesta flow within the reticulo-rumen followed a consistant pattern suggesting that the selection of digesta for onward passage to the omasum was by flotation. The pattern of gas movement suggested that the displacement of gas from the dorsal rumen into the caudal ventral blind sac initiated B sequences of contraction.

No movement of the omasum was observed radiographically other than that imposed by contiguous structures, especially the reticulum.

The most prominent feature of abomasal motility was peristaltic contractions moving towards the pylorus at a frequency which remained constant irrespective of the degree of abomasal distension. Abomasal distension was found to inhibit A sequences in the reticulo-rumen and to alter the pattern of digesta movement in the small intestine. The presence of peristaltic contractions on the abomasum was related to activity in the duodenum and orad jejunum.

The movement of digesta in the small intestine was of two basic forms; patterns of movement that were characteristic for a particular region and migrating patterns of movement. These patterns were associated with the electrical activity recorded from the intestinal wall. Alterations to the flow of digesta through the small intestine caused by increased flow through the pylorus, additions or subtractions through T cannulae or the insertion of re-entrant cannulae at certain sites caused marked changes in the patterns of digesta movement.

It was concluded that the basic motility pattern in both the stomach and the small intestine is migrating waves of contraction. The pattern in which these waves occur results from interactions between (a) the flow of digesta, (b) the degree of distension either local or in adjacent regions and (c) the pace-setter - imposed via the vagus, on the reticulo-rumen and by the slow wave frequency on the abomasum and small intestine.

PREFACE

For mammals to survive on a diet of herbage they must have an alimentary tract which provides a site, or sites, for the microbial breakdown of cellulose. In some herbivores such as the horse and rabbit the main site is provided by adaptions of caecum and colon, in others such as the macropods and ruminants the main site is a modified stomach. Of all the herbivores the ruminants are the most successful (Moir, 1965). The dominant feature of their alimentary tract is the complex stomach of which Hofmann (1973) says, "Since man first had scientific aspirations the ruminant stomach has been continuously studied in all its different aspects and by a great number of investigators, beginning, presumably, with Aristotle".

Up until comparatively recent times anatomists had merely speculated on the function of the ruminant stomach. Then the phenomenon of rumination was investigated by Flourens (1830), Haubner (1837) and Toussaint (1875). This work drew attention to the complex series of contractions of the compartments of the stomach and stimulated further research by individuals such as Colin (1871, 1886), Ellenberger (1881), Wester (1926), Czepa and Stigler (1926) and Schalk and Amadon (1928). Czepa and Stigler were the first to use radiological techniques as a method for investigating the movements of the stomach and they were followed by Magee (1932), Trautmann and Schmitt (1933), Phillipson (1939), Dougherty and Meridith (1955), Benzie and Phillipson (1957) and Akester and Titchen (1969). Although these radiological studies made valuable contributions to the understanding of the function of the ruminant stomach, more detailed information was obtained by recording the movements of partial exteriorisations of small areas of the reticulo-ruminal wall (Reid and Titchen, 1959; Reid, 1962, 1963) and by electromyographic techniques (Ruckebusch, 1970). Using these two systems the sequence of contraction of the compartments of the ruminant stomach was outlined and the variation with feeding demonstrated. However, there still remained a debate over the form of the contractions and the function of the various folds and pillars. It was to investigate these two points that the initial sections of this study were undertaken. Radiological techniques were used because observations could be made on animals with no, or only minor, surgical modifications and some recent developments in x-ray technology allowed longer and more detailed observations than had been possible previously.

There has been much less interest in the patterns of motility of the abomasum and small intestine of sheep probably because they resemble those of the stomach and intestine of other mammals. These patterns have been studied radiologically in a number of species by several investigators among whom are Cannon (1902), Czepa and Stigler (1926), Magee (1932), Phillipson (1939), Benzie and Phillipson (1957), Ehrlein and Hill (1970) and Ehrlein (1976). Other methods of demonstrating stomach and intestinal motility such as recording changes in intraluminal pressure or the electromyographic activity of the muscle in the walls of the viscus have also been used (Alvarez, 1914; Douglas and Mann, 1939; Douglas, 1948, 1949; Ruckebusch, 1970). There has been considerable discussion regarding the mechanisms controlling these patterns of motility and whether this control involved extrinsic or intrinsic nervous pathways or possibly hormonal influences (Code et al., 1968; Aeberhard et al., 1980). Initial observations in this study on the effects of abomasal distension on the patterns of digesta movement suggested that a major factor influencing these patterns was the distension that was associated with the flow of digesta through the alimentary tract; the investigations of the abomasum and small intestine were undertaken to examine this hypothesis.

The investigations reported in this thesis concern the inter-relationships of alimentary tract function, digesta movement and alimentary tract distension and, although confined to ruminants the results obtained have general application to studies of alimentary tract functions and characteristics.

Some parts of this work have already been published (Wyburn, 1980; Wenham and Wyburn, 1980).

ACKNOWLEDGEMENTS

Many people offered advice and assistance which contributed towards the completion of this thesis. The credit for initiating the project must go to Dr. C.S.W. Reid who has also acted as supervisor, mentor and good friend during its protracted production. The enthusiastic support of the second supervisor, Professor E.D. Fielden ensured that every encouragement and opportunity was given to finish the task. They both have given up much of their time to constructively criticise the writing of this thesis and have imparted skills that will be invaluable in the future. My wife, Paddy, also contributed a great deal to this work not only in coping with our family during some of my extended absences from home but also in the time and effort she put into mounting the numerous plates and figures.

Dr. R.N.B. Kay and his staff at the Rowett Research Institute must also be included in this acknowledgement for providing the facilities, expertise and encouragement during my six month stay with them. Particular thanks must go to Dr. G. Wenham who recorded the video-tapes of the effect of re-entrant cannulation 2 months after their insertion.

Part of the work carried out for this thesis involving the study of digesta movement within the rumen on 3 different diets (3:2:6, 3:3:6) was carried out in collaboration with Mr. G. Wagharn.

The photography of the radiographs and electromyographic recordings reproduced in this thesis were reproduced with the help and guidance of Mr. J Clouston and his staff in the Photographic Unit of Massey University.

The initial typing was done by Mrs. Betty Saunders who also helped with the many problems that arose during the final scramble to finish. The final typing was done by Miss Pat Audsley and my thanks to her for putting up with me and my writing.

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Chapter I

THE FUNCTIONAL ANATOMY OF THE DIGESTIVE TRACT

The mixing, propulsion, breakdown and absorption of digesta are the functions of the alimentary tract. How these functions are achieved is influenced by the size and shape of the various regions and the frequency, strength and form of the contractions of the various muscle layers in the viscus walls. Therefore a knowledge of anatomy of the alimentary tract is basic to the understanding of its function.

1:1 ANATOMY AND EMBRYOLOGY

1:1:1 The Oesophagus and Stomach.

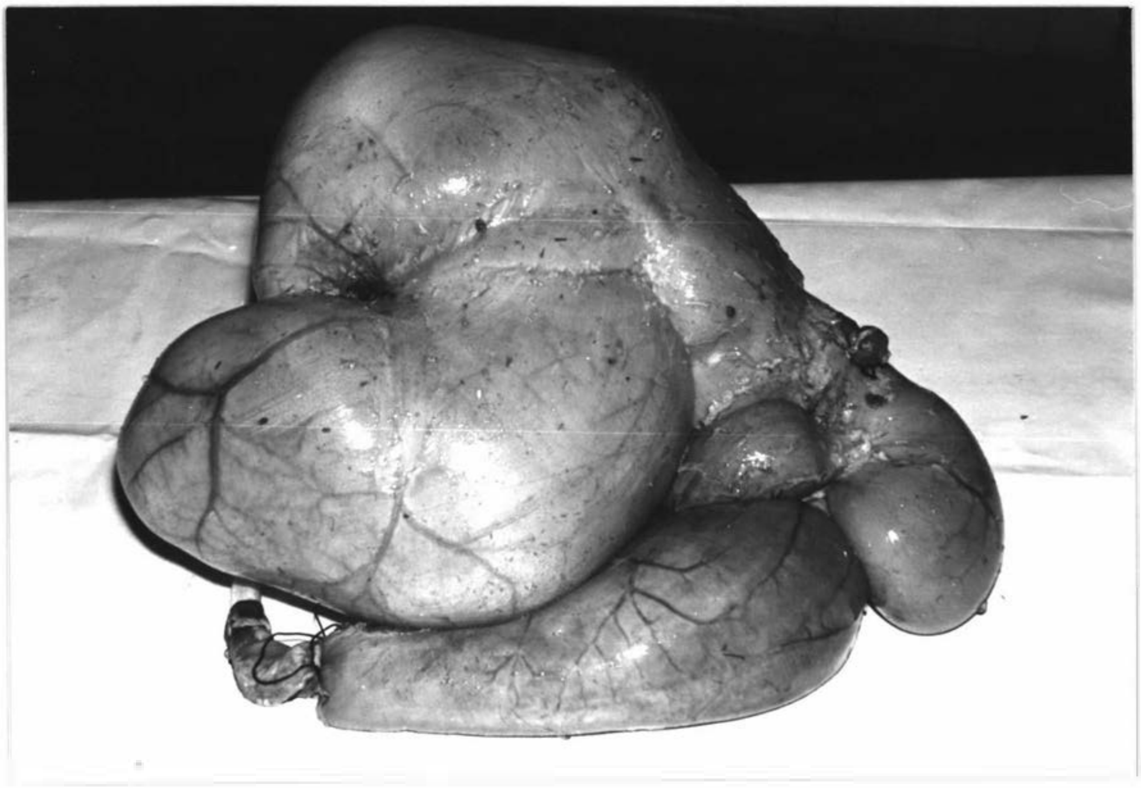
The sheep oesophagus is a muscular-walled tube approximately 45 cm long connecting the pharynx to the reticulum. The muscle of the oesophagus, which is entirely striated, is in two layers. The complex distribution of the fibres within these layers has been studied by Künzel (1961). The outer layer is in the form of a left hand spiral screw and the inner layer is formed of two opposite spirals which cross dorsally and ventrally. At the orad end of the oesophagus the pharyngoesophageal sphincter is formed by the overlap of pharyngeal and oesophageal musculatures.

The gross anatomy of the adult sheep stomach has been described by many authors among whom are Sisson and Grossman (1953), May (1964), Akester and Titchen (1969) and Nickel Schummer and Sierferle (1973). The reticulo-rumen (Plates 1 and 2) has six chambers partially separated by various muscular pillars and folds. The oesophagus (Oe) enters at the cardia in the dorsal, visceral (right) wall of the reticulum (Re), the most cranial of the chambers. Within the reticulum, running ventrally from the cardia to the reticulo-omasal orifice, is the reticular groove. The reticulum communicates with the cranial sac (CS) of the rumen (Ru) through the reticulo-ruminal orifice which is bounded by the reticulo-ruminal fold (RRF). This fold extends from the visceral (right) wall caudal to the reticular groove round and up the parietal wall to fade out just caudal to the cardia; there is a reticulo-ruminal groove on the outer surface in a

PLATE I.

The visceral (right) side of a sheep's stomach after it has been inflated.

(1) reticulum. (Re)
(2) cardia.
(3) reticulo-ruminal groove.
(4) cranial sac. (CS)
(5) omasum. (Om)
(6) right longitudinal groove.
(7) dorsal sac of the rumen. (DRu)
(8) dorsal blind sac. (DBS)
(9) right longitudinal groove.
(10) right dorsal coronary groove.
(11) ventral sac of the rumen. (VRu)
(12) right ventral coronary groove.
(13) caudal ventral blind sac. (CdVBS)
(14) abomasum. (Ab)
(15) pylorus. (P)



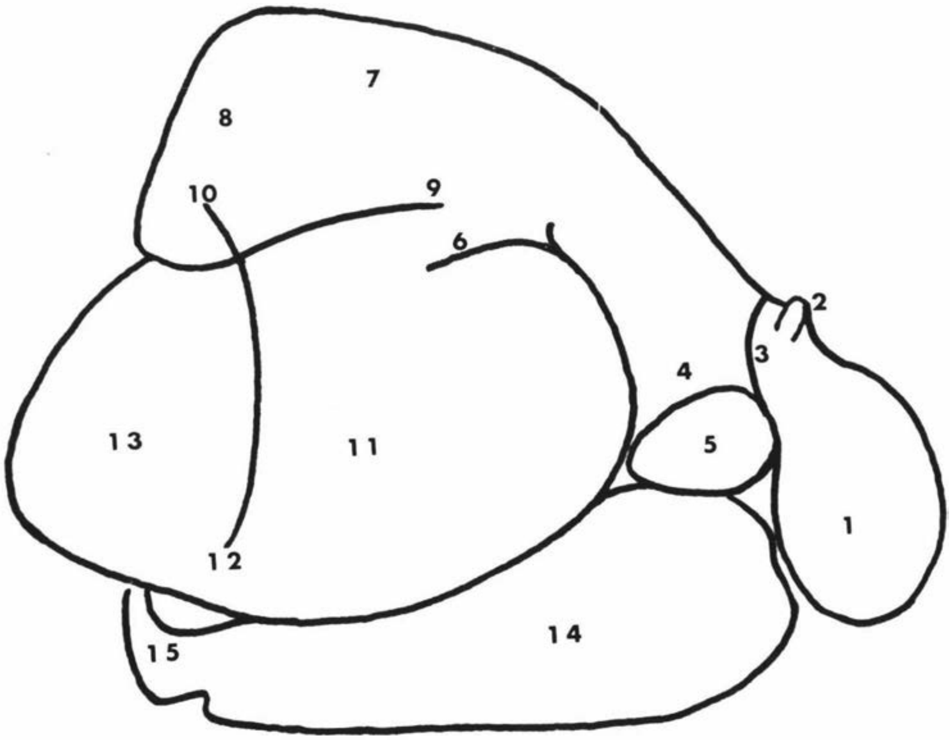

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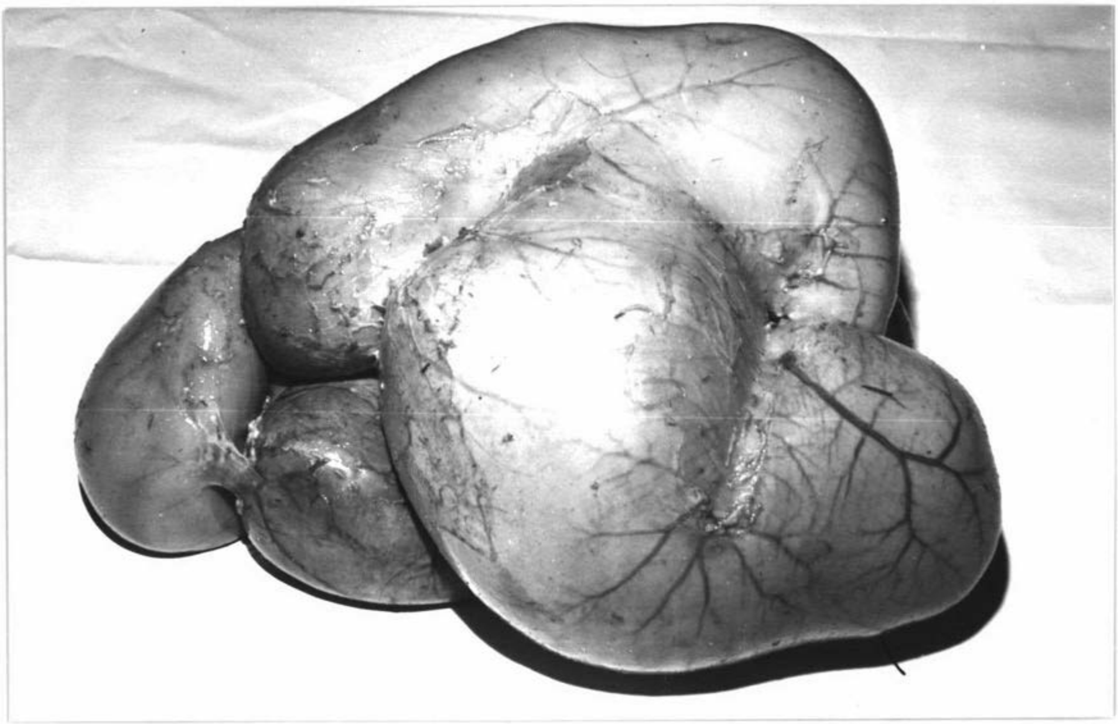
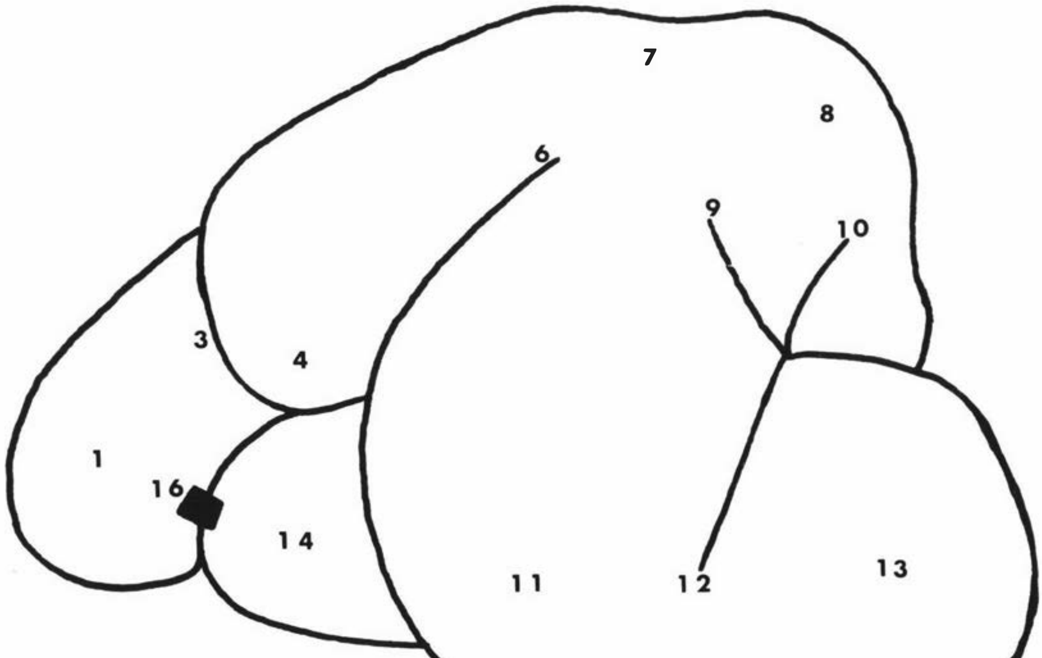
PLATE 2

The parietal (left) side of the same preparation as in Plate I.

(1) reticulum. (Re)
(3) reticulo-ruminal groove.
(4) cranial sac. (CS)
(6) left longitudinal groove.
(7) dorsal sac of the rumen. (DRu)
(8) dorsal blind sac. (DBS)
(9) left longitudinal groove.
(10) left dorsal coronary groove.
(11) ventral sac of the rumen. (VRu)
(12) left ventral coronary groove.
(13) caudal ventral blind sac. (CdVBS)
(14) abomasum. (Ab)
(16) reticulo-abomasal ligament.

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corresponding position. The cranial sac is small, lying between the reticulo-ruminal fold and the cranial pillar (CP). It opens into the dorsal sac of the rumen (DRu) over the cranial pillar which is a large dorso-caudally directed muscular flap connecting the visceral and parietal (left) longitudinal pillars. The cranial pillar is tilted with its parietal border more ventral than its visceral. The dorsal sac of the rumen is separated from the dorsal blind sac (DBS) by the incomplete visceral and parietal dorsal coronary pillars; there are corresponding visceral and parietal dorsal coronary grooves on the outer surface of the rumen. Ventrally the dorsal blind sac is bounded by the caudal pillar (CdP). The dorsal sac communicates with the ventral sac of the rumen (VRu) through a large opening the edges of which are formed by the cranial and caudal pillars, the visceral and parietal longitudinal pillars and the visceral and parietal accessory pillars; grooves in the outer surface are in corresponding positions to the two longitudinal and two accessory pillars. Caudal to the ventral sac and separated from it by the ventral coronary pillars is the caudal ventral blind sac (CdVBS).

The omasum (Om) is bean-shaped and situated on the visceral surface of the reticulum and cranial sac. A narrow neck connects it with the reticulum and there is an extensive connection between its wall and the wall of the abomasum (Ab). Within the omasum a groove, the omasal groove, which is an extension of the reticular groove, connects the reticulo-omasal orifice with the omaso-abomasal orifice. Much of the lumen is occupied by laminae which are attached to the wall and have their free borders directed towards the groove. The omaso-abomasal orifice is bounded cranially by the omasal pillar and is further protected by folds of the abomasal mucous membrane, the velae.

The abomasum is an elongated, tapering, tubular structure with its cranial blind end, the fundus, attached externally to the reticulum by a broad fibrous band. The body extends caudally between the omasum and the ventral rumen then inclines to the right and dorsally to form the pyloric part which connects with the duodenum through the pyloric sphincter. The visceral surface is mainly in contact with the abdominal floor. Within the lumen of the fundic region the mucous membrane forms a number of spiral folds which run obliquely towards the greater curvature. An area on the lesser curvature free of folds is called the abomasal groove and is considered to be a continuation of the omasal groove.

The lining of the oesophagus is a thick, stratified squamous epithelium which is flung up into longitudinal folds when the oesophagus is in its relaxed state. An abrupt change occurs at the cardia, the squamous epithelium giving way to a keratinised non-glandular epithelium which lines the reticulum, rumen and omasum. In the reticulum this lining is in ridges forming four, six or eight sided cells which gradually fade out towards the reticular groove and the reticulo-ruminal fold. The reticulo-ruminal fold is covered with papillae, and these extend throughout most of the rumen being largest in the cranial sac and the two blind sacs and fading out in the dorsal part of the dorsal rumen and on the lips of the major pillars. The degree of keratinisation, thickness of the epithelium and papillary growth have been related to the quality of the diet (Warner et al., 1956; Brownlee, 1965).

The lining of the omasum is also papillated; this papillated epithelium fades into glandular epithelium just before the omaso-abomasal orifice. Except for a small region of cardiac type glands close to this orifice, the fundic part of the abomasum is lined by mucosa with gastric glands which extend into the body region. The pyloric region of the abomasum corresponds with, and is similar to, the pyloric gland region of simple stomached animals.

The understanding of the function of an organ can be helped by knowledge of its ontogenesis, as the embryological development reflects its evolution. The embryology of the ruminant stomach was studied exhaustively by Pernkopf (1931). The development of the ruminant alimentary tract is similar to that of other mammals up to the 7 mm stage when an outpouching of the dorso-cranial aspect of the simple stomach occurs which will form the rumen. The reticulum and omasum then form from the cranial and caudal aspects of the ventral border of the stomach spindle. By the 12 mm - 15 mm stage all the parts of the stomach can be identified. Differential growth rate of the regions occur resulting in the rumen becoming largest. At the 50 mm stage the chambers start to rotate in a complex manner. The rumen rotates so that the original dorso-cranial aspect comes to be ventro-caudal and to the left, the omasum and abomasum rotate so that their dorsal aspects come to be ventral and to the right. When the rotation is completed the mesenteries have been changed in position and a strong adhesion develops between the dorsal sac and crura of the diaphragm which anchors the whole structure. Later the differential growth pattern changes so that at birth the abomasum is the most capacious structure. A further change occurs after birth which has been shown to be related to diet and microbial fermentation (Warner and Flatt, 1965) and results in the rumen becoming the largest structure.

The muscular coat of the ruminant stomach is comprised of smooth muscle except for a few striated muscle fibres which continue onto parts of the reticulum and rumen from the oesophagus. As in simple-stomached animals there are three layers of smooth muscle excluding the muscularis mucosus but their arrangement appears complicated because of the out-pouchings and rotations that occur during embryological development. The layer corresponding to the longitudinal muscle layer spreads out from the cardia in two parts. Part passes along the region of the reticular groove and over the omasum and abomasum becoming gradually thicker as it approaches the pylorus. The other part passes over the dorsal sac of the rumen. The next layer, corresponding to the circular muscle layer, spreads out from the cardia forming the floor of the reticular groove then spirals across the reticulum. It passes over the ventral rumen onto the caudal ventral blind sac. The circular muscle of the omasum, abomasum and pyloric sphincter are formed by this layer. Some recent studies by Lauwers et al. (1979) in the ox showed there was continuity of this layer with the circular muscle of the duodenum and there was also continuity of the longitudinal muscle but only by a few fibres. The layer corresponding to the internal oblique muscle layer is concentrated round the cardia and forms the lips of the reticular groove. It is a major component of the musculature of the reticulum and rumen and forms the pillars and encircles the two blind sacs. This layer does not appear in the walls of the omasum or abomasum.

1:1:2 The Small Intestine.

The sheep duodenum is about 1 metre in length. It passes from the pylorus to the surface of the liver where it forms the sigmoid flexure. From here it runs dorso-caudally passing round the root of the mesentery to the left side to join the jejunum at the duodeno-jejunal flexure. The common bile duct enters through the sphincter of Oddi on the second curve of the sigmoid flexure.

The jejunum forms loose coils, variable in position but usually in the supra-omental space to the right of the rumen. The small intestine continues as the ileum which is also in loose coils variable in position. The ileum terminates by entering the caecum and colon at the ileo-caecal junction.

The mucous membrane throughout the small intestine is in numerous circular folds and is covered with villi. Intestinal glands are distributed throughout its length and duodenal Brunner's glands occur in the more orad two thirds of the duodenum. The embryological development is unremarkable being the same as other mammals (Church, 1976). There is a longitudinal and a circular muscle layer.

1:1:3 The Large Intestine.

The entry of the ileum is considered to mark the junction of the caecum and colon. The sheep caecum, like those of other ruminants is small compared with many other herbivores. It is a blind-ending tube which is variable in position but is usually directed caudally with its blind end in, or close to, the left side of the pelvic inlet (MacRae *et al.*, 1973). The caecum runs into the colon which forms two elliptical coils before narrowing to form the centripetal and centrifugal coils. After leaving the spirals the colon passes cranial to the terminal duodenum then, just ventral to the right kidney, it turns caudally and forms an S curve before joining the rectum at the pelvic inlet (Ash, 1969).

The mucous membrane of the colon has no villi but does have intestinal glands. The increase in length of the colon in ruminants is embryologically derived from an elongation of that part called the ascending colon which lies to the right of the mesentery. The longitudinal and circular muscular layers are evenly distributed throughout the colon so there are no teniae.

1:2 MECHANICAL FUNCTION OF THE ALIMENTARY TRACT

1:2:1 The Oesophagus and Stomach.

The oesophagus of ruminants has to handle considerably more traffic than other animals. As well as handling the normal ingesta it has to pass digesta back up to the mouth for remastication and reswallow it, evacuate the gas produced in the reticulo-rumen and swallow the large volume of saliva produced (Kay, 1960). The reflex nature of the contractions of the sheep's oesophagus and its dependance on intact vagal nerves was demonstrated by Sellers and Titchen (1959). During normal swallowing a bolus passes down the oesophagus at 25 cm/sec. but boluses pass back up the oesophagus at 182 cm/sec. (Dougherty _et al_., 1971).

The function of the reticular groove in directing digesta past the reticulo-rumen has been described (Schalk and Amadon, 1928; Watson, 1944; Benzie and Phillipson, 1957; Orskov _et al_., 1970) and has been reviewed (Titchen and Newhook, 1975).

The closure of the groove occurs in two stages: first it shortens bringing the cardia and reticulo-omasal orifice closer together, then the lips - particularly the right lip - invert thus forming a complete tube connecting the oesophagus to the omasum.

The reticulo-rumen acts as a holding site for the microbial breakdown of digesta. It also mixes and sorts digesta for onward passage and eliminates the gas produced by the fermentation. This is achieved by a series of cycles of contractions of the various compartments, folds and pillars. The sequences in these cycles of events have been described by many authors among the most important of whom are Colin (1871), Ellenberger (1881), Wester (1926), Czepa and Stigler (1926), Schalk and Amadon (1928), Phillipson (1939), Weiss (1953), Reid and Cornwall (1959), Reid (1962, 1963) and Ruckebusch (1970). Two sequences of contractions have been described. The 'A' sequence commences with a biphasic contraction of the reticulum which is followed by sequential contractions of dorsal rumen, dorsal blind sac, ventral rumen and caudal ventral blind sac. The 'B' sequence, which is commonly associated with eructation, commences with a contraction of the caudal ventral blind sac followed by contractions of the dorsal blind sac, dorsal rumen and ventral rumen. It has been shown (Reid, 1963) that the form of these cycles and the ratio of one to the other is markedly influenced by diet and the degree of fasting.

Rumination was the process which first excited the attention of scientists and since the work of Toussaint (1875), there have been many contributions on this subject; the most significant of these are the reports by Colin (1886), Bergman and Dukes (1926), Downie (1954), Dougherty and Meridith (1955), Dussaudier (1959) and Stevens and Sellers (1960). The sequence of events commences with a reticular contraction associated with an inspiratory effort which impells a bolus from the cranial rumen into the oesophagus. This bolus is rapidly transported to the mouth where the fluid is expressed (and reswallowed) while the solid faction is remasticated rhythmically for a period of time before it too is reswallowed.

The reticulo-omasal orifice plays an important role as it controls the flow of digesta out of the reticulo-rumen. Flow of digesta into the omasum is most marked at the height of the second phase of the reticular contraction at which time the reticulo-omasal orifice is open (Balch *et al.*, 1951; Ohga *et al.*, 1956; Stevens *et al.*, 1960; Laplace, 1970; Ruckebusch, 1970; Bost, 1970; Ruckebusch and Kay, 1971; Bueno, 1975).

The omasum, with its large surface area, absorbs volatile fatty acids and electrolytes. Because of its position it also controls the passage of digesta into the abomasum. The two most extensive studies of the mechanical function of the omasum are those of Ehrlein and Hill (1969) and Bueno (1975). There are contractions of the dorsal two thirds of the omasal body which are in sequence with the reticular contractions. Contractions of the omasum closer to the abomasum occur independently, and possibly control the flow of digesta out into the abomasum. Completely independent of these two contractions are the contractions involving the leaves which occur about 2 - 3 times per minute.

The functions of the abomasum are to mix digesta with abomasal secretions thus acidifying them and exposing them to peptic enzymes, and to regulate their passage through the pylorus into the small intestine. The abomasum functions similarly to the stomach of simple-stomached animals except that the digesta that enters it is already in a liquid state, so passage time is comparatively rapid (Hill, 1968).

The mechanical activity of the abomasum and pylorus has been examined in detail by Ehrlein (1970, 1976). The only movement seen to involve the fundic region was that imposed by contraction of the reticulum. Over the body regular peristaltic waves started up and swept towards the pylorus with an increasing velocity at a frequency of about 6 per minute; this activity was continuous except for intervals of a few minutes. The contraction and relaxation of the pylorus was found to be synchronous with this peristalsis and no terminal antral contractions, as seen in simple-stomached animals, occurred.

1:2:2 The Small Intestine.

The contractions of the wall of the small intestine mix and propel digesta, and a number of patterns of contractions have been described (Code et al., 1968). The basic activity of the small intestine is made up of peristaltic waves (peristalsis). Peristalsis is defined by Davenport (1977) as a progressive wave of contraction of the circular muscle which moves a shorter or longer distance down the small intestine. Peristalsis is controlled by a slow wave or pace-setter potential which has been described by many including Bozler (1946), Ambache (1947), Bortoff (1961), and Ruckebusch et al. (1968). The frequency of this slow wave decreases down the small intestine causing the frequency gradient described by Alvarez (1914). There are two basic patterns of digesta movement:

(i) irregular movements associated with irregular contractions of the circular muscle - these occur randomly throughout the small intestine

(ii) regular coordinated movements associated with rhythmic sequences of contractions occurring at a frequency constant for a particular region of small intestine (segmental contractions).

1:2:3 The Large Intestine.

Further microbial digestion takes place in the caecum and that part of the colon orad of the spiral section. The mechanical activity of these regions has not been studied in great detail but the reports of MacRae et al. (1973) and Ulyatt et al. (1975) describe some of its features. Waves of contraction move orad and aborad over the caecum and adjacent colon. Intense contractions of the caecum evacuate its contents at intervals of 30 minutes to 4 hours. On entering the spiral colon the digesta are divided into small pellets and progress very slowly aborad. The pellets accumulate in the terminal colon where they remain until they are evacuated through the rectum and anus.

1:3 THE INNERVATION

As in other mammals the innervation of the alimentary tract of ruminants is organised so that there is voluntary control over either end and reflex control over the regions between. Central (vago-vagal) reflexes play a prominent part in the control of the orad portions of the stomach, their importance gradually decreasing towards the small intestine which can function without an extrinsic nerve supply.

1:3:1 The Oesophagus and Stomach.

The innervation to the oesophagus of the sheep has been described in detail by Dougherty et al. (1958) and is derived from the pharyngo-esophageal, recurrent laryngeal and vagus nerves. It has been shown that the peristaltic activity of the oesophagus is dependent on a centrally mediated reflex (Sellars and Titchen, 1959) and that this reflex can be modified by conditions in the reticulo-rumen.

The innervation of the ruminant stomach is basically similar to that of the simple stomach with a major contribution from the vagus nerves together with some sympathetic supply through the celiaco-mesenteric plexus; this has been described in detail by Habel (1956). The functional aspects of this innervation have been discussed by Titchen (1968). The dorsal vagus supplies the greater part of the rumen and the left aspect of the omasum and abomasum. The reticulum and right sides of the omasum and abomasum are supplied by the ventral vagus. The anatomical distribution of the sympathetic system has been described by Pintea et al. (1960). Both sets of nerves contain efferent and afferent components (Comline et al., 1968) but it has been shown that, whereas section of the vagal nerves stops the orderly contractions of the reticulo-rumen (Mangold and Klein, 1927; Duncan, 1953) section of the splanchnic nerves has no detectable effect (Duncan, 1953). The ruminant stomach appears to be more under the control of the central nervous system than the stomach of other mammals (Titchen, 1968).

The reflex closure of the reticular groove has been investigated (Watson, 1944; Comline and Titchen, 1951; Titchen and Newhook, 1975) and shown to be mediated through a centre in the medulla oblongata via the vagus nerves. The main stimuli that evoked closure of the groove were sucking or the anticipation of sucking (Orskov et al., 1970), or the presence of fluid in the back of the mouth (Comline and Titchen, 1951). In adult animals closure of the groove occurred after the administration of some organic salts.

Contractions of the reticulo-rumen have been shown to be controlled from centres in the medulla oblongata (Iggo, 1956; Dussardier, 1959; Titchen, 1958, 1960) and to be modified by vago-vagal reflexes. Two basic types of sensory receptors have been described in the reticulo-rumen (Iggo and Leek, 1970; Leek, 1971; Leek and Harding, 1975). Tension receptors are located in the muscle layers and are particularly concentrated in the reticulum and cranial sac, especially round the reticular groove. These respond to increased tension (stretch) and have an excitatory effect on reticulo-rumen contractions. Epithelial receptors are located superficially mainly in the reticulum and cranial sac of the rumen and on the cranial and longitudinal pillars. These receptors respond to mechanical and chemical stimulation and have an inhibitory effect on contractions.

The reflexes of the process of rumination are evoked by mechanical (tactile) stimulation of the more cranial parts of the rumen and especially the reticulo-ruminal fold (Ash and Kay, 1959; Reid, 1962, 1963). Eructation is stimulated by gaseous distention (Reid and Titchen, 1965) but may be inhibited by the presence of fluid in the region of the cardia (Dougherty *et al.*, 1958).

The neurological control of the reticulo-omasal orifice has been investigated but it has not been shown how it is effected (Newhook and Titchen, 1972; Titchen, 1974). However, it was shown that there was inhibitory vagal innervation and spontaneous activity.

The neurological control of the complex contractions of the various regions of the omasum has not been clearly established. Some of the contractions appear to be closely linked to the activity of the reticulo-rumen but others are not (Bueno, 1975).

The muscular activity of the abomasum is mostly intrinsic. Duncan (1953) showed that contractions of the pyloric antrum continued after vagotomy or splanchnotomy and that the major effect of this procedure was loss of tone in the fundic region. The two types of receptors found in the reticulo-rumen are also present in the abomasum (Leek and Harding, 1975).

Stimulation of the tension receptors results in inhibition of A sequences of reticulo-rumen contractions whereas stimulation of the mucosal receptors excites them. Gastric secretion into the abomasum is much less under vagal control than in simple-stomached animals and is mostly an intrinsic response to the flow and composition of digesta (Hill, 1960, 1968; Bell, 1980).

1:3:2 The Small Intestine.

The innervation of the small intestine appears to be the same as in other mammals; that is, there are contributions from the vagus and, through the coeliac plexus, from the sympathetic supply. The function of this nerve supply remains obscure and the small intestine will continue to function without it (Aeberhard et al., 1980). Van Harn (1963), working with cats, concluded that the autonomic nerve supply contained both excitatory fibres which cause contraction, and inhibitory factors which cause relaxation, and that their effect depends on the initial state of the intestine.

1:3:3 The Large Intestine.

Which regions of the caecum and colon receive the parasympathetic nerve supply from the vagus, and which receive it from the pelvic nerves, has not been established in the sheep. In the cat, stimulation of the vagus produces rhythmic contraction of the orad colon whereas stimulation of the pelvic nerves produces an expulsive movement of the colon. From the type of colonic activity observed in the sheep it is likely that the caecum and colon, to the aborad end of the spiral colon, receive their nerve supply from the vagus with the remainder of the colon and rectum receiving its supply from the pelvic nerves. Increased activity of the caecum and colon have been demonstrated with feeding and sham feeding (Ruckebusch, 1970; Ulyatt et al., 1975).

Chapter II

RADIOGRAPHIC TECHNIQUES

2:1 THE PROPERTIES OF X-RAYS

X-rays are part of the spectrum of electromagnetic radiation. Their wavelength is considerably shorter than that of light: the wavelength of x-rays used to produce an image is in the range 0.1 to 0.2 of an angström unit. X-rays form part of the excess energy given off when electrons rapidly decelerate or when electrons make a quantum jump inwards in one of the inner shells of an atom. In modern x-ray tubes the x-rays are produced when a stream of accelerated electrons collides with a tungsten target. The wavelength of the x-rays produced depends on the speed of the electrons, which is determined by the high voltage gradient (kV) between the source and the target. The number of x-rays produced is dependent on the number of electrons in the stream, a measurement of which is given by the resultant electric current (mA). Because of their high energy and short wavelength x-rays penetrate into materials. The degree to which they penetrate a given material is influenced by a number of factors:

(a) the energy of the x-ray (controlled by kV)

(b) the density of the material

(c) the atomic number of the material

(d) the thickness of the material.

As a result, when an x-ray beam passes through an object such as an animal body which is composed of various tissues of various thicknesses, a complex shadow of the regions passed through will be formed in the beam. As x-rays are not visible some method has to be used to convert this shadow into a visible image and two properties of x-rays can be used to do this.

X-rays affect a photographic plate in the same way as light, so if a photographic plate is placed in the beam, a photographic image can be developed. X-rays also cause certain crystals such as calcium tungstate to fluoresce, giving out light in proportion to the number of x-rays. Using a screen coated with such crystals the x-ray image can be converted to a visible light image for examination. Fluorescent screens can also be used to increase the efficiency of conversion of the energy in an x-ray beam into a photographic image by first converting the x-ray energy into light energy. To enhance the conversion of an image in an x-ray beam to an image on a photographic film the film is therefore sandwiched between two such screens (intensifying screens) in a light-proof cassette.

Producing a clearly defined image on an x-ray plate or on a fluorescent screen presents a number of problems for which there is no absolute solution. An x-ray beam cannot be produced from a point source so, inherent in the formation of an x-ray image is a degree of geometric "unsharpness". The degree of unsharpness depends on the size of the source, and the ratio of the distances between the source (focal spot) and the film or screen and between the object and the film or screen.

The main method by which an x-ray beam is attenuated as it passes through matter is by being "scattered". Scattered x-rays "fog" the image, decreasing the contrast range. They can be partly stopped from reaching the x-ray film by interposing a grid of alternating radio-opaque and radiolucent strips between the object being x-rayed and the film to act as a collimator. However, this grid will also stop a portion of the beam that is useful in forming the image.

X-rays, like other ionising radiations, damage tissues; they have both genetic and somatic effects, and the effects are cumulative. It is important that the total dose of x-rays to both the subject being examined and the people carrying out the examination be kept to an absolute minimum. Maximum permissible radiation doses for those working with ionising radiations have been derived and investigators using x-rays should monitor the dose received to ensure that it is not above this level.

The dose of radiation to the sheep used during the experimental procedures reported in this thesis requires consideration. Among mammals there is a great range of susceptibility to radiation damage and exact figures for sheep are not known. The average radiation dose quoted for mammals that will kill 50% of the population within 30 days is 500 rem as a single dose (Gillette et al., 1977). The dose of radiation received by each sheep used in this study at each procedure could only be estimated. During no single series of observations would the dose received by each sheep be greater than 100 rem but the accumulated dose over the period of the investigation could have been as high as 800 rem. This level of radiation spread over a period of time might be expected to cause some genetic damage but is well below the levels commonly used for radiation therapy. When the sheep were examined *post-mortem* no evidence of radiation damage could be found.

2:2 CONTRAST AGENTS

When the first attempts were made to carry out radiological investigations of the alimentary tract it was found that there was insufficient contrast from the surrounding and overlying tissues to make the viscera clearly visible either on fluorescent screens or on radiographs. The first agent introduced in an attempt to give contrast was iron oxide in gelatin capsules: it was not very effective. Cannon (1898) used bismuth subnitrate successfully, but because the nitrate preparation was not always reliable some deaths occurred from nitrite poisoning. This put the use of bismuth subnitrate into disrepute and the alternative found was barium sulphate. Suspensions of barium sulphate have been used to give contrast to the alimentary tract ever since.

Throughout these observations, the contrast media used was barium sulphate, either as a 100% weight for volume suspension (Micropaque, Nicholas) or as barium sulphate powder (Micropaque, Nicholas). On some occasions the barium sulphate was mixed with an equal volume of digesta before it was introduced into the digestive tract, on others it was mixed with the food material offered at a ratio which will be specified under the relevant section.

When barium sulphate or a barium sulphate-digesta mixture was to be instilled at a constant rate into the digestive tract an infusion pump (Harrod Apparatus) or a peristaltic infusion pump was used. The material being infused was heated to body temperature by passing it through coils of tubing immersed in a constant temperature water bath.

When certain specific points such as the rumen pillars had to be identified fixed radio-opaque markers made of stainless steel wire were attached to them.

2:3 APPARATUS

The first report of the use of x-rays to study alimentary tract function published by Cannon (1898) describes the methods used in considerable detail. The x-rays were produced in a Collidge tube which was supplied with the necessary high voltage by a small transformer. The high tension wires were not insulated and the remark was made that great care had to be taken not to come into contact with them.

The subjects used were cats and it was said that old females were best because they were less upset by the noise and sparks from the transformer. Bismuth subnitrate was the contrast material given to the cats and its movement through the alimentary tract was viewed on a fluorescent screen. Light output from the screen was extremely low and it had to be viewed in a blacked-out room after dark - adapting the eyes for twenty minutes. Cannon made records of what he saw by tracing the image on the screen and by taking photographic plates. The very low output of x-rays from the Coolidge tube can be gauged by the description of the method used for taking one of these plates. The exposure time required must have been extremely long by modern standards. As the film was being exposed a lead plate was used to block off the beam each time the cat breathed thus avoiding blurring of the image caused by movement.

The best method of analysing movement is to use moving film (cine-film) and the first to produce such an x-ray cine-film was MacIntyre who showed a short x-ray cine-film of the movement of a frog's leg to the Glasgow Philosophical Society in 1897. There were two methods of making x-ray cine-films. The direct method in which the film was exposed directly to the x-ray image, was used with some success initially but it had two major limitations: the size of field that could be filmed was very small, restricted by the dimensions of the film, while the long exposure times required limited the frame speed to 2 to 4 frames per second. The indirect method, in which the x-ray image was converted to a light image by using a fluorescent screen (hence the name cinefluoroscopy) had the distinct advantage that the light image could then be reduced and focused using lenses, thus increasing the possible size of the field filmed. As a half way stage between these two systems Alvarez (1914) used a machine which clamped the cine-film between two intensifying screens to expose each frame.

The development of more powerful x-ray machines and better cinefluoroscopic techniques made it possible for this method to be applied to the investigation of stomach motility in small ruminants. Czepa and Stigler (1926) first reported on its use and it has since been used by a number of others, (Magee, 1932; Phillipson, 1939; Dougherty and Meredith, 1955; Benzie and Phillipson, 1957) to add considerably to the understanding of the function of the ruminant alimentary tract. A major limitation to the use of cinefluoroscopy was the very high dose of x-rays that was required. The length of cine-film and the frame speed were kept down by the capacity of the x-ray tube to cope with the output required, and there was considerable hazard from the high levels of radiation used (Benzie and Phillipson, 1957).

In the late 1950's the image intensifier was introduced. This is a system of electronically intensifying the brightness of the fluoroscopy image many hundreds of times, thus allowing a much lower dose of x-rays to be used and increasing the perceptibility of detail of the final image. The system has other advantages - the image can be viewed by closed circuit television permitting the operator to be removed from the radiation hazard, while the image can be recorded in a number of ways such as on video-tape, cine-film or on single photographic films.

Akester and Titchen (1969) used an image intensification system to study various details of the contractions of stomachs of sheep and since then it has been used to investigate a number of aspects of ruminant alimentary tract function (Kay et al., 1972; Newhook and Titchen, 1974). During the course of research for this thesis two different x-ray facilities were used each of which had certain advantages for some of the procedures undertaken. One was installed in the Department of Veterinary Clinical Sciences, Massey University, New Zealand and the other in the Department of Physiology, Rowett Research Institute, Scotland.

The x-ray machine at Massey University (Plate 3) was powered from a Triplex Optimatic 1023 generator (Elema Schonander) which took a three phase alternating current supply and rectified and smoothed it to produce an almost constant voltage direct current. This generator had a maximum possible output of a 1000 milliamperes (mA) and 200 kilovolts (kV). It supplied a rotating anode x-ray tube BI200/30/50 (Siemens) which had a rating of 40 kilowatts on a 2 mm focal spot. The dimension of the x-ray beam emerging from the tube was controlled by an attached light-beam diaphragm (Siemens).

When plain radiographs of the sheep were taken the scatter in the x-ray beam was partially eliminated by inserting a 12:1 ratio, 100 lines per inch, focused grid in front of the cassette containing the x-ray film. The x-ray film used was RPX Royal (Kodak) which was sandwiched between two high speed intensifying screens (Kodak) and was protected from light in a cassette (Kodak). X-ray films were automatically processed by an RPXomat Processor (Kodak) on a 90 second cycle. A high kV technique was used to give a good cover of the large range of tissue densities and thicknesses through which the primary x-ray beam had to pass.

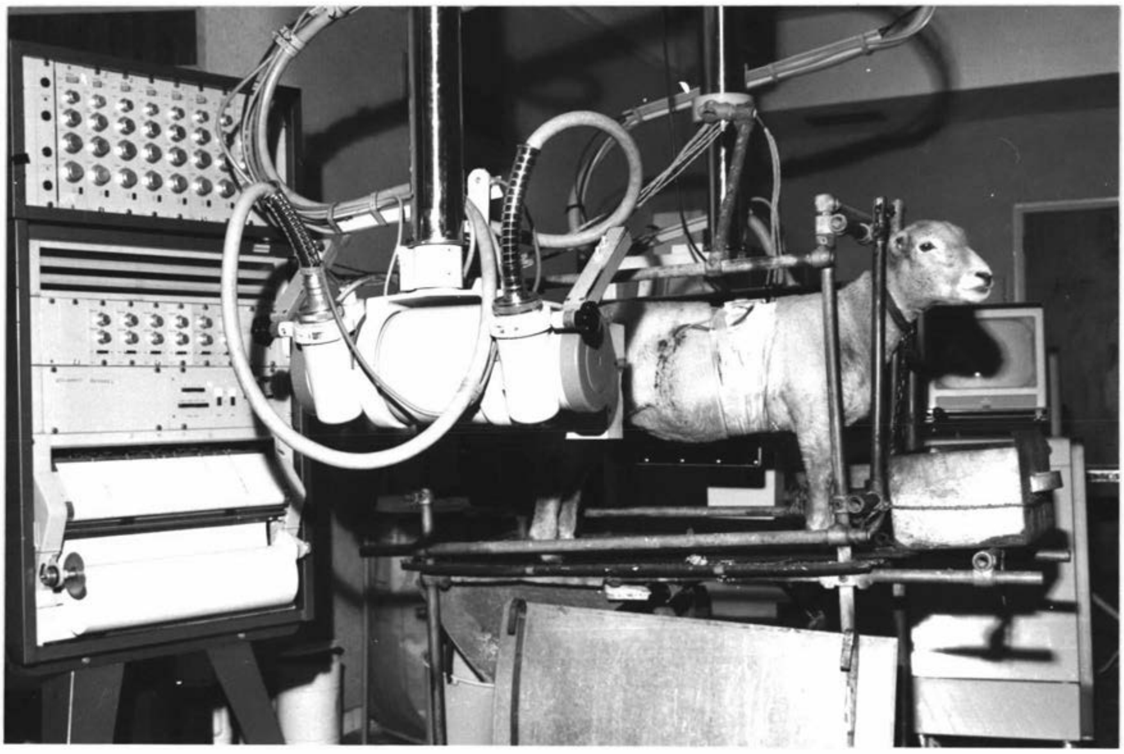
The x-ray image could also be viewed continuously by directing it onto a 10/6 image intensifier (Siemens) the output of which was viewed by a Plumbicon television camera and the final image displayed on a television monitor. This system permitted viewing of a 25 cm diameter circular field or provided for a 15 cm diameter field to be magnified up to 25 cm diameter. Exposure factors required to produce the best image on the television monitor were controlled through an automatic dose control unit (Siemens). A one inch Ampex video-tape recorder could be connected to the closed circuit television chain to provide a permanent record of the image.

