*J. Physiol.* (1974), **237**, *pp.* 415–430
*With 3 plates and 1 text-figure*
*Printed in Great Britain*



# EFFECTS OF VAGOTOMY, ATROPINE, HEXAMETHONIUM AND ADRENALINE ON THE DESTINATION IN THE STOMACH OF LIQUIDS SUCKED BY MILK-FED LAMBS AND CALVES

By J. C. NEWHOOK and D. A. TITCHEN*

*From the Department of Physiology and Anatomy, Massey University, Palmerston North, New Zealand and Department of Veterinary Preclinical Sciences, University of Melbourne, Parkville, Victoria 3052, Australia*

(*Received 13 August 1973*)

SUMMARY

1. The normal passage to the abomasum of liquid sucked by lambs and calves was confirmed in radiographic studies to be changed to passage of liquid to the reticulum and rumen after cervical or abdominal vagotomy.

2. The effects of hexamethonium (8–10 mg $kg^{-1}$ I.V.) were similar to those of vagotomy.

3. Atropine (200–800 $\mu g$ $kg^{-1}$ I.V.) had either no detectable effect on the destination in the stomach of liquid sucked by lambs or caused a partial failure of the reticular groove mechanism.

4. Fluid sucked by lambs passed wholly to the abomasum after adrenaline (5–40 $\mu g$ $kg^{-1}$ I.V.).

5. Atropine and adrenaline caused a greater dysfunction of the reticular groove mechanisms in calves than in lambs.

6. Contraction of the reticular groove was observed via rumen fistulae in three lambs. Eversion of the caudal oesophagus into the reticulum which occurred when saliva was swallowed into the reticulum and rumen was not observed when liquids were sucked from a bottle.

7. The continued passage to the abomasum of sucked liquid in atropinized lambs has been taken as an indication of the importance of caudal oesophageal reactions, tonic activity of the reticular groove and the atropine-resistant vagally induced opening of the reticulo-omasal orifice in the reticular groove mechanism.

* Address: Department of Veterinary Preclinical Sciences, University of Melbourne, Parkville, Victoria 3052, Australia.

## INTRODUCTION

Liquids sucked by young ruminants pass to the most caudal part of their stomach, the abomasum, without entering the reticulum and rumen. This is attributed to the reticular groove which forms a conduit from the oesophagus through the reticulum to the reticulo-omasal orifice. Contraction of the groove has been palpated when calves with rumen fistulae suck (Wester, 1926; Schalk & Amadon, 1928; Wise, 1939). The groove contracted in the foetal lamb (Duncan & Phillipson, 1951) as it did in decerebrate calves and lambs in response to stimulation of the vagus nerves (Comline & Titchen, 1951).

The effectiveness of contraction of the reticular groove in directing sucked liquid to the abomasum depends on the reticulo-omasal orifice being open so that liquid passing from the oesophagus into the reticular groove may enter the omasum and thence the abomasum. Whereas contraction of the reticular groove is blocked by atropine (Wester, 1926; Comline & Titchen, 1951) opening of the reticulo-omasal orifice in the sheep evoked by efferent vagus nerve stimulation is resistant to atropine (Newhook & Titchen, 1972). In the present work the effect of atropine on the destination of liquid sucked by lambs and calves was studied and a comparison made of its effects and those of cervical and abdominal vagotomy and hexamethonium. Brief preliminary reports of some of the observations have been presented (Newhook, 1970; Newhook & Titchen, 1969).

## METHODS

*Animals and their management.* These were lambs and calves of both sexes. In New Zealand the lambs studied were of the Romney or Cheviot breeds or their crosses, and in Australia Romney or Leicester crosses, obtained within 72 hr of birth and after they had received colostrum from their dams. In the laboratory they were kept in individual cages on wire floors without bedding. They were fed four times each day with a proprietary lamb rearing mixture ('Fostermilk', Glaxo, New Zealand) derived from dried cow's milk, or with reconstituted evaporated whole milk. The lambs sucked these from a bottle and teat. They were allowed as much as they would drink at each meal. From 3 weeks of age dried buttermilk powder was added to the lamb rearing mixture in increasing quantities until it formed three quarters of the ration. The lambs and calves always had access to water but never to solid food. The lambs were kept closely clipped about their forelegs and hindquarters to reduce wool eating. All were allowed each day to roam for a period in a pen on a concrete floor. The animals were accustomed to being fed from a bottle when restrained in headstocks.

*Radiographic apparatus and procedures.* The X-ray generator used was either of two mobile machines with stationary anode tubes (a 'Watvic D3', Watson Victor, Australia, with a mechanical timer and a 'Konrad 60', Watson Victor, Australia, with an electronic timer), or a G.E. (U.S.A.) 'Patrician' apparatus with rotating

anode tube. The two mobile machines were used without the aid of grids, but sometimes a 6:1 Liebel Flarsheim grid was used with the larger apparatus.

The *X*-ray films (Kodak 'Blue Brand', 3M type R, Ilford 'Red Seal') were used in cassettes fitted with intensifying screens (Du Pont 'High Speed' and 'Par Speed'). Development was with 'Phenisol' (Ilford) and fixation with 'Hypam' (Ilford).

The contrast media were an oesophageal paste ('Microtrast', Damancy) or powders ('Raybar', Bell Craig: 'Micropaque', Damancy). The paste (70 % w/w barium sulphate in an aqueous vehicle) was added to milk up to 30 % v/v. Both powders are readily suspended in liquid and were mixed with milk to make up to 30 % v/v of the liquid. All the mixtures used flowed readily through the teats and were sucked avidly by lambs and calves.

*Observations on the course of swallowed liquid* were made with all three machines *whilst* liquid was being sucked. Each mobile apparatus was used in the animals' usual quarters. The larger G.E. machine is a fixed installation to which animals had to be taken. In an effort to accustom them to this procedure the lambs were given at least one feed daily for 3 or 4 days of each week in the *X*-ray room. One animal consistently refused to suck in this room. It was excluded from the experimental observations.

Radiographic observations were made before, during and after sucking on at least one occasion before any experimental procedures or administration of drugs. The animals were fed from the same bottle and teat during normal feeding and experimental sessions. The rate at which they sucked was 2–12 ml.sec$^{-1}$. The amounts of contrast material received were usually limited by giving a maximum of 120 ml. milk contrast medium mixtures at each radiographic session except after vagotomy and during observations *per fistulam* when over 200 ml. have been given. The standard procedure adopted was to take a preliminary radiograph of each animal whilst standing and held by an acrylic sheet (Perspex, I.C.I.) against the film cassette. Three or more radiographs were taken, at the start of, during, and after sucking 100–120 ml. milk-contrast media mixtures. Some radiographs were also taken in a dorsoventral plane to confirm the distribution of contrast medium in the stomach.

The drugs used were all injected I.V. into a jugular vein. Atropine sulphate (B.D.H.) was given in doses of the base of 200–800 $\mu$g kg$^{-1}$, hexamethonium (Koch Light) 8–10 mg kg$^{-1}$, adrenaline hydrochloride 5–40 $\mu$g kg$^{-1}$.

*Surgical procedures* were undertaken with precautions to maintain asepsis and under anaesthesia induced and maintained with halothane (B.P.). Induction was undertaken with the aid of a Hall's dog mask (B.O.C.) in conjunction with a Fluotec (B.O.C.) vaporizer in a closed circuit anaesthetic apparatus. Maintenance was *via* a cuffed endotracheal tube.

Cervical or abdominal vagotomy was through mid-line cervical or epigastric incisions. Rumen fistulae used for direct observation of the reticular groove were prepared in the left side of the animal in the mid-dorsal sac with the two stage technique described by Jarrett (1948).

Markers placed on the lips of the reticular groove were Weck 'hemoclips' (Edward Weck & Co. Long Island City, N.Y.) the use of which with special forceps has been described by Samuels, Roedling, Katz & Cincotti (1966). In the present work medium size clips were used after being re-shaped so that when closed they had a quadrilateral outline, with a circumference of about 11 mm.

A speculum with its own illumination was used for viewing structures in the stomach. It had an external diameter of 2·5 cm and an internal diameter of 2 cm. The rumen and reticulum were emptied of fluid by suction and the intermittently deposited saliva was also removed by suction. The end of the suction tube was covered with gauze to prevent it holding to the mucosa.

*Acute experiments.* The completeness of vagus nerve section was confirmed at acute experiments under chloralose anaesthesia or after decerebration under halothane anaesthesia, when the effects were examined of electrical stimulation of the vagus nerve trunks cranial and caudal to the point of transection. The procedures were as described by Newhook & Titchen (1972). The observations on the effects of vagotomy reported all refer to animals in which stimulation of the cervical vagus nerve trunks failed to elicit movements of the stomach.

*Studies in calves.* Six Jersey or Jersey-cross calves (four males, two females) were used in the studies in New Zealand. Observations were made on calves 3–22 days of age. They were maintained in the same manner as lambs and subjected to similar experimental procedures. All radiography was undertaken on them in the room in which they were normally housed, using one or other of the mobile machines.

## RESULTS

The appearance of contrast material in the oesophagus and the stomach was followed radiographically in 47 milk-fed lambs 2–140 days old, during and after sucking.

*The abomasal destination* of sucked liquid was the invariable normal result. This was indicated by the accumulation of contrast material in a ventral position in association with outlines of the abomasal folds, the abomasal gas cap in the mid-epigastric region (Figs. 1 and 2, Pl. 1) and sometimes clear impressions of the pyloric antrum of the abomasum. Movement of contrast material from the abomasum into the duodenum has been detected within 200 sec of the commencement of its ingestion. Benzie & Phillipson (1957) and Kay, Orskov & Wenham (1972) reported rapid movement of material caudally from the abomasum.

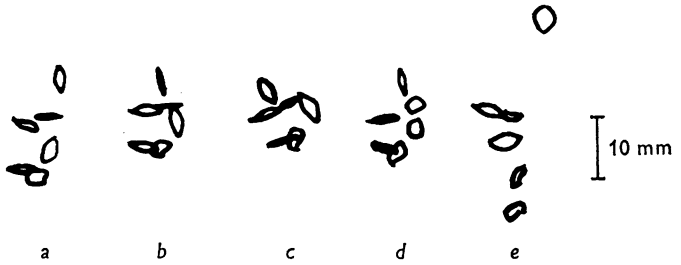
Two liquid-gas interfaces were present in the stomach. Liquid in the abomasum extended ventrally towards the floor of the abdomen and had overlying it the mid-epigastric abomasal gas cap which increased during sucking. The other liquid-gas interface was more dorsal and the liquid did not extend as far ventrally towards the floor of the abdomen; dorsal to it was a gas cap extending to the level of the vertebral column. This liquid and gas was in the rumen. Direct observation has shown that saliva swallowed at times when lambs are not sucking enters the reticulum and rumen. These different fluid levels were detected as early as in a lamb 4 days old.