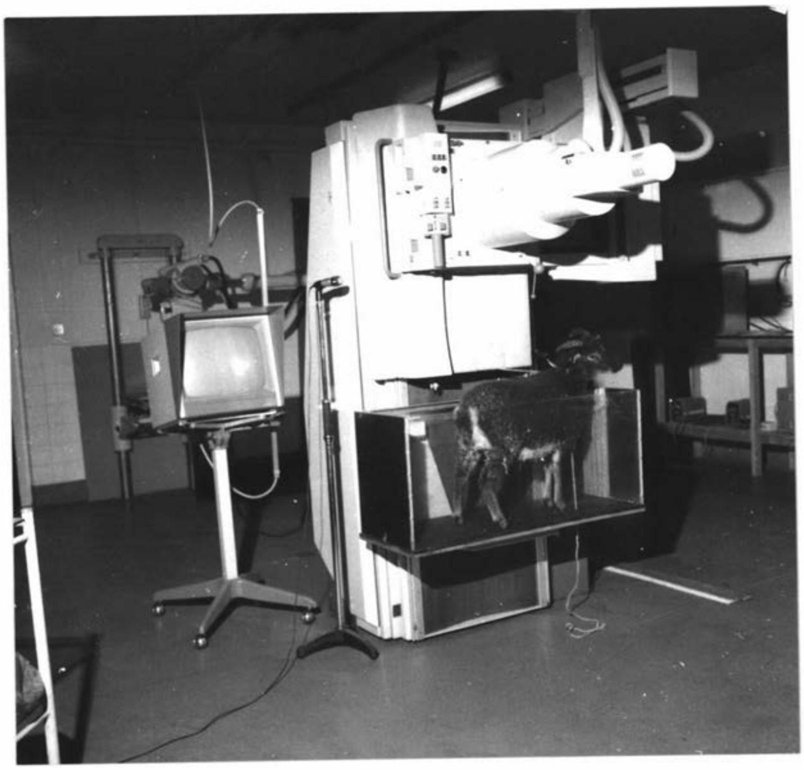
PLATE 3

The installation at Massey University with a sheep in position for a radiographic screening session. The sheep is restrained by head stalls and the sides of the metabolic crate are removed. This sheep was one of the animals used for studies on the small intestine, and the apparatus to the left is the Devices Multichannel recorder used for recording the electromyographic signal from the gut wall. The X-ray tube is on the side of the sheep nearest the camera. The switches for the magnetic brakes on the ceiling suspension can be seen on the handgrips.

PLATE 4

The installation at the Rowett Research Institute with a small Soay sheep in position for a radiographic screening session. The sheep is restrained in a small perspex-sided crush with a string from a neck collar attached to the floor of the crush. When screening is taking place, the motor driven table top elevates the sheep to come into line with the X-ray tube and image intensifier.





At the output of the image intensifier was a two way image splitter which allowed the mounting of either a 35 mm cine-camera or a 70 mm spot-film camera.

The 35 mm Arriflex cine-camera could be run at frame speeds of 12, 24, 37 or 75 frames per second. X-ray output was pulsed synchronously with the camera shutter opening so that, irrespective of the frame speed, the exposure time for each frame was 0.003 seconds. Brightness of the image on the cine-film was controlled by automatic variation of the kV after manual selection of the mA required. Incorporated in the cine-camera was a small light-emitting diode which, when activated, put a spot in the corner of a frame. This diode could be linked to the marker pen circuit of the pen recorders used so that marks could be made simultaneously on the film and on the pen recording. The cine-film used throughout was RAR2498 (Kodak) which was processed by the automatic processor.

The cine-camera could be replaced by a 70 mm spot-film camera (Sircom 70 Philips) which was fitted with an overframing lens. This camera could take either single frames or 1, 2, 3 or 4 frames per second. An Iontomat unit (Siemens) controlled the exposure factors automatically. The film used in this camera was Cronex SF2 (Du Pont) and this also was processed automatically.

The x-ray tube and the bracket carrying the image intensifier, the cassette and grid holder, were suspended from telescopic cranes mounted on rails on the ceiling. These ceiling cranes were cross-linked at the ceiling so that the x-ray tube was always centred on either the image intensifier or the cassette holder. This allowed the x-ray beam to be directed horizontally at the sheep as it stood in its crate.

The 35 mm cine-film was reviewed on a Tage-Arno projector which had a rotating prism rather than a shutter, allowing an infinite variation in frame speed up to a maximum of 50 frames per second both forward and reverse. A frame counter was incorporated in this machine which could be switched in and out as desired.

The x-ray machine installed at the Rowett Research Institute was basically similar to the Massey facility (Plate 4). The generator, x-ray tube and image intensifier were the same. The output of the image intensifier could only be viewed on closed circuit television via a Vidicon television camera and the exposure factors required to produce the best image on the display monitor were controlled by an automatic dose-control unit. A permanent record could be made on a 1 inch video-tape recorder Sirecord X, (Siemens) but there was no cine-camera, nor facility for any form of serial films. Another major difference was the method of mounting the x-ray tube and image intensifier. They were mounted on an explorator associated with a Pantaskop 3 table (Siemens), the tube being undercouch and the image intensifier overcouch. The explorator incorporated a device whereby spot-films could be taken on 35 x 35 cm or 24 x 30 cm films either using the entire film or dividing it into 2, 3 or 4 parts, exposing each part separately. When sheep were to be examined the table was tilted to its vertical position and a modified foot stand attached which protruded 47 cm from the table top and was 135 cm in length. On top of this platform was a perspex crush with 55 cm high walls which could be spaced between 20 and 40 cm apart.

The radiographic film used was Blue Brand (Kodak) coupled with fast intensifying screens (Ilford) which were mounted in cassettes (Siemens). The scattered x-rays were partially eliminated by a Bucky diaphragm. The film was processed manually.

The image recorded on video-tape could be transposed onto 16 mm cine-film by a Kinescope (Old Delft) and the film analysed by projecting with a 16 mm cine projector fitted with a stop frame facility. The cine-film (PlusX, Kodak) was processed by a commercial laboratory (Filmatic Laboratories, London).

The installation at Massey University had some distinct advantages for the type of investigation undertaken. The system of ceiling suspended mountings allowed the observations to be carried out without removing the sheep from its crate creating a minimum degree of disturbance to its daily routine. The high output of the generator and high rating of the x-ray tube permitted plain radiographs to be taken with a very short exposure time, thus eliminating blurr caused by rapid alimentary tract movements and respiratory movements.

The use of cine-film was an advantage for detailed analysis and timing of events because it could be replayed forwards and backwards or stopped; the frame counting gave very accurate timing. The ability to mark frames on the cine-film simultaneously with a marker on a pen recorder allowed for a close correlation to be made between phenomena observed radiographically and a specific type of E.M.G. recording.

The 70 mm spot-films were useful for recording some of the slower events that took place on a format that was large enough to be reproduced as illustrations, and more detail could be seen on these films than could be seen on the cine-film.

A disadvantage of the system was that there was no way of instantly making a record of an event seen on the display monitor. When full-sized 35 x 43 cm radiographs were being used it was not possible to observe events in the alimentary tract on the image intensifier so other means of predicting their occurrence had to be devised. When the cine-camera was attached to the image intensifier events could be observed continuously but there was a 2 second delay from switching on the cine-camera until it actually started running because of the time needed for the image splitter to change position. The high demand made of the x-ray tube when taking cine-film meant that the maximum length of each run was approximately 40 seconds at 12 frames per second and 6 to 10 minutes had to be allowed between each run to allow the x-ray tube to cool down. The cine-film used was very "fast" to keep the required exposure factors low and the maximum length of cine run as long as possible. This meant that the film was rather "grainy", particularly when viewed as a single frame and consequently, photographic reproduction from the cine-film was not satisfactory. The 2 second delay between pressing the button and actual exposure also applied to the spot-film camera, so any particular event or series of events that were to be recorded had to be predicted 2 seconds before they occurred. The 70 mm film allowed for good photographic reproductions but was considerably more difficult to analyse than cine-film because it had to be viewed as a series of still frames rather than as a moving picture. The maximum number of frames that could be taken at any one run was limited and again the limitation was imposed by the capacity of the x-ray tube to dissipate the heat generated. A further constraint was the size of the input end of the image intensifier tube (25 cm) which limited the size of field it was possible to view so that it was not possible to observe the entire reticulo-rumen even in the smallest of mature sheep.

During the earlier investigations undertaken for this thesis the image intensifier was nearing the end of its useful life and the quality of pictures obtainable was poor. Later a new image intensifier tube was installed which resulted in a marked improvement in picture quality.

The installation at the Rowett Research Institute had the additional disadvantage of lacking direct cine-radiographic facility. While it did have the capability of copying small selected runs from video-tape onto 16 mm cine-film, which was played through a standard projector, this process made it more difficult to analyse and time sequences of events accurately. A further disadvantage was the method of restraining the sheep between the table top and the image intensifier since this involved a change in the daily routine of the animals.

2:4 DISCUSSION ON THE USE OF RADIOLOGY AS A MEANS OF INVESTIGATING ALIMENTARY TRACT FUNCTION

Radiology is one of the few methods of observing the movements of the alimentary tract without surgical interference or the insertion of recording devices. Once the animals have been trained to stand in front of the x-ray machine there is no further stress. Being able to view large areas simultaneously allows the form of any contraction and its resultant effect on digesta movement to be observed more readily and in greater detail than can be determined from interpreting physiological recordings taken from a usually limited number of local sites. For this reason simultaneous radiological observation greatly aids the interpretation of such records. The various methods available for recording the radiographic image allowed different techniques to be adopted to illustrate particular points of interest. When considerable detail was wanted of a particular event single radiographs could be taken. Where the requirement was for prolonged periods of observation video-tape recordings could be made - this latter technique did not, however, allow easy detailed analyses of events as frames could not be stopped without considerable loss of image detail. When detail of movement was looked for in a step by step fashion the best method was to use serial spot-films taken at 2 per second. Observation on timing of movement, and the form of the movement, was analysed best on cine-film taken at 12 frames per second.

Radiology does have its limitations. The final image obtained is that of a shadow cast by the structures through which the beam has passed: therefore three dimensions are compressed into two. The interpretation of the image is subjective and is dependant to a considerable extent on the experience of the viewer. It is desirable to take radiographs in two planes to enable a 3 dimensional interpretation but, for a number of mechanical reasons, this was not feasible with the apparatus available in this study. For any structure to be radiographically visible it must differ from the surrounding structures in its ability to attenuate an x-ray beam. Most of the organs within the abdominal cavity have poor radiographic contrast, hence various markers have to be used. The introduction of the markers may then influence the events being observed. Barium sulphate is of high specific gravity (4) and tends to sink if mixed with fluid digesta. When barium sulphate was put into the ventral sac of the rumen, or into the abomasum, it sank to the lowest point unless the agitation of digesta was adequate to keep it mixed. Where coils of small intestine were filled with barium sulphate they tended to be more ventral in the abdominal cavity, especially when compared to gas filled loops. As far as can be determined the introduction of barium sulphate does not affect the pattern of motility when compared with the introduction of water (Ramsbottom et al., 1977).

Radiography gives the closest possible approximation to being able to view structures directly in vivo but there are three major differences: (i) the image is only two dimensional, (ii) the size of the field that can be observed is restricted, and (iii) the duration of each period of observation is limited. As with any observation, few results can be produced as figures or graphs: most have to be recorded in a descriptive manner and illustrated with a series of photographs, a subjective procedure open to variation in interpretation which cannot be avoided. Every effort was made to keep observations here as objective as possible. As much of the study is on radiographically observed movement, results could have been produced better as a cine-film than as series of static pictures. Successive pictures show change but not how the change came about, and so the gap has to be bridged by description.

The prolonged periods of radiographic observation used during these investigations had the potential to be a severe radiation hazard both to the animals and the observer. There was no detectable radiation damage to the sheep even although their total dose was high but had they been allowed to survive for a number of years it is possible that some of them might have shown effects, such as the development of malignant tumours. The observer had to take precautions to avoid excessive exposure to radiation and a double sided lead apron of 50 mm lead equivalent was worn at all times. Whenever possible a mobile lead protective screen was kept between the observer and the sheep and the distance from the sheep was kept as long as possible. The total body dose of radiation to the observer was constantly monitored using a film badge worn under the apron and never reached measureable levels.

Chapter III

THE RETICULO-RUMEN

3:1 LITERATURE REVIEW

There has been considerable debate about the form of the motor activity of the reticulo-rumen. Wester (1926) described a sequence of events in the cow, starting with a double contraction of the reticulum followed by a peristaltic wave passing caudally across the rumen, and an antiperistaltic wave passing cranially. The antiperistaltic wave was commonly associated with eructation or regurgitation. This was different from previous reports (Colin, 1871, 1886; Ellenberger, 1881) that the rumen contractions were completely independent of the reticular contractions and involved the whole organ as a single unit. Czepa and Stigler (1926, 1929) also found no relationship between the contractions of the reticulum and rumen but described the refilling of the reticulum from rumen. They said that there were total contractions of different chambers of the rumen and that the only sites at which peristalsis occurred were the caudal ventral blind sac of the rumen and the pyloric antrum of the abomasum. Wester's suggested relationship between the reticular and ruminal contractions was substantiated by the work of Schalk and Amadon (1928), Magee (1932) and Krzywanek and Quast (1936). However, none agreed with his suggestion of peristaltic and antiperistaltic contractions of the rumen. Schalk and Amadon (1928) agreed that there were two cycles of contraction of the rumen, one associated with reticular contractions and one not, but considered the sequence of events in both cycles to be similar and the contraction of each compartment to be a total rather than a sequential event. Using radiographic techniques Magee (1932) found only one cycle of events followed the reticular contraction, a total contraction of the ventral rumen and lastly a total contraction of the caudal ventral blind sac. A very complex series of events was described by Krzywanek and Quast (1936) which Phillipson (1939) suggested to be actually two cycles, a biphasic reticular contraction followed by two rumen contractions then a second biphasic reticular contraction followed by a single rumen contraction. Phillipson (1939) expressed the view that the many differences of opinion held by the various investigators were probably due to the differences in the methods of observation used. The two main points at issue, he considered, were the relationship between the reticular and ruminal contractions, and whether these were peristaltic or total in nature. Phillipson established that contractions of the rumen followed contraction of the reticulum but found that the ratio of rumen to reticulum contractions could range from 1:1 to 4:1 during the course of an experiment. He also found that the frequency and character of contractions changed with eating and rumination. Phillipson concluded that the contractions of the rumen were more total in nature than peristaltic but said "The real point of debate is the definition of peristalsis." The definition of peristalsis remains obscure and the term has been used to define a number of different manifestations of the results of muscle contractions (Farrar and Zfass, 1967).

The notion of two types of rumen contractions was revived by Weiss (1953) in reporting on his investigation of eructation. He considered that the first type moved caudally and that the second type moved cranially; and noted the second type frequently finished with eructation. He also demonstrated that the ratio of the first type to the second type of contractions could be changed by insufflating the rumen with gas.

The state of knowledge that pertained in 1952 was summed up by Balch (1952) as follows. A basic cycle of reticulo-ruminal contractions occurred but it was complicated by rumen movements independent of reticular contractions, by independent contractions of some parts of the ventral sac, and by the omission, in some cycles, of contractions of certain compartments and pillars. In 1956 the observations by Phillipson (1939) were reconfirmed and elaborated on by Radev and Stayonav (1956). During feeding the frequency of cycles increased and became stronger with an increased ratio of secondary to primary rumen sequences. When the animal was at rest, neither eating nor ruminating, the frequency of cycles decreased and the contractions became weak, frequently missing out contractions of the ventral sac entirely. The two sequences of contractions in cattle were described by Reid and Cornwall (1959) as the mixing and belching cycles. They found that the mixing cycle occurred in three phases. The first phase was a sharp contraction of the reticulum accompanied by a contraction of the reticulo-ruminal fold. The second phase comprised a second contraction of the reticulum and fold, and contractions of the cranial sac, cranial pillar, dorsal sac, caudal pillar and dorsal coronary pillars which occurred at slightly different rates. The third and final phase was the simultaneous contraction of the cranial, caudal and ventral coronary pillars, the ventral sac and the caudal dorsal blind sac. The belching cycle commenced with a contraction in the region of the dorsal coronary pillars which only slightly preceded a contraction of the cranial pillar, the dorsal sac and the ventral blind sacs. In the last phase, the cranial pillar, the ventral coronary pillars, the ventral rumen sac and the caudal dorsal blind sac all contracted.

A technique for partial exteriorisation of the reticulum originally described by van der Heyde (1927) was revived and modified by Bost (1958) and Titchen (1958a). Reid and Titchen (1959) extended this to various regions of the rumen and devised a system of pulleys which allowed graphic recording of movements of these exteriorised areas. This method allowed a much more detailed characterisation of the sequence of events in cycles of contractions of the reticulo-rumen (Reid, 1960, 1962, 1963; Titchen and Reid, 1965). The findings confirmed the presence of two cycles of contractions, which were called A and B sequences. It was also confirmed that the character and frequency of these sequences changed with changes in the state of the animal. The simplest form of cycle seen was in the fasted state and was an isolated A sequence. It commenced with a biphasic contraction of the reticulum, then the more cranial and dorsal rumen contracted followed by a contraction in the ventral regions which was not consistent. These contractions occurred so close together that they could be described as concurrent. When a B sequence was seen it generally followed an A but could occur in isolation. It commenced with a contraction of the caudal ventral blind sac which passed rapidly onto the dorsal rumen. Following feeding the contractions of the various regions of the rumen became stronger and more complex and consecutive. The series of events recorded during an A cycle was the sequential contraction of reticulum, cranial dorsal sac, caudal dorsal sac, ventral sac and finally caudal ventral blind sac. The B sequences became more frequent and commenced with a contraction of the caudal ventral blind sac which could be simply a continuation of an A sequence. A contraction of caudal and cranial dorsal sacs followed by a contraction of the ventral sac completed the sequence.

Study of the electrical events accompanying contractions of the reticulo-rumen was first undertaken by Toman (1928) but no further work using this technique was reported until the publications of Ruckebusch, Grivel and Santini (1968), Ruckebusch (1970), Ruckebusch and Kay (1971) and Tsiamitas (1972). The findings using this method confirmed those using partial exteriorisations. Contractions of the various compartments were shown to occur in sequence and the character and frequency of contractions to vary with the state of the animal. Strain gauges and pressure balloons were used by Kölling (1974, 1974a) and confirmed this sequence of events. Kölling also reported a correlation between the character of the contraction of the caudal ventral blind sac and the relationship of the A and B sequences.

The movements of the various folds and pillars as related to the sequence of contraction of the chambers has been investigated. Wester (1926) described the cranial pillar moving to divide the rumen into cranial and caudal sacs as the contraction passed over the cranial sac. The right and left longitudinal pillars then contracted to divide the rumen into dorsal and ventral sacs after which the dorsal coronary and caudal pillars contracted compressing the dorsal blind sac. During the secondary wave the pillars contracted in the sequence caudal pillar, dorsal coronary pillar, longitudinal pillars and cranial pillar. Schalk and Amadon (1926) reported that the contraction of the longitudinal, dorsal coronary and caudal pillars was a simultaneous event. In their report on the study of eructation Dougherty and Meridith (1955) suggested that the contraction of the reticulo-ruminal fold in conjunction with relaxation of the reticulum was important to hold back fluid contents and allow eructation.

The contraction of the pillars in cattle were investigated by direct inspection, palpation and by measuring the change in hydrostatic pressure in a fixed chamber alongside the animal and connected to the pillar by a column of water in a flexible tube (Reid and Cornwall, 1959). It was found that in the primary sequence the cranial pillar and dorsal coronary pillar started to contract together some short time after the reticulo-ruminal fold contracted but did not contract at the same rate. In the third phase of the mixing sequence the cranial, caudal and ventral coronary pillars all contracted simultaneously. During the belching sequence a contraction of the dorsal coronary pillars preceded a contraction of the caudal pillar.

The contractions of the reticulo-ruminal fold, cranial and caudal pillars were observed radiographically by placing radio-opaque markers on their free border (Akester and Titchen, 1969). The path taken by these markers was described in detail. The time of their displacement in relation to the contraction of the various chambers of the reticulo-rumen was similar to the previous reports. During the first phase of the reticular contraction the marker placed on the ventral free border of the reticulo-ruminal fold moved dorsally and slightly caudally. During the second phase it came back through its resting position then moved directly cranial, to remain in this position until the reticulum started to relax.

After the reticulum had relaxed a marker placed on the free border of the cranial pillar moved dorso-cranially then returned to its resting position within approximately 10 seconds. A marker placed in a similar position on the caudal pillar moved dorsally and caudally during both an A and B sequence.

The movement of digesta within the reticulo-rumen was observed by Reid and Cornwall (1959). During an A sequence contents were moved from the reticulum into the cranial and dorsal rumen. From the cranial rumen they moved back into the reticulum while from the dorsal rumen they moved down into the ventral rumen. The movement from the ventral rumen was over the relaxed cranial pillar into the cranial rumen and reticulum. This report did not conflict with previous reports (Wester, 1926; Czepa and Stigler, 1926, 1929; Schalk and Amadon, 1928; Magee, 1932; Phillipson, 1939; Benzie and Phillipson, 1957) except in some minor details. Czepa and Stigler (1926) observed digesta moving back and forth between the reticulum and cranial sac of the rumen in a rocking action and Magee (1932) reported seeing swallowed boluses dart about within the rumen.

The regurgitation of stomach contents for remastication is the process from which ruminants derive their name and it is this aspect which first aroused the interest of the early comparative anatomists and physiologists. Flourens (1830) and Haubner (1837) came to the conclusion that the reticular groove was responsible for forming the bolus for regurgitation and forcing it into the oesophagus. Colin (1871) disproved this by suturing up the reticular groove and demonstrating that rumination still occurred. He also made the observation that both the fluid and the solid of the remasticated bolus were returned to the rumen and not the abomasum. The method whereby the regurgitated bolus entered the oesophagus was the subject of much debate. Toussaint (1875) suggested that negative pressure was created in the thorax by an inspiratory effort against a closed glottis thus drawing material into the oesophagus. Colin (1886) argued that the material was propelled into the oesophagus by an increase in intraruminal pressure. A third hypothesis was brought forward by Wester (1926) suggesting that there was active dilation of the cardia and contraction of the oesophagus while the diaphragm was contracted thus creating a negative intra-oesophageal pressure.

Bergman and Dukes (1926) associated an extra contraction of the reticulum with regurgitation and confirmed Toussaint's (1875) findings. Downie (1954) also confirmed Toussaint's (1875) findings but added a rider that increased pressure caused by a ruminal contraction might play a part. However, it has been shown that an animal with a tracheal fistula placed below the glottis can still ruminate normally (Bell, 1958). Bell (1958) demonstrated that division of the phrenic nerves also had no effect on rumination but that a combination of division of the phrenic nerves and a tracheal fistula had a very marked effect. Investigations carried out by Dzuik and Sellars (1955), Dougherty and Meredith (1955), Bell (1958a) and Stevens and Sellars (1960) showed that the reticulum contraction associated with regurgitation caused a marked intra-reticular pressure rise without an associated rise in pressure in the rumen. This was associated with a fall in pressure in the oesophagus so that when the caudal oesophageal sphincter relaxed, material was forcibly ejected into the oesophagus.

Claims have been made that regurgitation can occur unassociated with a reticular contraction (Wester, 1926; Czepa and Stigler, 1929; Reid and Cornwall, 1959).

Tsiamitas (1972) recorded the series of events that occur in ruminating sheep as follows: A reticular contraction occurred with the amplitude of contraction of the caudal wall greater than that of the cranial wall. This was accompanied by inspiratory effort. The bolus entered the oesophagus and was then passed rapidly to the mouth where the fluid was expressed and reswallowed. Then followed a reticulo-rumen A sequence in one of its various forms, more usually of the less vigorous, resting, type.

The method of eliminating the gas produced by fermentation in the rumen has been another subject of much investigation. Wester (1926) was the first to suggest that eructation was commonly associated with a wave of rumen contractions passing from caudal to cranial. This point was disputed by Schalk and Amadon (1928) and Magee (1932). Weiss (1953) in agreeing with the findings of Wester suggested that eructation was commonly associated with a caudal to cranial rumen contraction unassociated with a reticular contraction and also showed that the frequency of this type of contraction could be increased by introducing air to the rumen. Using cine-fluoroscopy to investigate eructation, Dougherty and Meredith (1955) showed that contraction of the reticulo-ruminal fold and relaxation of the reticulum allowed the fluid level to drop below the cardia so that eructation could occur, and also that insufflation of the rumen with gas increased the frequency of eructation. Reid and Cornwall (1959) called the two sequences of contraction mixing and belching and confirmed the findings of Wester (1926) and Weiss (1953). They found that belching was most commonly associated with a B sequence, although not all B sequences were accompanied by belching and furthermore it could occur during an A sequence or unassociated with any reticulo-ruminal activity at all. These findings were further confirmed and elaborated upon during the subsequent few years (Reid, 1960; Reid, 1962; Reid, 1963; Titchen and Reid, 1965) and it was confirmed that the ratio of A to B sequences depended basically on the amount of gas present in the rumen. The B sequence was described by Ruckebusch and Tomov (1973) as commencing with a contraction of the caudal ventral blind sac which may or may not be a continuation of the contraction of this sac which concluded the preceding A sequence. This was followed by sequential contractions of the caudal dorsal blind sac, dorsal sac and ventral sac with eructation occurring at the height of the dorsal sac contraction. Many of these cycles were found to be weak or incomplete, and those which did not eventuate in an eructation generally had no ventral blind sac contraction; there was frequently simultaneous or reversed contractions of the dorsal and caudal dorsal blind sacs. Ventral sac contractions were frequently very weak or absent.

These findings were confirmed by Kölling (1974a) who added that eructation was only seen during a B sequence and that the time of the actual eructation depended on the strength of contraction of the caudal ventral blind sac. He went on to show that relaxation of the reticulum occurred after the contraction of the dorsal sac of the rumen in a B sequence. Kölling (1974a) further demonstrated that inflation of the rumen caused an increase in the relative frequency of B sequences so that the ratio of A to B sequences can become 1:2, which concurs with the findings of Dougherty (1961).

The sequence in which the major compartments of the reticulo-rumen contract under different conditions has been firmly established but the form of these contractions and whether they are peristaltic in nature has not been established. The aim of the first part of this investigation was to determine the form of the reticulo-ruminal contractions.

The movements of the various folds and pillars of the reticulo-rumen of sheep and the relationship to the contractions of the various compartments has also not been clearly defined: this was the objective of the second part of this study. Lastly the effects of the various sequences of contraction on the movements of digesta and gas, formed the objective of the third part.

3:2 MATERIALS AND METHODS

The study of the contractions of the reticulo-rumen and the movements of its contained digesta was divided into 8 sections. The aims of these sections were to observe:

- the reticulo-ruminal contractions and movements of digesta in the reticulo-rumen, and the changes that occur in both between the replete and the fasted state, in sheep in which there has been no surgical interference (3:2:1),
- details of the contractions of the reticulum, the reticulo-ruminal fold, the cranial sac of the rumen and the cranial pillar (3:2:2),
- details of the contractions of the cranial and caudal pillars and the dorsal rumen sac (3:2:3),
- details of the contractions of the ventral rumen (3:2:4),
- the contraction sequence of the reticulo-rumen in the replete sheep, for the purpose of illustration (3:2:5),
- the movement of digesta within the reticulo-rumen and the effects of different diets (3:2:6),
- the effects of abomasal distention on the contractions of the reticulo-rumen (3:2:7), and
- the effects of partial exteriorisation of the reticulum and of rumen fistulation on the contractions of the reticulo-rumen (3:2:8).

Details of the methods used are given below under the appropriate section.

Animals and their preparation: Twenty two animals were used to carry out these observations and experiments. Details of these animals are given in Table I.

The animals at the Rowett Research Institute were housed in individual pens and, unless otherwise stated, were fed dried grass ad libitum with a small amount of concentrate supplementation. Water was freely available. The animals at Massey University were kept in individual crates and were fed chaffed lucerne hay ad libitum, with water freely available.

Considerable time was spent training the animals and accustoming them to the routine in the x-ray room. This was particularly important at the Rowett Research Institute where the sheep had to be conveyed from their pens to the x-ray room and be restrained in the crush on the x-ray table.

Sheep 2 and 3 were bottle-trained so that radio-opaque marker mixed with cow's milk given by mouth from a bottle, would pass directly into the abomasum (Orskov et al., 1970). These sheep were removed from their mothers at birth and bottle-fed on cow's milk until 4 weeks old at which time they were offered dried grass. The amount of milk given each day was gradually decreased over the following three weeks, until the daily intake of milk was reduced to a single feed of 500 ml per day. This daily feeding with 500 ml of cow's milk from a bottle fitted with a teat was continued up to the commencement of observations, when the sheep were 7 months old, and was maintained for the 5 month period of observations.

As the animals got older their behaviour gradually changed. At about 5 months of age they would accept only their own bottle fitted with their own teat; and when a new teat was required they had to be coaxed to take the milk on the first one or two occasions. Also they would not accept the bottle if proferred by a person other than the one who fed them routinely. Some difficulty was encountered in getting these sheep to accept a mixture of barium and milk on the first 2 or 3 occasions it was offered.

Fistulation of the rumen was carried out on sheep 7, 9, 10, 11, 14,

TABLE I

DETAILS OF ANIMALS USED FOR INVESTIGATION OF RETICULO-RUMINAL CONTRACTIONS AND DIGESTA MOVEMENT.

Sheep No.	Age (months)	Breed	Sex	Where Housed	Preparations
1	7	So.	F	Rowett	-
2	7	So.	F	Rowett	B-tr. Ab.fist.
3	7	So.	F	Rowett	B-tr. Ab.fist.
6	13	Ro.	F	Massey	P.mark.
7	15	Ro.	F	Massey	Ru. fist.
8	15	Ro.	F	Massey	Re.exter.
9	14	Ro.	F	Massey	Ru.fist.
10	16	D/F	F	Rowett	Ru.fist.
11	36	D/F	F	Rowett	Ru.fist.
14	27	Ro.	F	Massey	Ru.fist.
15	29	Ro.	MC	Massey	Ru.fist.
16	32	Ro.	MC	Massey	Ru.fist.
17	25	Ro.	MC	Massey	Ru.fist.
18	26	Ro.	F	Massey	Re.exter.
19	25	Ro.	F	Massey	Re.exter.
20	25	Ro.	F	Massey	Re.exter.
21	3	D/F	M	Rowett	B-fed. Ab.fist.
25	13	Ro.	F	Massey	P.mark.
26	24	Ro.	F	Massey	P.mark.
27	27	Ro.	F	Massey	P.mark.
35	11	Ro.	F	Massey	Ru.fist.
36	11	Ro.	F	Massey	-

Ab.fist. - Abomasal fistula or cannula.
B-fed. - Bottle-fed.
B-tr. - Bottle-trained.
D/F - Dorset cross Finn.
F - Female
M - Male
MC - Castrated Male
P.mark. - Markers on pillars
Re.exter. - Partial exteriorisation of Reticulum.
Ro. - Romney
Ru.fist. - Rumen fistula.
So. - Soay

15, 16 and 17.

The Surgery was performed under general anaesthesia (Appendix I) in two stages. During the first stage an adhesion was created between the rumen wall and the skin. A high left flank laparotomy was performed midway between the last rib and the wing of the ilium. When the dorsal sac of the rumen was exposed, a stomach tube was passed down the oesophagus and the rumen gently inflated to bring it into its position in the replete state. It was then possible to select the site of the rumen wall adhesion so as to cause minimal distortion. This site on the left ruminal wall, eventually to be fistulated, was in the dorsal third of the dorsal sac somewhat cranial to the dorsal blind sac. The selected area of rumen wall was gently brought out through the laparotomy wound. A 6 cm vertical length of the rumen was sutured to the muscles of the abdominal wall with 2 rows of continuous sutures down either side separated from each other by a distance of about 2 cm. The exposed part of the rumen was then sutured to the skin down either side after dissecting away the panniculus muscle, and the remainder of the skin incision was closed.

During the second stage, carried out not less than 14 days later, the cannula was inserted. An incision was made over the site of the adhesion and the rubber cannula (Jarrett 1948) everted into position. The cannula had an internal diameter of 2.5 cm; it was held in place by an external plate of P.V.C. and closed with an expanding thermos flask stopper.

The reticulum was partially exteriorised in sheep 8, 18, 19 and 20 after the method described by Titchen (1958a), Bost (1958) and Reid (1963).

Before embarking upon surgery, the sheep were x-rayed in the replete state to establish the location of the reticulum with respect to the left ribs. It was found in all animals that the best location for an exteriorisation with minimal distortion was at the level of the eighth rib. This position also allowed the costophrenic angle of the pleural cavity to be crossed without encroaching on the lung.

After preparation of the site an incision was made over the midpoint of the eighth rib and carried on down to expose the rib. The periosteum was then carefully stripped off the rib from the level of the costochondral junction up to the point of maximum medial curvature. The rib was cut through as far dorsally as could easily be reached and was removed by disarticulating it from the costochondral junction. A small incision was made through the caudal edge of the periosteum and closely associated pleura and a small tent of diaphragm immediately drawn through to prevent air leaking into the pleural cavity. As the incision was being made digital pressure was used to keep the air out of the pleural cavity. The diaphragm was then cut, opening the peritoneal cavity. The incision through the periosteum, pleura, and diaphragm was gradually extended with the cut edge of the diaphragm being clamped to the periosteum to keep the defect in the pleural cavity air-tight. Once the incision had been extended to 6 cm in length the cut edges of the diaphragm were sutured to the periosteum and intercostal muscle with a continuous suture.

The reticulum was identified and a 6 cm length of the more dorsal part of its left wall brought out through the opening in the diaphragm. The dorsal and ventral borders of the exteriorised part were sutured to the muscles of the thoracic wall and then 3 or 4 sutures were placed down each side so that a piece of reticular wall 6 cm long and 2 cm wide was brought out through the pleural cavity. The panniculus muscle was then dissected away from the skin round the borders of the wound and the reticulum wall was sutured to the skin and the skin wound was closed.

Radio-opaque markers were fixed on the reticulo-ruminal fold, cranial pillar and caudal pillar of sheep 25, 26 and 27. After preparing the site a left flank laparotomy was performed and the dorsal sac of the rumen exposed. The dorsal sac was brought out through the laparotomy wound and a 10 cm vertical incision made in the mid point of the left wall taking care to keep clear of all pillars. A suction apparatus , was used to remove the rumen contents to allow identification of specific sites on the internal structures of the rumen. The markers used were made from 26 S.W.G. stainless steel suture wire (Zimmer, U.K.). Loops of a variety of shapes were made which were sutured into the required site, going through into the muscle layers. The different shaped loops allowed identification of any structure on radiographic examination.

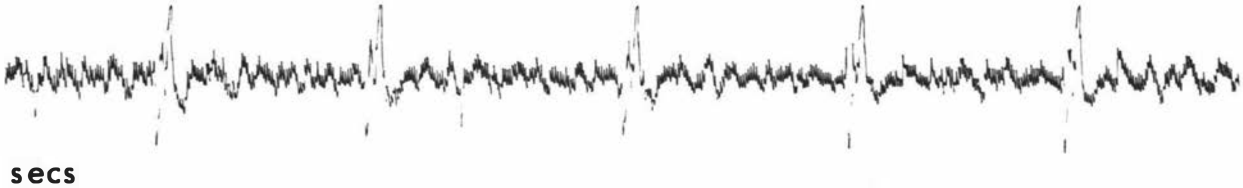
Four markers were placed on the reticulo-ruminal fold, the most dorsal at the level of the cardia and the most ventral on the ventral border of the fold. The other 2 were spaced equally between these. Markers were also placed on the mid point on the free borders of the cranial and caudal pillars.

The rumen contents, which had been maintained at 37^{o}C, were returned before the rumenotomy wound was closed with Czerny-Lembert sutures. Each layer of the body wall was sutured individually, with particular care being taken with the rumen wall and peritoneum to try to prevent adhesions occurring between the two surfaces.

Detecting reticulum contractions: In sheep 9, 14, 15, 16 and 17 the electrical signals of reticular contractions were recorded from skin electrodes by a slight modification of the method described by Itabisashi (1970) (Plate 5). Loops of 30 S.W.G. stainless steel suture wire (Zimmer, U.K.) were passed through the skin to act as electrodes. The reference electrode was positioned over the base of the tail. A second electrode was placed over the xiphoid cartilage and a third electrode was positioned on the left flank approximately at the level of the costochondral junction of the left, tenth rib. The exact positioning of the third electrode was determined in each individual sheep by trial and error with a needle electrode to find the position that gave the best signal. The signals were processed through an AC7 preamplifier (Devices) used in the differential mode and recorded with a heated stylus pen recorder (Devices). The settings that gave the best results were; time constant 0.3 sec., filter 3dB at 10Hz and a range of 0.5 mV. The paper speed selected was 5 cm/minute. To establish which recorded signal corresponded precisely with the first radiographically visible movement of the reticulum, cine-film of the reticular contractions was made simultaneously with the recording. The frame marker in the cine-camera and the recorder pen marker were in common circuit.

PLATE 5

A recording of the signal of reticular contraction. It was picked up by skin electrodes and processed through a differential amplifier. The large deflections indicate a reticular contraction. Cross checking with radiographic cine-film showed that the first downward deflection corresponded with the initiation of the dorsal movement of the reticulo-ruminal fold.


secs

Recording the radiographic image: A number of methods of recording the radiographic image were used depending on the type of information that was sought. Initially a general picture of the sequence of contractions was obtained by careful reviewing of video-tape recordings made from a number of sheep. The next step was to examine each part of the contraction cycles in detail and to time the interval of and between various events. Cine-film exposed at 12 frames per second was selected for this purpose as it could be examined frame by frame and replayed at different speeds through a variable speed projector. Accurate timing of events could be derived by counting the frames over which they occurred. The image on the cine-film was projected onto paper and the form of the movement of various regions traced out onto paper frame by frame.

When certain specific movements had to be illustrated in detail serial spot-films were taken at 2 per second. Where specific points in the contraction sequences or movement of digesta had to be illustrated radiographs were taken at a known time after the start of the reticular contraction. The start of the reticular contraction was determined either from an electrical recording or from observing a partial exteriorisation.

3:2:1 The reticulo-rumen contractions and movements of digesta in the reticulo-rumen, and the changes that occur in both between the replete and fasted state, in sheep in which there has been no surgical interference.

Sheep 1, 2, 3, 7 and 8 were submitted to 4 radiographic screening sessions of 150 minutes duration, each session separated by a minimum of 7 days and a maximum of 14 days. The sessions were alternated with the animal replete and fasted. For the sessions with the animal replete, food was freely available up to and throughout the period of screening. For the sessions with the fasted animal, food was withdrawn 18 hours beforehand.

Each session was commenced at 10.30 a.m. The routine followed was that for the first hour the activity of the reticulo-rumen was observed for a 5 minute period in every 15 minutes, then 50 ml of barium sulphate suspension was administered by dosing gun (Philips) and observations continued for 5 minutes in every 15 for the next hour. Following this, the sheep were given 100 g of normal food material mixed with either 20 g of barium sulphate powder or 20 ml of barium sulphate suspension and the destination and dispersion of the swallowed bolus observed. This procedure was carried out so that each sheep had each mixture once in the replete and once in the fasted state. Screening sessions were recorded on video-tape and were reviewed carefully afterwards, noting all movements of the reticulorumen and its contained digesta. No attempt was made to time the sequence of events observed.

In sheep 7 and 8, a series of 70 mm spot-films at 2 per second were taken of reticular contractions following the oral administration of 50 ml of barium sulphate suspension.

3:2:2 Details of the contractions of the reticulum, the reticulo-ruminal fold, the cranial sac of the rumen and the cranial pillar.

Three animals were used: sheep 9 which had no surgical interference, and sheep 26 and 27 which had markers placed on the reticulo-ruminal fold, cranial pillar and caudal pillar. No observations were made of the movement of the caudal pillar during this series. Sheep 9 had 50 ml of barium sulphate administered by dosing gun before the start of each session.

Each animal was submitted to 4 recording sessions which were a minimum 7 days and a maximum of 14 days apart, and alternating with the animal replete and fasted. As before, with the replete animal, food was available up to and during the recording session while in the fasted state, food was withdrawn 18 hours before the start of the session. At each session, which commenced at 9 a.m., a radiographic cine-film was taken of 5 separate series of contractions of the reticulum. For a number of reasons, this could take any length of time from 90 minutes to 4 hours. The maximum length of cine run possible was 40 seconds and between each run a 10 minute period was lost waiting for the x-ray tube to cool down. Furthermore it was essential that the cine-film run started before the reticulum commenced its contraction, but, because it was difficult to predict when a reticular contraction would occur, many runs were unsuccessful.

The change in shape and position of the reticulum, cranial sac, reticulo-ruminal fold and cranial pillar were traced out making allowances for respiratory movements by using the ninth rib as a reference point.

At each of the 4 sessions (two in the replete and two in the fasted state) for each of the 3 sheep the times of the following series of events were measured over 5 contraction sequences.

(1) Duration of the first phase of the reticular contractions (Re1).

(2) Duration of the second phase of the reticular contractions (Re2).

(3) Interval between the end of the second phase of the reticular contraction and the peak of the cranial pillar contraction (Re2-CP).

(4) Start of reticular contractions to the peak of the cranial pillar contraction (Re1-CP).

The times were derived by frame counting, with each count from each film being made 3 times, the mean taken, and the results expressed as a mean and a range.

Attempts were made to get cine-film of the activity during rumination in all 3 animals but the noise of the cine-camera continued to disturb sheep 9 and 26 even although considerable effort was made to accustom them to it. The only animal from which satisfactory films of rumination were obtained was sheep 27; in this animal timing of the duration of the reticular contraction of rumination (Rx) and each phase of the biphasic contraction was obtained on 10 occasions.

As well as the cine-film, a series of spot-films, at 2 frames per second, were taken of the movement of the reticulo-ruminal fold and cranial pillar to further illustrate the range of movement that occurred.

3:2:3 Details of the contractions of the cranial and caudal pillars and the dorsal rumen sac.

Four animals with radio-opaque markers on the cranial and caudal pillars were used, sheep 6, 25, 26 and 27.

Sheep 26 and 27 were submitted to 4 recording sessions which were commenced at 1 pm and were a minimum of 7 days and a maximum of 14 days apart. As before these sessions were alternated with the sheep in the replete and fasted state. The replete animal had food available up to and during the recording session, the fasted animal had food withheld for 18 hours before the recording session and during the recording session. At each recording session movements of the pillars were observed and 5 cine-radiographic runs of a complete cycle ending shortly after eructation, were obtained. As it was not possible to predict with any accuracy which cycles would continue on to a second contraction of the dorsal rumen, many filmed runs were incomplete. This was particularly so with the sheep in the fasted state and it could take up to 5 hours to obtain the desired 5 complete cine-runs.

Sheep 6 and 25 were also submitted to 4 sessions, 2 in the replete and 2 in the fasted state, each session being separated by a minimum of 7 days and a maximum of 14 days. However, no useful radiographic cine-film was obtained from these two animals in the fasted state because of the difficulty of predicting which cycles would continue on to a second contraction of the dorsal rumen, and the infrequency of such cycles.

The cine-film was projected onto paper and the path taken by markers on the free borders of the cranial and caudal pillars was traced out, making allowance for respiratory movement and movement of the sheep by using the fourth lumbar vertebra as a constant reference point. The time taken between various points of the movements of the pillars was obtained by frame counting with each count being done three times and the mean taken.

The intervals timed were:

1. The peak of the cranial pillar's dorsal excursion until the caudal pillar reached the peak of its dorsal excursion.
2. The peak of the caudal pillar's dorsal excursion to the return of the cranial and caudal pillars to their resting positions.
3. The point when the caudal pillar returned to its resting position to the peak of its first ventral displacement.
4. The peak of the first to the peak of the second ventral displacement of the caudal pillar.
5. The peak of the first to the peak of the second movement of the cranial pillar.

3:2:4 Details of the contractions of the ventral rumen.

The movements of the ventral rumen were observed in 2 animals, sheep 18 and 19: both had a reticulum exteriorisation and a rumen fistula which were prepared 3 weeks previously. The reticulum exteriorisations were made to indicate when a cycle of contraction had commenced. Each of these sheep was subjected to 4 screening sessions following the routine previously described. The sessions were separated by a minimum of 7 days and a maximum of 14 days and alternated with the sheep in the replete and fasted state. The sessions were started at 9 am. Before the start of each session, the rumen fistula was opened and a catheter passed down into the ventral rumen. Through this catheter 50 ml of barium sulphate suspension, warmed to body temperature, was slowly instilled to outline the ventral wall of the rumen. The ventral rumen was observed continuously for 30 minutes and videotape recordings made for later scrutiny; 5 cine-runs were taken at appropriate times following movement of the reticular exteriorisation.

3:2:5 Illustration of the contraction sequence of the reticulo-rumen in the replete sheep.

Sheep 16 and 17 were prepared for this investigation with rumen fistulae and skin electrodes. The pen recording from these electrodes allowed the contraction of the reticulum to be identified (see Plate 5) so that radiographs or a series of spot-films could be taken at a known time after the start of the reticulum contraction.

To give contrast, 50 ml of barium sulphate suspension was placed in the particular region of interest by injecting it through a catheter inserted through the rumen fistula and positioned with the aid of the image intensifier. More than 15 sessions extending over a period of 6 months were required to obtain an adequate series of radiographs and spot-films. At each of these sessions, the movements of the reticulo-rumen were observed, intermittently for up to 4 hours and the events recorded on video-tape for detailed analysis.

3:2:6 The movement of digesta within the reticulo-rumen and the effects of different diets.

Four sheep, 14, 15, 16 and 17 with rumen fistulae and skin electrodes were used for this experiment. However, sheep 15 demonstrated digesta movement different from the other three and lost condition over the period of the experiment. At post mortem examination, this animal had gross adhesions involving the rumen, terminal ileum, and colon. There was also a 5 cm diameter calcified hydatid cyst overlying the pylorus. Results from this animal were not used.

The sheep were fed 3 different diets, chaffed lucerne hay (chaff), ground and pelleted lucerne hay (pellets) and fresh perennial ryegrass (Grasslands Ruanui ryegrass). The dry matter intake on all diets was held at 2.5% of body weight with the chaff and pellets fed once daily at 9 am and grass twice per day at 9 am and 4 pm, the latter in equal portions. When the sheep were switched from one diet to another, a two-week period was allowed before a new recording session was embarked upon. The diets were given in the order, chaff, pellets, grass, chaff.

The routine of a recording session was that at 11 am water was withdrawn, at 1 pm food was withdrawn, and the session commenced at 1.30 pm with food and water being returned at 5 pm.

The radiological recording of the movement of the digesta was achieved by using a radio-opaque marker (barium sulphate) administered either by mouth, using a dosing gun, or intra-ruminally into the dorsal blind sac using a catheter inserted through the rumen fistula and monitoring its position radiologically. The dose of marker used in both instances was 50 ml. Radiographs were then taken at 5 minute intervals, continuing until the marker was so dispersed that it could no longer be followed. Between 5 and 20 plates were taken at each session. To ensure that the radiographs were all taken at the same stage of the cycle of activity of the reticulo-rumen, all exposures of the radiographs were made 45 seconds after an electromyographic pattern of a reticular contraction was noted on the pen recorder connected to the skin electrodes.

On each diet for the marker given orally, and for the marker put into dorsal blind sac, two series of lateral radiographs were made to illustrate the vertical plane of the dispersion, and one set of dorso-ventral radiographs to illustrate the horizontal dispersion. During the dorso-ventral series at every third radiograph, a lateral one was taken so that the two series could be correlated. This made a total of 72 observation sessions in the three sheep (3 sheep x 2 sites x 3 series x 4 diets).

Once a series of radiographs was obtained, it was photographed onto 35 mm slides which were projected onto the frosted screen of a daylight slide projector (Hiruma). The screen was then covered with an acetate sheet and the outline of the marker on each succeeding slide traced out using a different colour pen for each slide. This allowed composite pictures of the dispersion of the marker with time to be built up.