*Radiographic observations of the oesophagus.* The usual appearance of sucked material in the oesophagus was of distinct boluses with broad caudal faces and tapering cranially. 116 boluses measured in twenty-four lambs 3–140 days old were 25–100 mm long, another twenty-five were 110–180 mm long. The total length of the oesophagus was 240–370 mm. The entire oesophagus contained contrast material (Fig. 3, Pl. 2) in seven radiographs (six animals) of a total of forty-three in which all of

the oesophagus was included in the field. Discrete boluses occupying less than half the length of the oesophagus were also detected in one or more radiographs taken at the same session as that in which all of the oesophagus contained contrast material.

A dilatation of the caudal thoracic oesophagus has been detected (Figs. 1 and 2, Pl. 1). This corresponds to the description of the phrenic ampulla provided by Ruckebusch & Bost (1962). It was not invariably present (Fig. 3, Pl. 2).

*The passage into the reticular groove* of sucked material was marked by its change from a caudal direction in the thorax to a more ventral one in the abdomen (Figs. 1 and 3, Pl. 1 and 2), as is also apparent in the radiographs published by Watson (1944) and Benzie & Phillipson (1957). The caudal thoracic oesophagus may assume a caudo-ventral direction and appear to be more in line with the reticular groove specially when




Text-fig. 1. Position of markers in lateral radiographs of the reticular groove in a lamb 5 days old (*a*) before it was fed, (*b*) when the feeding bottle was in sight but had not been available, (*c*) during sucking from the bottle at 7 ml.min$^{-1}$, (*d*) 180 sec after atropine (200 $\mu$g kg$^{-1}$) was injected I.V. during sucking from the bottle at 5·5 ml.min$^{-1}$. The sucked liquid passed to the abomasum, (*e*) 4 hr after both vagus nerves had been cut in the neck during sucking at 6·3 ml.min$^{-1}$. In each case the head is to the left. The markers were situated dorsally on the cardia, on the middle of the length of the lips of the groove on the floor of the groove where it forms one border of the reticulo-omasal orifice and the ventral extremities of the lips of the groove.

there is ventriflexion of the hind limbs. The passage through the reticular groove was identified by the narrower shadow of contrast material immediately caudal to the diaphragm. The shadow widened on entry into the omasal canal and became more diffuse as the contrast medium adhered to, or spread between the leaves of the omasum (Fig. 4, Pl. 2), clear impressions of which were obtained in some radiographs. Shortening of the reticular groove in the sucking animal was shown by the movement of markers outlining its limits and labelling its lips. Text-fig. 1*a*, *b* and *c* provide a comparison of the position of markers before and during sucking. Contraction of the groove when the bottle could be

seen but before sucking started was detected with these markers (Text-fig. 1*b*). Wise (1939) and Orskov, Benzie & Kay (1970) reported the activation of the reticular groove mechanism as a conditioned response in the calf and lambs in anticipation of being allowed to suck.

*Effects of cervical and abdominal vagotomy*

After both vagus nerves were cut in the neck or in the abdomen immediately caudal to the diaphragm, sucked liquid passed to the reticulum and cranial sac of the rumen whence it flowed over the cranial pillar into the ventral rumen (Fig. 5, Pl. 3). Nine of the eleven animals subjected to complete vagotomy continued to suck avidly. They displayed the usual excitement and interest in anticipation of receiving the teat and drank vigorously taking all of the liquid made available. One lamb which had bilateral cervical vagotomy was reluctant to suck and when it did made only a few sucking movements at a time. It had a marked ruminal tympanities and sucked only 15 ml. during the radiographic observations. Another animal which had sucked to satiation 1 hr before cervical vagotomy did not suck at any time in the next 24 hr. The passage to the reticulum and rumen of the 120 ml. or more of liquid sucked led to clear outlines being obtained of the reticulum, cranial sac of the rumen between the rumino-reticular fold and cranial pillar, the ventral sac of the rumen and, as in Fig. 6 of Pl. 3, of the ventral margins of the caudal dorsal blind sac of the rumen. The ruminal gas cap which increased on sucking after vagotomy provided a less clear demarcation of the dorsal limits of the rumen than did the contrast medium ventrally – part of this was due to overlying intestinal gas shadows. These features provided clear evidence of the reticular and ruminal destination of liquid sucked after vagotomy. The passage of traces of sucked material into the abomasum was detected in seven of the lambs with vagotomy after they sucked; some of the liquid sucked was seen to have passed into the abomasum over the course of up to 6 hr after sucking (Fig. 7, Pl. 3).

Cervical vagotomy was followed by a failure of discrete bolus formation in the oesophagus caudal to the level of transection. The caudal cervical and thoracic regions of the oesophagus were distended throughout their length after cervical vagotomy, with narrowing at the level of the first rib and between this site and the heart. The caudal thoracic oesophageal dilatation identified as the phrenic ampulla was never detected after bilateral cervical vagotomy.

After the abdominal vagus nerve trunks were cut there was a tendency for greater lengths of the oesophagus to be filled with sucked liquid. Of forty-one radiographs made in lambs after abdominal vagus nerve section contrast medium was present in the whole length of the oesophagus

in twelve and in only four radiographs were there boluses of less than half the length of the oesophagus. This contrasts with the situation described in the normal lambs (p. 418–419).

Contrast medium was detected in the larynx and trachea of three animals with both abdominal vagus nerve trunks cut. None of these animals had any obvious difficulty or distress on sucking. Contrast material was detected in the trachea in one lamb in which both vagus nerves had been cut in the neck.