3:2:7 The effects of abomasal distension on the contractions of the reticulo-rumen.

Sheep 1, 2, 3 and 21 were used. Sheep 1 and 21 were fitted with abomasal fistulae, sheep 2 and 3 were bottle-trained and sheep 21 was bottle-fed with 800 ml of cow's milk 3 times per day. Abomasal distension in sheep 1 was caused by the introduction of:

(1) 600 ml of cow's milk,

(2) 600 ml of cow's milk and 200 ml of air, or

(3) 200 ml of air.

In sheep 2 and 3 abomasal distension was caused by bottle-feeding 600 ml of cow's milk or whey, which was augmented by a volume of air swallowed as they sucked. The volume of swallowed air in the abomasal gas cap was estimated using a simple computer programme (Appendix II). Abomasal distension in sheep 21 was caused by:

(1) bottle-feeding 600 ml of cow's milk,

(2) injecting 600 ml of cow's milk and 150 ml of air through the abomasal catheter,

(3) injecting 600 ml of cow's milk and 500 ml of air through the abomasal catheter.

All sheep were dosed with a 6.35 mm diameter stainless steel ball bearing to act as a marker in the reticulum.

Each sheep was submitted to three screening sessions, the routine of which was as follows. The sheep were screened for 30 minutes and a count made of the A and B sequences observed. The abomasum was then distended and the screening continued, noting the time elapsed until the first B sequence was observed, the first contraction of the reticulum, and the first normal A sequence. Notes were also made on some occasions of the time taken for the abomasal gas cap to start to be eliminated as well as its route of elimination.

3:2:8 The effects of partial exteriorisation of the reticulum and rumen fistulation on the contractions of the reticulo-rumen.

Five animals were used, sheep 10, 11, 20, 35 and 36. Sheep 10, and 11 had rumen fistulae and sheep 20 a reticular exteriorisation. Sheep 35 and 36 were intact when first observed (first session), but had reticular exteriorisations prepared 3 weeks before the second session. Sheep 10, 11 and 20 were submitted to one 30 minute session in the replete state and a video-tape recording made of reticulo-ruminal activity which was compared with normal sheep used in 3:2:1. Sheep 35 and 36 were submitted to two 30 minute sessions, one before and one after exteriorisation of the reticulum. At each session a video-tape recording and three series of serial spot-films of the reticular movement were taken.

3:3 RESULTS

3:3:1 The reticulo-ruminal contractions and movements of digesta in the reticulo-rumen, and the changes that occur in both between the replete and the fasted state in sheep in which there has been no surgical interference.

Contraction sequences in replete sheep.

The most extensive series of events in the reticulo-rumen were seen in the replete sheep. They were initiated by a biphasic contraction of the reticulum and ended with a contraction of the cranial ventral rumen which occurred shortly after eructation. The contraction sequence was similar in all 5 sheep in the replete state but there were some minor differences in the fasted state. A description of the contraction cycle in the replete state is given and a discussion of the modifications seen in the fasted state follows:

The first movement of the reticulo-rumen seen at the start of a contraction sequence was a straightening of the caudal wall of the reticulum and a slight caudal movement of its pole. The contraction of the reticulum lifted its pole in a shallow arc dorsally and slightly cranially causing its outline to become rounded. At a point approximately half way between its position at rest and at maximum contraction, the pole stopped momentarily and was observed on some occasions in sheep 1, 2 and 7, in the replete state, to drop back a short distance ventrally. On the majority of occasions, it only paused in this position then continued dorsally with the second phase of its contraction. During this second phase, the pole's dorsal arc of movement was inclined slightly caudally and the walls of the reticulum moved closer together until, at the height of contraction, the lumen was almost obliterated.

Immediately after the reticulum started to contract, the cranial sac of the rumen began to distend, reaching its maximum degree of distension as the reticulum reached its maximum degree of contraction. The cranial sac enlarged mainly in a cranial and ventral direction so that it occupied the space vacated by the contracting reticulum.

Following a very brief pause at the height of reticular contraction and cranial sac dilation, the reticulum started to relax, its pole returning to its resting position along the same route followed during contraction. As the reticulum relaxed the cranial sac contracted. When the reticulum had returned approximately half way to its resting position, and the cranial sac was half way to its contracted state, the cranial pillar started to move dorsally and caudally. The contractions of the cranial sac and the cranial pillar occurred as a unit so the peak of contraction of the cranial sac and cranial pillar occurred simultaneously. The contracted ventral wall of the cranial sac and the cranial pillar formed a curve running approximately parallel to the dorso-cranial aspect of the rumen. To illustrate this sequence of events, a series of 70 mm spot-films were taken of sheep 7 and 8, (Plate 6).

As the cranial pillar approached the furthest extent of its travel the raft in the dorsal rumen lifted and the gas cap from the dorsal rumen was displaced caudally into the dorsal blind sac, distending it. Following rapidly on this, the more caudal dorsal rumen and the dorsal blind sac contracted, displacing the gas cap, usually in three directions simultaneously. The largest volume was displaced cranially across the dorsal rumen and down into the dorsal part of the reticulum

PLATE 6

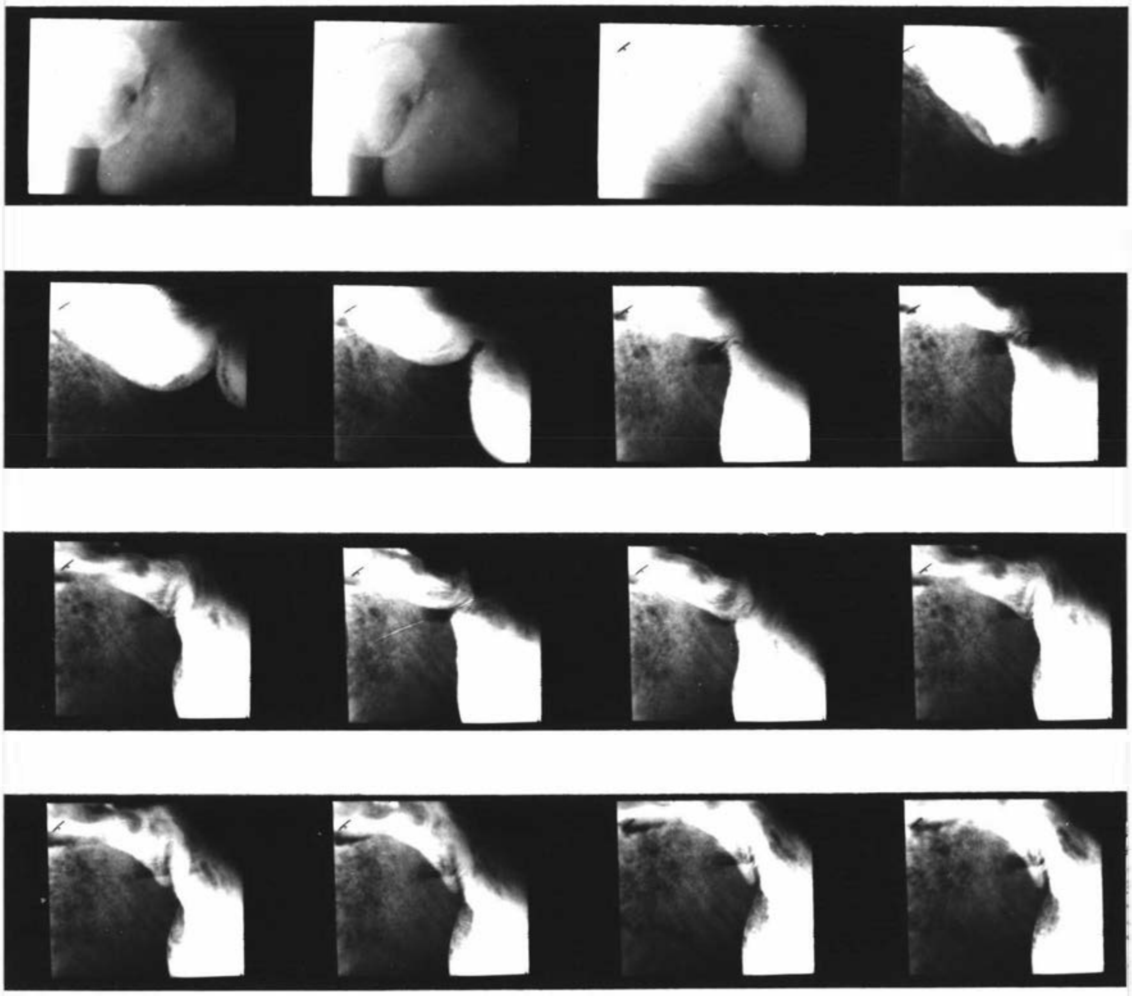
This is a series of spot-films taken of a reticulum contraction followed by a cranial sac contraction. The films were taken at 1 second intervals. Before the series started, the sheep was dosed with 50 ml of barium sulphate suspension by mouth. The sheep's head is on the right.

The first row. Contraction of the reticulum and distension of the cranial sac. The second frame shows the straightening of the caudal border of the reticulum indicating the start of a contraction sequence and the last frame shows the cranial sac dilated with the contrast pushed out of reticulum so that the reticulum is no longer visible.

The second row. Contraction of the cranial sac and refilling of the reticulum. In the first two frames of this row the ventral part of the reticulo-ruminal fold can be seen returning towards its resting position. By the last frame the cranial sac has reached the height of its contraction.

The third row. The contraction of the cranial sac is maintained as the gas cap is pushed cranially from dorsal rumen into the dorsal reticulum and under the cranial pillar.

The fourth row. The cranial sac relaxes and the gas cap returns to the dorsal rumen except for a small amount trapped under the cranial pillar which even by the last frame has not relaxed.



causing it to be distended beyond its normal resting state. A smaller volume was displaced cranio-ventrally, down the lateral walls of the dorsal rumen and under the cranial pillar. The smallest volume was displaced ventrally round the caudal pillar into the caudal ventral blind sac. Whether the gas was displaced into all three positions and how far it was displaced depended on its size and, to a lesser extent, on the consistency of the rumen contents. With a decreased volume of gas in the dorsal rumen there was no displacement of gas into the caudal ventral blind sac, and if this volume was decreased still further none was pushed under the cranial pillar. When no gas was displaced into the caudal ventral blind sac eructation did not occur. However, the converse did not hold.

The cranial pillar was held at the height of its contraction during the contraction of the dorsal rumen and dorsal blind sac. It then started to relax, returning towards its resting position, and relaxation of the dorsal rumen and dorsal blind sac followed. All the gas except that displaced into the caudal ventral blind sac returned to the dorsal rumen. On no occasion was eructation observed to occur during this phase of the cycle.

Shortly after the cranial pillar arrived back at its resting position the cranial wall of the ventral rumen contracted causing its rounded outline to straighten. At a site cranial of the mid point of the ventral rumen wall the apparently simultaneous contraction of the cranial section of the ventral rumen wall was replaced by a distinct wave of contraction which migrated slowly caudally across the ventral rumen onto the caudal ventral blind sac. When this wave arrived at the pole of the caudal ventral blind sac the pole contracted, displacing most of the small gas cap round into the dorsal rumen. The pole of the caudal ventral blind sac then relaxed and after a brief pause contracted a second time, followed by a wave of contraction which migrated cranially across the caudal ventral blind sac onto the ventral rumen. Very shortly after the second contraction of the caudal ventral blind sac the dorsal blind sac contracted, displacing the gas cap cranially along the dorsal rumen. The contraction moved rapidly onto the dorsal rumen and as it did so, the cranial pillar moved a short distance caudally and slightly dorsally. While this was happening, the wave of contraction on the caudal ventral blind sac was moving slowly cranially. If eructation occurred it took place when the cranial pillar had reached the maximum extent of its second movement. At eructation, one or two boluses of gas would pass into the oesophagus and move rapidly orad. In many instances the bolus of gas was split in the intrathoracic oesophagus somewhere between the thoracic inlet and the base of the heart, and the more aborad part returned to the rumen.

Immediately following eructation, the dorsal rumen relaxed and the cranial pillar returned to its resting position. At the same time the wave of contraction passed off the caudal ventral blind sac onto the ventral rumen. The cranially migrating wave on the ventral rumen disappeared at a position closely approximating the point of origin of the caudally migrating wave and was followed immediately by a contraction of the cranial ventral rumen which completed the contraction sequence.

To summarise, the sequence of events observed in these normal replete sheep from the start of a reticular contraction until shortly after eructation occurred was as follows:

1. Biphasic contraction of reticulum.
2. Contraction of cranial sac and cranial pillar.
3. Contraction of the dorsal rumen.
4. Contraction of the dorsal blind sac.
5. Contraction of cranial ventral rumen.
6. Wave of contraction migrating caudally across the caudal ventral rumen and caudal ventral blind sac.
7. Contraction of the pole of the caudal ventral blind sac.
8. Second contraction of the pole of the caudal ventral blind sac.
9. Second contraction of the dorsal blind sac.
10. Second contraction of the dorsal rumen and cranial pillar.

11. Eructation.
12. Wave of contraction migrating cranially over the ventral rumen.
13. Second contraction of the cranial ventral rumen.

Less than half the cycles in the replete animal were as complete as this-often some events were missing. Thus eructation did not occur every time this form of the cycle was seen. Many contraction sequences dropped out the second contraction of the pole of the caudal ventral blind sac, the dorsal blind sac, dorsal rumen and cranial pillar. When this happened eructation was never seen to occur. It was also frequently observed that all the steps in the contraction cycle took place except that there was no second contraction of the pole of the caudal ventral blind sac, this being replaced by a prolonged first contraction.

Contraction sequences in fasted sheep.

When observations were made on the fasted animals a number of changes in the form of contraction sequences were apparent. The time interval between the various events decreased so that they tended to become more concurrent than consecutive. The contractions appeared less forceful but tended to cause more displacement of the contents, which became more fluid after fasting. Lastly the sequence of events in a cycle was commonly abbreviated with many steps being left out. The shortest version of the cycle seen and the one most common in the fasted animal was as follows:

1. Biphasic contraction of the reticulum.
2. Contraction of the cranial sac and cranial pillar.
3. Contraction of the dorsal rumen.
4. Contraction of the dorsal blind sac.
5. Contraction of the cranial ventral rumen.

Should the cycle proceed to eructation, which was much less common than in the replete animal, the sequences of events most commonly observed was:

1. Biphasic contraction of the reticulum.
2. Contraction of the cranial sac and cranial pillar.
3. Contraction of the dorsal rumen.
4. Contraction of the dorsal blind sac.
5. Contraction of the cranial ventral rumen.
6. Wave of contraction migrating caudally across the caudal ventral rumen onto the caudal ventral blind sac.
7. Contraction of pole of caudal ventral blind sac.
8. Second contraction of dorsal blind sac.
9. Second contraction of dorsal rumen and cranial pillar.
10. Eructation.

Contraction sequences during rumination.

When rumination was taking place and the sheep was masticating in the typical rhythmical fashion, which was generally late in the radiographic screening sessions in the replete sheep, the following events were seen to take place before one of the previously described cycles of contractions started:

1. Mastication stopped.
2. Bolus swallowed.
3. Sharp contraction of the reticulum and contraction of abdominal muscles.
4. Bolus regurgitated.
5. Bolus swallowed.
6. Mastication started.
7. Biphasic contraction of reticulum leading into a

rumen contraction sequence.

There was frequently a long pause between the first bolus being swallowed (2) and the contraction of the reticulum (3). This contraction of the reticulum was very sharp and caused the pole to jump approximately quarter of the distance between its positions at relaxation and contraction. After this contraction and before the biphasic contraction, the reticulum almost returned to its normal position.

Destination of boluses swallowed during eating.

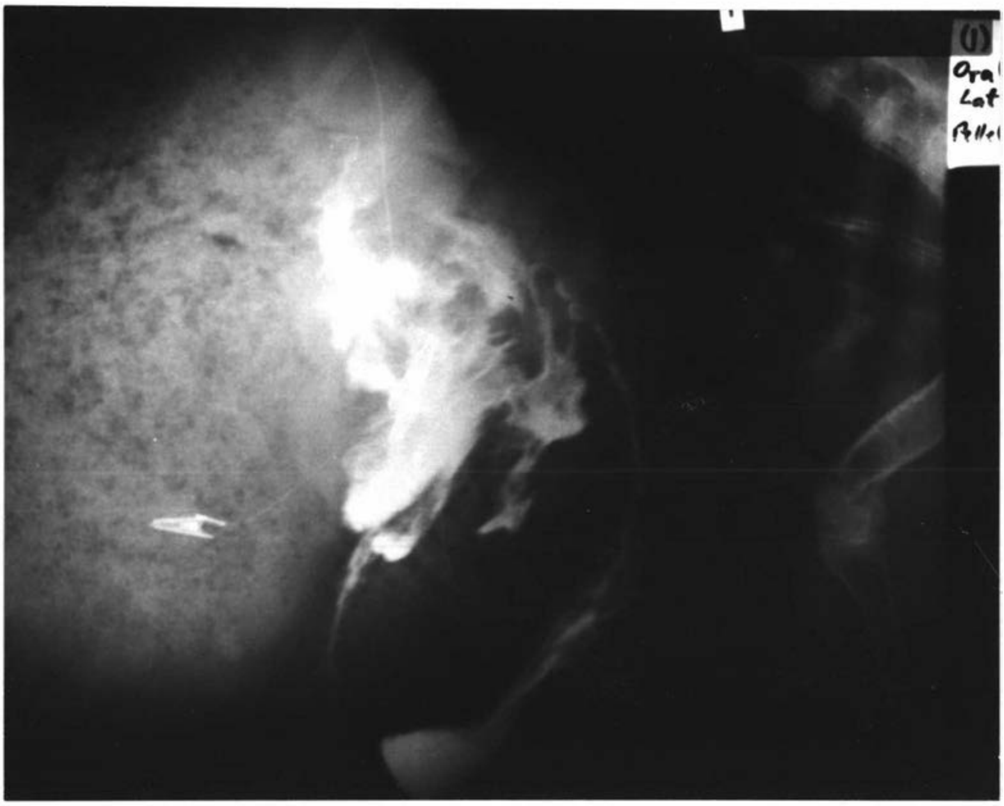
When the sheep in the replete state ate chaff mixed with barium sulphate suspension, the boluses generally gravitated into the reticulum but on some occasions they passed into the cranial sac; in both instances, however, they were rapidly mixed with contents of the reticulum and cranial sac as they were tipped back and forth at each contraction sequence. The contrast medium was commonly seen in the omasum after 3 or 4 contraction sequences. On the other hand, when these replete sheep were fed chaff mixed with barium sulphate powder, the boluses remained in the region of the cardia until the next reticular contraction which pushed them up into the cranial part of the raft in the dorsal rumen: here they amalgamated to the extent they were difficult to see radiographically.

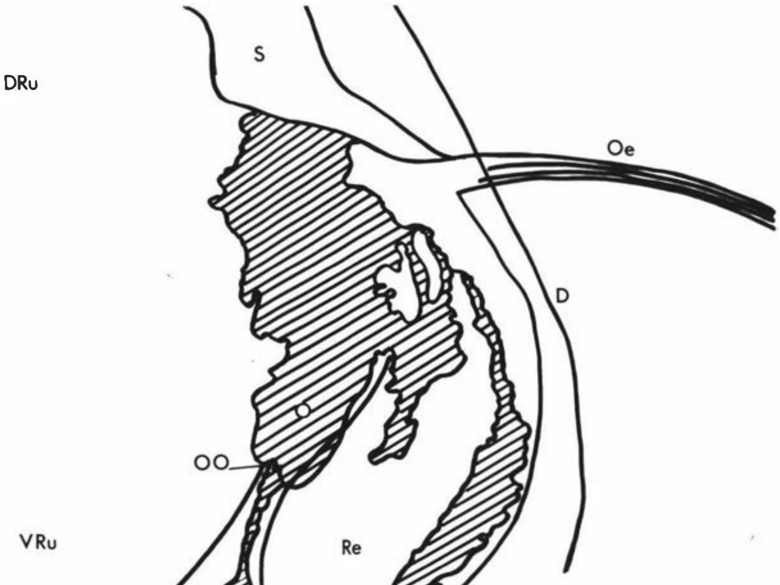
Barium sulphate suspension administered as a 50 ml dose with a drenching gun was deposited in the reticulum and cranial sac and was rapidly mixed with the contents of these two compartments by the following contraction sequences. Infrequently, the barium sulphate could be seen running through the omasum into the abomasum before any contractions had taken place (Plate 7). In sheep numbers 2 and 3, which were maintained bottle-trained, drenching resulted in most of the barium sulphate passing directly into the abomasum. On a very few occasions boluses of drench passed through the cardia as the reticulum or cranial sac of the rumen contracted in which case they were carried by the stream of digesta into which they had been injected. For example if a bolus was delivered through the cardia just as the reticulum was starting to contract it was carried into the dorsal rumen.

PLATE 7

A radiograph was taken immediately after dosing the sheep with 50 ml of barium sulphate. It illustrates the distribution of barium sulphate before any contraction cycles have taken place. Note how the barium is passing through the omasum into the abomasum. The shaded areas in the line drawing represents the barium sulphate. The bulldog clip is an electrode lead for recording reticular contractions.

Ab abomasum, D diaphragm, DRu dorsal rumen, O omasum,
OO omasal-abomasal orifice, Oe oesophagus, Re reticulum,
S spleen, VRu ventral rumen.


(I)
Ora
Lat
Pellet


S
DRu
Oe
D
OO
VRu
Re
Ab

When the sheep were fasted and then fed the chaff marked with either barium sulphate suspension or barium sulphate powder, the boluses landed in a greater variety of positions. As these animals started to eat, reticulo-ruminal contraction sequences followed rapidly one after the other. Inevitably many boluses passed through the cardia during contractions and were carried by the flow passing the cardia irrespective of their composition. However, some trends could be established. The boluses with barium sulphate suspension again generally gravitated into the reticulum or cranial sac although a number passed over the cranial pillar into the cranial ventral rumen. Where boluses were marked with barium sulphate powder, however, they tended to float up into the dorsal rumen if they were not caught in a moving tide of digesta as they emerged from the cardia.

Unlike the course of events in replete animals, in fasted animals no contrast media was seen in the omasum during the period of observation. Barium sulphate suspension administered by drenching gun was distributed in the same pattern as the replete animal but was dispersed rapidly and did not pass into the omasum except in the bottle-trained sheep where it passed directly through the omasum into the abomasum.

Following drenching with 50 ml of barium sulphate suspension the movement of digesta associated with each event in the contraction sequence was observed. The observations could only be made in the replete animals because in fasted animals the barium sulphate dispersed too rapidly to give the digesta adequate contrast.

In the early stage of the first phase of the reticular contraction a small amount of digesta in the dorsal reticulum and rumen adjacent to the dorsal part of the reticulo-ruminal fold was pushed caudally into the mid-rumen underneath the raft in the dorsal rumen. During the later stages of the first phase of the reticular contraction and throughout the second phase, the digesta in the reticulum was displaced over the reticulo-ruminal fold into the cranial sac. As the reticulum approached the height of its contraction some contrast was frequently seen to pass into the omasum. This observation could only be made at the first contraction sequence following the administration of barium sulphate suspension because the first pulse of marker to reach the omasum obscured any subsequent arrival.

As the cranial sac and cranial pillar contracted, the contents of the cranial sac were tipped back over the reticulo-ruminal fold into the relaxing reticulum. At the height of contraction of the cranial sac and cranial pillar, as the dorsal rumen started to contract, a small part of the cranial end of the raft in the dorsal rumen was moved cranio-ventrally into the reticulum and cranial sac. The raft in the dorsal rumen was moved cranially in association with the contraction of the dorsal rumen and dorsal blind sac with the greatest movement taking place as the dorsal blind sac contracted. With the contraction of the cranial part of the ventral rumen, digesta was displaced dorsally. The digesta closest to the ventral wall moved the furtherest, some being displaced over the relaxed cranial pillar into the cranial sac. The wave of contraction moving across the ventral rumen onto the caudal ventral blind sac pushed digesta into this sac, and particularly into the dorsal aspect, distending it. The contraction of the pole of the caudal ventral blind sac caused a marked movement of digesta out into the ventral rumen which was then continued by the cranially moving wave of contraction passing onto the ventral rumen. The second contraction of the cranial part of the ventral rumen resulted in more digesta being displaced over the cranial pillar into the cranial sac. The second and cranially moving contraction of the dorsal blind sac and dorsal rumen resulted in a further cranial movement of the raft in the dorsal rumen.

3:3:2 Details of the contractions of the reticulum, the reticulo-ruminal fold, the cranial sac of the rumen, and the cranial pillar.

Sheep number 9 was included to determine if the surgical interference on sheep 26 and 27 had any affect on the form of the movements seen. Because there were no radio-opaque markers in sheep 9, precise details of the paths taken by the reticulo-ruminal fold and the cranial pillar could not be obtained but the extent of their movement could be visualised due to contrast with the administered barium sulphate.

The form of the movements seen in the reticulum and cranial rumen of sheep 26 and 27 could not be distinguished from those seen in sheep 9 and were no different from those seen in the sheep used for the first series of observations (3:2:1). This indicated that the surgery carried out to place the radio-opaque markers had not altered the pattern of motility and that the movement of the markers could be taken as a true representation of the movements of the reticulo-ruminal fold and the cranial pillar.

The contractions of the reticulum and cranial sac are illustrated by a series of spot-films (Plate 6) and the movement of the markers on the reticulo-ruminal fold and cranial pillar by a further series (Plate 8). Figure 1 (1-12) is drawings derived by tracing outlines of a projected cine-film and illustrates the combined movements of the reticulum and cranial rumen. The paths taken by the markers on the ventral aspect of the reticulo-ruminal fold and cranial pillar, similarly derived, are illustrated by Figure 2 (a,b,c).

The most ventral radio-opaque marker on the reticulo-ruminal fold started to move dorsally simultaneously with straightening of the caudal wall and the caudal movement of the pole of the reticulum seen at the beginning of a contraction sequence. Of the 4 markers on the reticulo-ruminal fold, the marker at the cardia did not move at all while the most ventral marker moved the greatest distance. The intermediate 2 markers moved in paths generally similar to that of the ventral marker but covered a shorter distance with the more dorsal marker moving the lesser distance. Just before the end of the first phase of the reticular contraction the markers abruptly changed direction. They started to move ventrally in a path slightly cranial to the dorsal movement. During the first part of the second phase of the reticular contraction the ventral movement of the reticulo-ruminal fold markers continued until they reached a position slightly cranial and dorsal to their resting positions. Throughout the remainder of the second phase the movement of the ventral three markers was cranial until, at the height of the reticular contraction, they came to lie very close to, and approximately parallel to, the cranio-dorsal wall of the reticulum. As the reticulum relaxed, the markers travelled caudally passing through their resting positions and arriving at their most caudal position coincident with the height of the cranial pillar

PLATE 8

This is a series of spot-films taken 1 second apart. There are four wire loops on the reticulo-ruminal fold, the most dorsal one is close to the cardia. The ventral one is on the mid-point of the free ventral border and the remaining two are equally spaced on the left border. A fifth wire loop is on the mid-point of the free border of the cranial pillar. The sheep's head is to the right. The top group is of a reticular contraction followed by a cranial sac contraction.

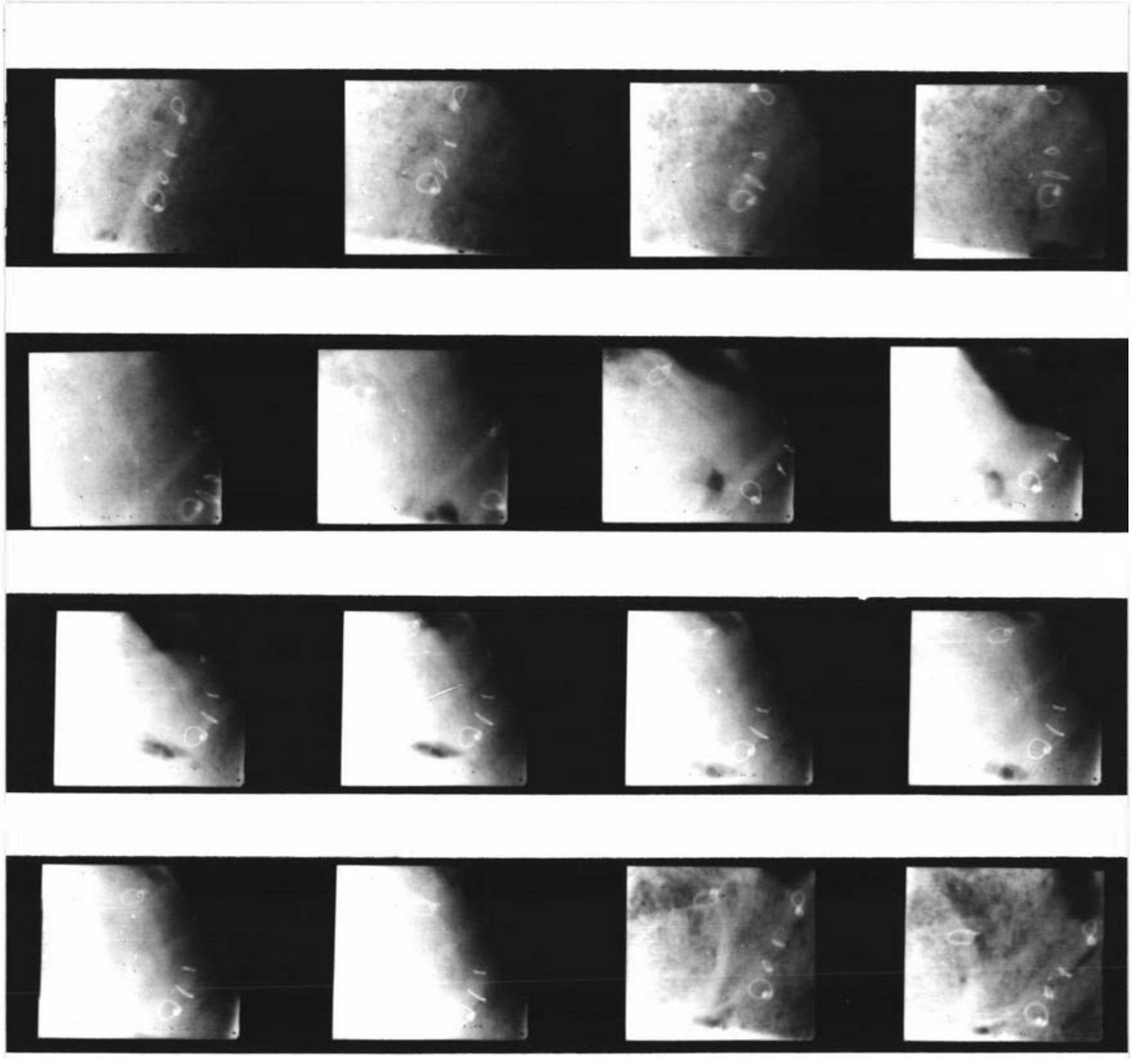
The first row. The marker on the cranial pillar is not visible because the framing was concentrated on the reticulo-ruminal fold. By the second frame, the dorsal displacement of the ventral wire loop can be detected and by the last frame it has started to move cranially.

The second row. The framing has been moved caudally to encompass the movement of the cranial pillar, the marker on which can be seen in the first frame as it commences its dorsal movement. By the last frame, it has reached the height of its contraction and the gas cap has been pushed cranially. The reticulo-ruminal fold has returned almost to its resting position.

The third row. The cranial pillar remains almost stationary at the height of its contraction until the third frame where it starts to return towards its resting position along a route somewhat more cranial than that taken during its dorsal excursion. The gas cap returns to the dorsal rumen. On this occasion, none was displaced under the cranial pillar.

The fourth row. The cranial pillar returns to its resting position.

The bottom group shows the second movement of the cranial pillar associated with eructation. The four loops are on the reticulo-ruminal fold and the single loop is on the cranial pillar.



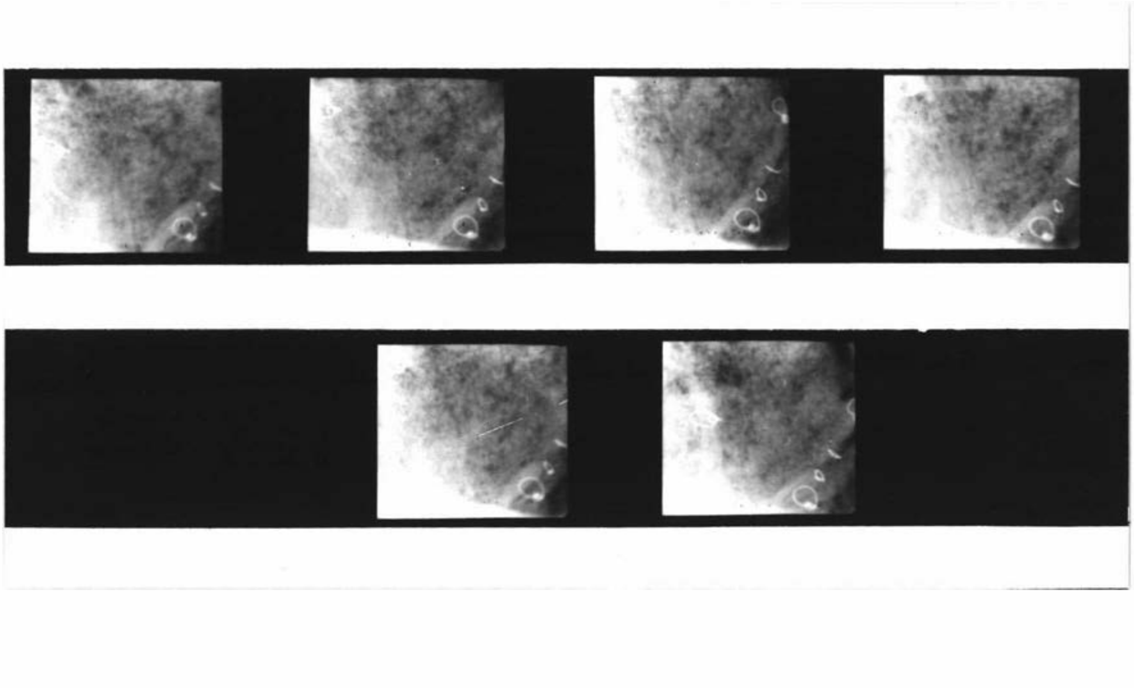


FIGURE I

This series of drawings was derived by taking tracings from projected radiographic cine-films. It gives, in detail, the movements and changes in shape of the reticulum and cranial rumen.

CP cranial pillar, CS cranial sac of rumen, DRu dorsal rumen,
Re reticulum, RRF reticulo-ruminal fold, VRu ventral rumen.

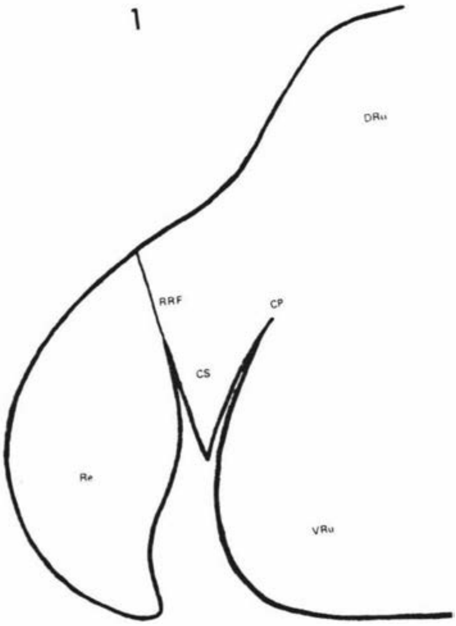
1. The resting position. The space between the reticulum and ventral rumen is occupied by the abomasum and to a much lesser extent by the omasum. In a sheep that has been fasted and then allowed to feed, the shape of the reticulum may be more rounded due to a degree of distension.

2. As a contraction sequence commences, the first detectable movement is an upward movement of the ventral border of the reticulo-ruminal fold. The other parts of the fold do not move at this time.

3. The ventral border of the reticulo-ruminal fold continues to move dorsally. All parts of the fold except that close to the cardia also start to move dorsally. The caudal border of the reticulum straightens out and the pole of the reticulum is pulled slightly caudally.

4. The reticulum starts to contract with its pole moving dorsally and slightly cranially. The ventral border of the reticulo-ruminal fold starts to return ventrally and the cranial sac starts to dilate.

1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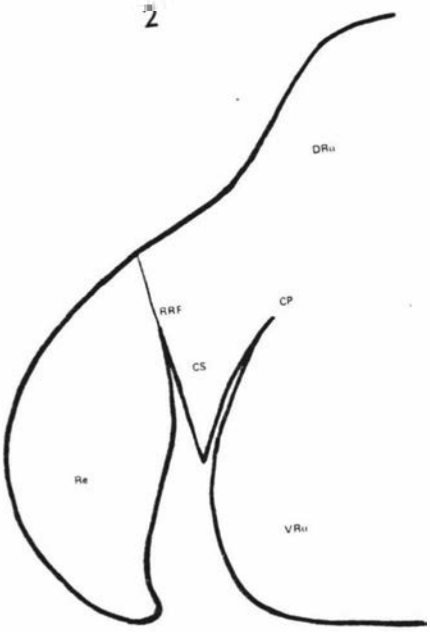
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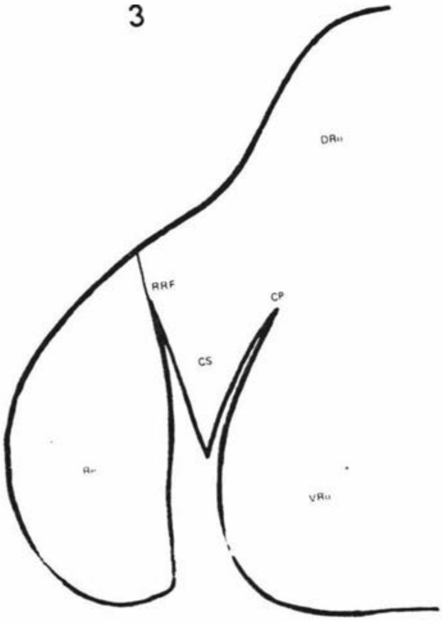
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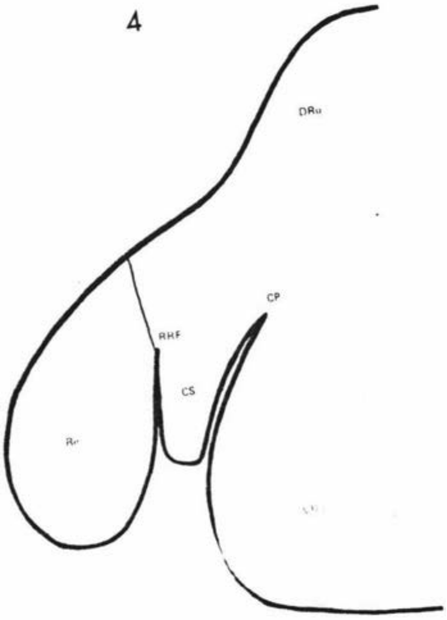
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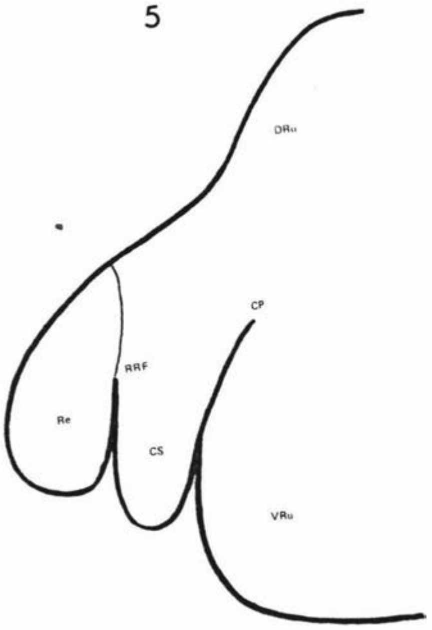
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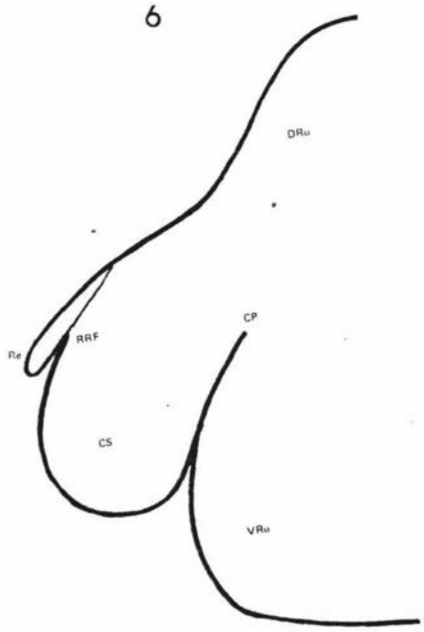
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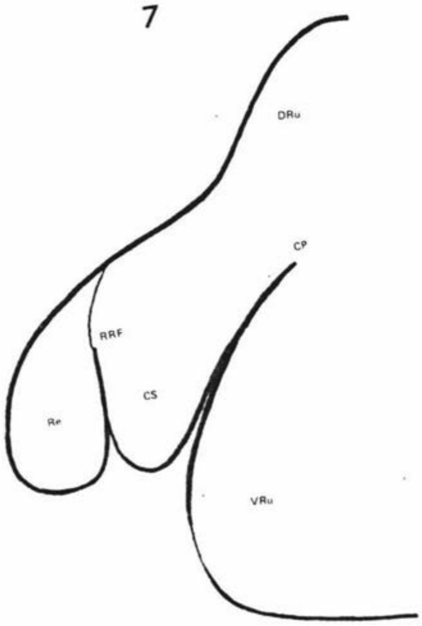
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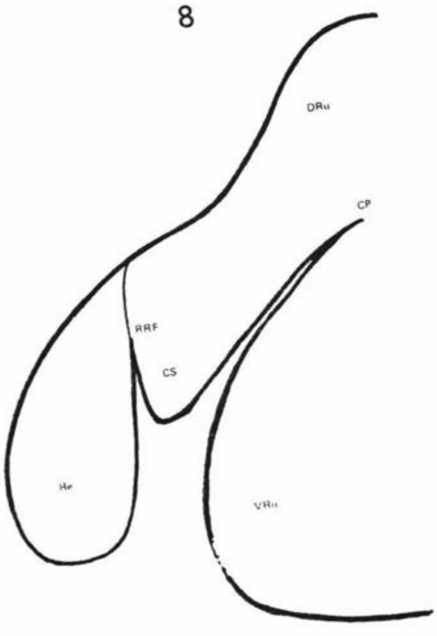
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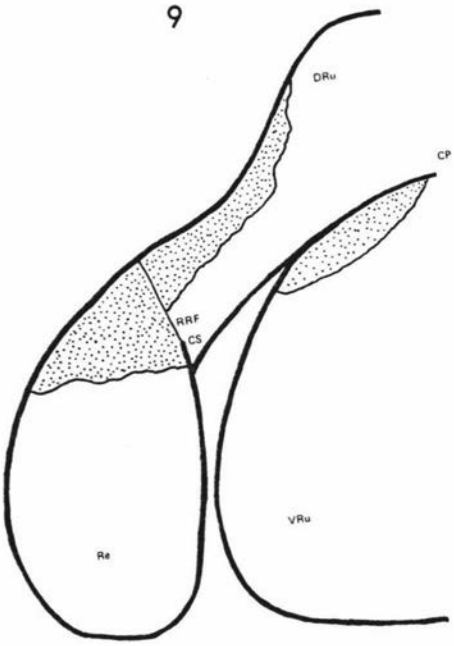
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CS
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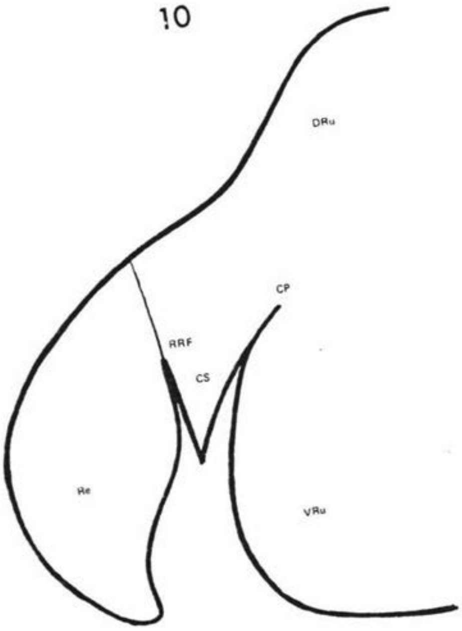
10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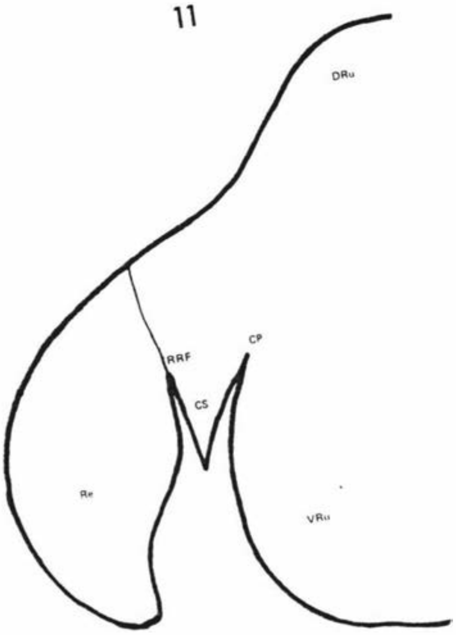
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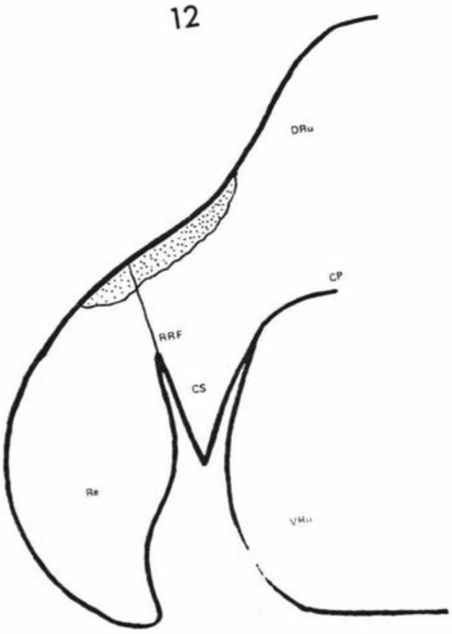
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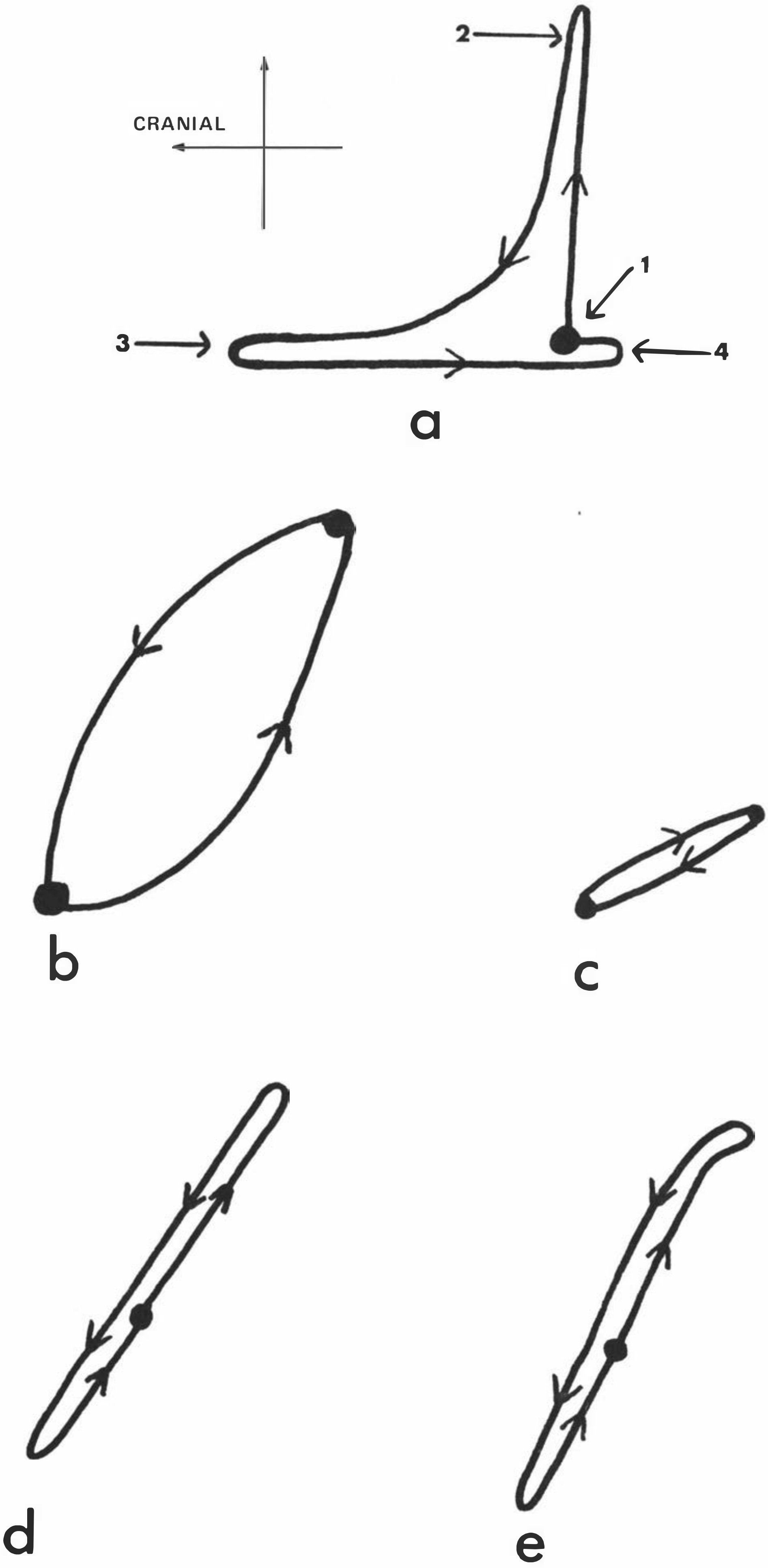

2
CRANIAL
1
3
4
a
b
c
d
e

contraction. As the cranial pillar started to relax the markers on the reticulo-ruminal fold returned to their resting positions, where they remained throughout the rest of the contraction sequence.

As the reticulum was approaching half way to relaxation the marker on the mid point of the free border of the cranial pillar started to move dorsally and caudally (Figure 2b). It reached the maximum of its excursion coincident with the peak of the cranial sac contraction and the reticulum returning to its resting position. Immediately following this the major part of the gas cap in the dorsal rumen was displaced cranially. In the replete sheep part of this gas cap was commonly displaced under the cranial pillar lifting and bulging it dorsally but this was much less common in the fasted sheep. After being held at this point of maximum excursion for a brief period, the cranial pillar returned to its resting position along a more cranial arc. It arrived at its resting position as the cranial sac also returned to its resting position. During this time the gas returned to the dorsal rumen. Should the cycle continue on to the stage where eructation could occur, the marker on the cranial pillar started to move a second time, simultaneously with the second contraction of the dorsal sac of the rumen. On this occasion the movement was more caudally directed and was less than half the magnitude of the first excursion (Figure 2c). Only on very rare occasions was a small volume of the gas from the dorsal rumen displaced under the cranial pillar at this second movement. If eructation occurred, it did so as the cranial pillar reached the furthest extent of its second excursion. The pillar returned to its resting position along a slightly more dorsal route. A contraction of the cranial ventral rumen followed and the pillar moved a short distance ventrally and remained in this position until the next cycle. This last event was never observed in the fasted sheep.

The times of and between various events in the reticulum and cranial rumen in the replete and fasted sheep, expressed as means and ranges, are given in Table II.

Taking the mean from all three sheep, the time taken for the first

TABLE II

TIMING OF EVENTS IN THE RETICULUM AND CRANIAL RUMEN.

	Duration Re 1		Duration Re 2	
	Replete	Fasted	Replete	Fasted
Sheep 9:				
Session 1	1.56(1.3-1.8)*	1.84(1.6-2.0)	2.60(1.9- 3.2)	1.92(1.7-2.1)
Session 2	1.50(1.3-1.8)	1.83(1.6-2.0)	2.52(2.2- 2.9)	1.92(1.5-2.6)
Sheep 26:				
Session 1	1.74(1.4-2.0)	2.04(1.7-2.3)	2.48(1.9- 2.8)	1.96(1.8-2.3)
Session 2	1.72(1.4-2.1)	2.16(1.9-2.3)	2.68(2.5- 3.0)	2.28(2.1-2.5)
Sheep 27:				
Session 1	1.62(1.4-1.8)	2.06(1.7-2.3)	2.04(1.4- 2.4)	1.50(1.3-1.7)
Session 2	1.75(1.4-1.9)	2.00(1.5-2.3)	2.56(2.2- 2.7)	2.02(1.5-2.1)

	Peak Re 2 - Peak CP		Start Re 1 - Peak CP	
	Replete	Fasted	Replete	Fasted
Sheep 9:				
Session 1	5.88(5.6-6.7)	4.31(3.3-4.8)	10.08(9.8-10.3)	7.92(7.6-8.3)
Session 2	5.74(5.3-6.1)	4.12(3.5-5.3)	9.78(9.4-10.1)	8.42(7.1-8.4)
Sheep 26:				
Session 1	6.44(5.8-6.8)	6.06(5.3-7.3)	10.66(10.2-11.2)	7.94(6.4-9.0)
Session 2	5.40(4.9-5.8)	5.36(5.0-6.3)	11.80(11.0-12.4)	9.88(9.6-10)
Sheep 27:				
Session 1	3.50(3.2-4.3)	3.10(2.7-3.5)	7.64(7.3- 8.0)	6.22(5.8-2.8)
Session 2	5.49(4.9-5.7)	4.85(4.4-5.2)	10.19(9.6-10.3)	8.18(7.8-8.4)

* The mean time and range in seconds over 5 readings.

Re 1 - Duration of 1st phase of reticular contraction.

Re 2 - Duration of 2nd phase of reticular contraction.

Re 2 - CP - Peak of second phase of reticular contraction to peak of cranial pillar contraction.

Re 1 - CP - Start of 1st phase of reticular contraction to peak of cranial pillar contraction.

phase of the reticular contraction in the replete state was 1.65 seconds and for the second phase was 2.48 seconds. The first phase was therefore shorter by 0.83 seconds (33.5%). In the fasted state the first phase lengthened to 1.99 seconds, an increase of 0.34 seconds (20.6%) while the second phase shortened to 1.93 seconds, a decrease of 0.55 seconds (22.2%). Therefore the first phase became longer than the second phase by 0.06 seconds (3.1%). The time interval between the peak of the reticular contraction and the peak of the cranial pillar contraction in the replete sheep had a mean of 5.41 seconds and in the fasted state shortened to 4.73 seconds, a reduction of 0.68 seconds (12.6%). The total mean time from the start of the reticular contraction to the peak of the cranial pillar contraction in the replete sheep was 10.03 seconds while in the fasted sheep this shortened to a mean of 8.09 seconds, a reduction of 1.94 seconds (19.3%).

The major differences between the replete and fasted state were that in the fasted state the first phase of the reticular contraction occurred over a longer time and all the other time intervals shortened.

Observations of the movements of the reticulum and cranial rumen during rumination were obtained from sheep 27 only. The movement of the reticulum during rumination was the same for this sheep as described in the first series of observations. There was no movement of the reticulo-ruminal fold or the cranial pillar associated with the initial sharp contraction of the reticulum which coincided with regurgitation. The sequence of events that followed on from this were the same as those seen in contraction cycles not associated with rumination. The timing of the reticular contractions during rumination is given in Table III.

3:3:3 Details of the contractions of the cranial and caudal pillars and the dorsal rumen sac.

As the cranial pillar approached the peak of its first excursion the raft of digesta in the dorsal rumen moved dorsally and the gas cap was displaced caudally. Immediately after the cranial pillar reached its furthest extent of movement, the dorsal blind sac contracted,

TABLE III

TIMING OF RETICULAR CONTRACTIONS DURING RUMINATION.

	Rx	Re 1	Re 2
Sheep 27	7.7 (7.4-7.9)*	2.2 (1.8-2.9)	2.1 (1.8-2.4)

* The mean time and range in seconds taken over 10 readings.

Rx	-	Start of reticular contraction of rumination to 1st phase of biphasic reticular contraction.
Re 1	-	1st phase of reticular contraction.
Re 2	-	2nd phase of reticular contraction.

displacing the gas cap cranially as previously described (3:3:1). Simultaneously with this, the marker on the caudal pillar started to move dorsally and slightly caudally. The path followed by this marker is shown in Figure 2(d), derived by tracing the projected image of an x-ray cine-film as described above (3:3:2). The cranial pillar remained stationary at the height of its contraction as the dorsal movement of the caudal pillar continued. When the caudal pillar reached the peak of its dorsal excursion, it did not pause but immediately started to travel back towards its resting position along a slightly more cranial path. The cranial pillar started to return towards its resting position at the same time as the caudal pillar, which also coincided with the relaxation of the dorsal sac and dorsal blind sac of the rumen. The cranial and caudal pillars returned to their resting positions simultaneously. The cranial pillar remained in this position until its second movement, associated with eructation, but the caudal pillar continued to move ventrally and slightly cranially. There was no pause at the peak of this ventral excursion before the pillar started to return to its resting position along a path slightly caudal to that taken in its ventral movement. There was a slight pause in this return movement at a point just ventral to the resting position at which time the caudal ventral blind sac contracted. Following this the caudal pillar returned to its resting position. The movement of the caudal pillar is illustrated by a series of spot-films (Plates 9 and 10). The contractions of the caudal rumen derived by tracing from a projected cine-film are illustrated in Figure 3 (1-16).

Immediately after a second contraction, or prolonged first contraction, of the caudal ventral blind sac, the caudal pillar started to move dorsally a second time. The path taken by the marker on the midpoint of the free edge of the caudal pillar on this occasion is illustrated in Figure 2(e). The route taken during the second movement was slightly more caudal than that for the first movement, and there was a sharp caudal change in direction just before the height of the excursion. During this time a cranially moving contraction passed over the dorsal blind sac and dorsal sac, and the cranial pillar started on its second movement. The two pillars reached the peak of their second movement together, at which point eructation occurred if

PLATE 9

This is a series of spot-films of the caudal pillar of the rumen taken at 1 second intervals. Barium sulphate suspension was placed on top of the caudal pillar using a catheter passed in through a rumen fistula. The sheep's head is to the right.

The first row. The first frame is taken just as the gas cap starts to move caudally. The next frame shows the caudal pillar start to curl dorsally as the dorsal rumen contracts. By the last frame in this first row, the caudal pillar has reached the height of its excursion and the dorsal blind sac has contracted, lifting the caudal part of the rumen dorsally.

The second row. The caudal pillar and dorsal rumen are relaxing.

The third row. The completion of the relaxation of the caudal pillar and dorsal rumen with return of the gas cap.

The fourth row. The caudal pillar is displaced ventrally then returned to its resting position similar to that seen in the first frame of the first row.

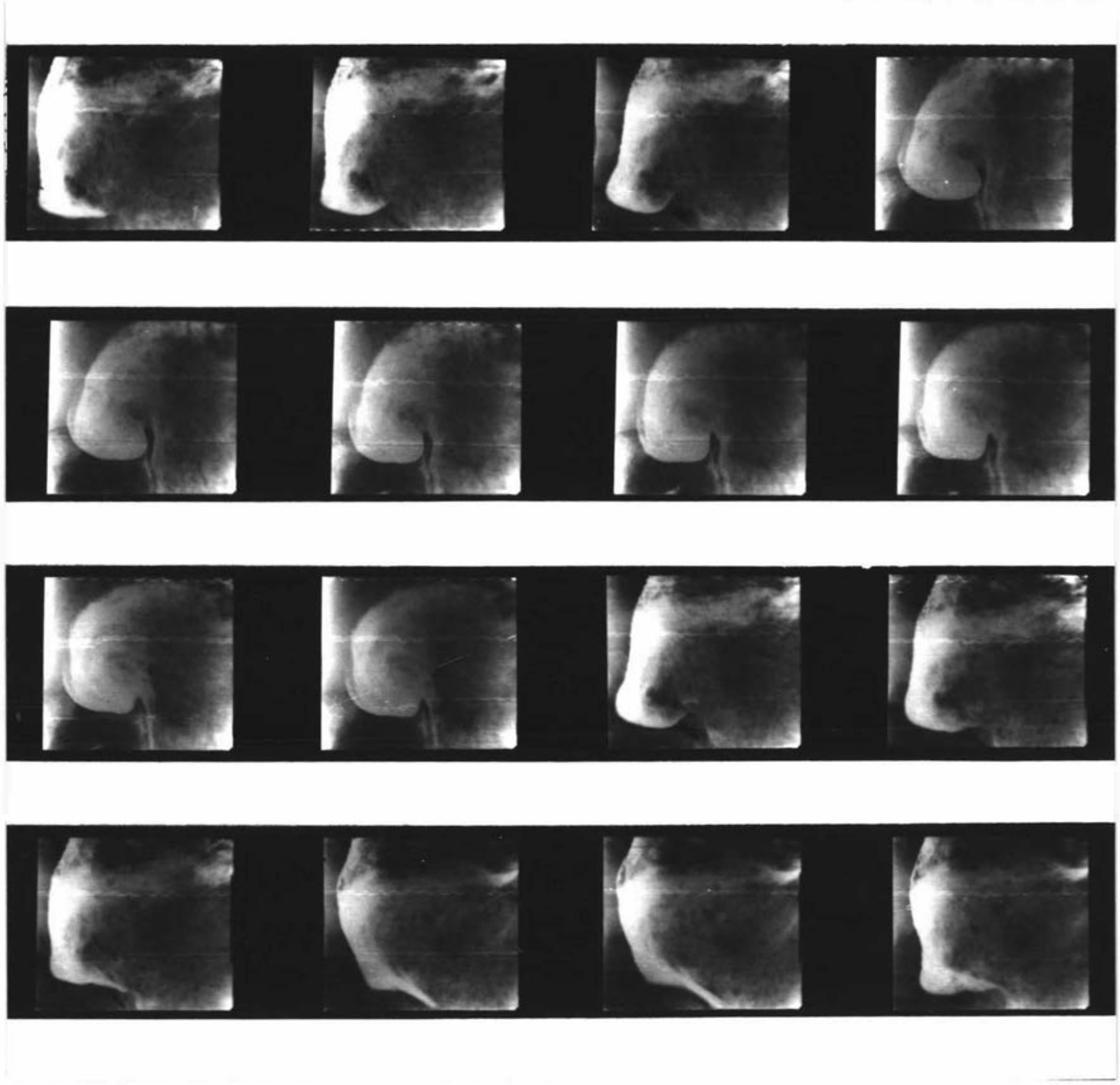


PLATE 10

This is a series of spot-films of the caudal pillar of the rumen taken at 1 second intervals. This series follows on from the first series, should eructation be going to take place.

The first row. The caudal pillar starts to curl dorsally for a second time then the dorsal blind sac contracts.

The second row. The dorsal rumen contracts lifting the dorsal blind sac then the pillar starts to relax followed by the dorsal blind sac and the dorsal rumen.

The third row. The caudal pillar is displaced ventrally then returns to a position slightly ventral to its previous resting position.

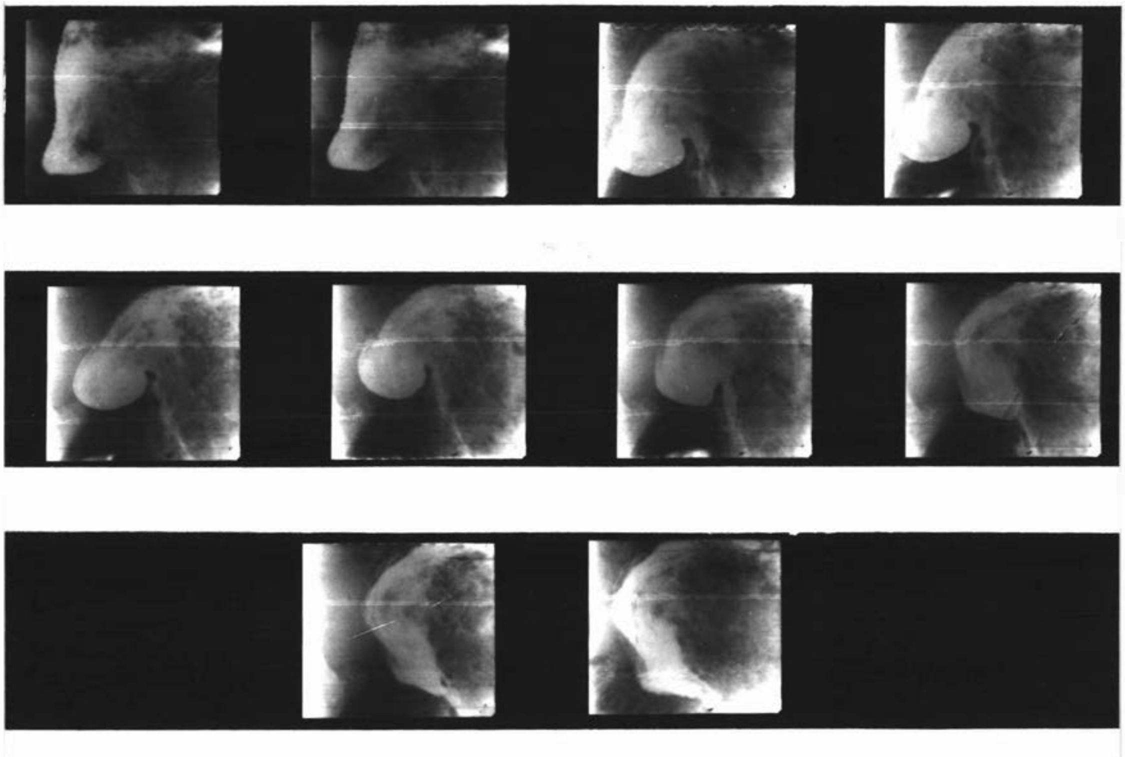


FIGURE 3

This series of drawings was derived by taking tracings from radiographs and spot-films. It gives in detail the movements and changes in shape of the caudal rumen. The dotted regions represents gas.

CdP caudal pillar, CdVBS caudal ventral blind sac, DBS dorsal blind sac.

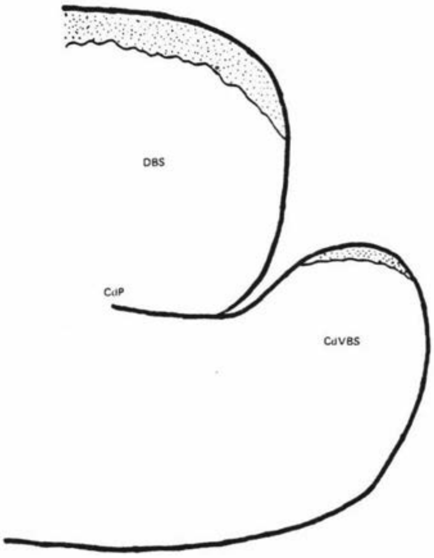
1. The resting stage. The resting position of the caudal pillar depends on whether the preceeding cycle included a second ventral displacement of this pillar. If it did, the resting position would be slightly more ventral than that depicted.

2. The gas cap in the dorsal rumen pushed into the dorsal blind sac. This stage coincides with drawing (8) of the reticulum and cranial rumen series as the cranial pillar starts to contract.

3. Contraction of the dorsal rumen. As the dorsal rumen contracts, the caudal pillar starts to curl dorsally and the gas cap gets pushed further round the dorsal blind sac.

4. Contraction of the dorsal blind sac. The caudal pillar curls dorsally and the dorsal blind sac contracts, pushing the gas cap round cranially as shown in drawing (9) in the series on reticulum and cranial rumen. Some of the gas cap is also displaced under the caudal pillar into the caudal ventral blind sac. The combined contraction of the dorsal blind sac and caudal pillar lifts the whole dorsal blind sac.

1



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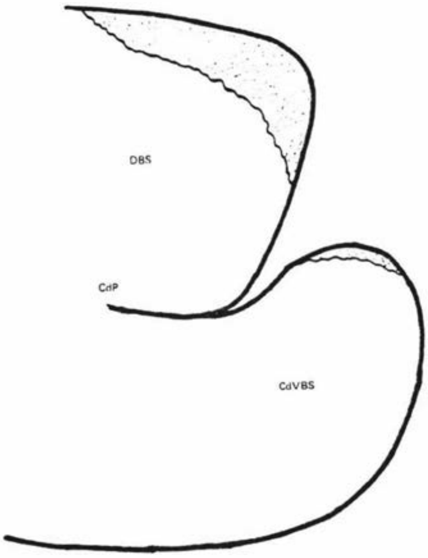

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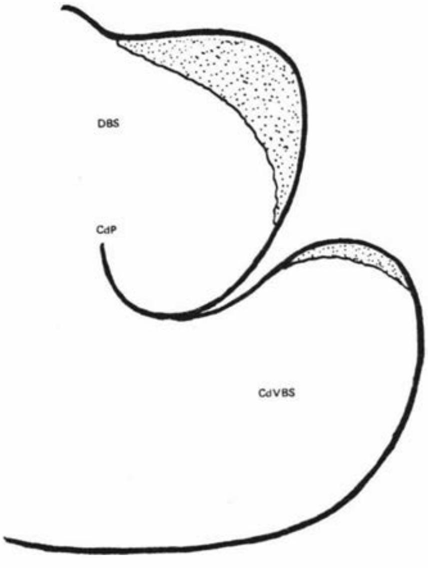

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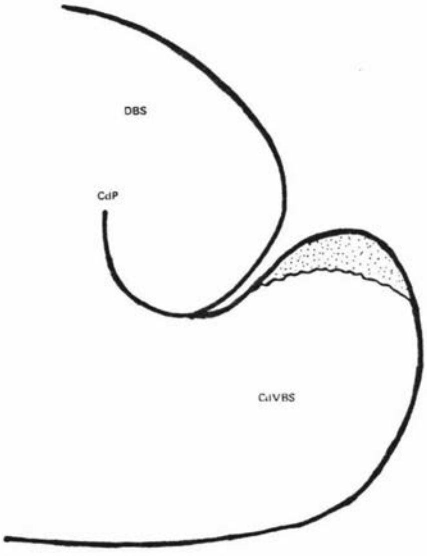

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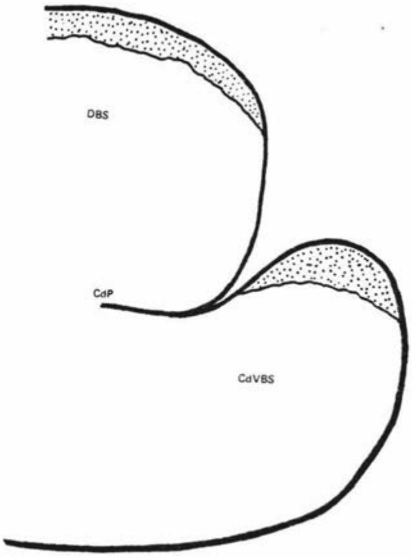

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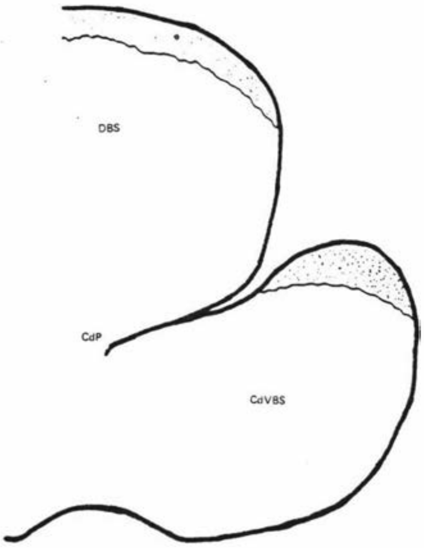

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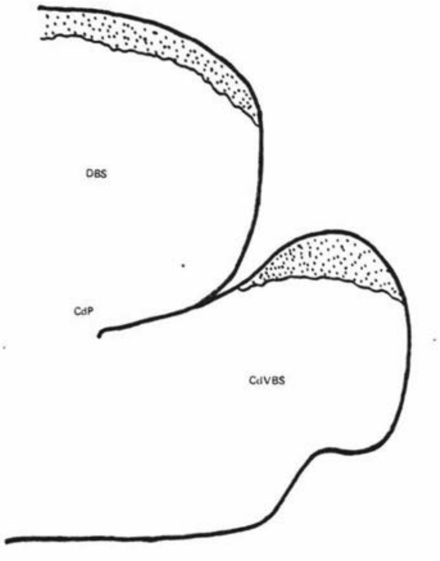

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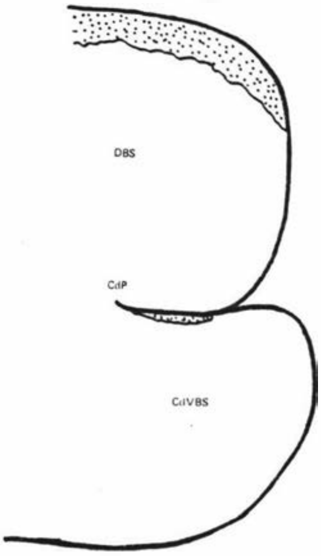


FIGURE 3

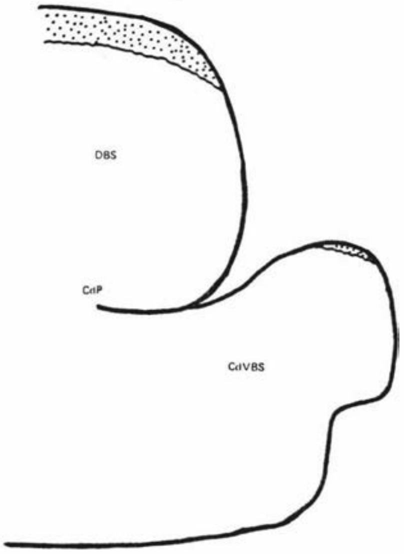
9. The pole of the caudal ventral blind sac relaxes and the gas that was trapped under the caudal pillar returns to form a much reduced gas cap. A wave of contraction now starts to migrate cranially across the caudal ventral blind sac.

10. When this cranially moving wave of contraction reaches the level of the ventral coronary pillars, there is a second ventral displacement of the caudal pillar.

11. The cranially moving wave of contraction moves onto the ventral rumen then the cranial wall of the ventral rumen contracts, as is shown in drawing (11) of the series on the reticulum and cranial rumen. The caudal pillar returns to a position somewhat ventral to that depicted in the first drawing of this series.

12. Should the contraction series be extended into one allowing eructation, the following series of events supercedes from drawing (9). Either the pole of the caudal ventral blind sac relaxes and contracts a second time or the initial contraction is protracted. The caudal pillar then starts to curl dorsally and as the pole of caudal ventral blind sac relaxes, the dorsal blind sac contracts pushing the gas cap cranially. At the same time, a cranially-moving wave of contraction is passing across the caudal ventral blind sac.

9



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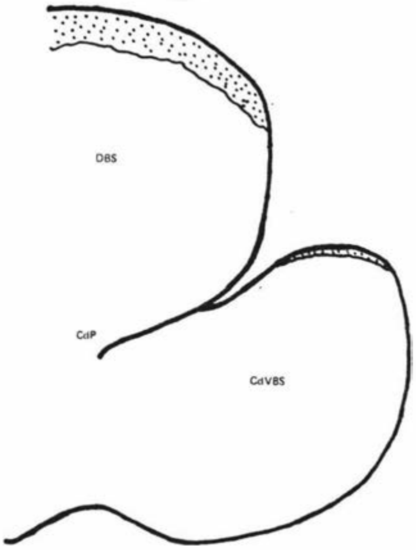

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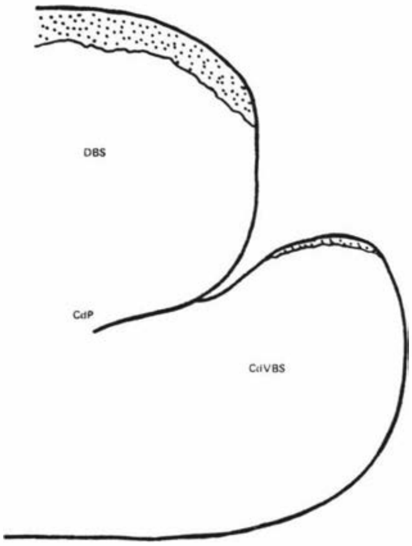

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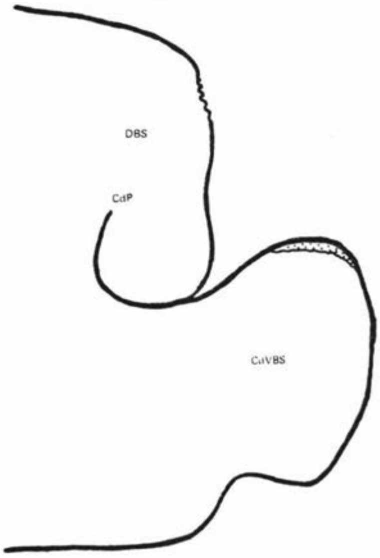


FIGURE 3

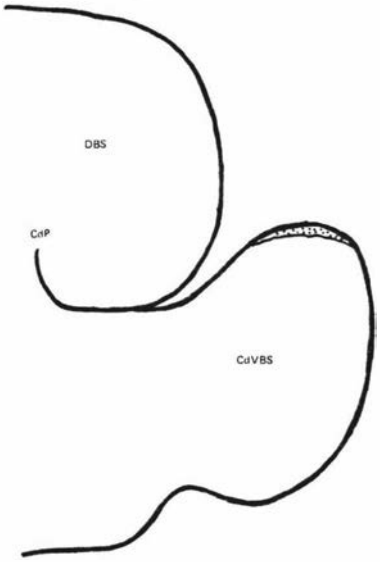
13. The caudal pillar starts to return towards its resting position and the dorsal blind sac starts to relax. The wave of contraction continues to move cranially across the caudal ventral blind sac. This drawing coincides with drawing (12) of the series on reticulum and cranial rumen and it is at this point that eructation occurs.

14. The wave of contraction travelling across the caudal ventral blind sac reaches the level of the coronary pillars and there is a second ventral displacement of the caudal pillar. The gas cap returns to the dorsal rumen.

15. As the wave of contraction passes onto the ventral rumen, the caudal pillar starts to move back towards its resting position.

16. The caudal pillar has returned to its resting position which is somewhat ventral to the position shown in drawing (1) in this series and it will stay in this position until the next contraction begins.

13



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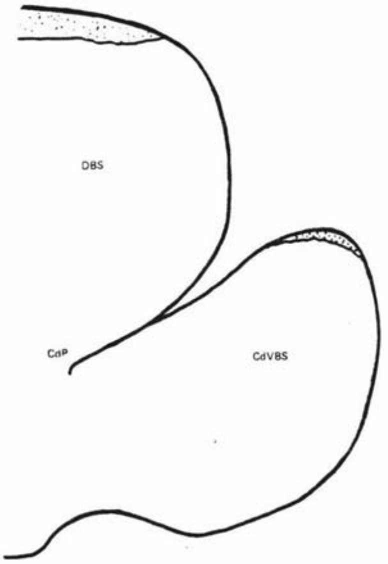

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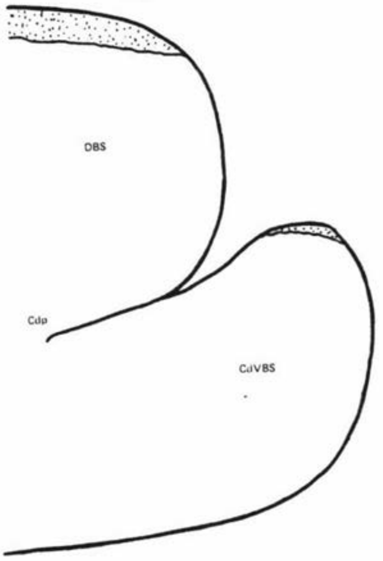

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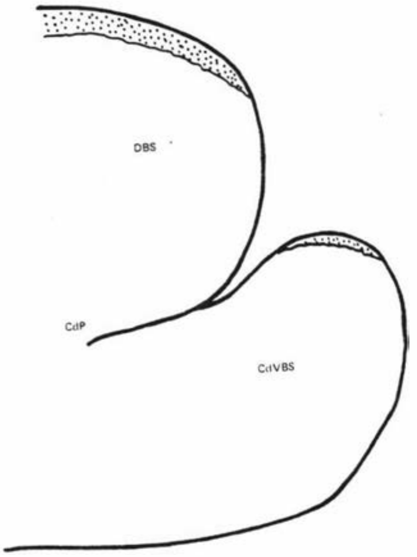


it was going to. Both pillars then returned to their resting positions but the caudal pillar continued on through into a second ventral movement following the same path as its first ventral movement. This time and without pause, it returned dorsally to its resting position where it remained until the next series of contractions.

In the replete sheep, in those contraction sequences which terminated without a second cranially moving contraction of the dorsal sac, the first movements of the cranial and caudal pillars occurred, but there was no second movement of the cranial pillar. The second movement of the caudal pillar was modified in that the dorsal range of movement did not occur. It started from its resting position and moved ventrally, then returned to its resting position.

The first movements of the cranial and caudal pillars were not modified in form in the fasted sheep, except that on some occasions the caudal pillar did not move ventrally from its resting position. The large majority of cycles in these sheep did not proceed on to a second, cranially moving contraction of the dorsal rumen, and in this type of cycle, the caudal pillar would only move dorsally and return to its resting position.

The time intervals between these various events in the replete state in sheep 6 and 25, and in the replete and fasted-state in sheep 26 and 27, are given in Tables IV and V.

A comparison of the mean times between the various movements of the two pillars in the replete and fasted state in sheep 26 and 27 is given in table VI.

3:3:4 Details of the contractions of the ventral rumen.

In the replete state the first movement of the ventral sac of the rumen was observed to take place immediately the cranial pillar returned to its resting position after its first contraction. This contraction of the ventral sac involved the cranial ventral aspect which

TABLE IV

THE RELATIONSHIPS BETWEEN CRANIAL PILLAR CONTRACTIONS.

	CP1 - CP2		CP1 - CdP1	
	Replete	Fasted	Replete	Fasted
Sheep 27:				
Session 1	31.3(27.1-35.7)*	20.7(18.8-23.6)	4.0(3.4-4.4)	2.7(2.3-3.5)
Session 2	31.0(26.7-34.1)	22.3(18.7-25.6)	4.1(2.9-4.8)	3.2(2.3-2.6)
Sheep 26:				
Session 1	32.7(28.8-35.4)	22.6(19.8-25.3)	5.2(4.3-6.0)	3.9(3.2-4.1)
Session 2	37.2(33.7-39.7)	27.4(27.8-30.0)	5.8(5.2-6.3)	4.6(4.3-4.8)
Sheep 25:				
Session 1	33.2(29.7-36.7)		5.3(4.8-6)	
Session 2	32.9(29.3-37.1)		5.3(5.1-5.8)	
Sheep 6:				
Session 1	34.1(29.6-36.8)		5.2(4.7-5.4)	
Session 2	33.2(28.9-37.2)		5.0(4.8-5.3)	

* Mean time and range in seconds over 5 readings.

CP1 - CP2	-	The peak of the first contraction to the peak of the second contraction of the cranial pillar.
CP1 - CdP1	-	The peak of the first cranial pillar contraction to the peak of the first dorsal movement of the caudal pillar

TABLE V

THE TIMING OF CAUDAL PILLAR CONTRACTIONS.

	CdP1 - CdP		CdP - CdPv1		CdPv1 - CdPv2	
	Replete	Fasted	Replete	Fasted	Replete	Fasted
Sheep 27						
Session 1	10.2(9.7-10.5)*	8.0(7.3- 8.3)	4.8(3.8-5.8)*	3.1(2.5-3.5)	11.6(8.3-14.1)	7.0(6.3-10.2)
Session 2	10.1(9.7-10.8)	8.1(7.6- 8.4)	4.8(4.1-5.6)	3.2(2.3-3.7)	11.9(8.4-14.2)	7.7(6.1-10.8)
Sheep 27						
Session 1	10.4(9.6-11.6)	7.9(6.4-9)	5.2(4.5-6.4)	4.0(3.2-4.7)	12.0(10.6-14.8)	7.0(5.6-9)
Session 2	11.8(11-12.3)	9.2(8.4-10.3)	6.0(5.8-6.4)	4.6(4.1-5.6)	14.5(11.6-17.1)	9.5(7.1-11.3)
Sheep 25						
Session 1	7.8(7.5-8)		4.7(4.5-4.8)		15.1(14.9-15.3)	
Session 2	7.9(7.4-8.3)		4.5(4.1-4.9)		15.2(14.8-15.4)	
Sheep 6						
Session 1	7.6(7.4- 7.8)		5.1(5-5.4)		15.6(15.4-15.8)	
Session 2	7.6(7.4- 7.8)		5.2(4.9-5.4)		15.6(15.1-15.9)	

* Mean time and range in seconds over 5 readings.

CdP1 - CdP - The peak of the first dorsal movement of the caudal pillar to the return of the cranial and caudal pillars to their resting positions.

CdP - CdPv1 - The resting position of the caudal pillar to the peak of its first ventral displacement.

CdPv1 - CdPv2 - The peak of the first ventral displacement to the peak of the second ventral displacement of the caudal pillar.

TABLE VI

A COMPARISON OF THE MEAN TIMES IN SECONDS BETWEEN THE EVENTS IN TABLES IV, V IN THE REPLETE AND FASTED SHEEP 26 AND 27.

Events	Mean time replete	Mean time fasted	Decrease in fasted	Percentage decrease in fasted
CP1 - CdP1	4.80	3.60	1.20	25%
CdP1 - CdP	10.64	8.30	2.34	22%
CdP - CdPv1	5.19	3.74	1.45	27.93%
CdPv1 - CdPv2	12.51	7.80	4.71	37.64%
CP1 - CP2	33.05	23.26	9.79	29.62%

appeared to contract as a unit (Plate 28). The effect of this was to straighten out the well-rounded outline of this part of the rumen. As it relaxed a marked indentation of the ventral wall of the ventral sac developed at a site approximately 5 cm cranial to the ventral coronary pillars (Plate 29). This indentation, or wave of contraction, migrated caudally and its arrival at the ventral coronary pillars coincided with the peak of the first ventral displacement of the caudal pillar. It continued caudally across the caudal ventral blind sac to involve the pole which underwent marked ventral and cranial contraction, relaxed and then contracted a second time. Sometimes this double contraction was replaced by a single prolonged contraction. In either case as soon as it had relaxed, a wave of contraction started to move cranially across the caudal ventral blind sac. The arrival of this cranially moving contraction at the ventral coronary pillars coincided with the peak of the second ventral displacement of the caudal pillar.

The wave of contraction continued cranially to the same point from which the caudally moving contraction had originated. It then disappeared and was immediately followed by a second contraction of the cranio-ventral part of the ventral sac, which completed the contraction sequence.

In the replete sheep there was no detectable difference in the cycle of movements of the ventral part of the rumen between those cycles which had a cranially moving contraction of the dorsal rumen and those that did not. However, in some cycles the second contraction of the cranial ventral part of the ventral rumen did not occur.

The contractions of the caudal rumen derived by tracing the outline from projected cine-film is illustrated in Figure 3 (1-16).

In the fasted state there was considerable modification of the sequence of events. In its simplest form there was only one contraction of the cranial ventral part of the ventral rumen. This could on occasions be extended to the formation of a wave of contraction which would only move a short distance caudally before disappearing. In those few sequences where there was a cranially-moving contraction of the dorsal rumen the first contraction of the cranio-ventral rumen would occur and the wave of contraction would develop and migrate caudally to the pole of the caudal ventral blind sac, but, following the contraction of the pole, the cranially moving wave of contraction would only move a short distance before disappearing.

In the fasted state, between the periods of regular cyclical activity, waves of contraction could frequently be seen to form apparently at random positions on the wall of the ventral rumen and to migrate short distances either caudally or cranially before disappearing.

3:3:5 Illustration of the contraction sequence in the replete sheep.

The results of this series of observations are illustrated in Plates 11 - 39. Accompanying each photograph of a radiograph there is a labelled line drawing to aid with interpretation because the process of photographing and reducing the size of the original radiograph results in considerable loss in visible detail.

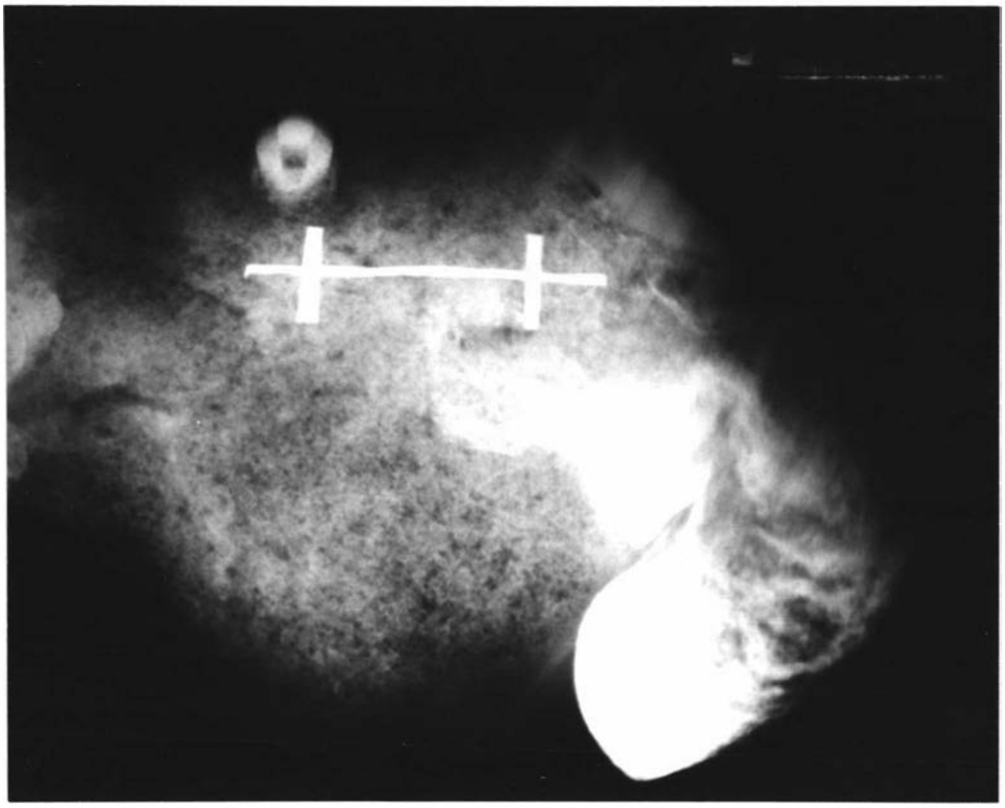
Some additional observations on the movement of the caudal pillar and dorsal caudal blind sac were obtained while screening these two animals after barium sulphate had been deposited on top of the caudal pillar. The dorsal movement of the free border of the caudal pillar really represented a dorsal curl of the pillar rather than a linear dorsal movement (See Plates 9 and 10). As the contraction passed onto the dorsal sac of the rumen the caudal pillar started to curl dorsally and was held there while the dorsal blind sac contracted. As both the dorsal blind sac and caudal pillar contracted, the whole caudal part of the rumen was lifted dorsally and slightly cranially.

When contractions of the dorsal rumen were moving from caudal to cranial regions the ventral part of the dorsal blind sac started to contract before the caudal pillar started to curl dorsally. The curl in the caudal pillar was more pronounced than during its first movement and frequently creasing of the caudal wall of the dorsal blind sac could be seen. Also instead of this pillar and the caudal wall of

PLATE 11

A radiograph of reticulum and cranial rumen taken in the resting phase between contractions. The sheep had been dosed with 50 ml of barium sulphate suspension and one reticulo-rumen contraction cycle had taken place. The bar with cross pieces was included to give a scale of maximum possible distortion (the distance between the cross pieces being 10 cm).

CdP caudal pillar, CP cranial pillar, CS cranial sac of rumen, D diaphragm, DRu dorsal rumen, F rumen fistula, G gas cap, Re reticulum, RRF reticulo-ruminal fold, S spleen, VRu ventral rumen.



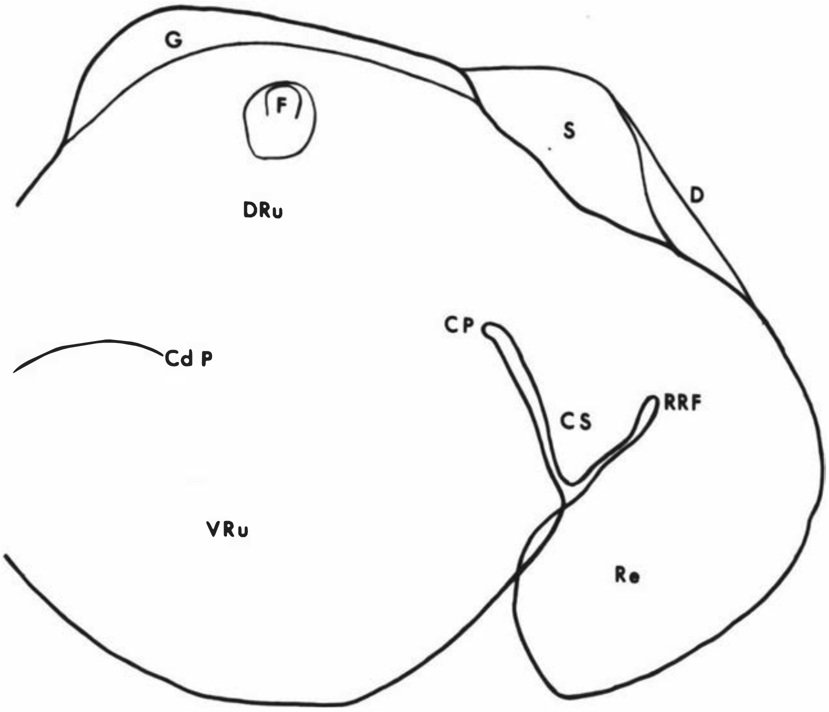
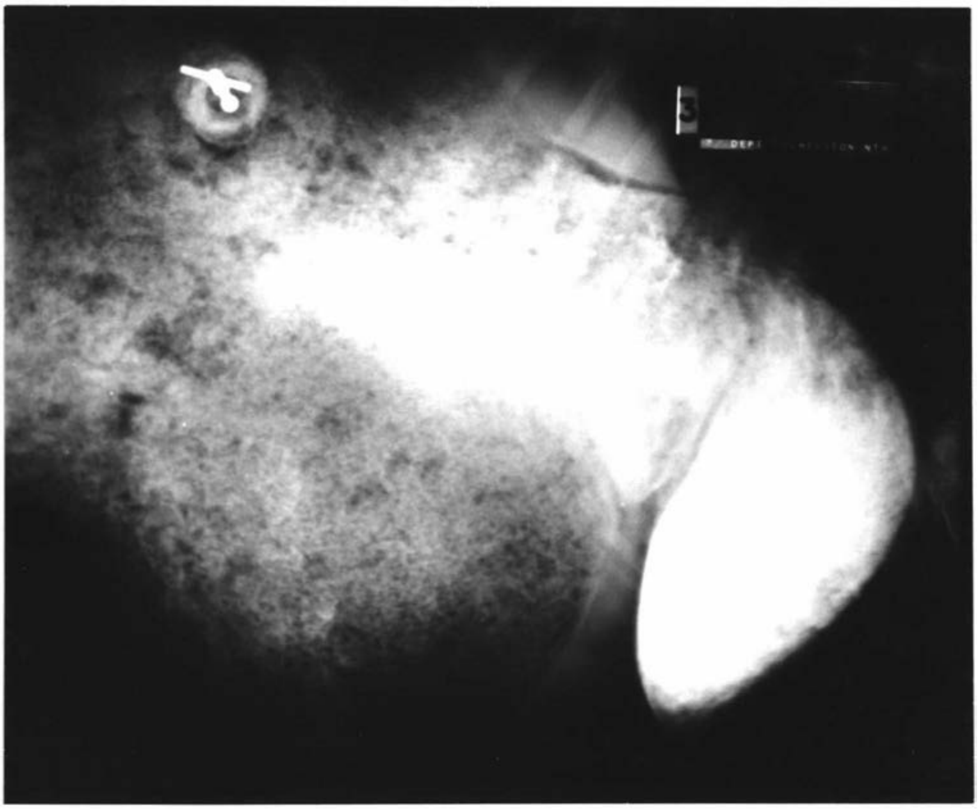

G
F
S
D
DRu
CP
Cd P
CS
RRF
VRu
Re

PLATE 12

The first indication of the commencement of a reticular contraction is a dorsal movement of the reticulo-ruminal fold and a straightening of the caudal border of the reticulum.

Ab abomasum, CP cranial pillar, CS cranial sac, D diaphragm, DRu dorsal rumen, F rumen fistula, Re reticulum, RRF reticulo-ruminal fold, S spleen, VRu ventral rumen.