*Effect of atropine on the course of sucked liquid*

Lambs continued to suck avidly after atropine was injected into a jugular vein in doses of 200–800 $\mu$g kg$^{-1}$. The greatest effect produced was a failure of some swallowed liquid to pass to the abomasum, which occurred on twenty occasions in eighteen lambs 7–48 days old. All sucked liquid passed to the abomasum on eighteen occasions in twelve lambs (7–29 days old) after atropine. The radiographic appearance when the administration of atropine I.V. was followed by some material entering the reticulum is presented in Fig. 8 of Pl. 3. Contrast medium was noted in the trachea in five animals after they had received atropine (500 $\mu$g kg$^{-1}$). None had displayed reluctance, difficulty or clumsiness on sucking after atropine was given.

The omasum appeared dilated after the I.V. injection of atropine. In the absence of quantitative measures this must be clearly identified as an impression. The passage caudally from the abomasum into the duodenum of contrast medium was detected within 10 min of the start of sucking in one of these animals after atropine (500 $\mu$g kg$^{-1}$) was given. A comparison of the position of markers on the reticular groove under resting conditions, during sucking in the untreated lamb, after it received atropine and, on another occasion, after the vagus nerves were cut is provided in Text-fig. 1 made by tracing the outlines of markers from radiographs.

*Effect of hexamethonium*

In contrast to the range of responses after atropine the administration of hexamethonium (8–10 $\mu$g kg$^{-1}$ I.V.) was followed by the entry of liquid swallowed during sucking, into the reticulum and rumen. Observations were made in five lambs on a total of six occasions, on each of which the 100–120 ml. they were allowed to suck was taken avidly and without difficulty.

*Effect of adrenaline*

The I.V. injection of adrenaline in doses of 5–40 $\mu$g kg$^{-1}$ to three lambs on a total of eight occasions was without effect on the eagerness with

which the animals sucked. They did so eagerly and apparently effectively since all the contrast medium sucked passed to the abomasum without evidence of entering the reticulum or rumen.

*Direct observations of the reticular groove*

These were made in three lambs 44–93 days old fed only by sucking from a bottle, and which had fistulae in the mid-dorsal rumen. When the animals were not sucking the lips of the reticular groove were in contact with each other along their whole length and showed localized contractions of the length of the lips and movements in which the right lip moved to cover the left. When saliva was swallowed the lips of the groove were separated in their dorsal parts by the oesophagus protruding between them and delivering saliva into the reticulum and cranial sac of the rumen.

During sucking the reticular groove shortened and rotated along its length. The reticulum adjacent to the groove also contracted, and thus overlay and partially obscured the groove from view. When the lambs sucked after the administration of atropine (500 $\mu$g kg$^{-1}$ I.V.) the lips of the groove simply remained in contact. They were not seen to shorten or twist although they showed localized contractions similar to those seen before atropine was given. In these three lambs after the administration of atropine, sucked material passed largely to the abomasum. They received up to 240 ml. milk at one time, an estimated 10 ml. of which escaped into the reticulum passing in a sheet between the lips along nearly their entire length. Eversion of the oesophagus still occurred when saliva was swallowed by the atropinized lamb.

Direct observations were made of the reticular groove during and for 10 min after the administration of 5–40 $\mu$g/kg of adrenaline in one lamb. On one occasion a separation of its lips in the dorsal part of the reticular groove was observed which persisted for 15 sec. It was thought that the spontaneous contractions of the groove diminished after adrenaline was injected on two occasions. Apart from this, the form of the contractions of the groove during sucking remained substantially as they were on occasions when adrenaline had not been given. Fluid was not observed escaping between the lips of the groove when the lamb sucked.

Direct observation was made of the reticular groove in one animal 4–5 hr after both vagus nerves were cut in the neck. The lips of the groove, which were in contact with one another over their full length, did not exhibit any spontaneous activity. Saliva dribbled from the oesophagus, the dilated lumen of which could occasionally be seen during respiratory movements. When the animal sucked the fluid flooded into the reticulum along the whole length of the reticular groove.

*Observations on stimulation of the vagus nerves*

These were made in the course of testing the completeness of section of the vagus nerves. The reticulum, reticular groove and reticulo-omasal orifice were observed during stimulation of the vagus nerves of lambs after decerebration or under chloralose anaesthesia. The absence of reticular and reticular groove contractions on stimulation of each of the vagus nerves in the neck (cranial to the site of transection with cervical vagotomy) was the criterion of complete section of the vagus nerves. In the course of confirming the reactivity of the preparations to stimulation of the vagus nerves responses of the reticular groove to cervical vagus nerve trunk stimulation (caudal to the point of previous section) were examined.

TABLE 1. Destination within the stomach of suckled fluid in six calves subjected to the procedures listed before being suckled

| | Destination of suckled fluid | | |
|---|---|---|---|
| Treatment of animals | Abomasum | Abomasum and reticulo-rumen | Reticulo-rumen |
| Controls including six observations in three animals after saline I.V. | 12 | — | — |
| Atropine 200 μg/kg three calves | — | 2 | 1 |
| Atropine 500 μg/kg six calves | 1 | 5 | — |
| Atropine 600 μg/kg three calves | — | 3 | — |
| Atropine 800 μg/kg six calves (3 twice) | 1 | 7 | 1 |
| Adrenaline 5 μg/kg three calves | 3 | — | — |
| Adrenaline 10 μg/kg three calves | 2 | 1 | — |
| Adrenaline 20 μg/kg six calves | — | 3 | 3 |
| Bilateral cervical vagotomy (three calves) | — | — | 3 |

Before atropine, stimulation of the vagus nerves caudal to the point of their section in the neck caused bradycardia, a marked blanching of the mucosa of the lips of the reticular groove and surrounding regions of the reticulum, a shortening of the groove and thickening and a rolling movement of the lips, specially of the right lip. After the stimulus there was commonly a separation of the lips of the groove at their omasal end which persisted for 2–5 sec after stimulation of the vagus at 5, 10 or 20 $sec^{-1}$ for 10 sec. After atropine, a reduced but definite thickening of the right lip of the groove and a slight rolling movement of it have been observed on stimulation of the vagus nerves although the other effects were abolished. When the lips of the groove which normally lay lightly

apposed were separated, the reactions of the reticulo-omasal orifice previously reported with vagal stimulation (Newhook & Titchen, 1972) were obtained.