3

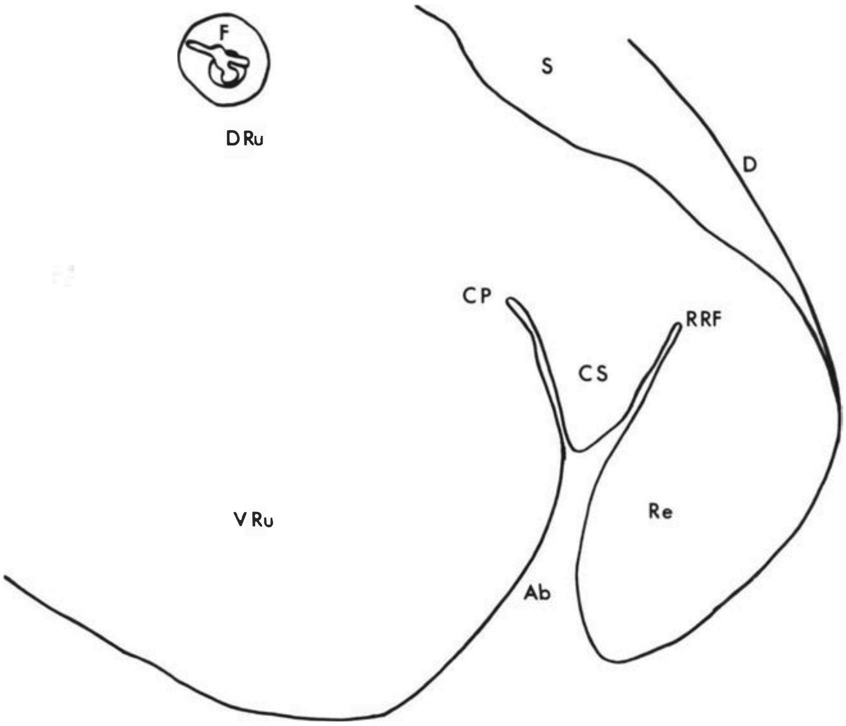
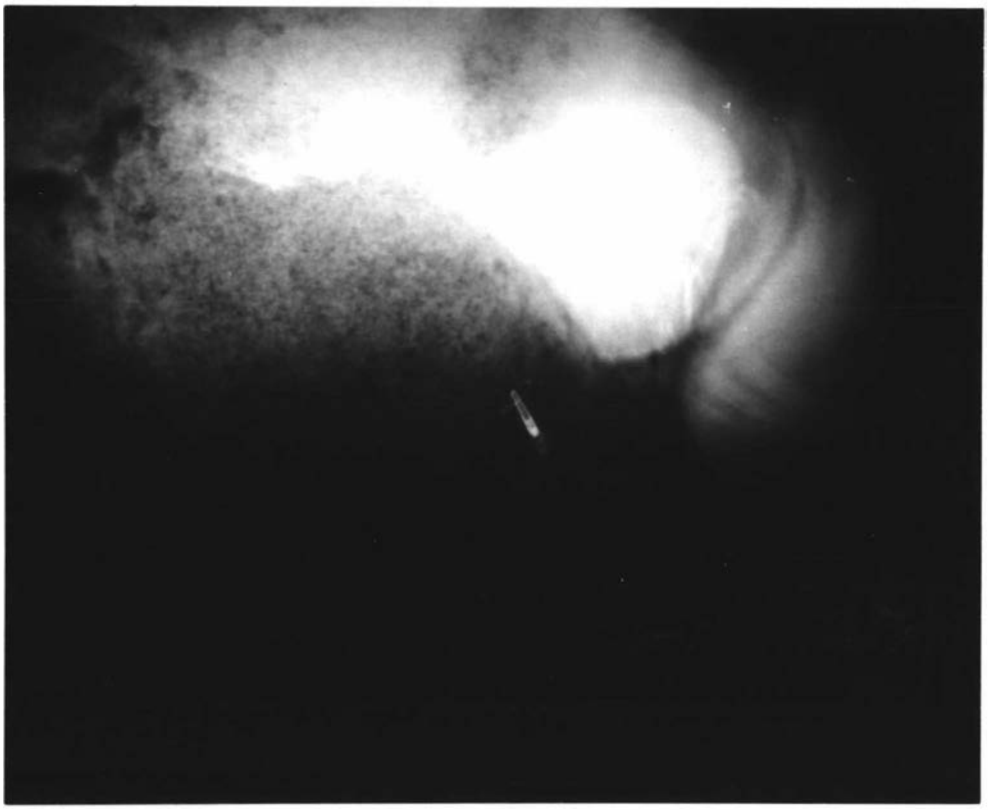

F
DRu
S
D
CP
RRF
CS
VRu
Re
Ab

PLATE 13

One second after the start of a reticular contraction. The pole of the reticulum has started to lift and the reticulo-ruminal fold has continued to move dorsally.

CP cranial pillar, CS cranial sac, DRu dorsal rumen, E electrode, O omasum, Re reticulum, RRF reticulo-ruminal fold, S spleen, VRu ventral rumen.



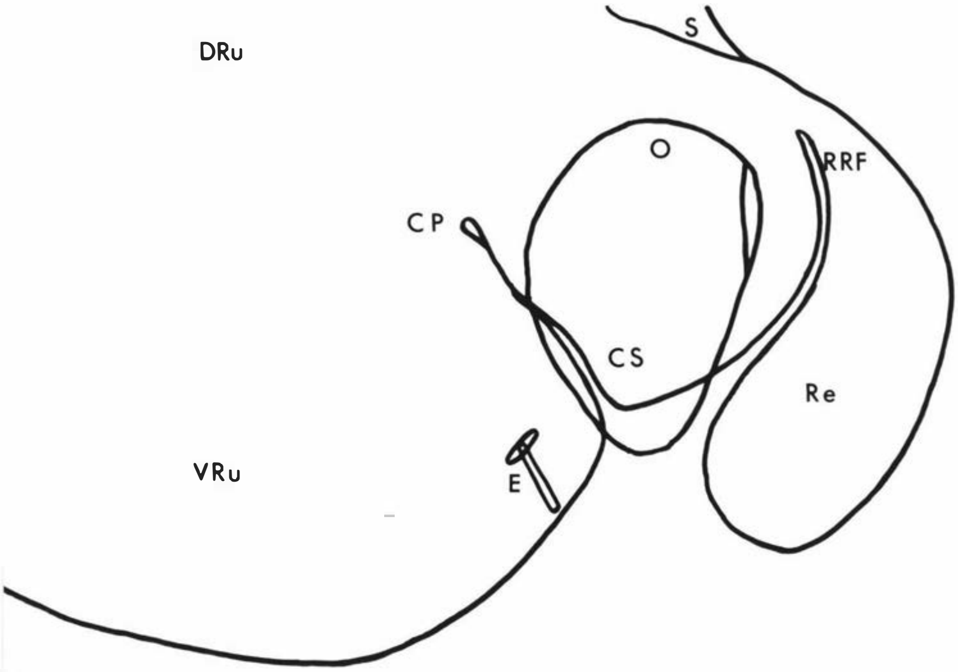
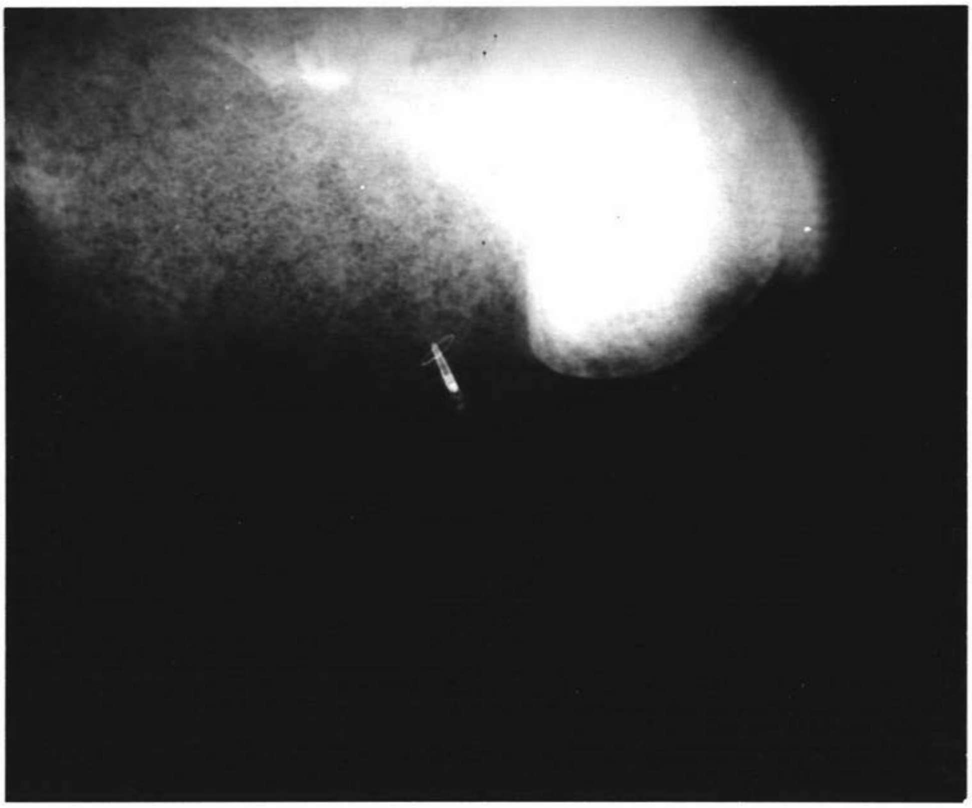

DRu
S
O
RRF
CP
CS
Re
VRu
E

PLATE 14

Two seconds after the start of a reticular contraction. The reticulum has completed its first phase of contraction and its pole has travelled approximately half the distance between its starting point and point of maximum contraction. The cranial sac is dilating, receiving the contents of the reticulum.

CP cranial pillar, DRu dorsal rumen, E electrode, Re reticulum, RRF reticulo-ruminal fold, VRu ventral rumen.



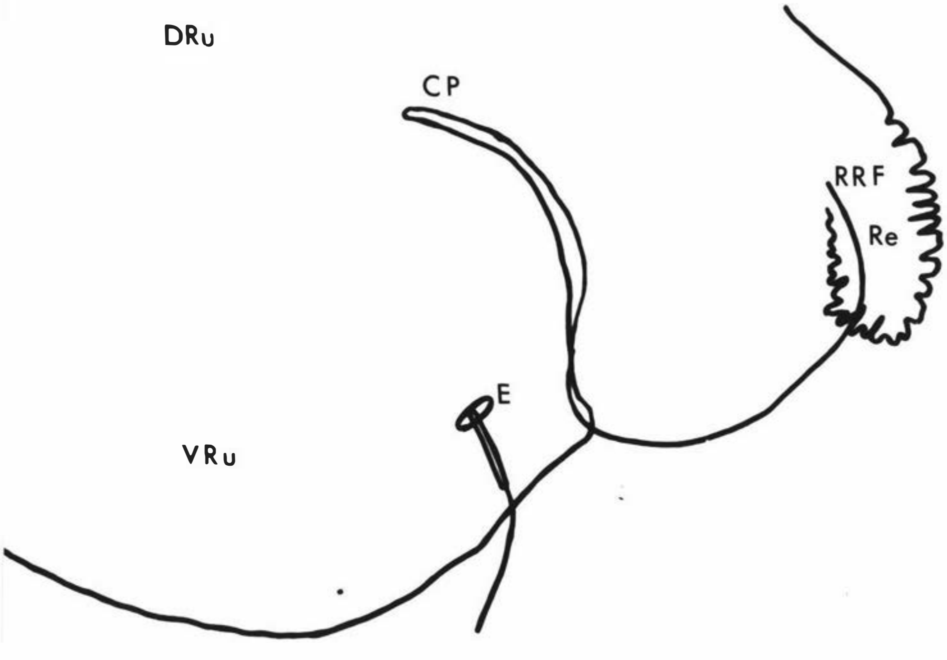
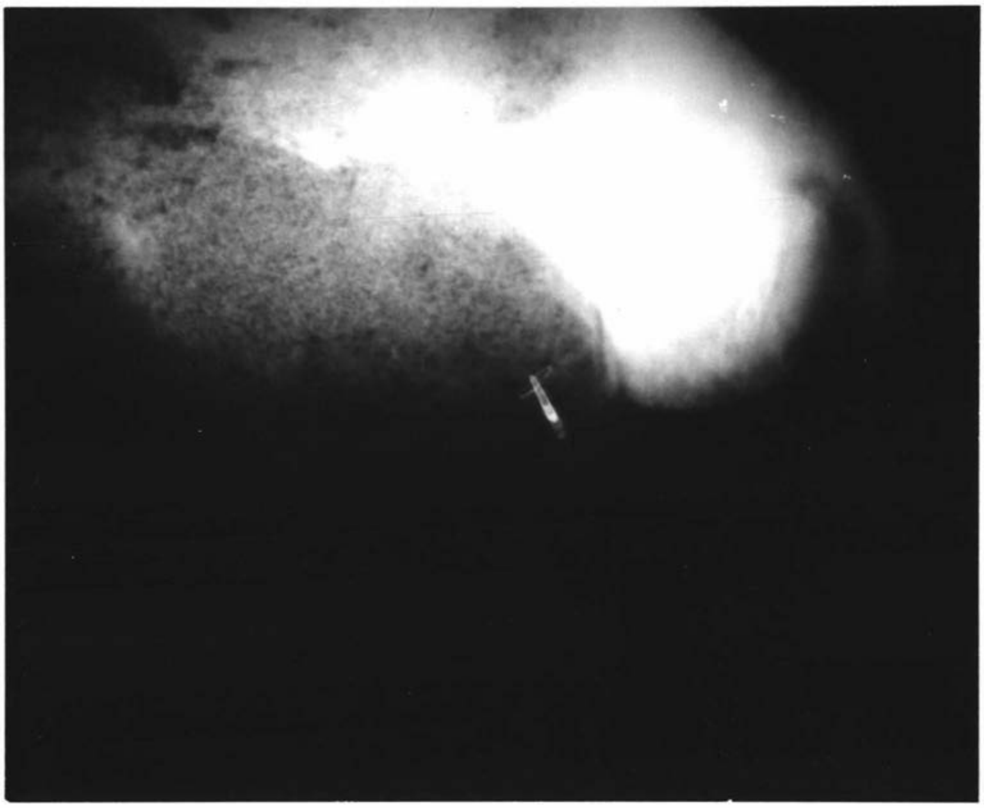

DRu
CP
RRF
Re
E
VRu

PLATE 15

Four seconds after the start of a reticular contraction. The reticulum has now reached its maximum contraction, virtually eliminating its lumen. The reticulo-ruminal fold has reached its maximum cranial movement with the greatest degree of dilation of the cranial sac of the rumen.

CP cranial pillar, CS cranial sac, DRu dorsal rumen,
E electrode, Re reticulum, RRF reticulo-ruminal fold,
VRu ventral rumen.



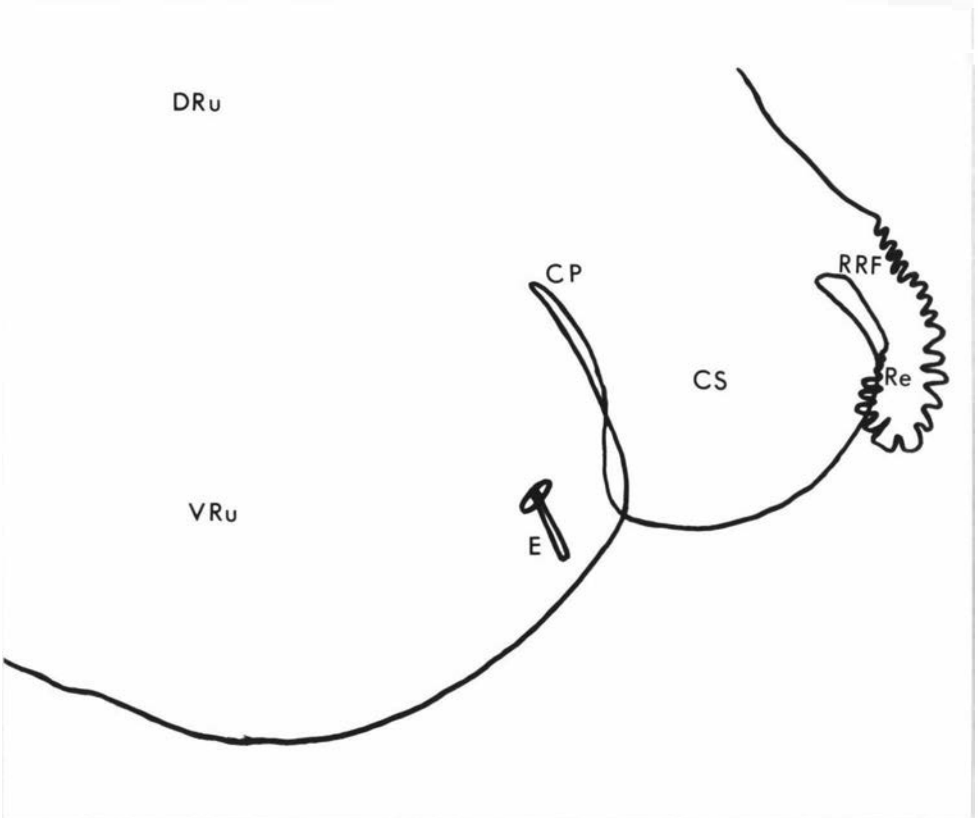
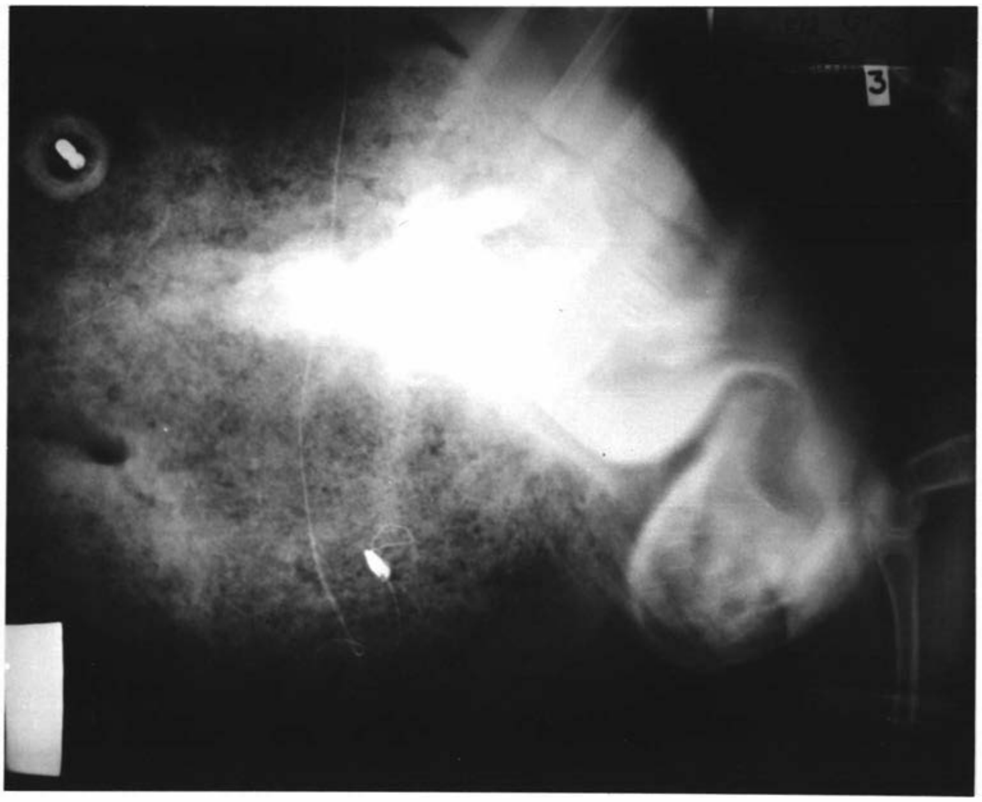

DRu
CP
RRF
CS
Re
VRu
E

PLATE 16

Six seconds after the start of the reticular contraction. The cranial sac is now contracting, tipping its contents over the reticulo-ruminal fold back into the relaxing reticulum. The reticulo-ruminal fold is returning towards its resting position as the cranial pillar starts to contract and move dorso-caudally.

CP cranial pillar, CS cranial sac, DRu dorsal rumen, E electrode, F rumen fistula, Re reticulum, RRF reticulo-ruminal fold, VRu ventral rumen.


3

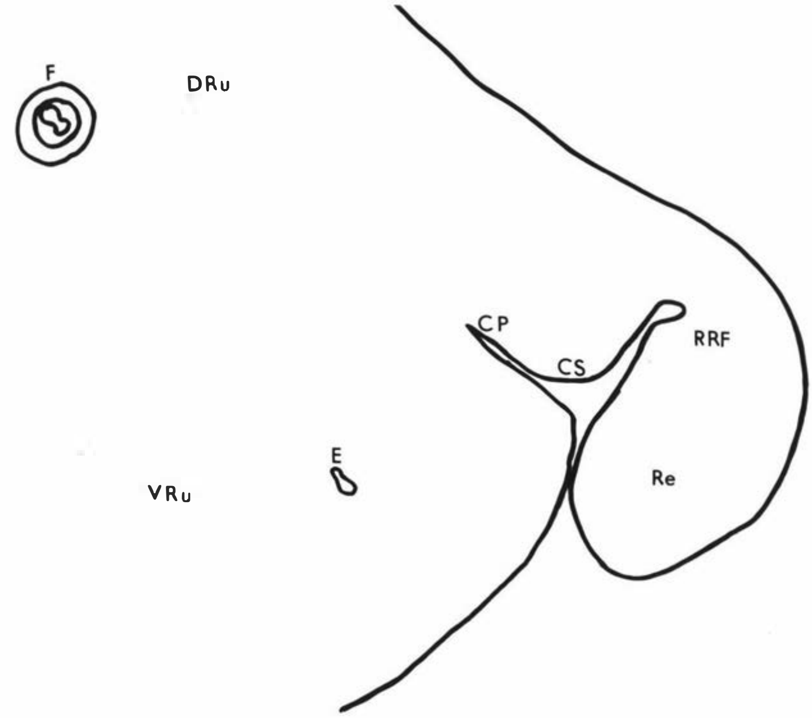
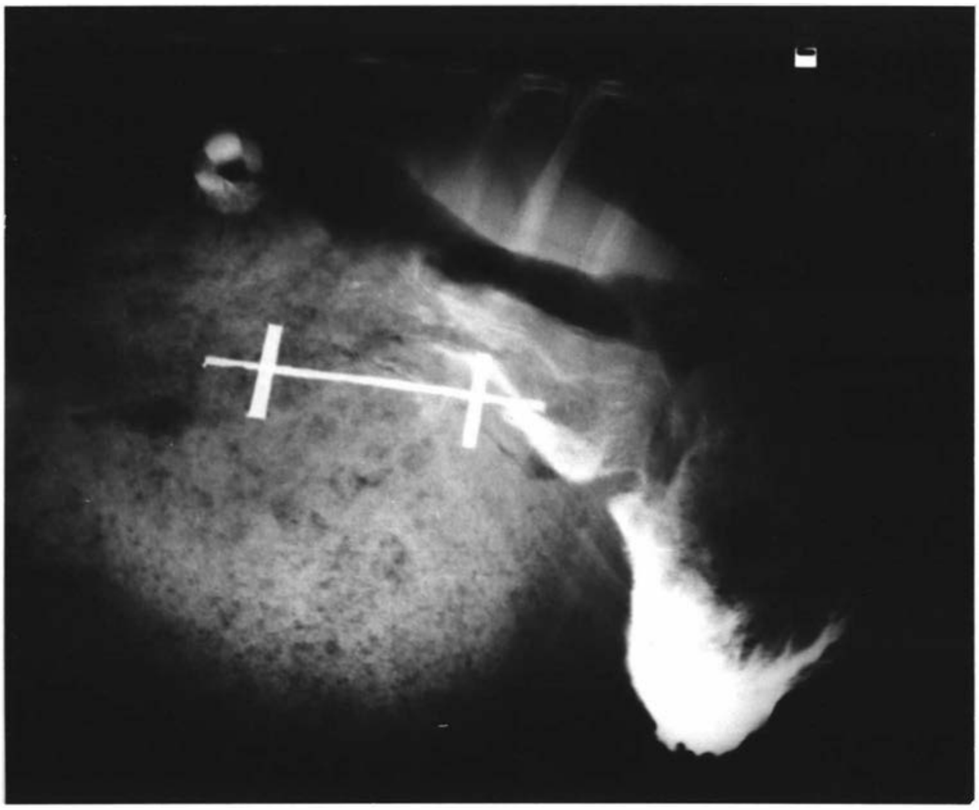

F
DRu
CP
CS
RRF
Re
E
VRu

PLATE 17

Ten seconds after the start of the reticular contraction. The cranial sac and cranial pillar have reached their maximum state of contraction and the reticulo-ruminal fold has been pulled slightly caudal to its normal resting position. The dorsal rumen has contracted displacing the gas cap cranially. The reticulum is distended slightly beyond its normal resting state.

CP cranial pillar, DRu dorsal rumen, F rumen fistula, G gas cap, Re reticulum, RRF reticulo-ruminal fold, VRu ventral rumen.



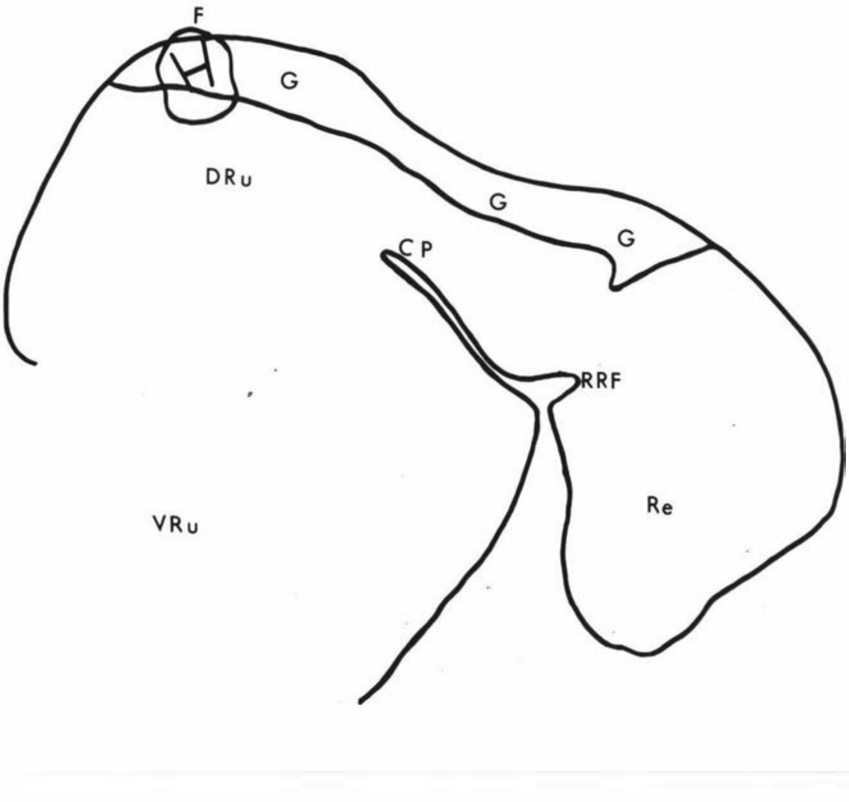
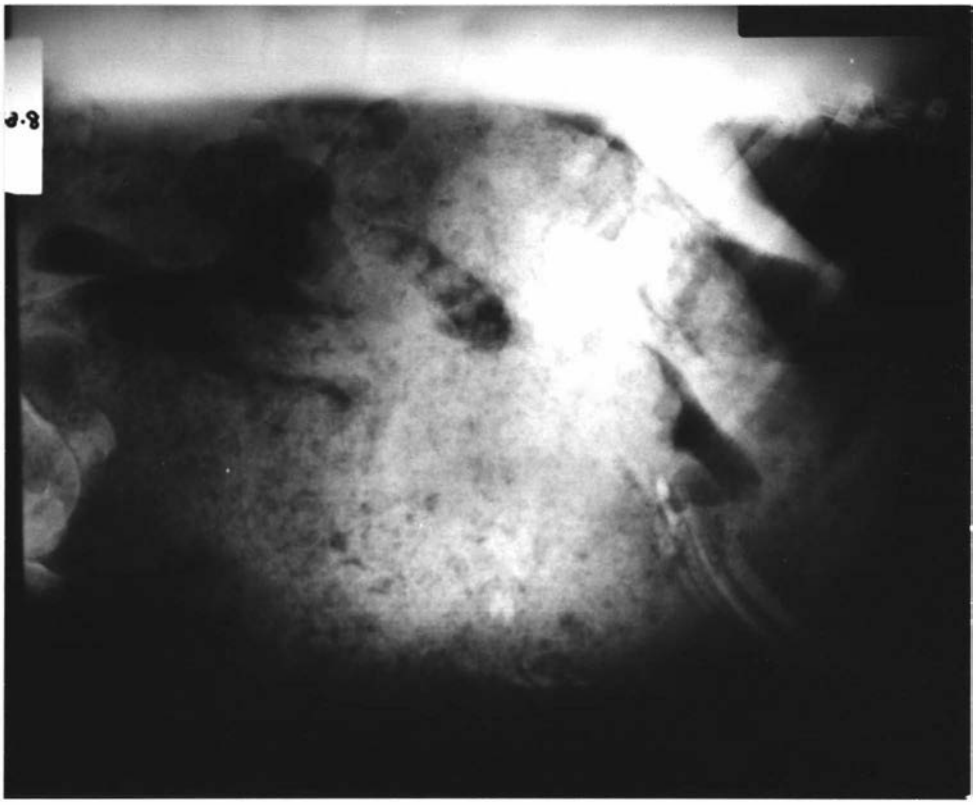

F
G
DRu
G
G
CP
RRF
Re
VRu

PLATE 18

Ten seconds after the start of a reticular contraction. This sheep had no rumen fistula to hinder the contraction of the dorsal rumen and it demonstrates the more commonly seen displacement of the gas cap. The gas has not only been displaced cranially into the cranial rumen and reticulum, but also underneath the cranial and caudal pillars. The gas shadows not depicted in the line drawing are caused by gas within other overlying parts of the alimentary tract.

CP cranial pillar, CdVBS caudal ventral blind sac, DRu dorsal rumen, G gas, Re reticulum, VRu ventral rumen.



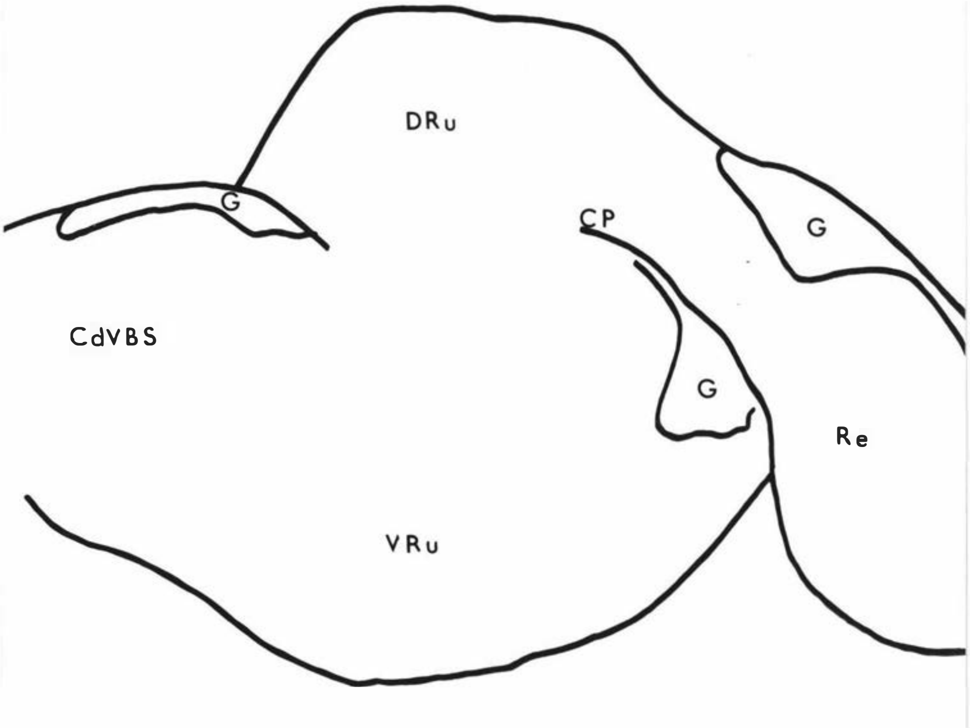
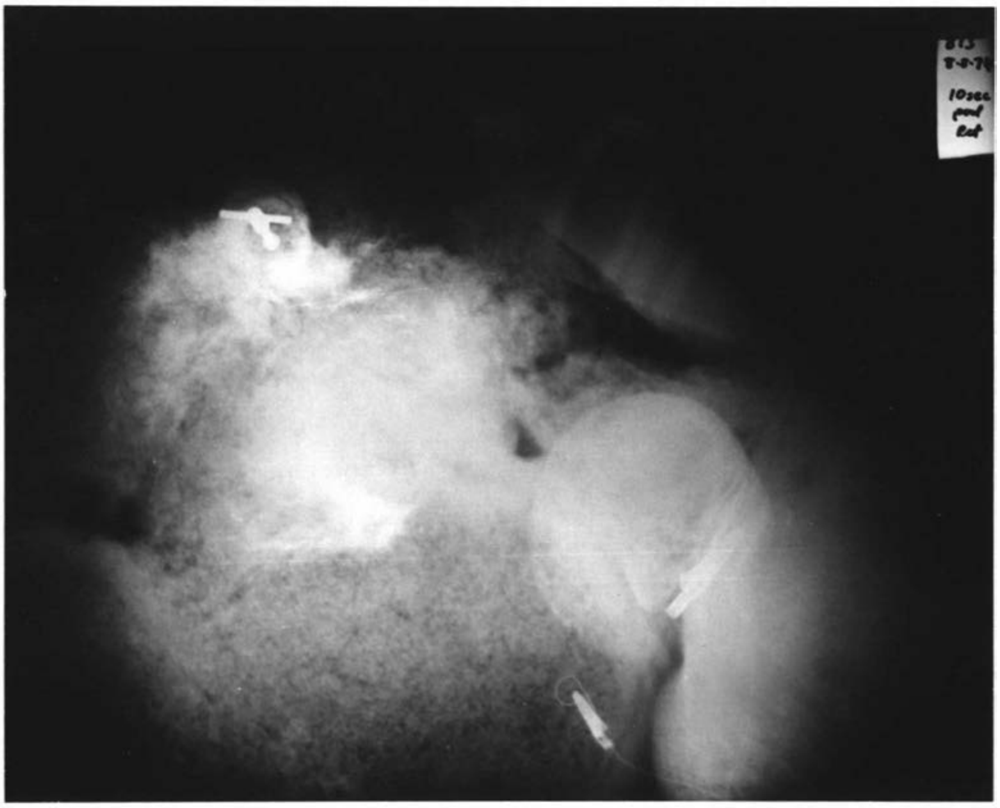

DRu
G
CP
G
CdVBS
G
Re
VRu

PLATE 19

Twenty seconds after the start of a reticular contraction. The cranial part of the dorsal rumen, the cranial sac of the rumen and the cranial pillar are relaxing. The gas cap is returning to the dorsal rumen.

CS cranial sac, CdP caudal pillar, CdVBS caudal ventral blind sac, DRu dorsal rumen, E electrodes, F rumen fistula, G gas, O omasum, Re reticulum, S spleen, VRu ventral rumen.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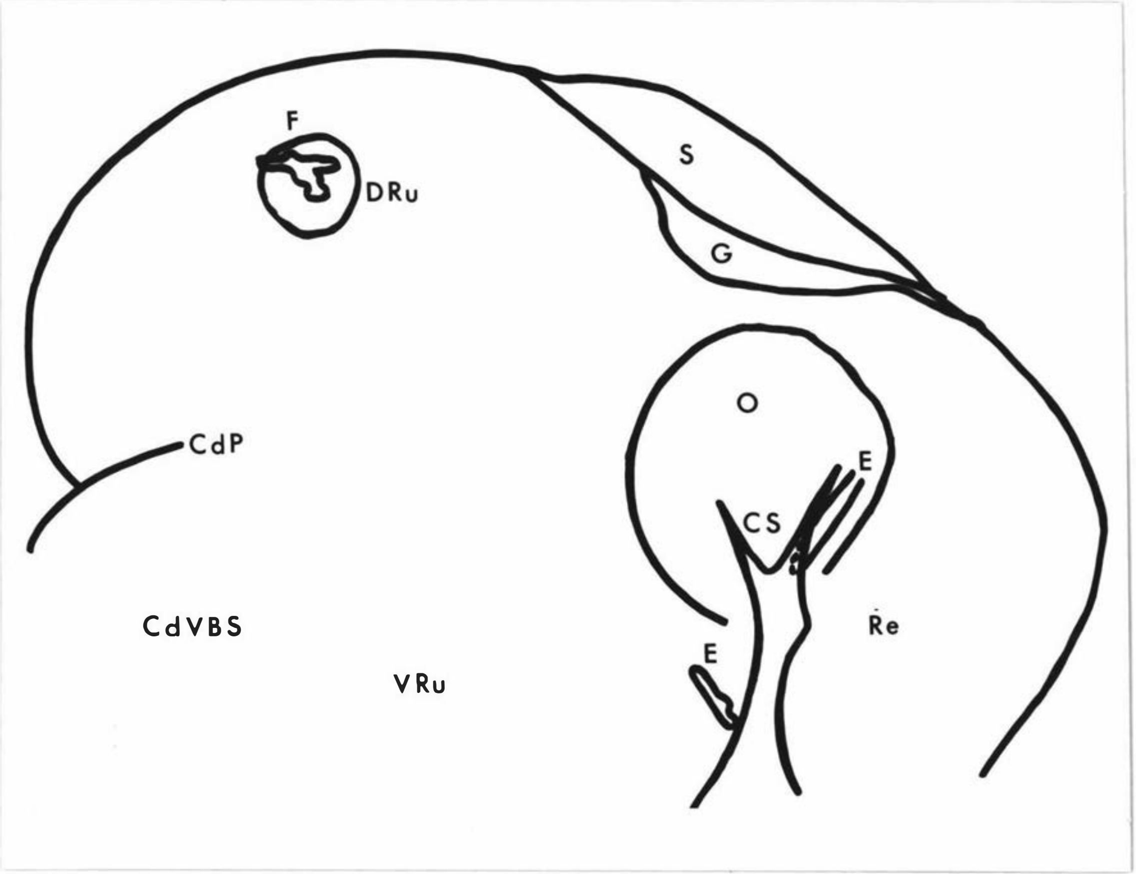
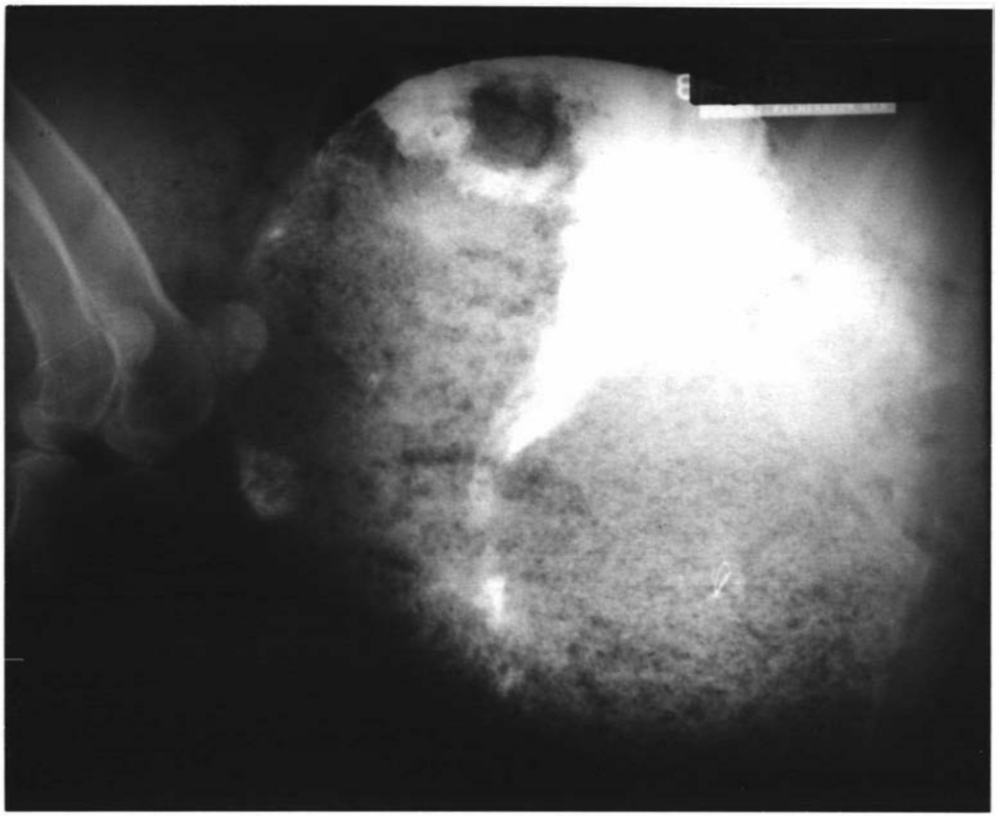

F
DRu
S
G
O
E
CS
CdP
CdVBS
VRu
E
Re

PLATE 20

Thirty seconds after the start of a reticular contraction. The caudal part of the dorsal rumen has just started to contract for the second time but on this occasion the contraction is moving from caudal to cranial rumen.

CdVBS caudal ventral blind sac, DRu dorsal rumen, E electrode, F fistula, G gas, VRu ventral rumen.



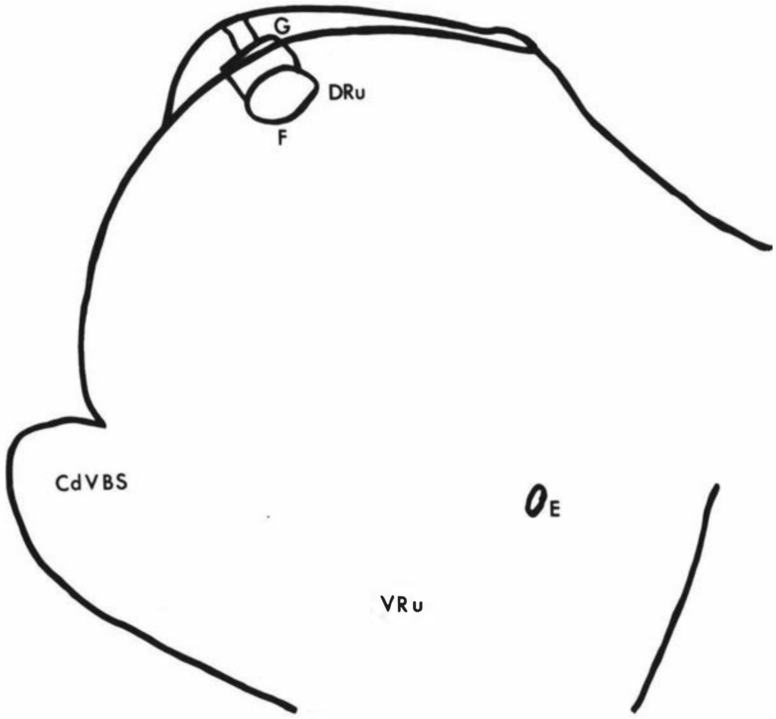
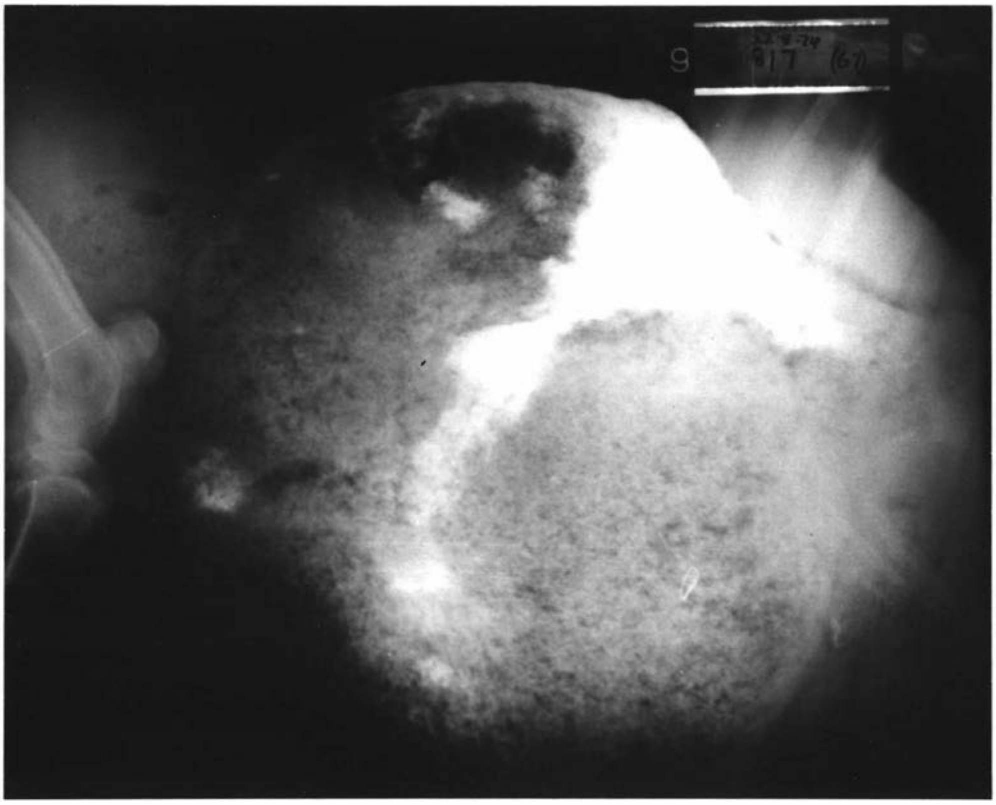

G
DRu
F
CdVBS
E
VRu

PLATE 21

Thirty five seconds after the start of a reticular contraction. The wave of the contraction continues to pass cranially over the dorsal rumen pushing the gas cap cranially.

CdVBS caudal ventral blind sac, CS cranial sac, DRu dorsal rumen, E electrode, G gas, Re reticulum, VRu ventral rumen.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22-8-74
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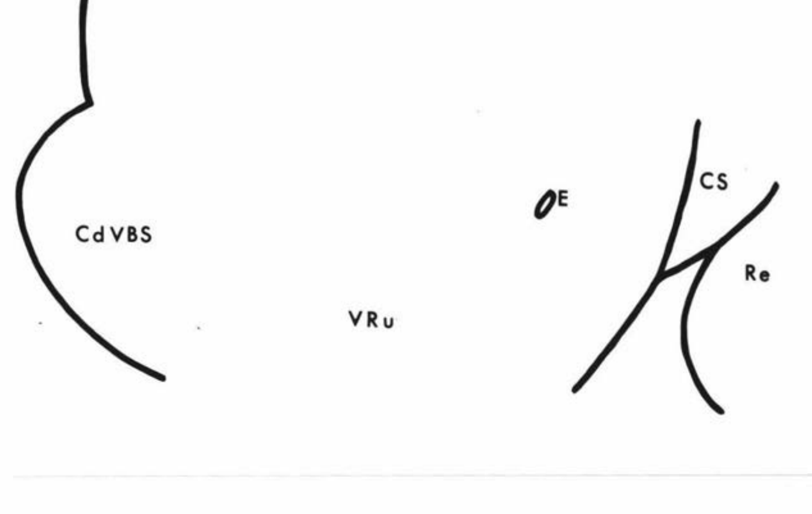
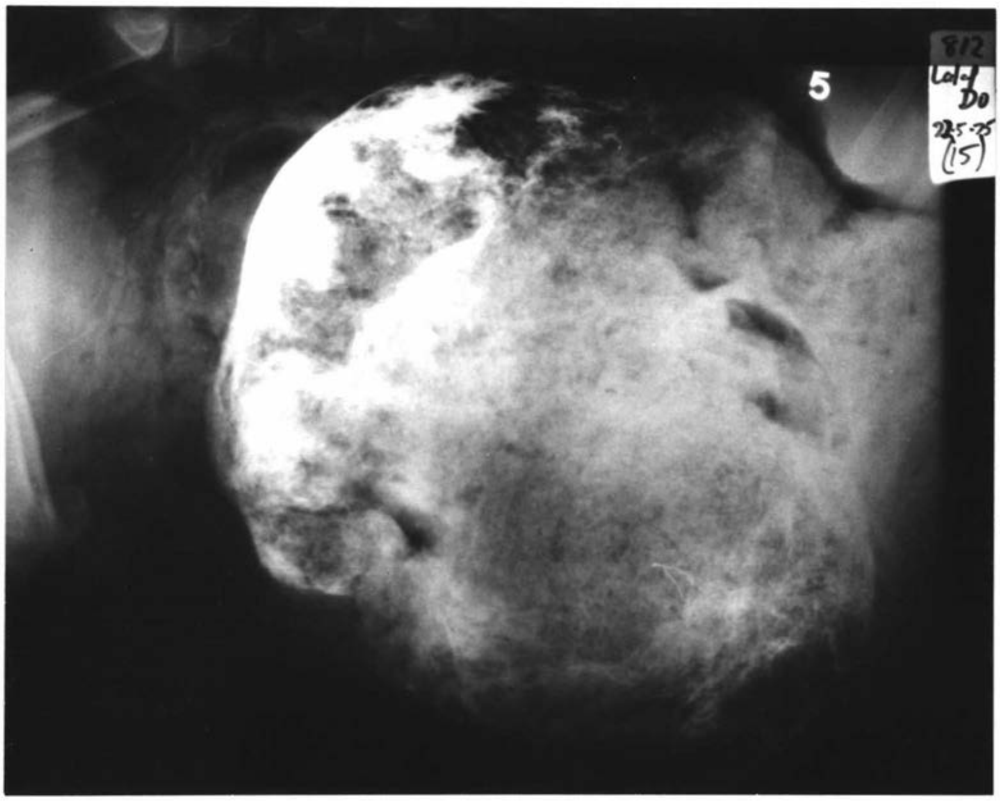

G
G
DRu
CdVBS
VRu
E
CS
Re

PLATE 22

Thirty seven seconds after the start of a reticular contraction. The contraction of the dorsal rumen continues to move cranially and the cranial pillar starts to contract again. The gas cap is pushed further cranially and some of it gets displaced under the cranial pillar.

CdP caudal pillar, CdVBS caudal ventral blind sac, CS cranial sac, DRu dorsal rumen, G gas, VRu ventral rumen.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(15)

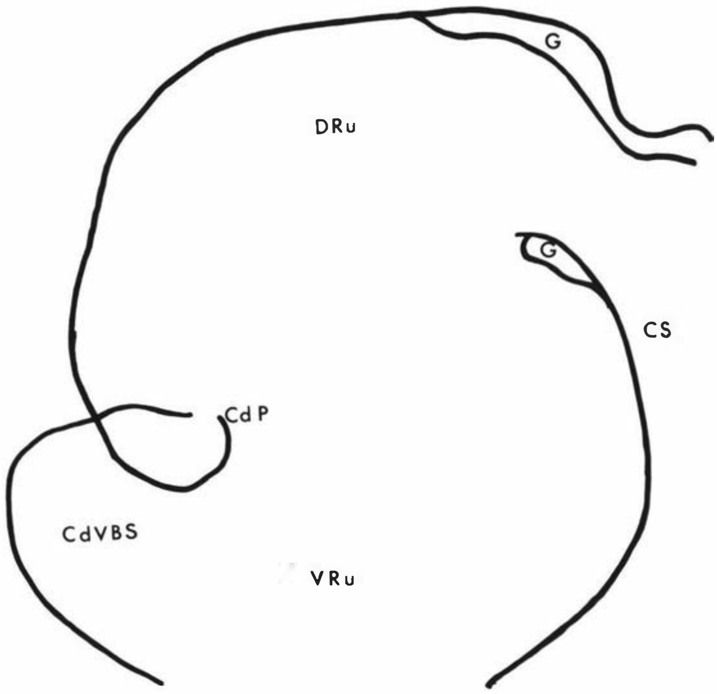
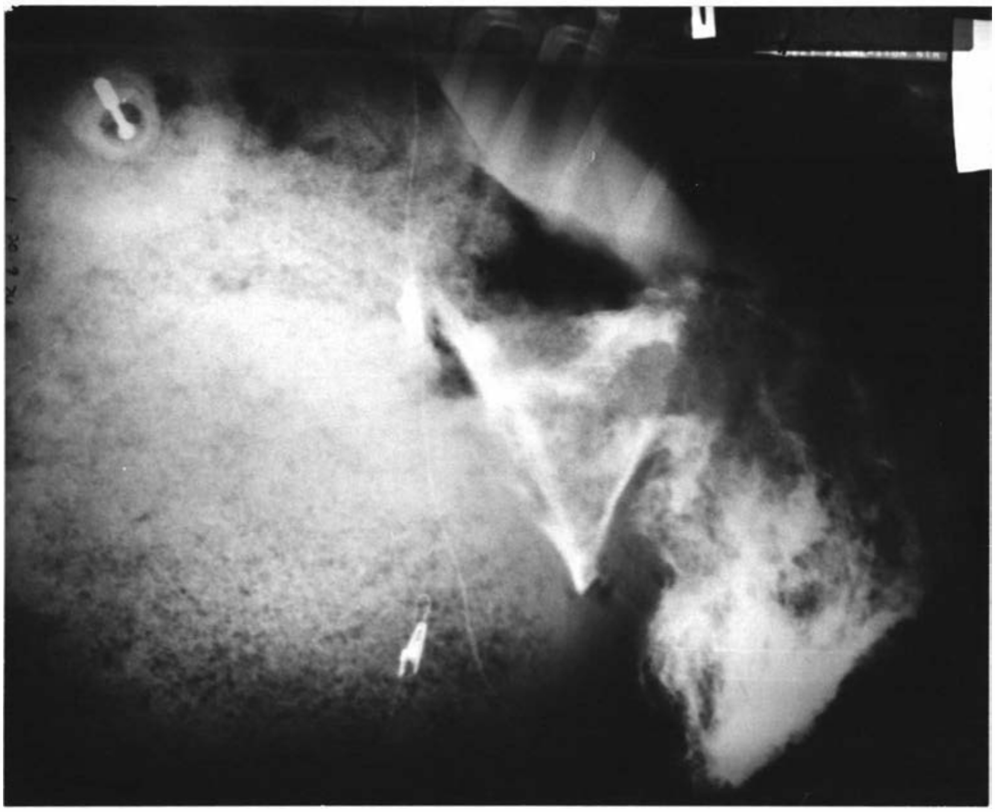

G
DRu
G
CS
CdP
CdVBS
VRu

PLATE 23

Forty seconds after the start of a reticular contraction. The dorsal rumen is contracted, the cranial pillar has moved a short distance caudally and the gas is displaced cranially. Eructation is occurring and a small bolus of gas can be seen passing through into the oesophagus. The gas is clearly seen in the photograph but as it has poorly-defined borders and is somewhat intermingled with digesta, its outline was not included in the line drawing.

CP cranial pillar, CS cranial sac, DRu dorsal rumen, E electrode, F fistula, G gas, Oe oesophagus, Re reticulum, RRF reticulo-ruminal fold, VRu ventral rumen.



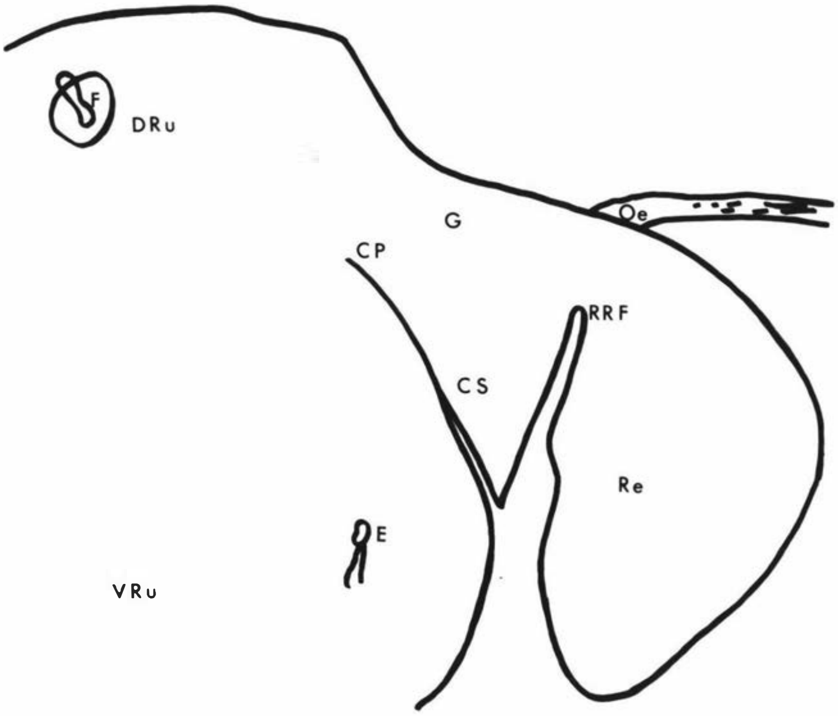
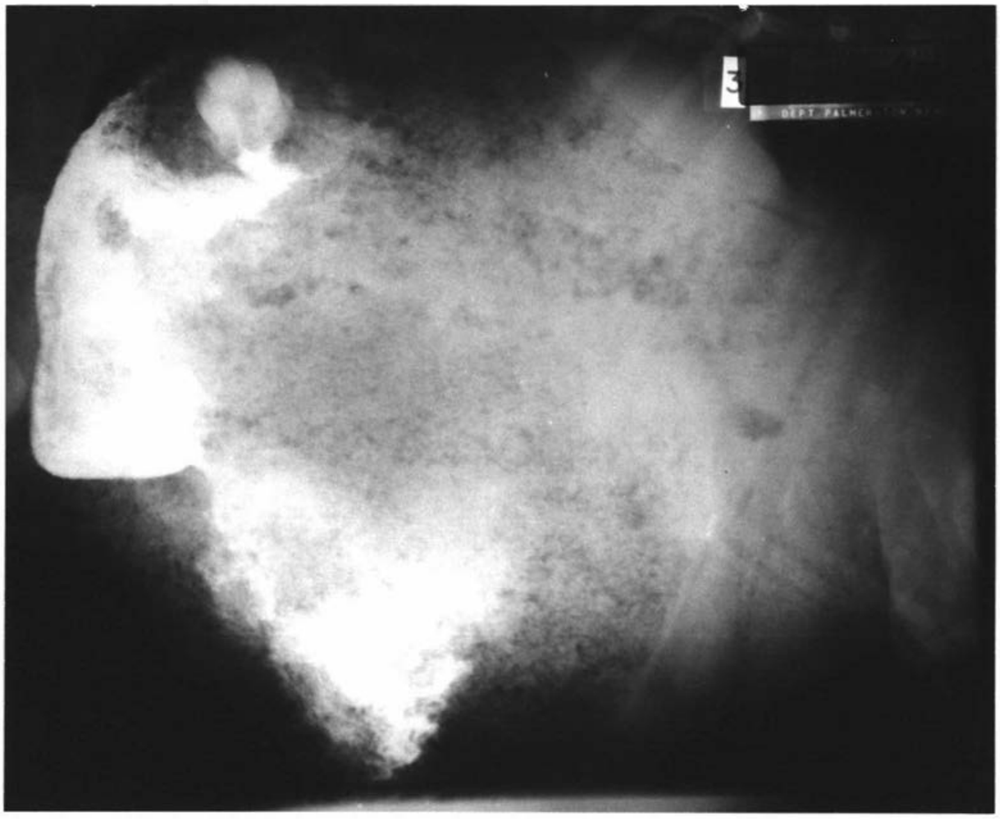

F
DRu
G
Oe
CP
RRF
CS
Re
E
VRu

PLATE 24

The reticulum has started to contract. No movement of the caudal part of the rumen has taken place. The contrast media (barium sulphate suspension), was placed dorsal to the caudal pillar by inserting a catheter through the rumen fistula. Some of the contrast media has spilled over the caudal pillar into the ventral rumen. In the line drawing of this radiograph, and all subsequent radiographs, no attempt was made to outline the contrast media.

CdP caudal pillar, CdVBS caudal ventral blind sac, CP cranial pillar, DRu dorsal rumen, E electrode, F fistula, G gas cap, Re reticulum, VRu ventral rumen.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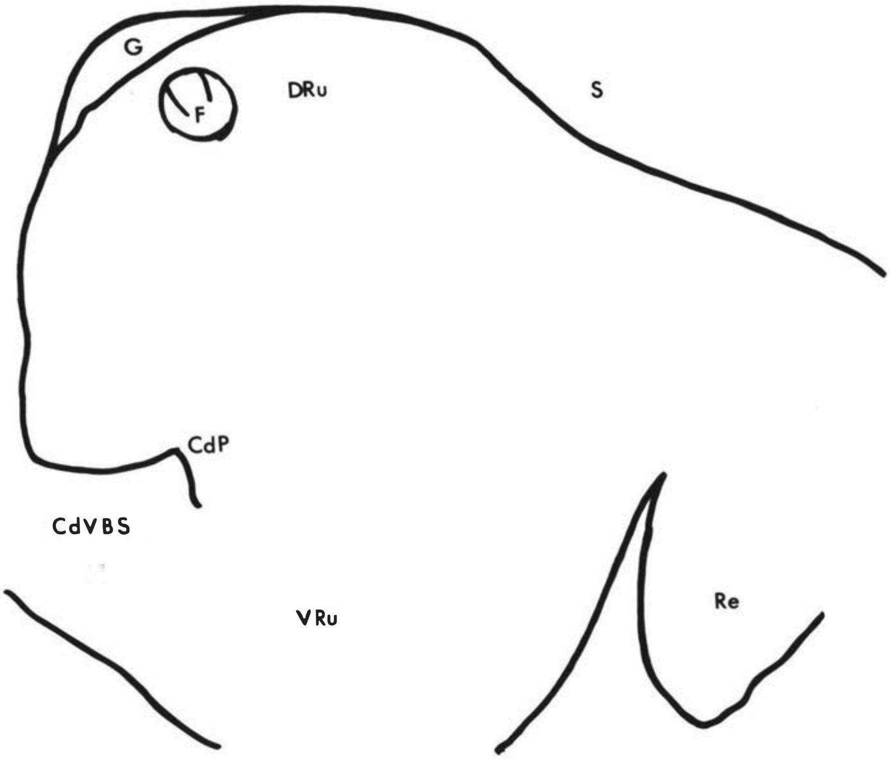
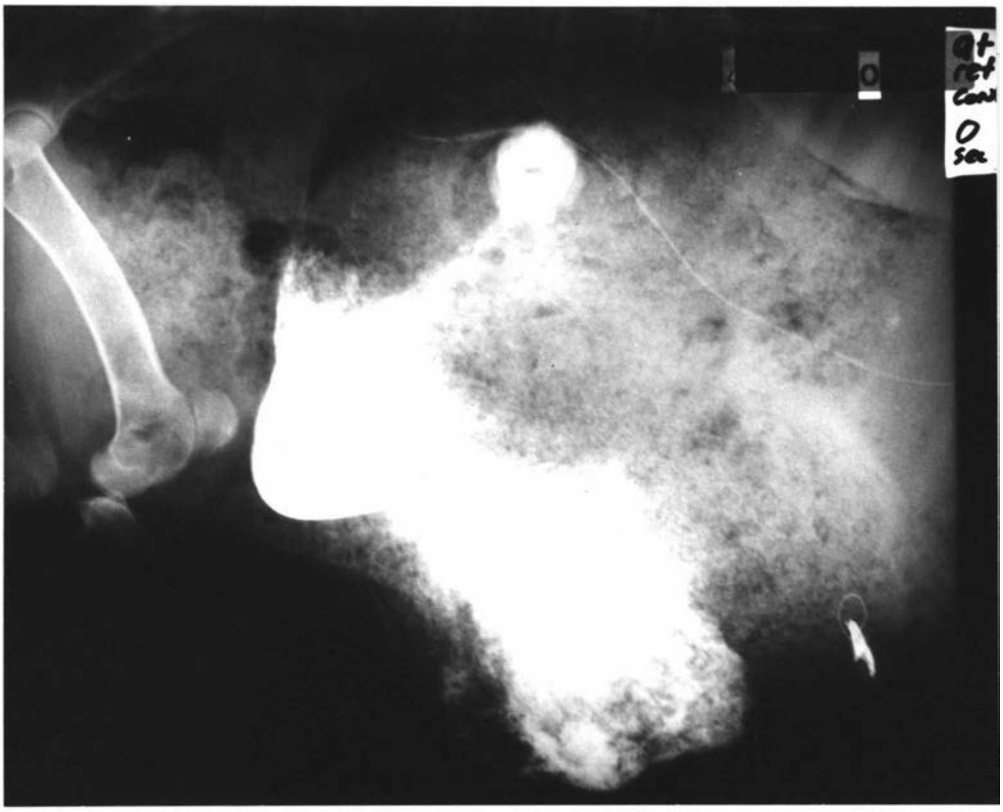

G
F
DRu
S
CdP
CdVBS
VRu
Re

PLATE 25

Ten seconds after the start of the reticular contraction. The more caudal part of the dorsal rumen wall has contracted pushing the gas cap cranially and ventrally.

CdP caudal pillar, CdVBS caudal ventral blind sac, DRu dorsal rumen, F fistula, G gas cap, Re reticulum, S spleen, VRu ventral rumen.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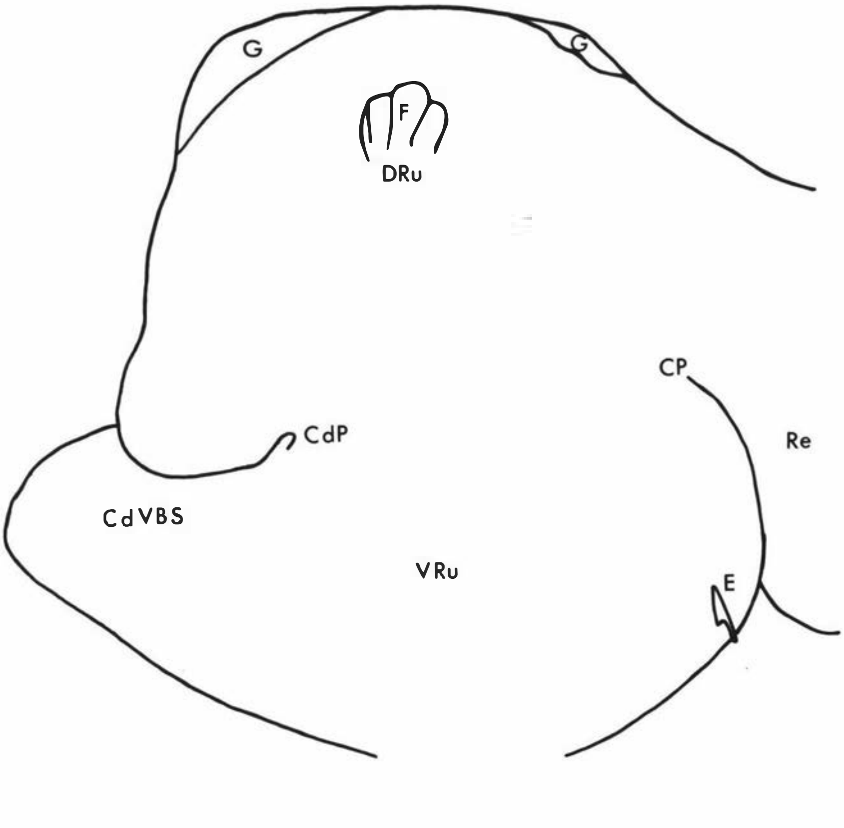
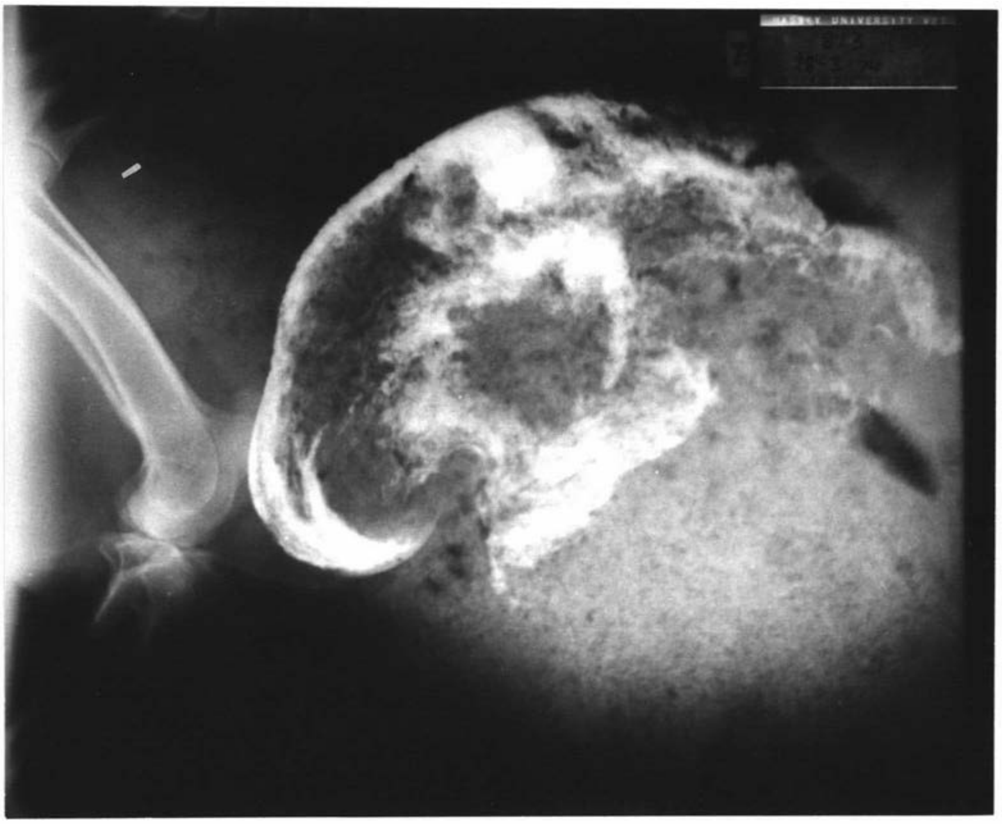

G
G
F
DRu
CP
CdP
Re
CdVBS
VRu
E

PLATE 26

Twelve seconds after the start of the reticular contraction. The contraction of the dorsal rumen has moved round further caudally and has displaced the gas cap cranially along the dorsal rumen and cranially and ventrally under the cranial pillar. The caudal pillar has curled dorsally and has reached its maximum dorsal excursion while the cranial pillar was held at its maximum cranio-dorsal excursion. The ventral rumen has been somewhat distended.

CdP caudal pillar, CdVBS caudal ventral blind sac, CP cranial pillar, DRu dorsal rumen, F fistula, G gas cap, VRu ventral rumen.


MASSEY UNIVERSITY

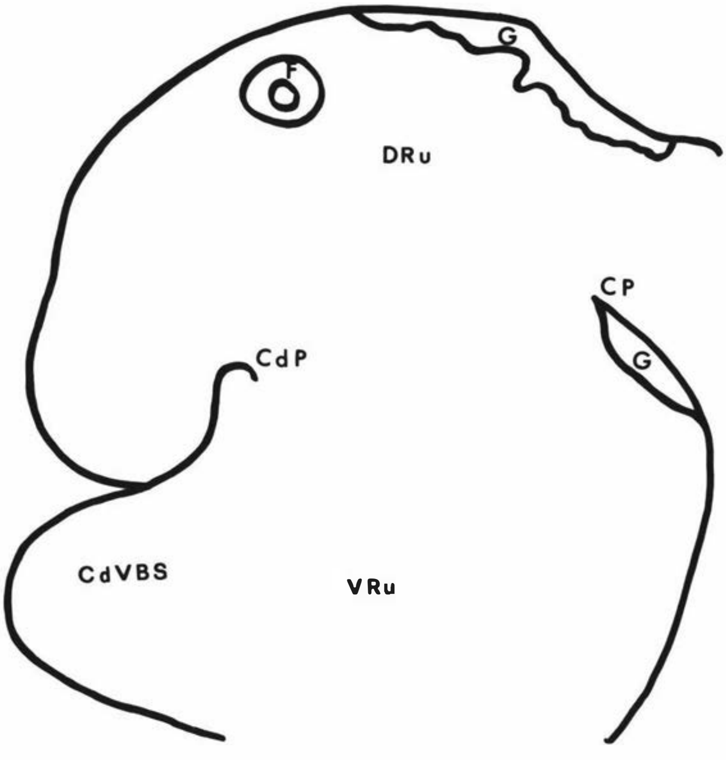
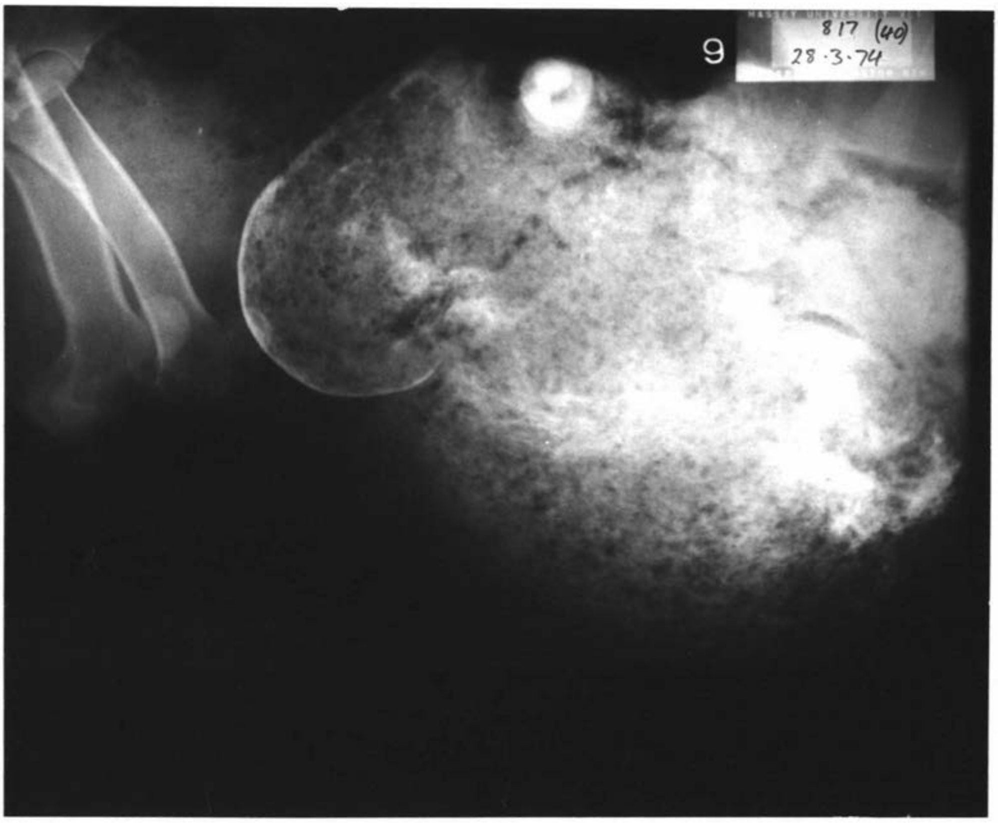

G
F
DRu
CP
CdP
G
CdVBS
VRu

PLATE 27

Fourteen seconds after the start of the reticular contraction. The contraction of the dorsal rumen has moved round onto the dorsal blind sac lifting the caudal part of the dorsal rumen and caudal part of the caudal pillar. The gas cap is still displaced cranially.

CdP caudal pillar, CdVBS caudal ventral blind sac, DRu dorsal rumen, F fistula, G gas cap, S spleen, VRu ventral rumen.


9
817 (40)
28·3·74

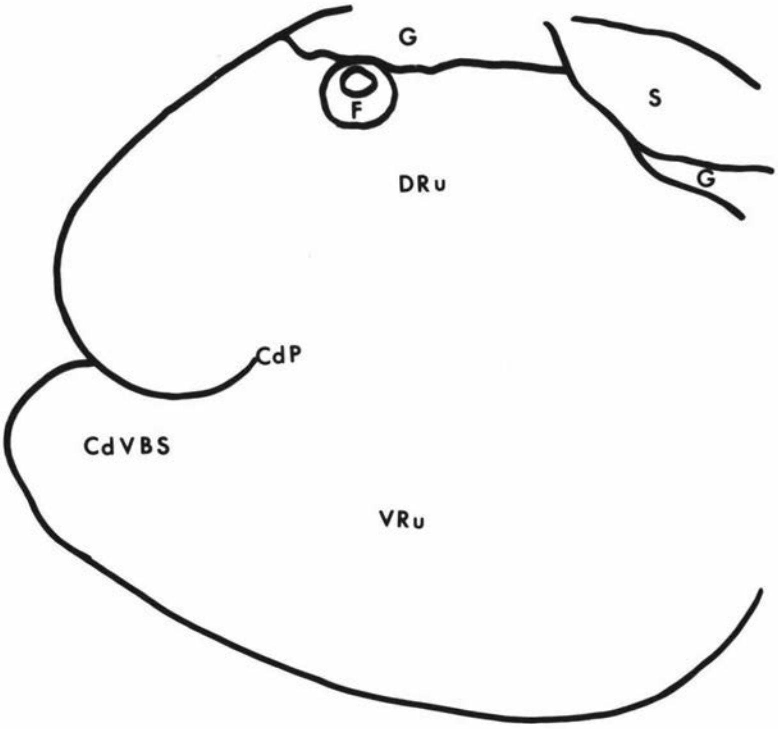
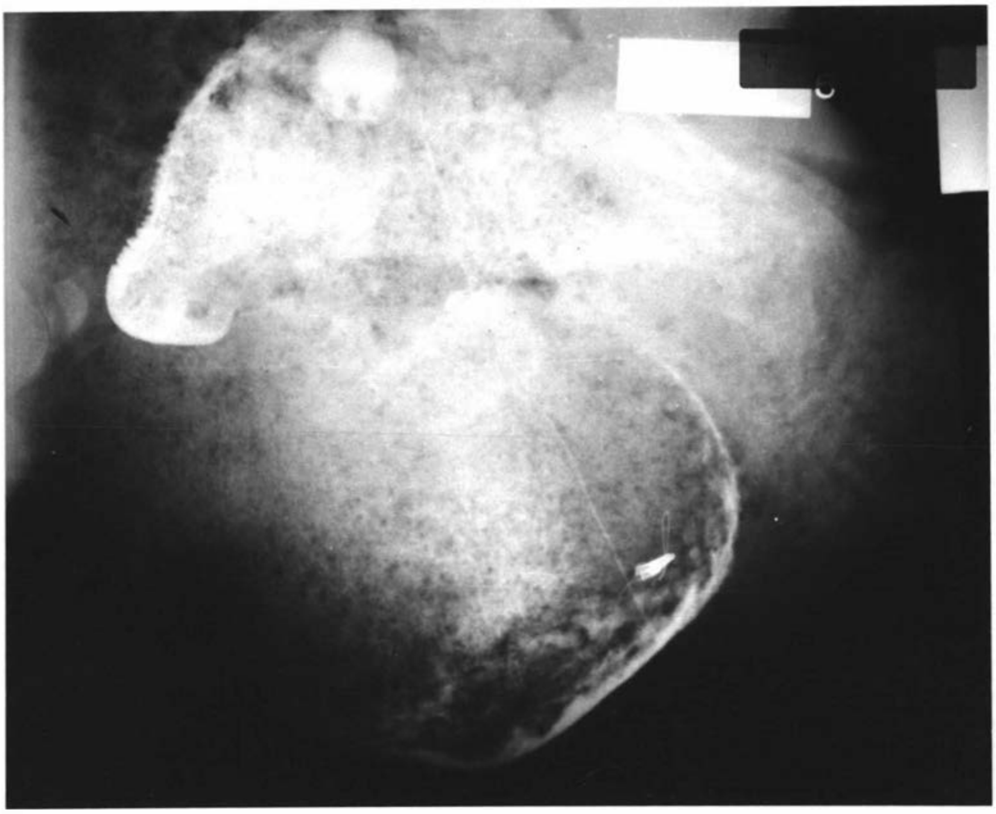

G
F
S
DRu
G
CdP
CdVBS
VRu

PLATE 28

Fifteen seconds after the start of the reticular contraction. The contraction has now moved onto the more ventral part of the caudal dorsal blind sac causing a marked crinkling of the inner aspect of the rumen wall. A contraction of the more cranial part of the ventral rumen has taken place as is shown by the straightening of this particular part of the rumen wall. The gas cap is still displaced cranially.

CdP caudal pillar, CdVBS caudal ventral blind sac, CP cranial pillar, DRu dorsal rumen, E electrode, F fistula, G gas cap, Re reticulum, S spleen, VRu ventral rumen.



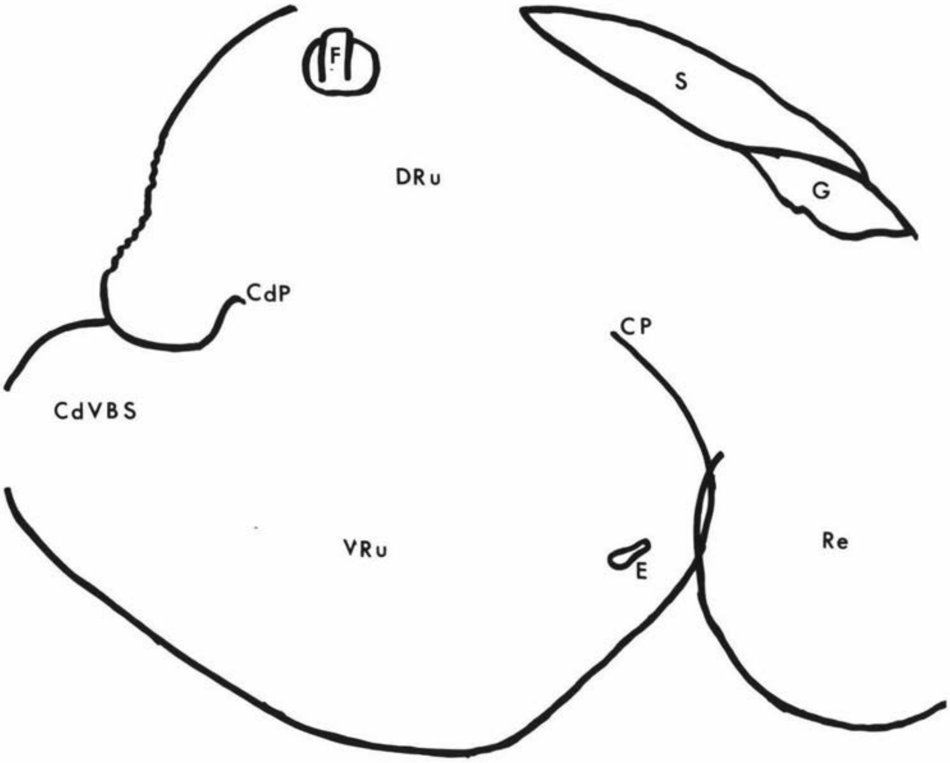
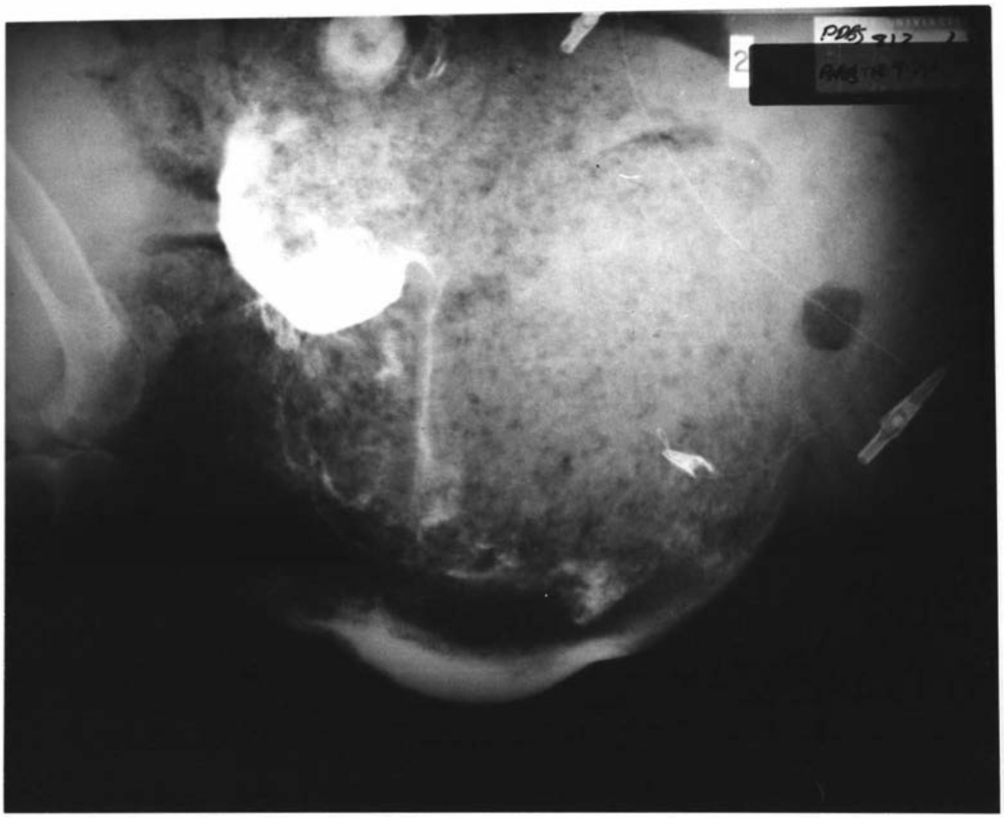

F
S
DRu
G
CdP
CP
CdVBS
VRu
E
Re

PLATE 29

Twenty seconds after the start of the reticular contraction. The dorsal rumen has relaxed and the caudal pillar is returning towards its resting position. The gas cap has returned to the dorsal rumen. The contraction of the more cranial part of the ventral rumen is now seen as a wave travelling caudally.

CdP caudal pillar, CdVBS caudal ventral blind sac, DRu dorsal rumen, E electrode, F fistula, G gas cap, Re reticulum, VRu ventral rumen.



[redacted]

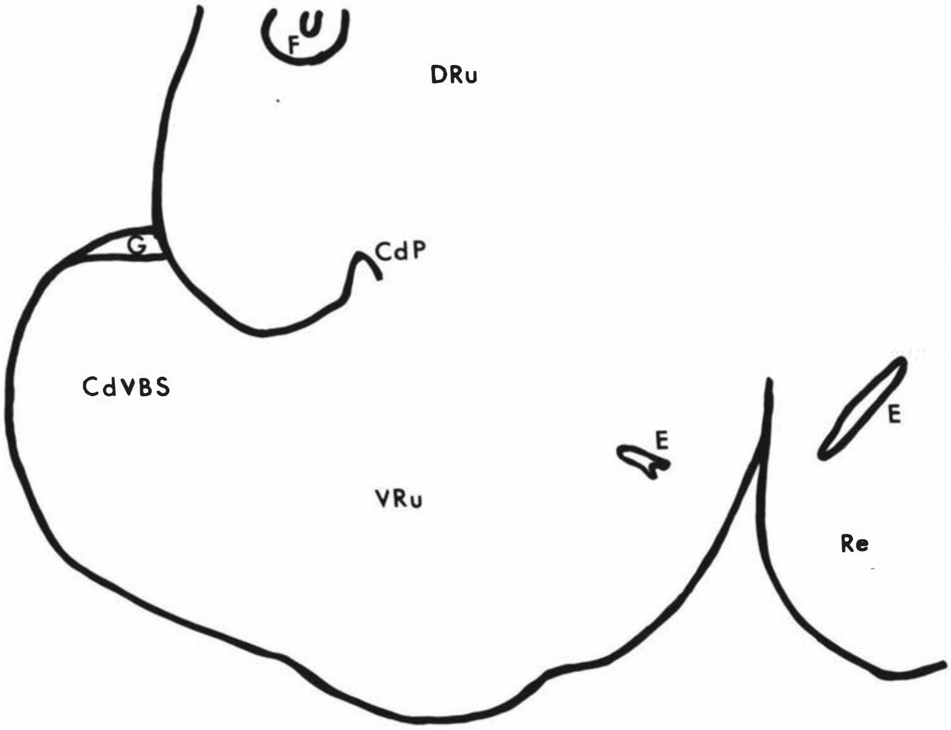
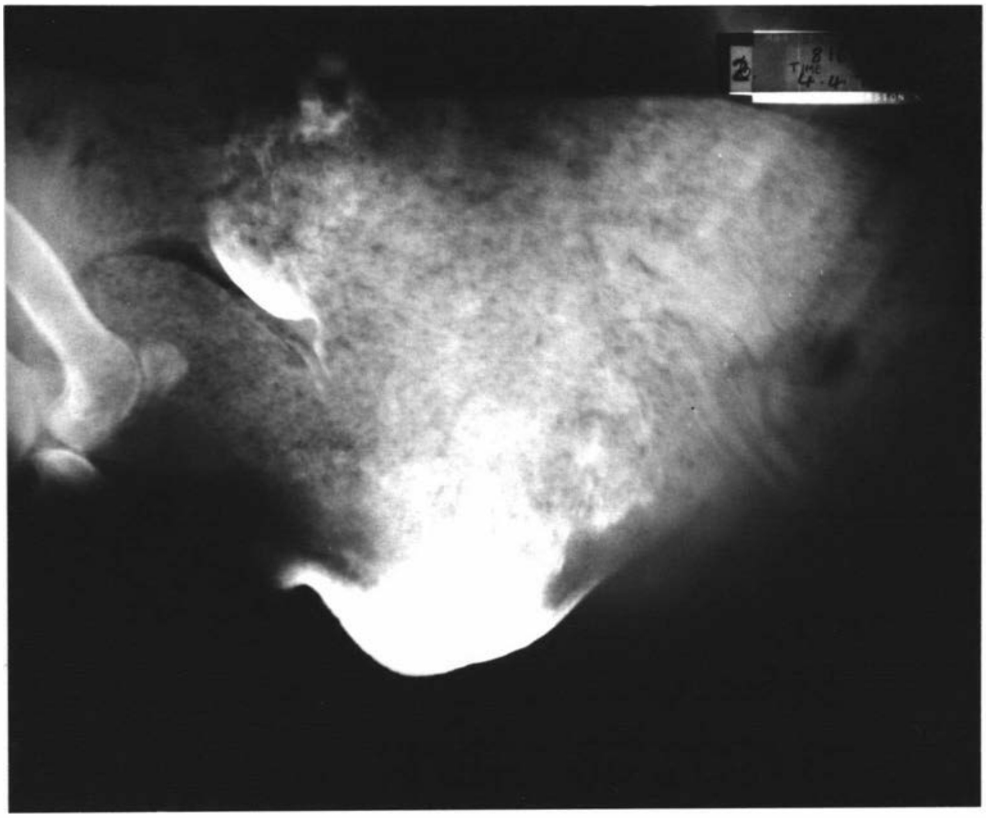


PLATE 30

Twenty five seconds after the start of the reticular contraction. The dorsal rumen has now completely relaxed and the gas cap has returned to the dorsal part of the dorsal rumen. The wave of contraction has passed caudally across the ventral rumen and its arrival at the regions of the ventral coronary pillars coincides with a marked ventral displacement of the caudal pillar.

Ab abomasum, CdP caudal pillar, CdVBS caudal ventral blind sac, CP cranial pillar, DRu dorsal rumen, F fistula, G gas cap, Re reticulum, S spleen, VRu ventral rumen.


2
TIME
4-4

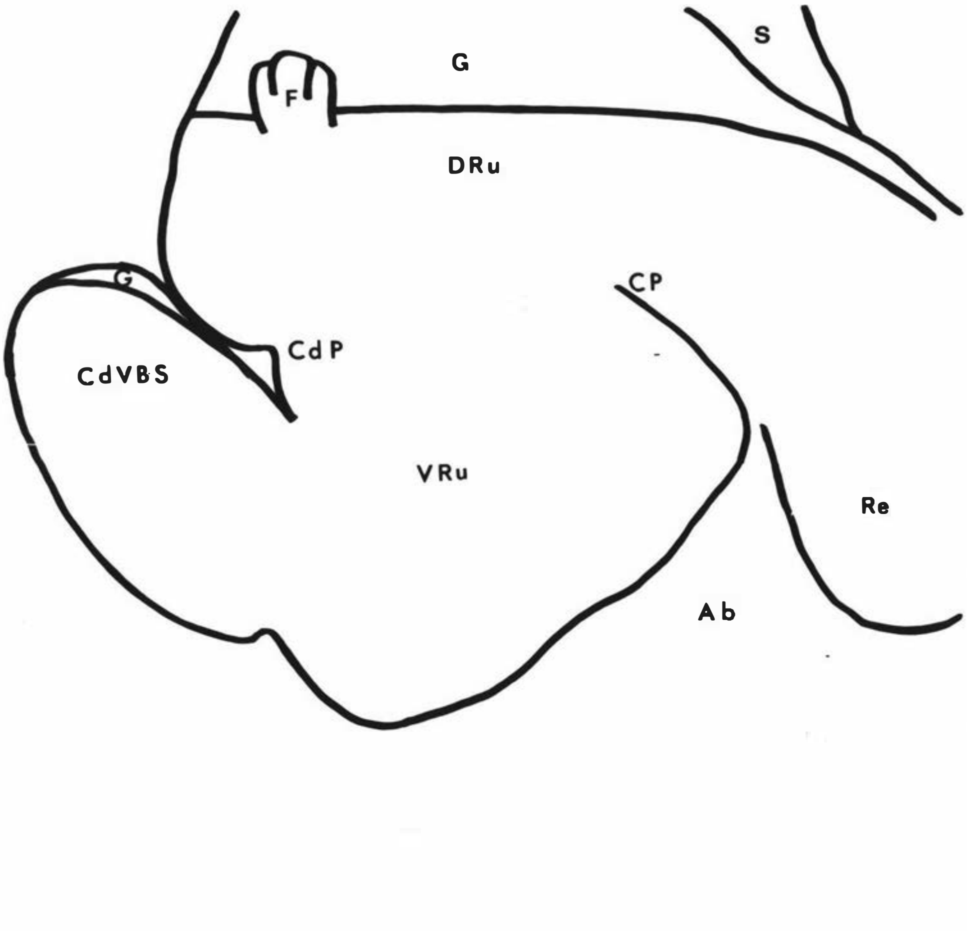
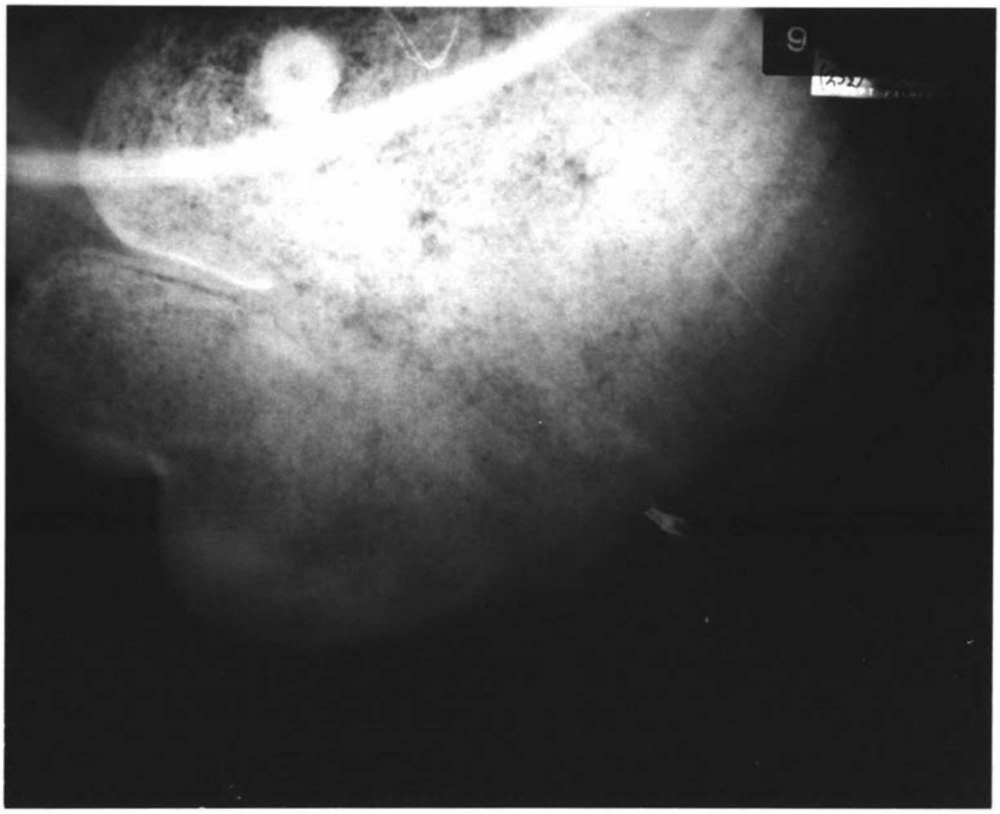

G
S
F
DRu
G
CP
CdP
CdVBS
VRu
Re
Ab

PLATE 31

Twenty seven seconds after the start of a reticular contraction. The wave of contraction continues caudally along the caudal-ventral blind sac as the caudal pillar starts to return towards its resting position.