*Observations in calves*

Four sets of observation of the destinations of suckled fluid were undertaken in calves, namely, (1) control observations including six made after the I.V. injection of saline, (2) observations made in all of the calves after atropine had been injected I.V., (3) observations made after the injection I.V. of adrenaline (5–20 $\mu$g/kg) and (4) observations made in three calves after both vagus nerves were cut in the neck. The results are summarized in Table 1. All of the observations recorded were made when the animals sucked vigorously. None of the procedures seemed to affect the ability or desire of the animals to suck at the time the observations were made.

## DISCUSSION

*Experimental conditions*

Since animals continued to suck avidly following all of the procedures adopted, the results are presented as effects of the experimental procedures adopted and not due to loss of a desire to suck, or the forced ingestion of liquid. The importance of this is clear from the studies reported by Watson (1944), Orskov *et al.* (1970) and Lawlor, Hopkins & Kealy (1971) in which the reticular groove mechanism was shown to be active when liquid is taken in the course of sucking but not when lambs drink to slake their thirst, nor when they bite at a teat rather than suck from it. When they swallow liquids with which they are dosed these pass to the rumino-reticulum unless they have some particular taste characteristic (Watson & Jarrett, 1944). The importance of behavioural factors was also shown in studies in conscious animals in which it was observed that the groove may contract when animals anticipate being fed (Wise 1939). Orskov *et al.* (1970) showed the effectiveness of the reticular groove mechanism as a psychic response. They demonstrated the passage to the abomasum of a suspension of contrast material injected into the oesophagus at times when lambs were teased with a bottle; in the absence of teasing contrast material injected into the oesophagus passed to the rumino-reticulum. Markers placed on the reticular groove clearly permitted identification of its contraction in lambs in anticipation of receiving milk from a bottle (Text-fig. 1).

Duncan (1953) reported that vagotomized lambs continued to suck but made no comment on their behaviour when they did so. In the same report it was noted that adult sheep also continued to eat after

vagotomy and that this led to distension of the rumino-reticulum with food. In the present work, nine of the eleven lambs subjected to complete vagotomy sucked vigorously post-operatively taking all of the liquid offered them. Lambs may have been more readily satiated than before vagotomy: this possibility was not examined. Sucking was limited to one episode post operatively at which the lambs were given up to about 200 ml. Similarly observations on the effects of atropine, hexamethonium and adrenaline were made without apparent effects on the avidity with which animals sucked. A limited amount of the liquid was usually given whilst these agents had their effects, and thus large loads of barium in the gut, and possible untoward effects of milk in the rumino-reticulum were avoided.

### *Observations in normal animals*

The features used here to identify the passage in the stomach of sucked liquid have been described by Czepa & Stigler (1926), Watson (1944) and in detail by Benzie & Phillipson (1957). These and the present studies included observations both whilst animals were sucking and on the destination of liquid after sucking was complete. Our identifications have been aided by the use of markers placed on the reticular groove and have led to a conservative indication of the extent of the reticular groove. In studies made whilst animals were sucking there are indications of the intermittent passage of liquid in the oesophagus and the reticular groove. Benzie & Phillipson (1957) identified, in cineradiographic studies, its passage in a pulsatile manner from the oesophagus through the groove. An intermittent flow of liquid through the groove was palpated by Schalk & Amadon (1928). This pulsed delivery is most probably referable to oesophageal activity and in particular that of the phrenic ampulla.

The rapid passage of some sucked liquid into the duodenum confirms observations made by Benzie & Phillipson (1957) and Kay *et al.* (1972). This may be basically a reflex response. Andersson, Landgren, Neil & Zottermann (1950) found that intestinal motility was reflexly stimulated when the central end of the superior laryngeal nerve was stimulated in the cat. This explains the well known augmentation of intestinal motility on swallowing. Similarly an increase in intestinal motility was noted in reflex studies on the reticular groove in decerebrate preparations when swallowing was stimulated (Comline & Titchen, 1951). Orskov *et al.* (1970) provided clear evidence in lambs of contractions of the caudal part of the abomasum and the presence of liquid in the duodenum 20 min after they sucked liquid or it was injected into the oesophagus during teasing. It seems that many, if not all, of the characteristic reactions during sucking have been evoked as a conditioned response.

*Effects of vagotomy*

Duncan (1953) showed that the reticular groove mechanism failed following vagotomy after which liquid sucked by lambs was found in the rumen. This observation has been confirmed in the present work. Radiographic evidence presented here suggests that after vagotomy sucked liquid enters the reticulum and antrum of the rumen and then flows into the ventral rumen. There are confusing reports in the literature on the effects of vagotomy on the reticulo-omasal orifice (see Duncan, 1953). Our observations indicate that it is not completely closed after vagotomy after which some liquid has been detected passing from the reticulum into the abomasum (Fig. 7, Pl. 3). Recurring rhythmic opening and closing movements of the reticulo-omasal orifice were recorded in spinal and anaesthetized preparations of lambs and sheep which had both vagus nerves cut (Newhook & Titchen, 1972). If these movements are present in the conscious lamb and calf after vagotomy they would provide some opportunity for the passage of liquid towards the abomasum. Recurrent e.m.g. discharges have been recorded from circular muscle of the reticulo-omasal orifice in adult sheep after hexamethonium and vagotomy (R. Derrick, B. Patten & D. A. Titchen, unpublished). Movement through the reticulo-omasal orifice would be expected to be slow however, in the absence, after vagotomy, of sustained opening mediated by the vagus (Newhook & Titchen, 1972) and without propulsive movements to contribute to the passage of material through the orifice (Stevens, Sellers & Spurrell, 1960).

*Effects of atropine, hexamethonium and adrenaline*

Atropine blocks contraction of the reticular groove (Wester, 1926; Comline & Titchen, 1951) but in the present study did not invariably block the activity of the reticular groove mechanism. Radiographic evidence suggests some shortening of the groove may still be present in lambs after atropine (Text-fig. 1). This shortening after atropine may be due to contraction of the band of skeletal muscle which passes from the oesophagus through the floor of the reticular groove towards the reticulo-omasal orifice (Trautmann & Fiebiger, 1957) and even as far as the reticulo-omasal orifice (Watson, 1944). Contraction of this band of skeletal muscle might account for the movements of the reticular groove seen after atropine in the present experiments with stimulation of the vagus nerves. Direct observations reported now in the lamb and previously in the calf (Wester, 1926) indicate the loss, after atropine, of the full shortening of the groove and the inversion movements of its lips (the movement recorded in acute experiments by Comline & Titchen, 1951).

Watson (1944) discussed the relation between the morphology and function of the reticular groove indicating that the groove might be able to contribute to the passage of liquid towards the reticulo-omasal orifice in the absence of contraction. Our observations suggest that the mechanism continues to operate in lambs in the absence of complete groove contraction. The importance of caudal oesophageal and reticulo-omasal orifice activity in this continued operation of the reticular groove mechanism must be considered. The eversion of the oesophagus between the lips of the groove when saliva was swallowed into the rumen suggests there are different caudal oesophageal reactions which contribute to the destination of liquid in the stomach. The oesophageal eversion on swallowing saliva persisted after atropine was given. Lambs 10–12 weeks old, although entirely milk fed, have been found to have some atropine resistant spontaneous parotid salivary secretion (J. Patterson & D. A. Titchen, unpublished). It could be suggested that there was a similar reaction of the caudal oesophagus with the delivery of saliva and of sucked liquid but that contraction of the groove prevented eversion of the oseophagus on sucking. This is not supported by the observations that after atropine blocked full groove contraction sucked liquid continued to pass to the abomasum and that it did so without any sign of eversion of the oesophagus. Caudal oesophageal motility was not obviously modified by atropine. The sensitivity to atropine and the function of the well developed circular layer of smooth muscle in this region of the oesophagus (Abe, 1959) has not been studied. The continued passage of sucked liquid to the abomasum after atropine would depend on the reticulo-omasal orifice being open. The vagal opening of this sphincter persists after atropine but is blocked by hexamethonium (Newhook & Titchen, 1972). This loss of vagal control of the reticulo-orifice could account for the markedly different effects of atropine and of hexamethonium.

Adrenaline and adrenal medullary secretion were shown in decerebrate preparations to reduce reflexly stimulated contractions and tonic activity of the reticular groove (Comline & Titchen, 1951). We have no explanation of the failure of adrenaline to do so in the present experiments in lambs, even with very large doses. The site of the effect on the reticular groove of adrenaline and of circulating catecholamines released in response to stimulation of the splanchnic nerves has not been demonstrated. Complex effects of adrenaline have been noted in conscious and decerebrate preparations of adult sheep. Kay (1959) showed that rumination (a procedure commonly taken as an indication of animals being at ease) regularly followed the intravenous injection of adrenaline. This was related to facilitation of receptors concerned in the initiation of regurgitation. The complexity of reactions to adrenaline is indicated by the

observations that inhibition of reticular contractions, stimulation of a single slow reticular contraction or a series of reticular contractions may follow I.V. injections of adrenaline in decerebrate preparations (Titchen, 1958).

The observations of complete failure of the reticular groove mechanism after vagotomy and hexamethonium but not atropine yield evidence to support the views advanced by Watson (1944) and Phillipson (1970) that the reticular groove contraction is one part of a mechanism contributing to the passage of sucked fluid to the abomasum. The reactions of the caudal oesophagus, the morphology, tonic contraction and reflex contractions of the reticular groove and opening of the reticulo-omasal orifice are important parts of this mechanism.

The skilled assistance received from Mrs M. Nandrup S.R.N. and Mr J. Patterson B.Sc. is acknowledged with gratitude. One of us (D.A.T.) is pleased to record the aid received from the Australian Research Grants Committee and from the Melbourne University Veterinary Research Fund. J. C. N. was able to continue these studies whilst on leave spent in part in the University of Melbourne.

## REFERENCES

ABE, S. (1959). On the histology and the innervation of the oesophagus and the first forestomach of goat. *Archos histol. jap.* **16**, 109–129.

ANDERSSON, B., LANDGREN, S., NEIL, E. & ZOTTERMANN, Y. (1950). Reflex augmentation of intestinal motility caused by stimulation of the superior laryngeal nerve. *Acta physiol. scand.* **20**, 253–257.

BENZIE, D. & PHILLIPSON, A. T. (1957). *The Alimentary Tract of the Ruminant.* Edinburgh: Oliver and Boyd.