Ab abomasum, CdP caudal pillar, CdVBS caudal ventral blind sac, DRu dorsal rumen, E electrode, F fistula, VRu ventral rumen.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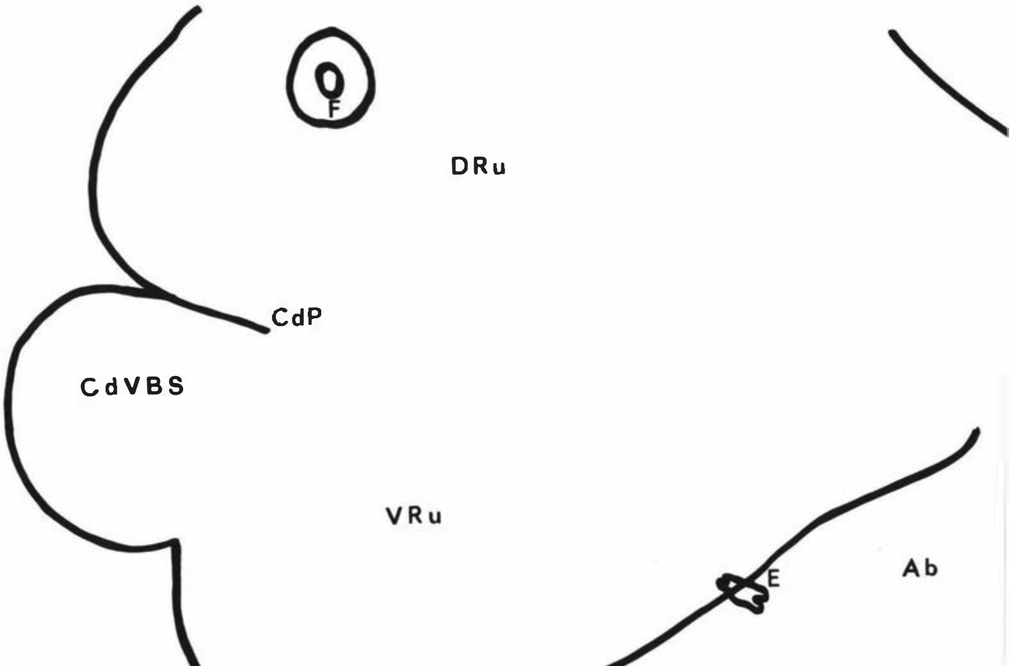
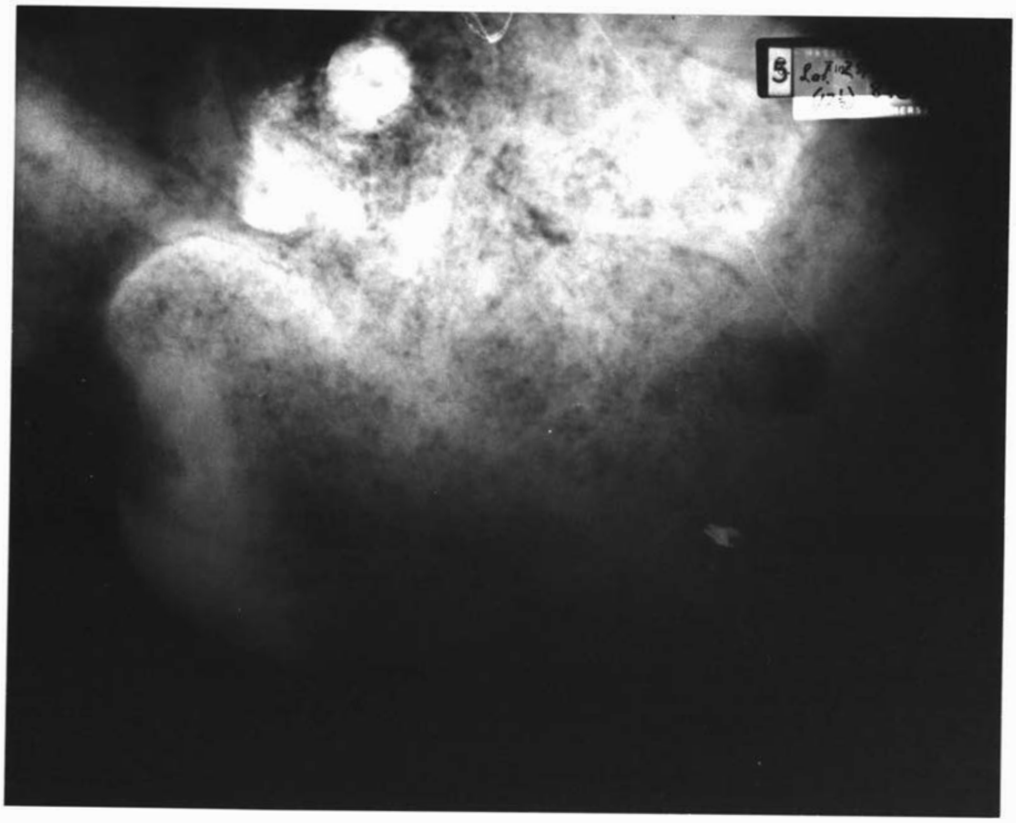

F
DRu
CdP
CdVBS
VRu
E
Ab

PLATE 32

Thirty seconds after the start of a reticular contraction. The pole of the caudal ventral blind sac has contracted down displacing the caudal pillar a short distance dorsally. The cranial part of the ventral rumen becomes slightly distended.

CdP caudal pillar, CdVBS caudal ventral blind sac, DRu dorsal rumen, E electrode, F fistula, Re reticulum, S spleen, VRu ventral rumen.


5
Lat.

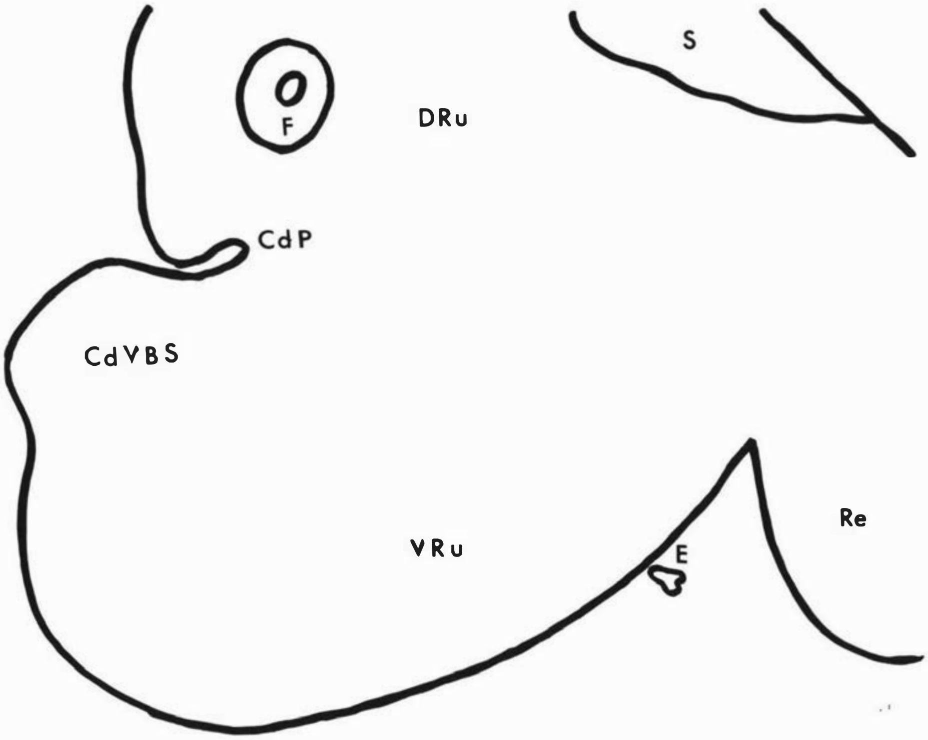
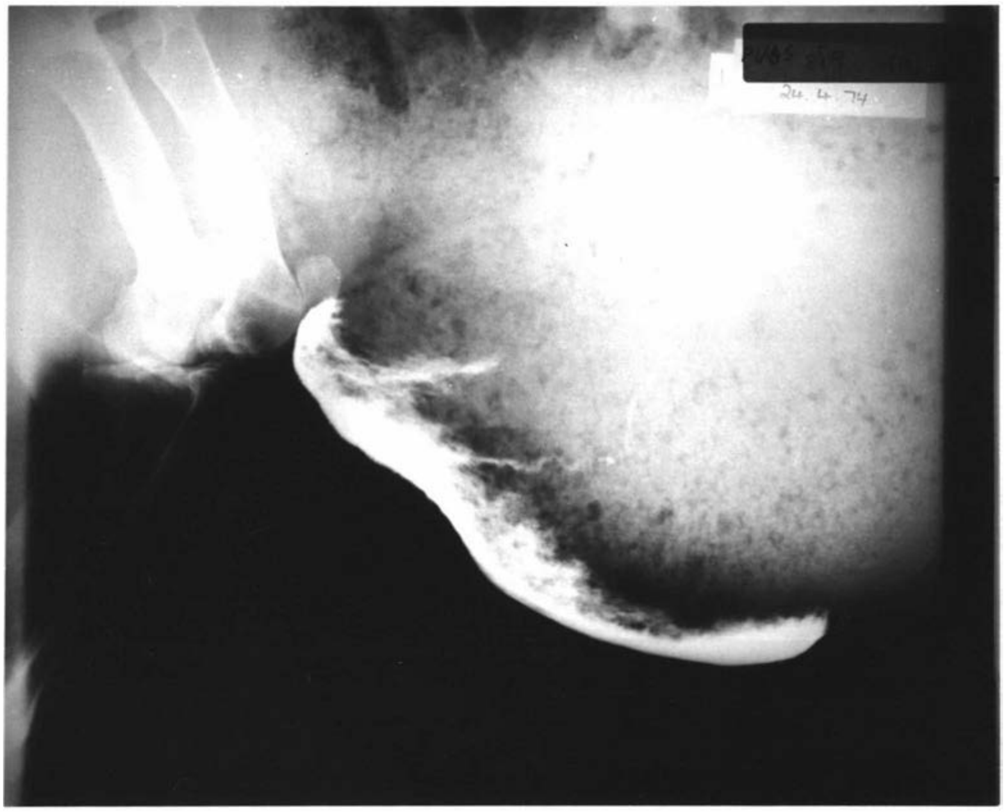

S
F
DRu
CdP
CdVBS
VRu
E
Re

PLATE 33

Thirty five seconds after the start of the reticular contraction. The pole of the caudal ventral blind sac has started to relax and the caudal pillar has returned to its resting position. A wave of contraction now starts to travel cranially across the caudal ventral blind sac.

CdVBS caudal ventral blind sac, DRu dorsal rumen, F fistula, VRu ventral rumen.


24. 4. 74

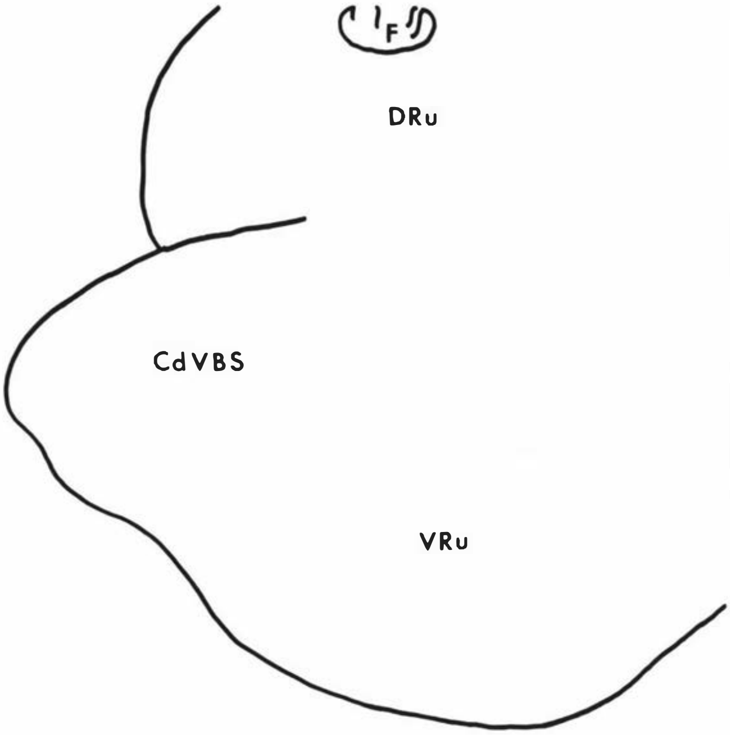
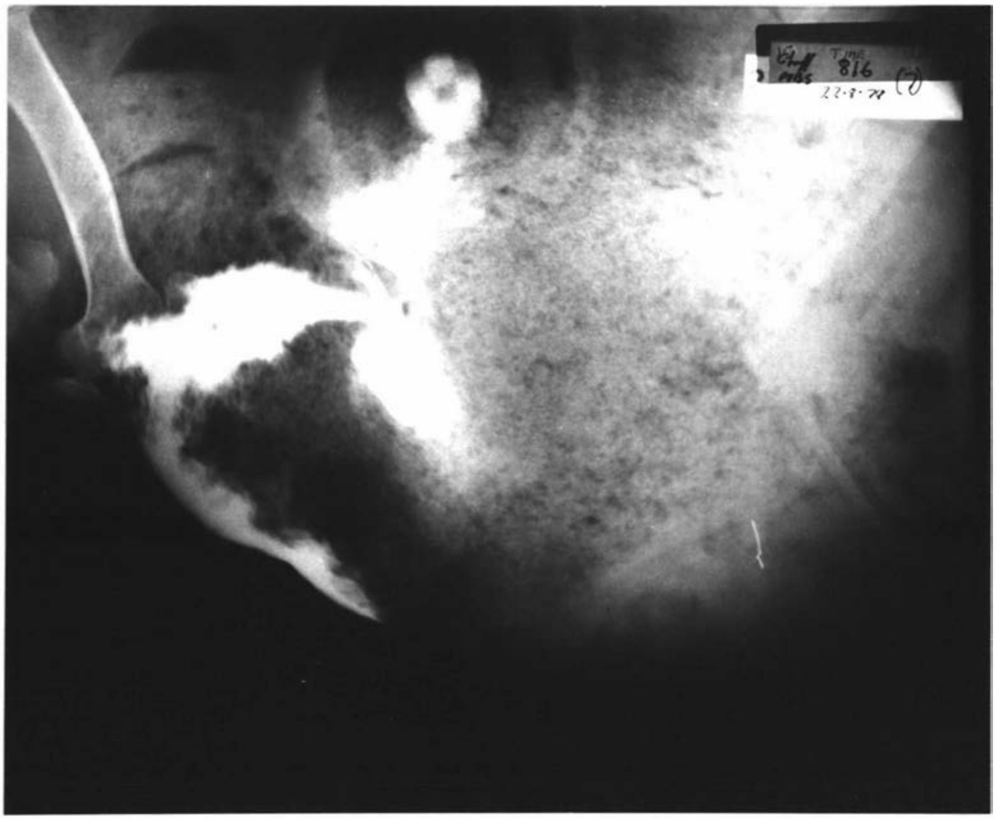

IF
DRu
CdVBS
VRu

PLATE 34

Thirty seven seconds after the start of the reticular contraction. The wave of contraction has travelled cranially to the level of the ventral coronary pillars and there is an associated second ventral displacement of the caudal pillar.

CdP caudal pillar, CdVBS caudal ventral blind sac, DRu dorsal rumen, E electrode, F fistula, Re reticulum, VRu ventral rumen.


TIME
816
22.8.78

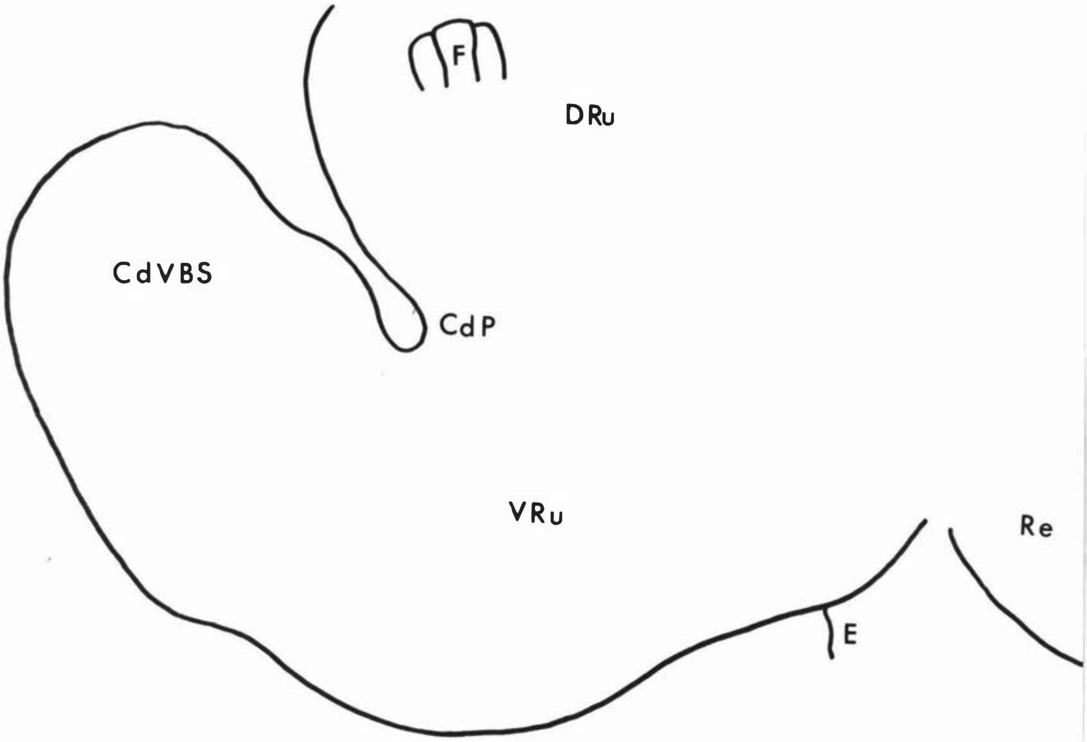
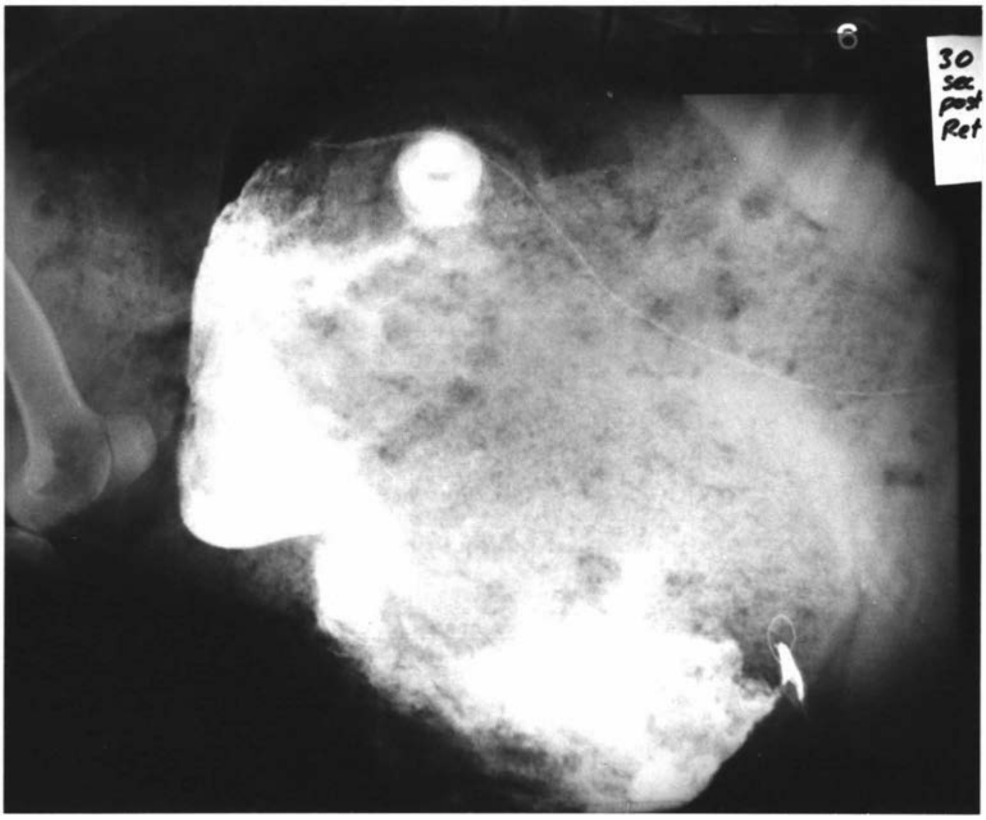

F
DRu
CdVBS
CdP
VRu
Re
E

PLATE 35

Forty five seconds after the start of the reticular contraction. The cranial aspect of the ventral rumen has contracted as can be seen by straightening of this part of the rumen wall. The caudal pillar has returned to its resting position. This completes the sequence of contractions that occur if no eructation is going to take place.

CdP caudal pillar, CdVBS caudal ventral blind sac, DRu dorsal rumen, E electrode, F fistula, G gas cap, Re reticulum, S spleen, VRu ventral rumen.


6
30 sec post Ret

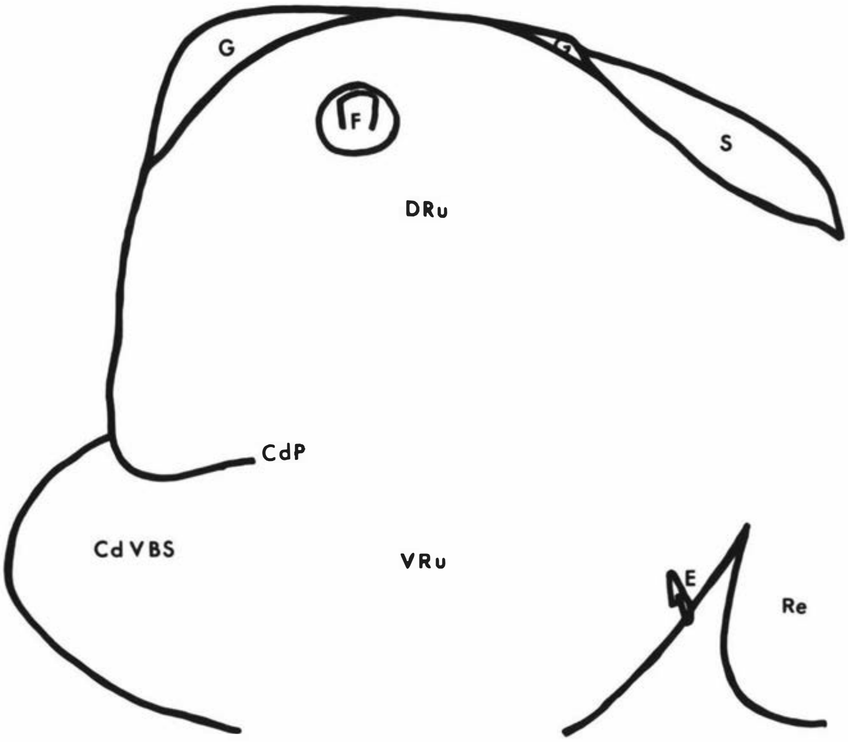
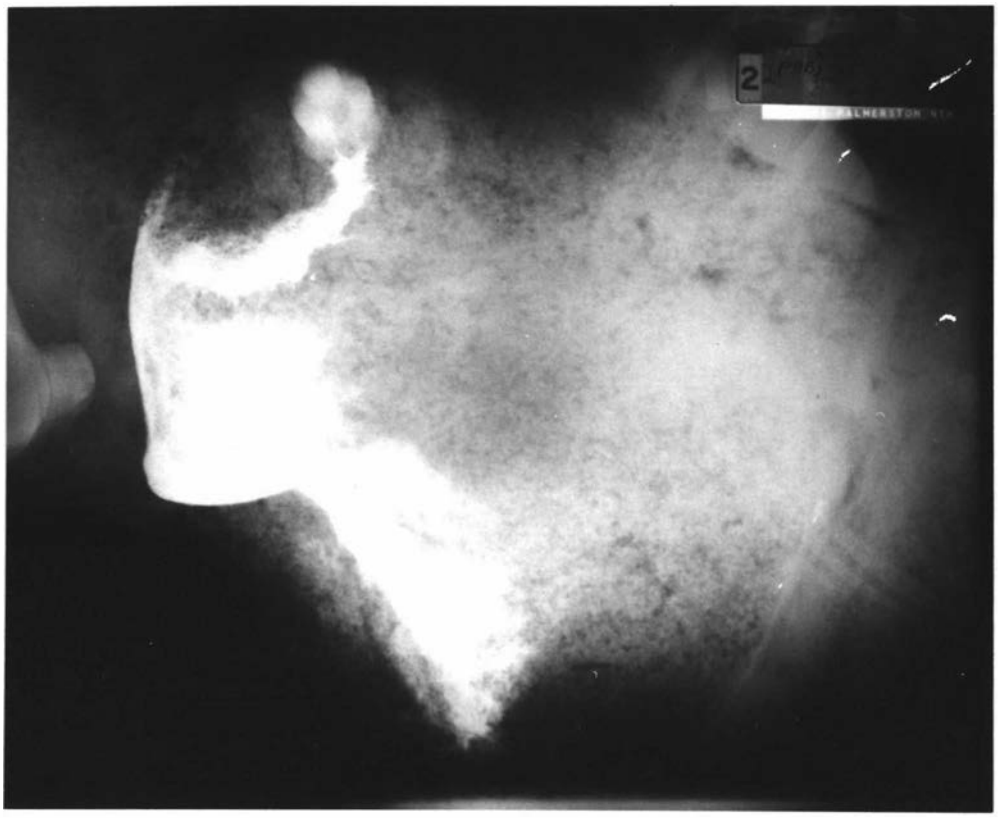

G
G
F
S
DRu
CdP
CdVBS
VRu
E
Re

PLATE 36

Thirty five seconds after the start of the reticular contraction during a sequence of contractions that eventually culminated in eructation. The pole of the caudal ventral sac is just starting to contract for the second time and the caudal pillar is just starting to move dorsally.

CdP caudal pillar, CdVBS caudal ventral blind sac, DRu dorsal rumen, F fistula, G gas cap, Re reticulum, S spleen, VRu ventral rumen.


2
PALMERSTON NTH

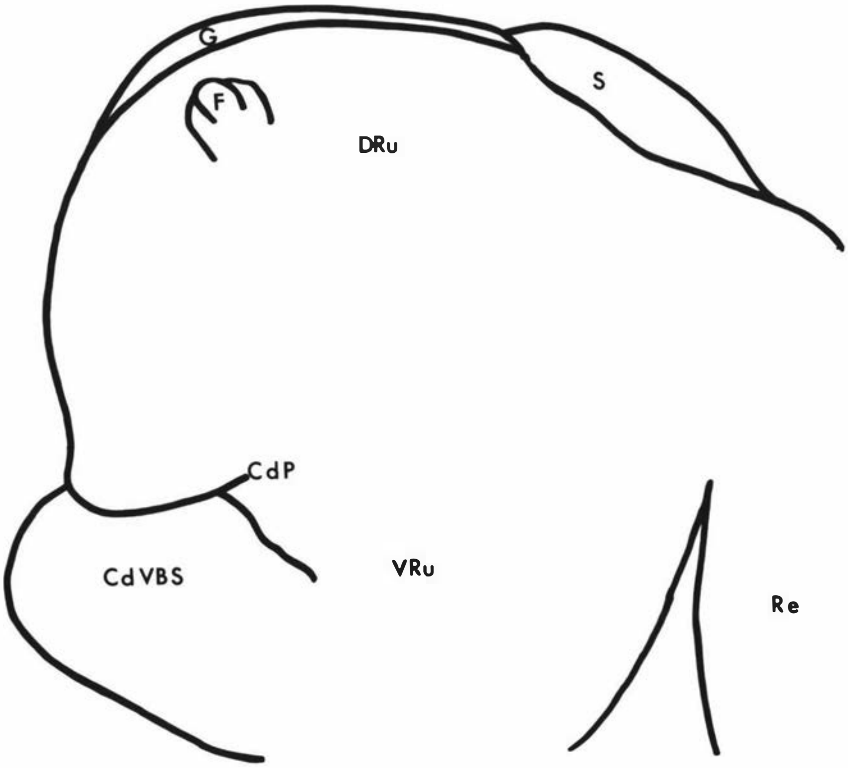

G
F
DRu
S
CdP
CdVBS
VRu
Re

PLATE 37

Thirty six seconds after the start of a reticular contraction. The caudal pillar continues to curl dorsally and a contraction of the more caudal part of the dorsal rumen displaces the gas cap cranially. The pole of the caudal ventral blind sac is starting to relax and from it a contraction wave starts to move cranially.

CdP caudal pillar, CdVBS caudal ventral blind sac, CP cranial pillar, DRu dorsal rumen, F fistula, G gas cap, VRu ventral rumen.


3
MASSE
4. 4. 74
2 DEPT PALMERSTON NTH
(12)

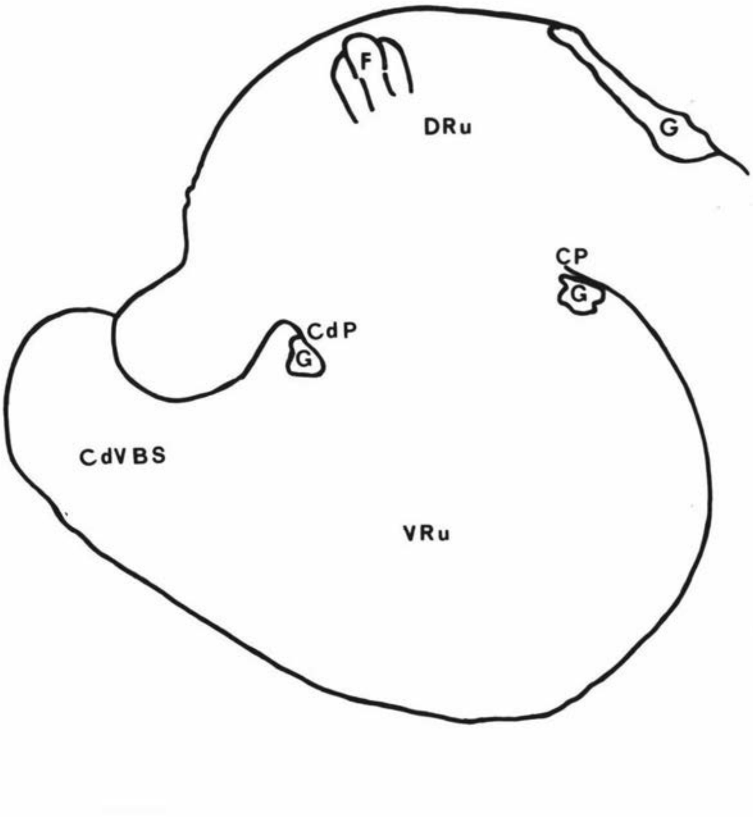
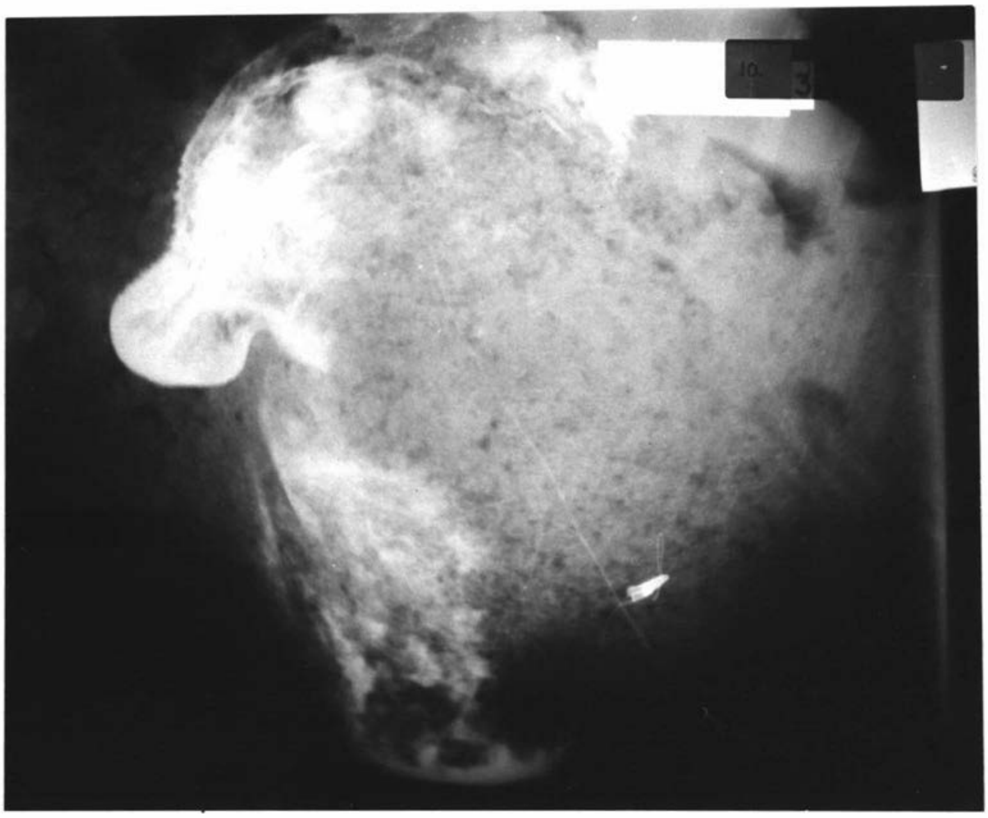

F
DRu
G
CP
G
CdP
G
CdVBS
VRu

PLATE 38

Thirty seven seconds after the start of the reticular contraction. The contraction of the dorsal rumen moves cranially elevating its more ventro-caudal region along with the caudal pillar. The gas cap is displaced further cranially.

CdP caudal pillar, CdVBS caudal ventral blind sac, DRu dorsal rumen, E electrode, F fistula, G gas cap, Re reticulum, S spleen, VCP ventral coronary pillar, VRu ventral rumen.



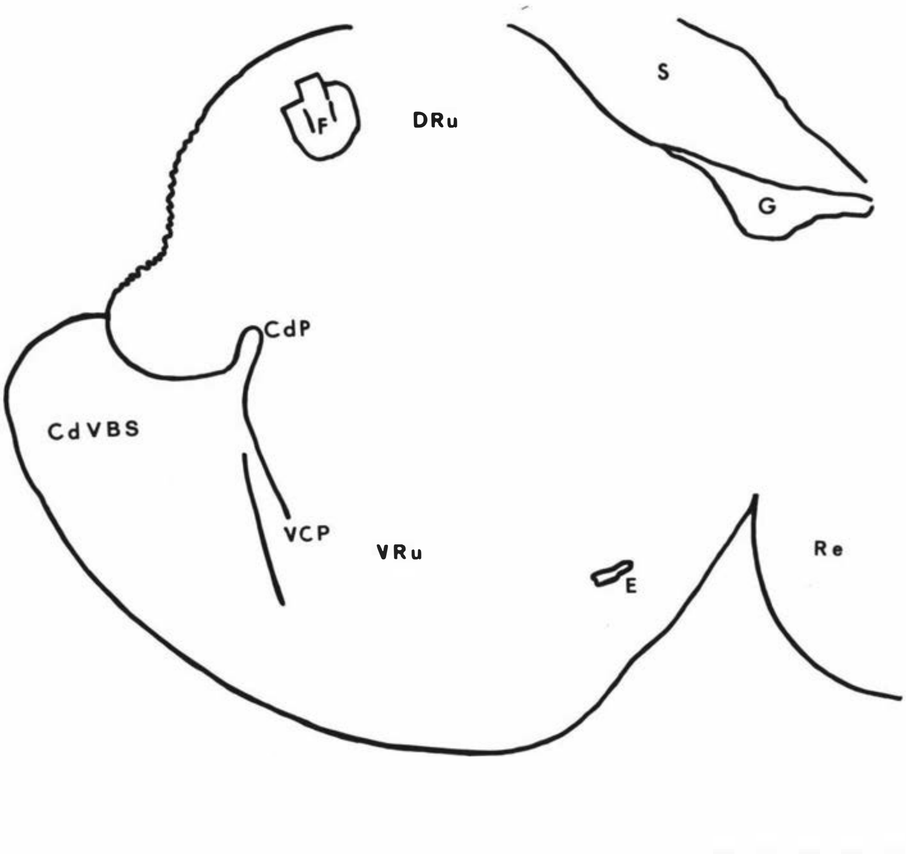
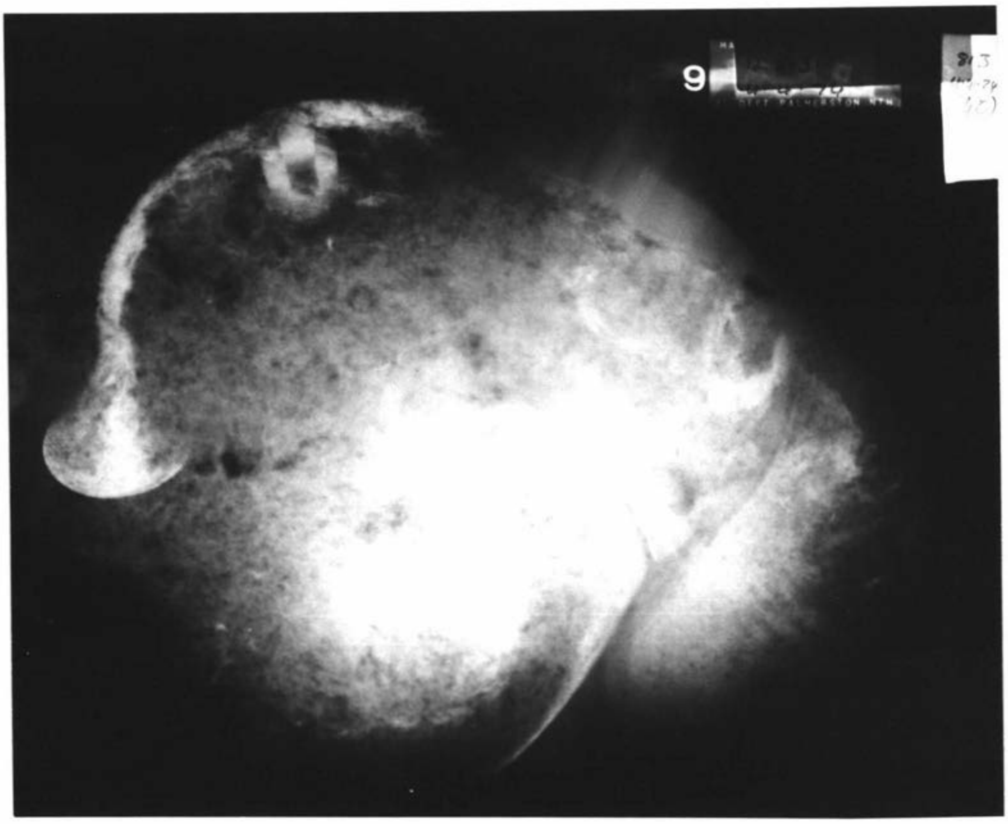
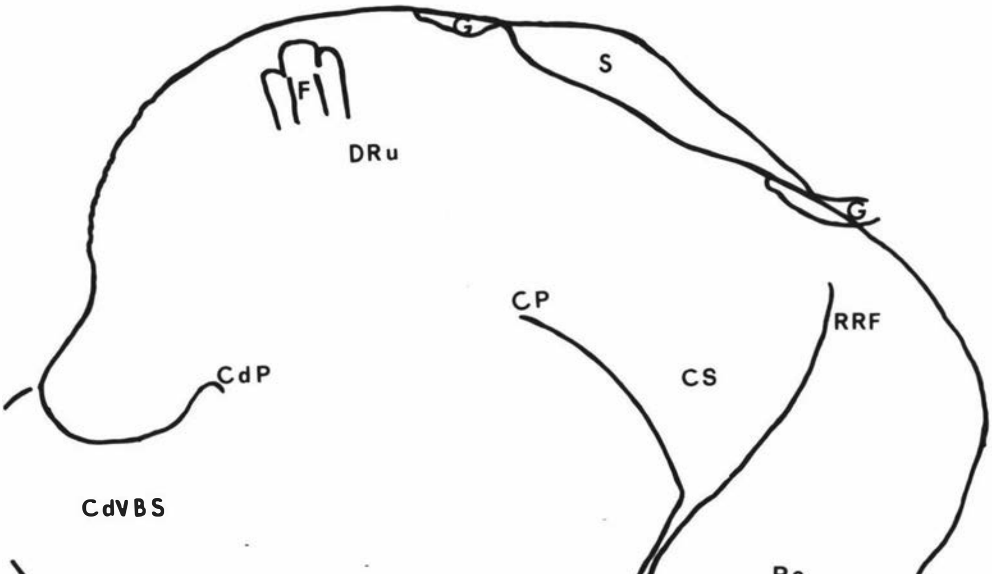

F
DRu
S
G
CdP
CdVBS
VCP
VRu
E
Re

PLATE 39

Thirty eight seconds after the start of the reticular contraction. The caudal pillar has started to return to its resting position as the cranial pillar moves caudo-dorsally. Eructation occurs.

CdP caudal pillar, CdVBS caudal ventral blind sac, CP cranial pillar, CS cranial sac, Dru dorsal rumen, F fistula, G gas cap, Re reticulum, RRF reticulo-ruminal fold, S spleen, VRu ventral rumen.


9
PALMERSTON NTH
81.3


G
S
F
DRu
G
CP
RRF
CdP
CS
CdVBS
Re
VRu

the dorsal blind sac forming a simple continuous curve they tended to form a more complex S shape.

The outline of the caudal aspects of the rumen at different stages of the contraction cycle was derived from cine-films and is illustrated in Figure 3 (1-16).

3:3:6 The movement of digesta within the reticulo-rumen and the effects of different diets.

The flow pattern of the digesta within the reticulo-rumen was similar in the three sheep and on the three diets although there were some differences detected in the rate of digesta movement associated with the different diets.

The pattern of flow derived from these observations is illustrated in Figure 4. When the marker was given orally some was always deposited in the reticulum and cranial sac with the proportions going into each being variable. There was no relationship either with the sheep or with diets as to the proportions deposited in these two sites. At the first contraction of the reticulum following the administration of the marker, the tipping of the reticulum contents into the cranial sac and their return meant that the marker became distributed between these two chambers. On occasions some of the marker could be deposited into additional sites such as the cranio-dorsal rumen, omasum, or omasum and abomasum, but again the sites of deposition of the marker could not be related to the sheep or the diet. When the marker was deposited into the cranial dorsal rumen it passed cranially into the reticulum or cranial sac at the next contraction sequence. Thus when the marker was given orally, irrespective of where in the reticulo-rumen it was initially deposited, it ended up in the reticulum and cranial sac, being tipped from one to the other at each contraction sequence. On many occasions following oral administration of the marker, a small amount of it could be seen to pass into the omasum at the height of the second phase of the first ensuing reticular contraction and then to trickle through into the abomasum. However, after the marker had initially outlined the omasum, it was not possible to detect any additions of marker at subsequent reticular contraction.

FIGURE 4

These two drawing illustrate the movement of digesta within the reticulo-rumen in the vertical plane (1) and in the horizontal plane (2).

In the vertical plane (1) swallowed material may be deposited in the reticulum, cranial sac, dorsal rumen, or may pass directly through the omasum into the abomasum. Where the swallowed material is deposited depends on (a) the type of material, (b) the consistency of the reticulo-ruminal contents, (c) the amount of digesta in the reticulo-rumen, (d) the stage of the contraction cycle at which the bolus of material was delivered through the cardia.

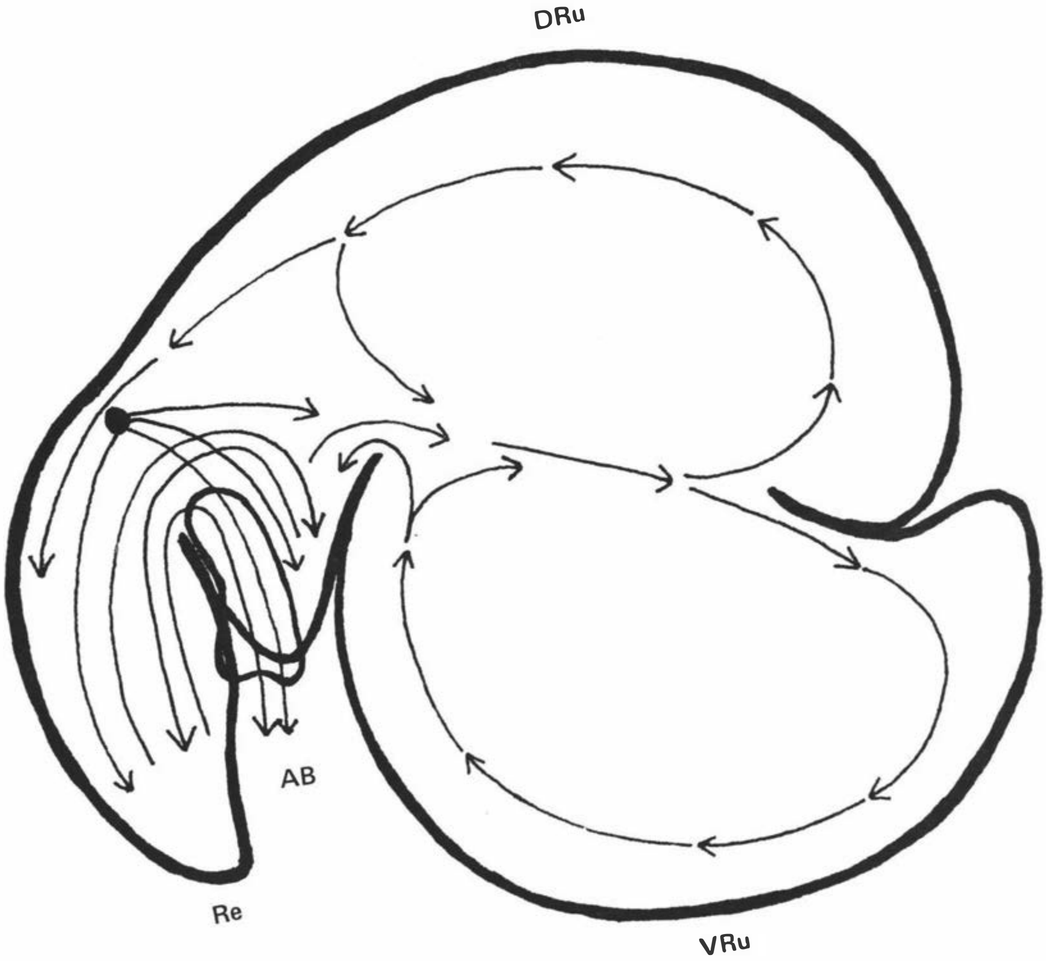
From the reticulum, digesta is passed into the cranial sac or into the omasum and abomasum.

From the cranial sac, digesta either passes back into the reticulum, or into the dorsal rumen.

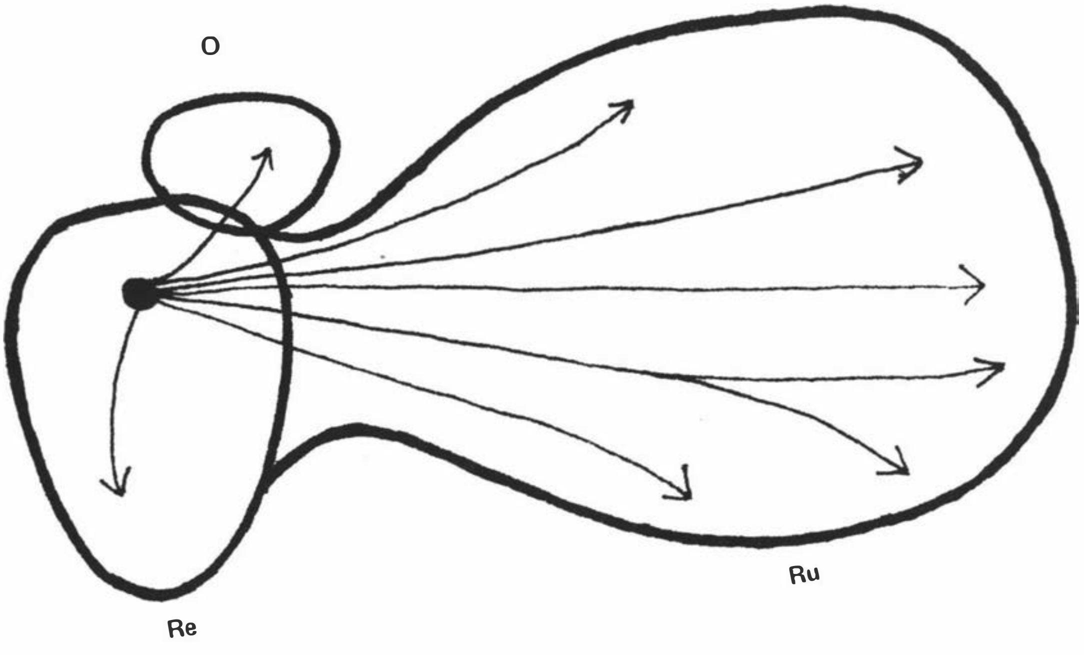
Once the digesta enters the rumen, it passes caudally towards the caudal pillar where it is split into a dorsal and a ventral stream. The dorsal stream moves anticlockwise round the dorsal rumen, dividing cranially into a stream which enters the reticulum and a stream which rejoins the caudally-moving stream in mid-rumen. The ventral stream moves clockwise round the ventral rumen, dividing cranially with one stream entering the cranial sac and the other rejoining the caudal mid-rumen flow.

In the horizontal plane (2), marked digesta is much more difficult to follow radiographically, but it can be seen to move from the cardia into the reticulum, into the omasum and to pass caudally across the rumen.