COMLINE, R. S. & TITCHEN, D. A. (1951). Reflex contractions of the oesophageal groove in young ruminants. *J. Physiol.* **115**, 210–226.

CZEPA, A. & STIGLER, R. (1926). Der wiederkäuermagen im Röntgenbild. *Pflügers Arch. ges. Physiol.* **212**, 300–356.

DUNCAN, D. L. (1953). The effects of vagotomy and splanchnotomy on gastric motility in the sheep. *J. Physiol.* **119**, 157–169.

DUNCAN, D. L. & PHILLIPSON, A. T. (1951). The development of the motor responses in the stomach of the foetal sheep. *J. exp. Biol.* **28**, 32–40.

JARRETT, I. G. (1948). Production of rumen and abomasal fistulae in sheep. *J. Coun. scient. ind. Res. Aust.* **21**, 311–315.

KAY, R. N. B. (1959). Rumination in sheep caused by injection of adrenaline. *Nature, Lond.* **183**, 552–553.

KAY, R. N. B., ORSKOV, E. R. & WENHAM, G. (1972). Radiographic studies of the oesophagus and stomach of the suckling lamb and kid. *J. Physiol.* **227**, 2–3*P*.

LAWLOR, M. J., HOPKINS, S. P. & KEALY, J. K. (1971). The functioning of the oesophageal groove reflex and comparison of the performance of lambs fed individually and in groups. *Br. J. Nutr.* **26**, 439–448.

NEWHOOK, J. C. (1970). Visual studies of the oesophageal groove in lambs and its responses to intravenous atropine. *J. Anat.* **106**, 199.

NEWHOOK, J. C. & TITCHEN, D. A. (1969). Radiographic study of the oesophageal groove in lambs. *J. Anat.* **104**, 405.

NEWHOOK, J. C. & TITCHEN, D. A. (1972). Effects of stimulation of efferent fibres of the vagus on the reticulo-omasal orifice of the sheep. *J. Physiol.* **222**, 407–418.

ORSKOV, E. R., BENZIE, D. & KAY, R. N. B. (1970). The effects of feeding procedure on closure of the oesophageal groove in young sheep. *Br. J. Nutr.* **24**, 785–795.

PHILLIPSON, A. T. (1970). Ruminant digestion. In *Dukes' Physiology of Domestic Animals*, 8th edn., chapt. 22, ed. SWANSON, M. J. Ithaca: Comstock.

RUCKEBUSCH, Y. & BOST, J. (1962). Aspects fonctionnels du cardia chez les ruminants. *Rev. Méd. vét.* **113**, 211–227.

SAMUELS, P. B., ROEDLING, H., KATZ, R. & CINCOTTI, J. J. (1966). A new hemostatic clip: 2-year review of 1007 cases. *Ann. Surg.* **163**, 427–431.

SCHALK, A. F. & AMADON, R. S. (1928). Physiology of the ruminant stomach (bovine). *Bull. N. Dak. agric. Exp. Stn* No. 216.

STEVENS, C. E., SELLERS, A. F. & SPURRELL, F. A. (1960). Function of the bovine omasum in ingesta transfer. *Am. J. Physiol.* **198**, 449–455.

TITCHEN, D. A. (1958). Reflex stimulation and inhibition of reticulum contractions in the ruminal stomach. *J. Physiol.* **141**, 1–21.

TRAUTMANN, A. & FIEBIGER, J. (1957). *Fundamentals of the Histology of Domestic Animals.* Translated and revised by HABEL, R. E. & BIBERSTEIN, E. L. Ithaca: Comstock.

WATSON, R. H. (1944). Studies on Deglutition in Sheep. I. Observations on the course taken by liquids through the stomach of the sheep at various ages from birth to maturity. *Bull. Coun. scient. ind. Res. Melb.* **180**, 1–94.

WATSON, R. H. & JARRETT, I. G. (1944). Studies on Deglutition in Sheep. II. Observations on the influence of copper salts on the course taken by liquids into the stomach of the sheep. *Bull. Coun. scient. ind. Res. Melb.* **180**, 95–126.

WESTER, J. (1926). *Die Physiologie und Pathologie der Vormagen beim Rinde.* Berlin: Richard Schoetz. Cited by PHILLIPSON, A. T. (1970) Ruminal Digestion. In *Dukes' Physiology of Domestic Animals*, 8th edn., chapt. 22, ed. SWANSON, M. J. Ithaca: Comstock.

WISE, G. H. (1939). Factors affecting the reactions of the esophageal groove of dairy calves. *J. Dairy Sci.* **22**, 465.

## EXPLANATION OF PLATES

All of the radiographs were made of lambs whilst standing and except in Figs. 6 and 7, *whilst* sucking. In each, cranial is to the left, dorsal uppermost. The figure numbers are in the top right hand corner.

### PLATE 1

Fig. 1. Radiograph made during sucking of milk-contrast mixture by a lamb 4 days old. Contrast medium is present in three sites in the thoracic oesophagus, the most cranial bolus dorsal to the shoulder joint (S) is separate from more caudally situated material in the mid-thoracic oesophagus which is partly separated from the caudal phrenic ampulla (P.A.) by a distinct constriction. Contrast medium presents a continuous shadow from the phrenic ampulla, through the reticular groove (R.G.), the omasum (OM) into the abomasum (AB). Liquid-gas interfaces present are in the epigastric position between the abomasal gas (AB.G.) and liquid (AB), and in the dorsal position between the ruminal gas (RU.G.) and liquid.