1



2



With each contraction of the reticulum some of the marker was pushed into the mid-rumen region from where it was passed caudally towards the caudal pillar. When this caudally-moving stream arrived in the vicinity of the caudal pillar it was split, part moving dorsally and part ventrally. The dorsal stream moved into the dorsal blind sac then turned cranially into the dorsal rumen. From here it continued cranially towards the reticulum. Once it reached a position approximately level with the cranial pillar at the height of its contraction, this stream was again divided into two portions. The major portion passed ventrally to join the caudally moving stream in the mid-rumen. The smaller dorsal portion moved into the reticulum from where the majority of it was pushed caudally again to join the caudally moving stream in mid-rumen. The portion of the marker which had passed ventral to the caudal pillar flowed caudo-ventrally into the caudal ventral blind sac from where it started to move cranially across the more ventral parts of the ventral rumen. The marker then passed dorsally up the cranial wall of the ventral rumen then up the caudal aspect of the cranial pillar. At the lip of the cranial pillar the stream was divided with the part closest to the pillar passing over into the cranial sac. The remainder joined the caudally moving stream in the mid-rumen.

When the marker was deposited in the dorsal blind sac on top of the caudal pillar by introducing it through the rumen fistula it moved through the reticulo-rumen in a pattern very similar to that seen with oral administration. As the marker was being deposited some of it slowly flowed over the lip of the caudal pillar and fell directly onto the floor of the ventral rumen. The marker remaining in the dorsal blind sac moved dorsally and cranially into the dorsal rumen, from where it followed the same path as that described for the dorsally moving stream when the marker was administered orally. That portion which had spilled over the caudal pillar into the ventral rumen was only rarely displaced caudally into the caudal ventral blind sac. On the majority of occasions it immediately started to move cranially taking the same path from this point on as described for the orally administered marker.

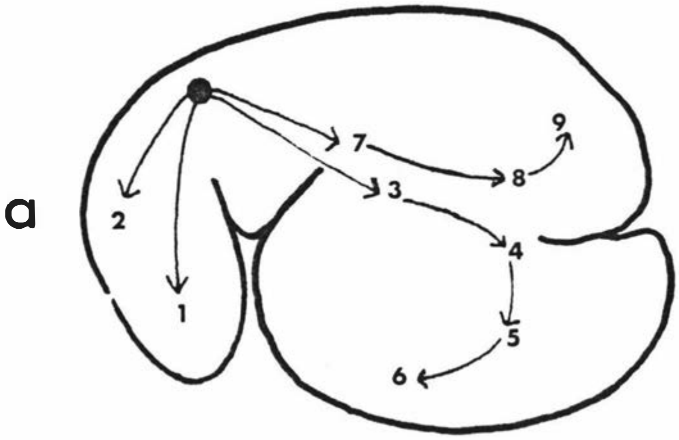
When the flow pattern in the horizontal plane was observed with the marker administered orally it was again seen to be deposited mainly in the reticulum and cranial rumen with a small amount frequently passing into the omasum. The portion from the reticulum and cranial rumen was then dispersed caudally across the rumen. Cross check radiographs taken of the movement in the vertical plane showed that this horizontal caudal dispersion was the caudally moving stream in mid-rumen. When the marker was deposited in the dorsal blind sac it was seen to disperse cranially in the horizontal plane until it arrived in the reticulum. Cross check radiographs taken of the movement in the vertical plane showed that this cranial dispersion was the cranial flow both in the dorsal and ventral rumen, superimposed on each other.

The rate of flow of digesta on the three diets (chaff, pellets and grass) was determined by measuring the time taken for a radio-opaque marker given orally, or placed on top of the caudal pillar, to reach pre-determined positions, and is illustrated in Figure 5. The mean times taken for the marker to reach these locations on the three diets is given in Table VII. When the marker was placed on the caudal pillar it moved fastest on the pellet diet, slightly slower on the grass diet, and approximately half the speed on the chaff diet. The differences in speed when the marker was administered orally were not so great but it again moved most rapidly on the pellet diet and slowest on the chaff diet. These differences appeared to be related to the consistency of the rumen contents on the three diets.

A subjective impression of the consistency of the rumen contents on each of the three diets was obtained by radiographic observation. On the chaff diet a comparatively solid raft formed in the dorsal rumen. This raft had various fissures or clefts through it, which remained constant over a large number of contraction sequences. Contraction of the dorsal rumen on top of the raft did not detectably alter its shape and the tract made through the raft when the catheter was passed into the dorsal blind sac remained clearly visible over a number of contraction sequences. With the grass diet on the other hand, although a definite raft was discernible in the dorsal rumen, it had no fissures or clefts in it, and contraction of the dorsal rumen did obviously alter its shape. Furthermore, the tract made by passing the catheter into the dorsal blind sac disappeared within a very short

FIGURE 5

The diagrams and table illustrates the flow pattern and rates of movement of a radio-opaque marker administered orally (a) and placed on top of the caudal pillar (b).



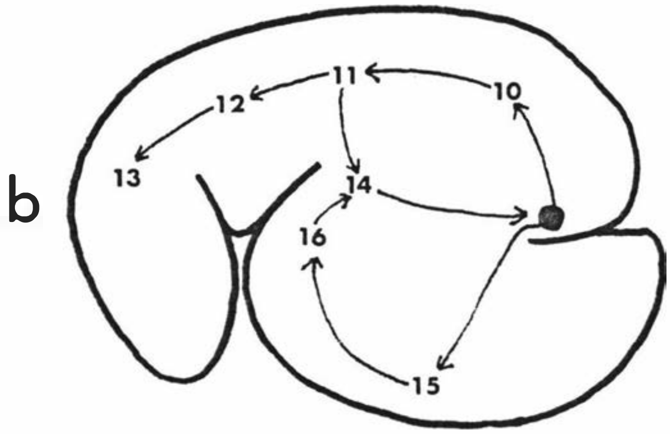


TABLE VII

THE EFFECT OF THREE DIETS ON THE MEAN TIMES (MINUTES) TAKEN FOR THE RADIO-OPAQUE MARKER TO REACH THE NUMBERED POSITIONS.

Starting Site	Oral									Caudal pillar						
Location	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Chaff diet	2	4	3	9	13	27	1	3	17	8	30	42	52	42	9	31
Grass diet	2	3	2	11	19	22	1	4	14	4	15	19	24	27	5	16
Pellet diet	1	2	2	8	13	-	1	4	14	5	13	6	20	-	6	20

time after the catheter had been withdrawn and certainly was never visible after one contraction of the dorsal rumen. When the pellet diet was fed no distinct raft in the dorsal rumen could be seen and each contraction of the rumen set up fluid waves in the dorsal rumen. No tract was left on withdrawal of the catheter from the dorsal blind sac. With these sheep the marker was rapidly dispersed throughout the rumen digesta so it could not be traced for as long a time as when the sheep were on a chaff or grass diet.

3:3:7 The effects of abomasal distension on the contractions of the reticulo-rumen.

When sheep 2, 3 and 21 sucked either milk or whey from a bottle they also swallowed considerable volumes of air, estimated to range from 250 ml to 460 ml, so that the abomasum was distended by total volumes ranging from 850 ml to 1060 ml. This degree of distension did not appear to cause the sheep any discomfort and they were willing to suck more from the bottle if it was offered. The distended abomasum caused the reticulum to be markedly flattened against the diaphragm and thus emptied of most of its contents (Plate 40). The swallowed gas formed a large cap at the fundic end of the abomasum, but only on two occasions did it pass back through the omasum into the reticulo-rumen, and it did so within a minute of the sheep stopping sucking. In all other instances the gas was eliminated from the abomasum through the pylorus over a long period of time.

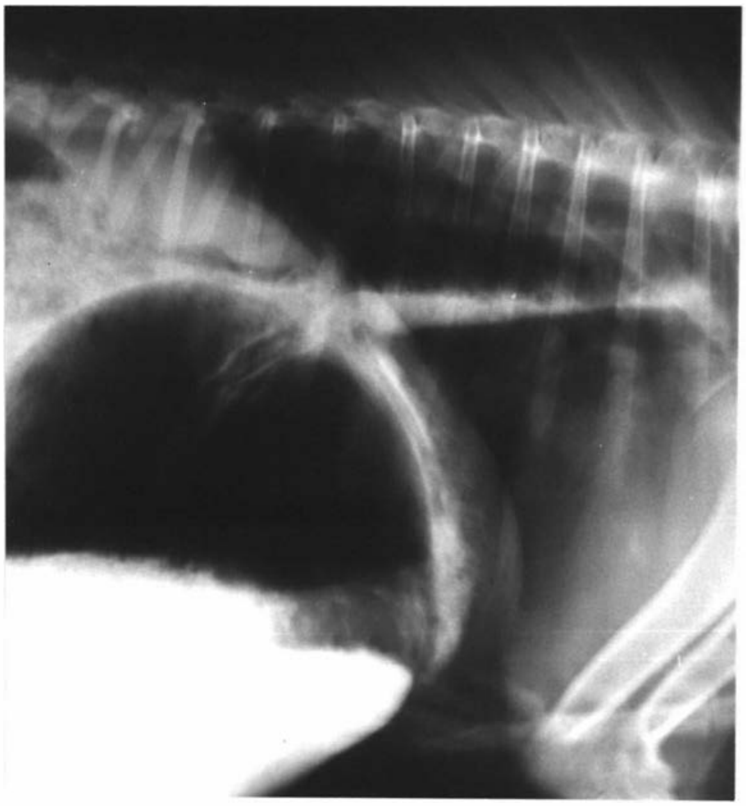
The immediate effect of abomasal distension was to interrupt the normal cyclical activity of the reticulo-rumen, sometimes for prolonged periods (Table VIII). On one occasion normal cyclical activity was not seen for 130 minutes after the abomasum was distended. The cranially-moving contraction of the dorsal sac of the rumen always returned first and on some occasions was not eliminated by abomasal distension. Whether or not this contraction was abolished, and the length of time for which it was abolished, could not be related to the degree of distension or the route of administration of the distending material.

In sheep 1, 2 and 3 distension of the abomasum with 600 ml of fluid

PLATE 40

Abomasal distension with gas and milk following bottle feeding. The reticulum is compressed between the distended abomasum and the diaphragm.

Ab abomasum, D diaphragm, DRu dorsal rumen, O omasum,
OO omasal orifice, Oe oesophagus, Re reticulum, S spleen.



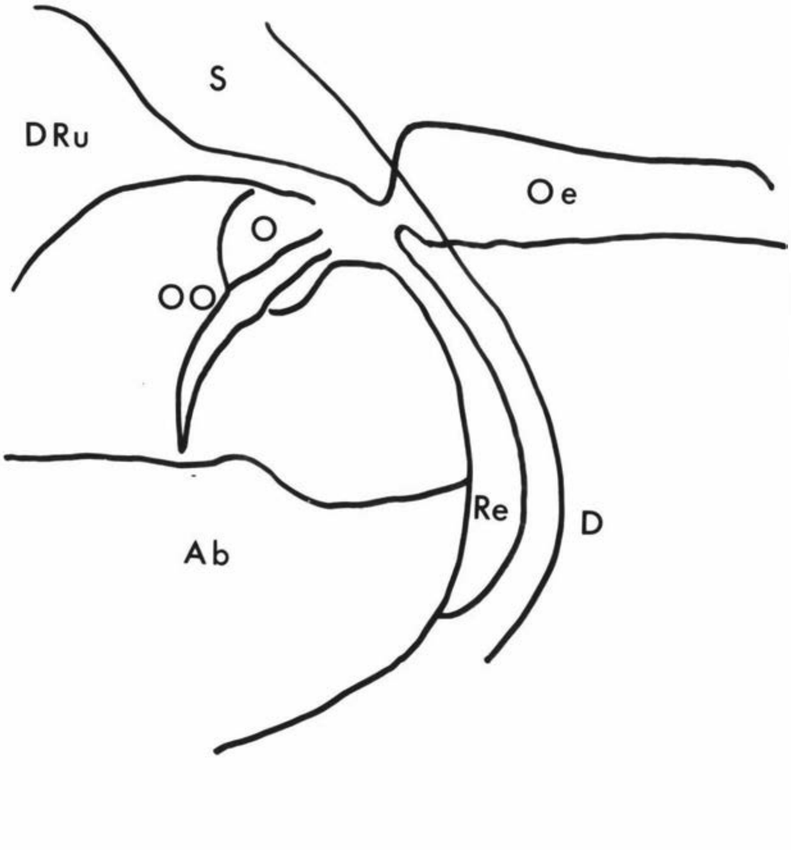

S
DRu
Oe
O
OO
Re
D
Ab

TABLE VIII

EFFECTS OF ABOMASAL DISTENSION ON RETICULO-RUMINAL MOTILITY.

Observation Session	Mean time (mins) between Re contractions before Ab distended	Ab distending material (ml)		Route of Administration	Time (mins) to first contraction			Route of gas elimination from abomasum
		Fluid**	Air		DRu	Re	Complete sequence	
1A	1.15	600	0	Per catheter	6.67	17	130	-
2A	1.02	600	200	Per catheter	1.83	3.33	14	Pylorus
3A	1.13	-	200	Per catheter	0.53	0.75	6	Pylorus
1B	0.92	600	300*	Per os	2.50	6.23	8.07	Pylorus
2B	1.00	600	350*	Per os	0.95	11.3	29.0	Pylorus
3B	0.93	600	460*	Per os	2.67	15.0	16.6	Pylorus
1C	1.22	600	250*	Per os	2.83	24.50	58.2	Pylorus
2C	1.10	600	360*	Per os	2.08	38.33	102	Pylorus
3C	1.00	600	300*	Per os	0.38	5.03	13	Omasum
1D	0.95	600	150	Per catheter	0.50	0.83	28	Pylorus
2D	0.82	600	470*	Per os	1.04	0.85	55	Omasum
3D	0.87	600	500*	Per catheter	1	1.18	65	Pylorus

* Volume of air estimated using BUBIL programme (See Appendix 2)

** The fluid was milk except in sessions 2B and 3B when it was whey.

Re - Reticulum
DRu - Dorsal rumen
Ab - Abomasum

with or without an associated volume of gas, caused inhibition of reticular contractions whereas the introduction of 200 ml of gas alone into the abomasum of sheep 1 through a catheter did not inhibit reticular contractions. The length of time for which the reticular contractions were inhibited could not be related to the degree of distension of the abomasum. The return of the reticular contractions took place gradually. Initially there was a weak simple contraction which gradually increased in strength then eventually became biphasic. The first reticular contraction was taken at the first detectable dorsal movement of the ball bearing in the reticulum. The first strong biphasic contraction of the reticulum corresponded with the first complete caudally moving contraction sequence. In sheep 21 the reticulum was never completely inhibited but its contractions became weak and monophasic. This sheep had not been weaned and its reticulorumen appeared relatively small and certainly less full than in the other 3 sheep, with the result that the distended abomasum did not compress the reticulum against the diaphragm to the same extent.

While observing the abomasal activity of these sheep an impression was formed that the clotting of the milk in the abomasum was considerably slowing down its rate of emptying and acting as an obstruction to the elimination of the gas cap through the pylorus. Whey, which did not clot in the abomasum, was fed to sheep 2 and 3 on one occasion, but did not alter the rate of elimination of the gas cap or the rate of emptying of the abomasum.

An interesting observation was made when administering the stainless steel ball bearings which were to act as markers in the reticulum. The sheep were given the ball bearings by placing them as far back on the tongue as was possible with the fingers then holding the mouth shut until they swallowed. When sheep 1, which was not bottle fed, swallowed the ball bearing, it dropped straight down into the reticulum. When sheep 2, 3 and 21, which were bottle fed, swallowed ball bearings administered by the person who fed them, they passed straight through into the abomasum. This was repeated once in each of the three sheep with the same results. When an individual who was a stranger to the three sheep gave the ball bearings, they dropped into the reticulum.

3:3:8 The effects of partial exteriorisation of the reticulum and rumen fistulation on the contractions of the reticulo-rumen.

Exteriorisation of the reticulum affected both the movement of digesta from the reticulum and the movement of the cranial pillar. The adhesion of the reticular wall at the site of exteriorisation prevented the usual almost complete obliteration of the lumen that takes place during contraction so that some digesta remained in the reticulum. In sheep 20 the movement of the cranial pillar was seen to be dorso-cranial rather than dorso-caudal. Observations with sheep 30 showed that prior to surgery the cranial pillar contracted dorso-caudally but, following exteriorisation of the reticulum, the contraction was dorso-cranial. This change in the direction of contraction brought the midpoint of the free border of the cranial pillar much closer to the dorso-cranial wall thus increasing its effectiveness as a barrier to the flow of digesta from the cranial dorsal rumen into the reticulum.

The effects of rumen fistulation were not so obvious. The adhesions of the rumen to the abdominal wall prevented the dorsal sac of the rumen contracting down as far as it did in intact sheep, which resulted in the gas cap in the dorsal rumen not being displaced as far cranially as normal (Plates 17 and 18). There was no recognisable alteration to the pattern of movement of the cranial or caudal pillars.

3:4 DISCUSSION

The sequence of events observed during the contraction cycles of the reticulo-rumen in this study is basically similar to previous descriptions (Reid and Cornwall, 1959; Reid, 1960, 1962, 1963; Titchen and Reid, 1965; Tsiamitas, 1972; Ruckebusch and Tomov, 1973; Kölling, 1974, 1974a). An A sequence commenced with a biphasic contraction of the reticulum followed by contractions progressing caudally across the rumen and a B sequence commenced with a contraction of the caudal ventral blind sac followed by contractions moving cranially across the rumen - this latter sequence was usually associated with eructation.

A summary of the contraction sequences is shown in Figure 6 (1-21).

The motility pattern was as reported by Reid (1963), a series of A sequences interspersed with B sequences. However, on no occasion in this present study was a B sequence seen to occur other than following on immediately from an A, whereas Reid (1962) recorded a number of isolated B sequences. This difference could be due to the different states of the animals at the time of observation since the sheep in this study were either fasted for 18 hours or were feeding ad libitum, while most of the isolated B sequences observed by Reid (1962) occurred in sheep feeding after an 18 - 24 hour fast. Others (Weiss, 1953; Dougherty, 1961; Sellers and Stevens, 1966) have reported an increase in rumen contractions, presumably B sequences, in response to insufflation of the rumen with gas suggesting that the occurrence of isolated B sequences could be related to the rate of gas production.

The first radiologically detectable movement at the start of an A sequence was a dorsal movement of the ventral border of the reticulo-ruminal fold, an observation which is compatible with the suggestion that the contraction sequence is initiated somewhere in the region of the reticular groove (Wester, 1962; Schalk and Amadon, 1928). However, this conflicts with the finding of Akester and Titchen (1969) who reported that the reticulo-ruminal fold started to move after the reticulum had started to contract. Such a discrepancy in observations could be explained by the short time interval of approximately 0.25 seconds between the first movement of the reticulo-ruminal fold and the start of the dorsal movement of the pole of the reticulum.

As has been reported (Dziuk and McCauley, 1965) there was not complete relaxation of the reticulum between its two phases of contraction. In two animals some relaxation was manifest by a slight ventral movement of the pole of the reticulum. As the dorsal sac and dorsal blind sac of the rumen contracted the reticulum became distended beyond its normal resting size confirming reports by Phillipson (1939) and Benzie and Phillipson (1957), but this was much more pronounced in an A sequence than a B sequence. The series of events in the reticulum associated with eructation described by Dougherty and Meredith (1955)

FIGURE 6

The following series of drawings of the reticulo-rumen has been derived from information obtained in the described observations and represents a summary of the events that occur during a contraction sequence. The part of the outline drawn with a thicker line indicates the region that is actively contracting. The dotted areas indicate the position of the gas caps.

1. The resting stage with no contractions taking place. The double dotted line represents the point of attachment to the dorsal wall of the abdomen.

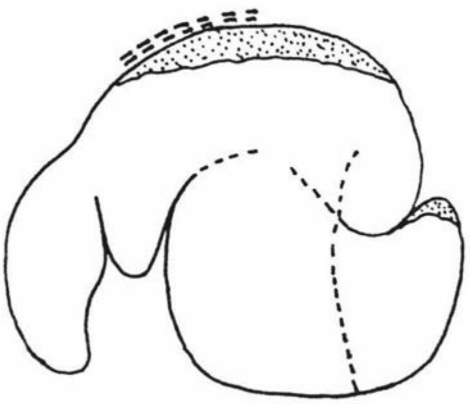
2. The start of a sequence of contraction. Dorsal movement of the ventral part of the reticulo-ruminal fold, contraction of caudal border of the reticulum, slight caudal displacement of the pole of the reticulum.

3. The end of the first phase of reticular contraction. The pole of the reticulum and the reticulo-ruminal fold move dorsally, the cranial sac starts to dilate.

4. The end of the second phase of reticular contraction. The pole of the reticulum has been lifted further dorsally, the reticulo-ruminal fold has moved ventro-cranially, the cranial sac is dilated. The gas cap in dorsal rumen starts to move caudally.

5. Contraction of the cranial sac. The reticulum relaxes, the reticulo-ruminal fold moves caudally, the gas cap is pushed further caudally.

6. Contraction of cranial pillar. The contraction moves caudally across the dorsal rumen, the cranial pillar moves dorsally and slightly caudally, the gas cap is pushed further caudally round the dorsal blind sac.



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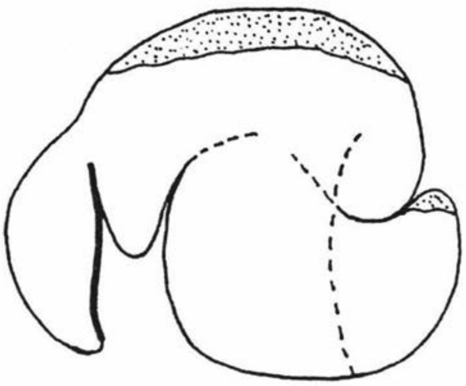

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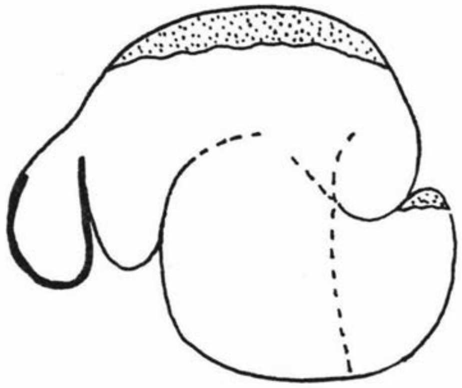

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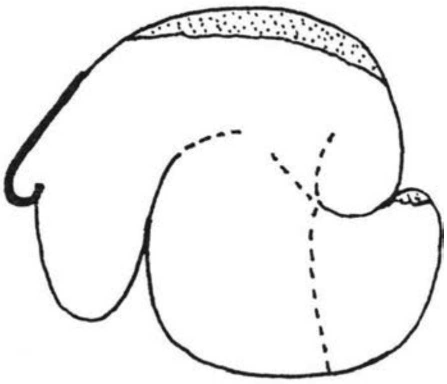

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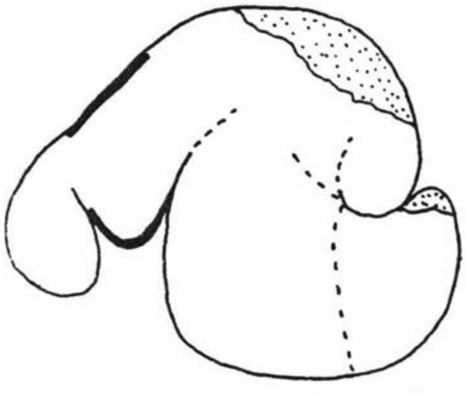

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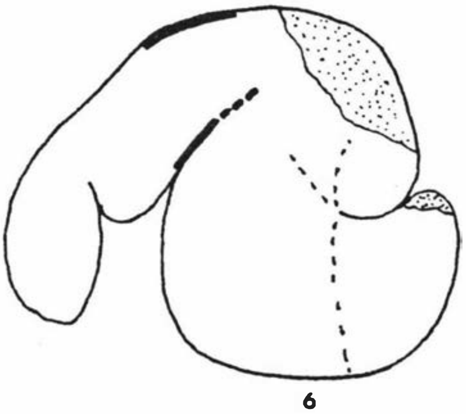

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FIGURE 6

7. Contraction of the dorsal rumen. The cranial pillar continues to move dorsally and slightly caudally, the contraction moves further caudally across the dorsal rumen displacing the gas cap down the lateral walls of the dorsal rumen.

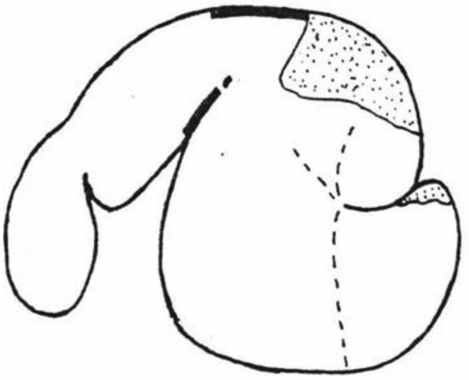
8. Contraction of the dorsal blind sac. The cranial pillar remains at the height of its contraction. Contraction of the dorsal blind sac occurs with a marked dorsal curling of the caudal pillar; the gas cap is displaced cranially as far as the dorsal part of the reticulum, under the cranial pillar and if reasonably large, round under the caudal pillar into the caudal ventral blind sac.

9. Contraction of cranial ventral rumen. The cranial and caudal pillars return to their resting positions simultaneously and the dorsal rumen relaxes allowing the gas cap to return to the dorsal rumen except for that part trapped in the caudal ventral blind sac. The cranio ventral part of the ventral rumen contracts straightening this part of the outline. (When the sheep were in a fasted state, the contraction sequence rarely progressed past this point).

10. Contraction of ventral rumen. A wave of contraction migrates caudally across the more caudal part of the ventral rumen.

11. Ventral movement of the caudal pillar. When the migrating wave of contraction reaches the ventral coronary pillar, there was a marked ventral displacement of the caudal pillar.

12. Contraction of the caudal ventral blind sac. The wave of contraction continues caudally across the caudal ventral blind sac.



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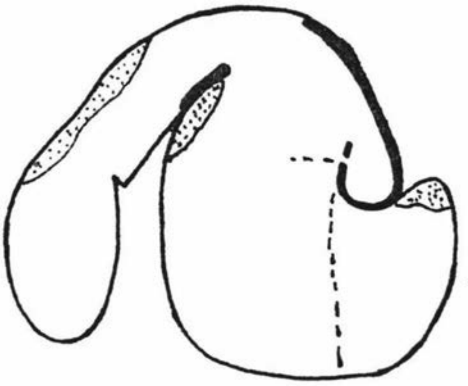

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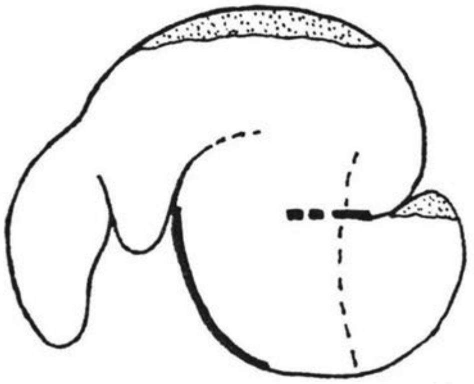

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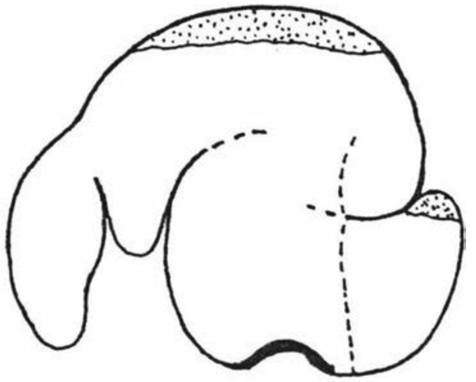

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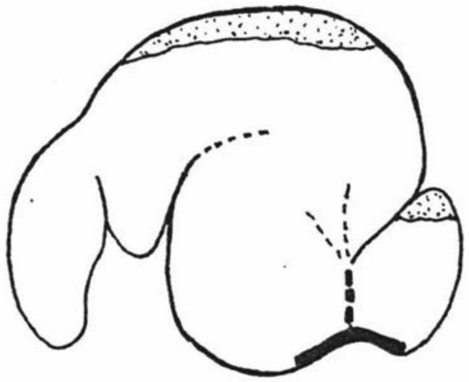

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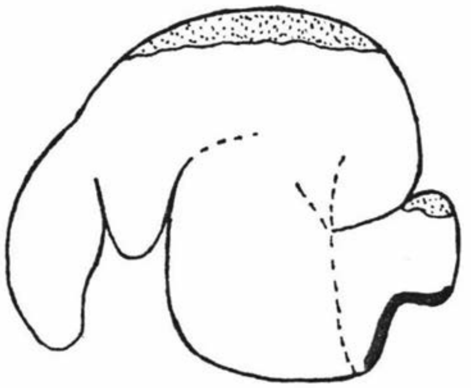

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FIGURE 6

13. Contraction of the pole of the caudal ventral blind sac. When the caudally moving wave of contraction reaches the pole of the caudal ventral blind sac, it is pulled cranially displacing most of its gas cap round the caudal pillar into the dorsal rumen.

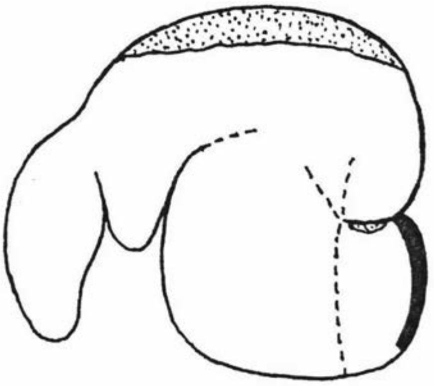
14. Second contraction of the caudal ventral blind sac. Following relaxation of the pole of the caudal ventral blind sac, a wave of contraction starts to migrate cranially across the caudal ventral blind sac.

15. Second ventral contraction of the caudal pillar. When this cranially migrating wave of contraction reaches the ventral coronary pillars, there is a second ventral displacement of the caudal pillar.

16. Second contraction cranial ventral rumen. The wave of contraction continues to migrate cranially then the cranial ventral rumen contracts for the second time completing the sequence of contractions.

NOTE: As the animals approach the fasted state, parts of this cycle are gradually dropped off starting with (16) and working back to where a cycle may cease at the stage illustrated in drawing (9).

Should eructation be going to take place, the following sequence of events supercedes at the stage of contraction of the pole of the caudal blind sac (13).



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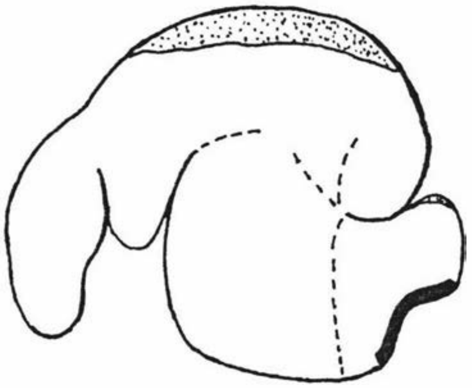

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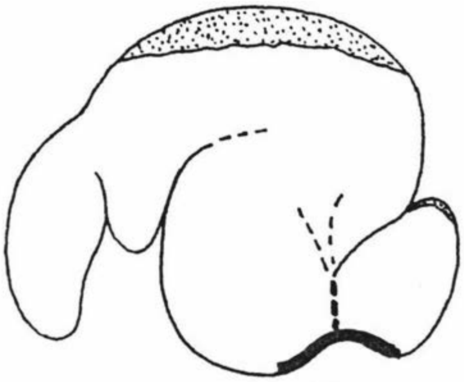

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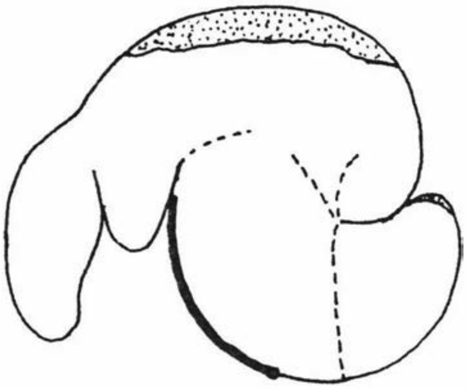

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FIGURE 6

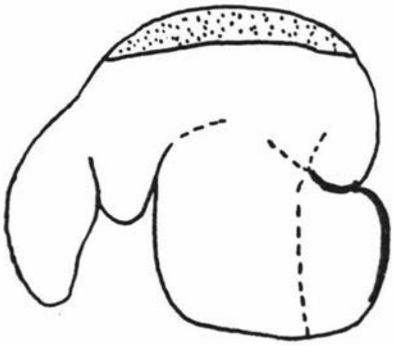
17. Second contraction of the pole of the caudal ventral blind sac. Either the first contraction of the pole of the caudal ventral sac is sustained over a prolonged period or it relaxes and contracts a second time coinciding with the second contraction or the prolonged first contraction, the caudal pillar starts to curl dorsally.

18. Second dorsal movement of the caudal pillar. The caudal pillar continues to curl dorsally and the caudal wall of the dorsal blind sac contracts starting to move the gas cap cranially. A cranially moving wave of contraction starts across the caudal ventral blind sac.

19. Second contraction of the dorsal rumen. The wave of contraction moves cranially over the dorsal rumen displacing the gas cap further cranially. The cranial pillar moves dorso-caudally and as it reaches its height of contraction, eructation occurs. The contraction on the caudal ventral blind sac continues to move cranially.

20. Second ventral movement of the caudal pillar. The cranial pillar relaxes as the wave of contraction reaches the ventral coronary pillars causing ventral movement of the caudal pillar.

21. Second contraction of the ventral rumen. The wave of contraction moves onto the ventral rumen then the cranial part of the ventral rumen contracts completing the sequence.



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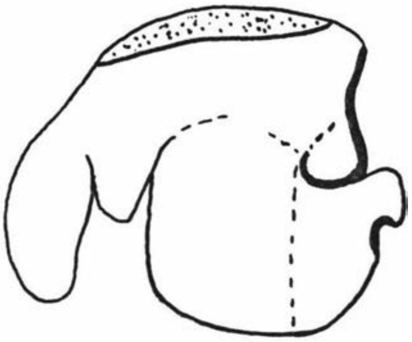

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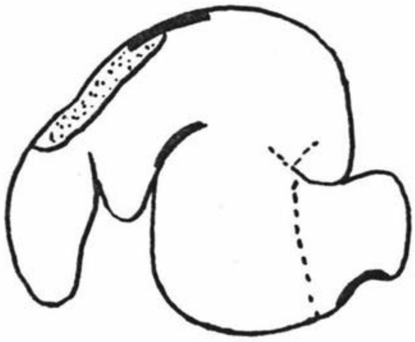

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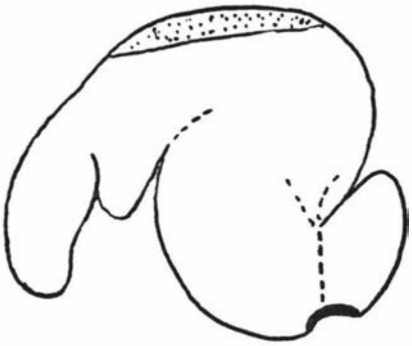

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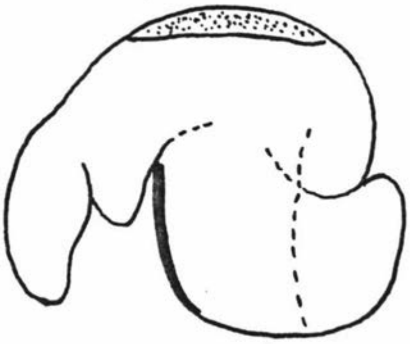

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with the virtual total replacement of the fluid contents by gas, was never seen nor was anything remotely resembling it. It can only be suggested that their techniques produced a bizarre effect perhaps due to over-inflation of the rumen with gas.

The dilation of the cranial sac of the rumen that occurred as the reticulum contracted was reported by Czepa and Stigler (1926) but has not been remarked on since. This is an important observation because the greatest volume of reticular contents are tipped into the cranial sac and are then tipped back to the reticulum as the cranial sac contracts. Very little digesta moves from the reticulum into the dorsal sac of the rumen. There is general agreement that contractions move from dorsal sac to dorsal blind sac in an A sequence and from the dorsal blind sac to dorsal sac in a B sequence (Wester, 1926; Weiss, 1953; Reid and Titchen, 1959; Reid, 1962; Tsiamitas, 1972; Ruckebusch and Tomov, 1973). Radiological observation of contractions of the dorsal sac is complicated by the attachment to the crura of the diaphragm in this region, but it could be seen that the contraction spread across the dorsal rumen onto the dorsal blind sac or vice versa. This contraction propagated rapidly and was then maintained, with the result that there was a period during which the dorsal sac and dorsal blind sac were contracted simultaneously. The debate as to whether various regions of the rumen contracted as a total unit or whether a propagated wave of contraction passed over them is answered by this observation, that a wave of contraction spreads rapidly over the dorsal rumen but is sustained long enough for there to be a point when there is a total contraction of the dorsal sac and dorsal blind sac. The different pattern of movement of the wall of the dorsal blind sac seen in A and B sequences (Akester and Titchen, 1969) was caused by the contraction moving towards or away from the fixed point of attachment of the dorsal rumen.

The sequence of events observed in the ventral rumen conflicts with descriptions by Reid (1962) and Tsiamitas (1972). After the dorsal sac of the rumen relaxes, it appears that a wave of contraction starts ventral to the longitudinal pillars and migrates slowly towards the cranial ventral rumen. It was not possible to directly visualise this contraction because it was not moving across the outline of the rumen as seen from the lateral projection, but, movement of digesta in the region indicated this to be what was happening. When the wave of contraction reached the cranial ventral rumen it appeared as a simultaneous contraction of the whole region. It then migrated caudally across the more caudal ventral sac and caudal ventral blind sac then returned cranially as reported and illustrated by Czepa and Stigler (1926). The discrepancy with the descriptions of Reid and Tsiamitas can be explained because records made from single sites on the caudal rumen and caudal ventral blind sac would produce a variety of patterns of activity depending on the sites selected. Should the sites chosen be the more cranial part of the ventral sac and a region adjacent to the pole of the caudal ventral blind sac, the patterns of contractions seen would be similar to those described by these two workers. Had the recording site on the ventral rumen been closer to the ventral coronary pillars, it would have been found that, in the replete state, contraction sequences terminated in a contraction of the ventral sac irrespective of whether they were A sequences, or A followed by B sequences, because the contraction frequently did not migrate to the more cranial regions of the ventral rumen at the end of an A sequence. Similarly, if the area of the caudal ventral blind sac recorded from was not close to the pole, a much greater incidence of apparent double contraction of the caudal ventral blind sac would have been recorded as the wave of contraction first migrated caudally and then returned cranially passing the recording site twice. Thus, by recording from single sites it would be possible to obtain a number of patterns of events in the ventral rumen which did not directly reflect the flow of a single contraction across the rumen caudally then returning a variable distance cranially.

During a contraction sequence the path taken by a marker placed at the mid-point of the ventral aspect of the reticulo-ruminal fold was found to be the same as described by Akester and Titchen (1969), but its timing in relationship to the reticular contractions differed. The marker started to move fractionally before the pole of the reticulum and reached its maximum dorsal displacement slightly ahead of the end of the first phase of the reticular contraction. The maximum cranial movement coincided with the peak of the second phase. During the first phase of the reticular contraction the array of markers placed on the reticulo-ruminal fold all closed up on the one closest to the cardia, indicating that the reticulo-ruminal oriface was narrowest just before the end of the first phase of the reticular contraction. There was no movement of the reticulo-ruminal fold associated with regurgitation or eructation and no evidence could be found to support Dougherty and Meridith's (1955) claim that the fold played an important role in eructation by acting as a dam holding back digesta.

The first illustration of the movement of the cranial pillar in sheep was presented by Akester and Titchen (1969) and they showed the path taken by a marker on the mid-point of the free border of the pillar moving dorsocranially from its resting position. This conflicts with the present series of observations that showed the path taken by a similarly placed marker to be dorsocaudal. However, in those sheep with partial exteriorisations of the reticulum, the plane of movement of the marker was described by those authors. The most likely explanation for this is that fixing the reticulum to the abdominal wall results in the cranial rumen and cranial pillar being pulled towards the point of fixation as they contract. Akester and Titchen did not report the second movement of the cranial pillar associated with a B sequence.

The movement of the caudal pillar was observed to be considerably more complex than described by Akester and Titchen (1969). The range of movement they describe was seen in fasted animals during an A sequence. However, when a B sequence followed, or in an A sequence in the replete state, the pillar moved ventrally from its resting position twice.

Changes in the frequency of the contractions and the ratio of A to B sequences depended on whether the sheep was replete or fasted and were similar to previous observations made by Phillipson (1939), Radev and Stayonav (1956), Reid (1960, 1962, 1963) and Reid and Titchen (1965). The more rapid progression of the sequence in the fasted sheep was compatible with previous reports (Reid, 1962, 1963) but the increased duration of the first phase of the reticular contraction, which was found consistently, has not been described before. There is no obvious explanation reconciling these contrasting effects.

Previous descriptions of the movement of the gas cap have been incomplete (Magee, 1932; Dougherty and Meridith, 1955; Akester and Titchen, 1969). The displacement of the gas cap during an A sequence was not only cranial into the reticulum but also ventral to below the cranial and caudal pillars. Throughout this series of observations eructation was only seen to occur in association with a B sequence when the gas cap was displaced less cranially. This is contrary to the observations of Dougherty and Meridith (1955), Reid (1960) and Sellars and Stevens (1966) who reported seeing eructation at other times. However, their observations were made under different circumstances such as after inflating the reticulo-rumen with gas or through an open rumen fistula. The presence of a small gas cap in the caudal ventral blind sac, which is periodically added to from the gas in the dorsal rumen, may play an important role in initiating B sequences particularly as it has been demonstrated that B sequences originate in that sac (Ruckebusch and Tomov, 1973). This possibility requires further investigation.

The series of events observed during rumination did not differ from those that have been previously reported and summarised by Stevens and Sellars (1968). It has been shown that rumination plays an important role in the reduction of particle size (Pearce and Moir, 1964; Reid et al., 1979) but it may also play a part in the sorting of digesta for onward passage. Fluid expressed from the regurgitated bolus and reswallowed is likely to be retained in the reticulum or cranial sac and passed on rapidly through the reticulo-omasal orifice. The remasticated bolus returns to the dorsal rumen (Balch, 1950) where it is further processed before passing on.

The form of the contractions of the reticulo-rumen has been debated since they were first described by Wester (1926) as being peristaltic in nature. There is now general acceptance of the sequential nature of the events (Reid, 1962, 1963; Titchen and Reid, 1965; Titchen, 1968; Tsimitas, 1972). The form and sequence of the contractions of the walls, folds and pillars of the reticulo-rumen as seen radiographically could be explained by the effects of a wave of contraction migrating caudally from the reticulum across the dorsal rumen, down onto the ventral rumen, then onto the caudal ventral blind sac and a second wave migrating cranially from the caudal ventral blind sac onto the ventral rumen and rapidly across the dorsal rumen. The origin appeared to be in the region of the reticular groove from where the wave spread out to first involve the reticulo-ruminal fold and the reticulum. It then moved rapidly caudally, sequentially involving cranial sac, cranial pillar, dorsal sac, dorsal coronary pillars, dorsal blind sac and caudal pillar. The progression across the ventral rumen was much slower and it travelled from the longitudinal pillars over the cranial ventral rumen then to the ventral coronary pillars and caudal ventral blind sac. The cranially moving contraction started in the region of the caudal ventral blind sac and spread rapidly across the dorsal rumen with the sequential contractions of the caudal pillar, dorsal blind sac, dorsal coronary pillars, dorsal rumen and cranial pillar. It did not involve the cranial sac or reticulum. The wave moved slowly across the caudal ventral blind sac onto the ventral coronary pillars, ventral rumen and cranial ventral rumen. The difference in the rate of migration of this wave over the dorsal and ventral rumen may be a function of the different distribution of muscle fibres. The longitudinal muscle fibres which extend over the reticulum and dorsal rumen may facilitate rapid propagation rates: this layer does not occur over the ventral rumen (Pernkopf, 1931). Such migrating waves of contraction explain all the events observed and the sequence in which they occur. Whether this wave is peristaltic or not was discussed by Phillipson (1939) and his statement that the debate really hinges on the definition of peristalsis remains true. The definition given by Bayliss and Starling (1899) was that peristalsis is a zone of relaxation followed by a zone of contraction, but the term has come to be used loosely to describe a variety of migrating muscle contractions. In many regions of the reticulo-rumen a zone of relaxation or distension could be seen preceding the wave of contraction: during the caudal migration there was a preceding distension of cranial sac, dorsal blind sac, cranial ventral rumen and caudal ventral blind sac; during the cranial migration there was distension of the reticulum and cranial ventral rumen. This lends support to the concept proposed by Wester (1926) that the waves are peristaltic and anti-peristaltic. Whatever the nature of these migrating waves of contraction, this study has further established their existence and they do explain sequences of contraction of all parts of the reticulo-rumen.

The variations seen in the form of the sequences would be explained by the wave of contraction fading out before it had completed its normal course across the rumen. The most obvious factor which would affect its persistence would seem to be distension of the reticulo-rumen by its contents. Stretch of the reticulum and rumen walls and pillars has been shown to stimulate contractions (Titchen, 1958, 1960; Reid, 1962; Reid and Titchen, 1965). Presumably the tension receptors in the walls of the reticulum and rumen (Iggo and Leek, 1970; Leek, 1971; Leek and Harding, 1975) are involved. High degrees of distension are inhibitory to reticulo-ruminal mobility (Reid and Titchen, 1965; Leek and Harding, 1975) and may result in gastric paralysis: This situation may occur in severe tympanites (Boda et al., 1956). Moderate degrees of distension however, are predominantly excitatory and would be expected to facilitate the maintenance of a contraction wave. That is, contraction waves would travel longer distances, tending towards the most extended form of the rumen contraction sequence, seen after eating. On the other hand, low degrees of distension would likely be insufficiently excitatory to favour maintenance of contraction waves: the contraction waves would then tend to die out before completing their passage across the rumen, resulting in the abbreviated sequences characteristic of fasting animals.

The activity of the reticulo-rumen not only mixes and propels digesta but sorts it so material that is in suitable form is passed out through the reticulo-omasal orifice. It is difficult, with the pattern of digesta movement described, to understand how this selection is made. Balch (1950) showed that finely ground hay passed through the reticulo-rumen more rapidly than long hay and it has been suggested that selection for passage is based on particle size (Ewing and Wright, 1918; Balch and Campling, 1962; Ulyatt et al., 1976; Poppi et al., 1980). How the movements would bring about selection on particle size alone is not clear. The possibility that specific gravity of particles is important in relation to passage has been suggested (Campling and Freer, 1962). Sellers and Stevens (1966) proposed that sorting is done by floatation. That an interaction between particle density, particle size and reticulo-ruminal motility determines the route of movement of digesta is plausible. Further, with most forms of diet, there is likely to be a relationship between particle size and whether the particles sink or float in the rumen (Schalk and Amadon, 1928). Thus smaller, heavier particles would be expected to move towards the ventral regions to be carried forward from there to the reticulum where they become available for onward passage.

That distension of the abomasum can profoundly affect the motility of the reticulo-rumen has been known for more than 40 years. The first report appears to be by Phillipson (1939). He observed that distension of the abomasum of conscious sheep by a balloon introduced through an abomasal cannula was followed by a reduction of reticulum and associated rumen contractions (A sequences) but not of rumen contractions independent of reticulum contractions (B sequences). Since then, other workers have reported a variety of effects reviewed by Titchen (1968) and Carr et al. (1970). These range from excitation to apparent inhibition of reticulum contractions and from apparent inhibition of the rumen contractions to excitation of B sequences. In the present experiments the effects seen radiographically were similar to those reported by Phillipson (1939). Here, varying degrees of abomasal distension resulted in the complete disappearance of reticular contractions for a period of time that was not related to the degree of distension. The contractions of the more caudal parts were reduced to a lesser extent - indeed there was some suggestion that the activity of the caudal regions was slightly increased. The mechanisms by which abomasal distension affects reticulo-ruminal motility are not fully understood. Titchen (1958) has provided evidence that sensory nerve fibres involved in inhibitory effects of abomasal distension pass along the splanchnic nerves. Following section of these nerves a previously inhibitory degree of distension may have excitatory effects on reticulo-ruminal motility. Vagal afferent fibres are also involved (Titchen, 1968). Tension and other receptors in the abomasum have been described by Leek and Harding (1975). They have reported that abomasal distension inhibited gastric centre neurones in the medulla and gastric efferent vagal fibre activity (Harding and Leek, 1973). Such effects would certainly alter motility of the reticulo-rumen. The possibility that the hormone gastrin may also be involved has been suggested by Carr et al. (1970). The form of the responses seen here suggests they reflect varying degrees of inhibitions. However, changes in excitatory stimulation due to redistribution of the contents of the reticulo-rumen may have contributed as well. Emptying the reticulum of its contents, as occurred when the distended abomasum compressed it against the diaphragm, would remove a potent excitatory stimulus for reticulum and to a lesser degree, rumen contractions (Titchen, 1958, 1960). On the other hand aborad displacement of the rumen contents would result in distension of the caudal regions and would be likely to increase rumen motility especially the occurrence of B sequences. These changes would at least reinforce the effects of stimuli originating in the abomasum. The interaction between the contents of the alimentary tract and alimentary tract motility will be returned to in Chapters 4 and 5.