Fig. 2. The 4-day-old lamb in which this radiograph was taken was sucking at the time. Contrast medium in the caudal thoracic oesophagus is partially separated by

a constriction cranial to the phrenic ampulla (P.A.). The reticular groove (R.G.) is free of contrast material which is present in the omasum (OM) and abomasum (AB) and has passed into the pyloric antrum (PYL).

PLATE 2

Fig. 3. The entire oesophagus is shadowed by contrast material without the clear impressions of a phrenic ampulla as in Figs. 1 and 2. The reticular groove (R.G.) is a region of narrowing of the shadow between the caudal oesophagus and the omasum (OM); the contrast material thus provides a continuous shadow from the mouth to the abomasum (AB).

Fig. 4. The presence of contrast material in the omasum (OM) provides an impression of its leaves. Although the most caudal region of the oesophagus does not contain contrast medium, an indication of the shortness of the reticular groove is provided by the narrow distance between the omasum and diaphragm. The abomasal gas cap (AB.G.) is distinct. Indentations in this and Figs. 1, 2 and 3 in the shadow of the contrast material in the abomasum (AB) which extends to its pyloric antrum are due to the folds of abomasal mucosa.

PLATE 3

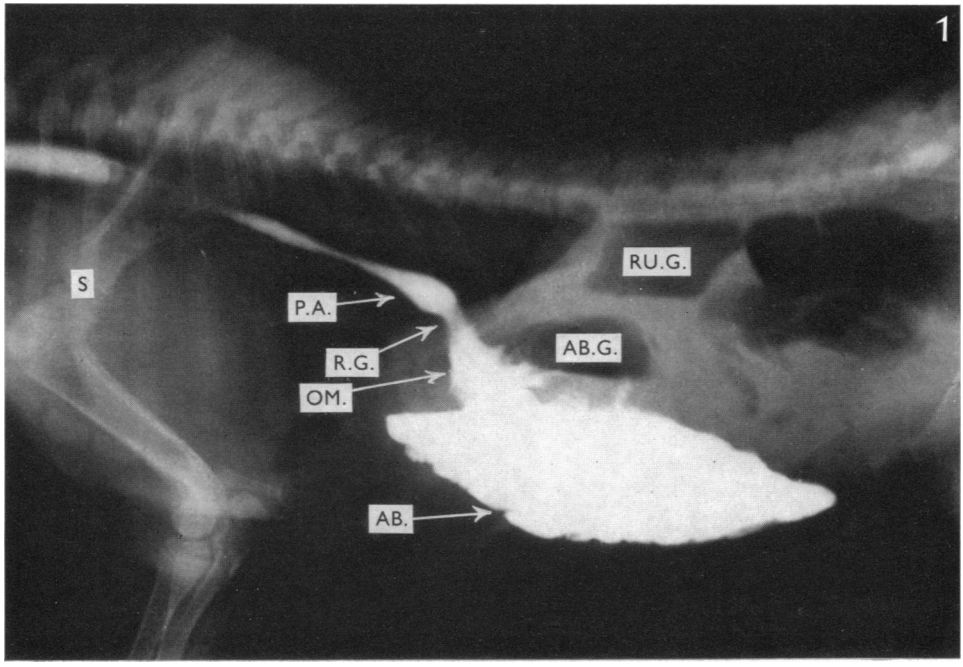
Figs. 5, 6 and 7 were radiographs made in a 10-day-old lamb after both vagus nerves were cut in the abdomen.

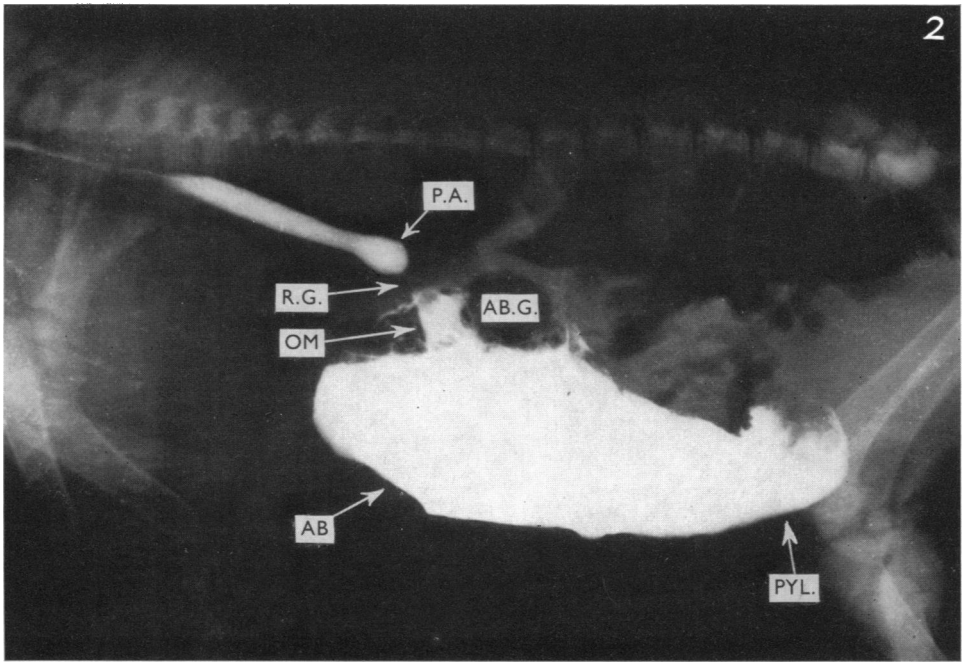
Fig. 5. 60 ml. liquid had been sucked. It entered the reticulum (RE) and cranial sac of rumen (C.S.) cranial and dorsal to the cranial pillar over which it is flowing into the ventral rumen (V.R.).

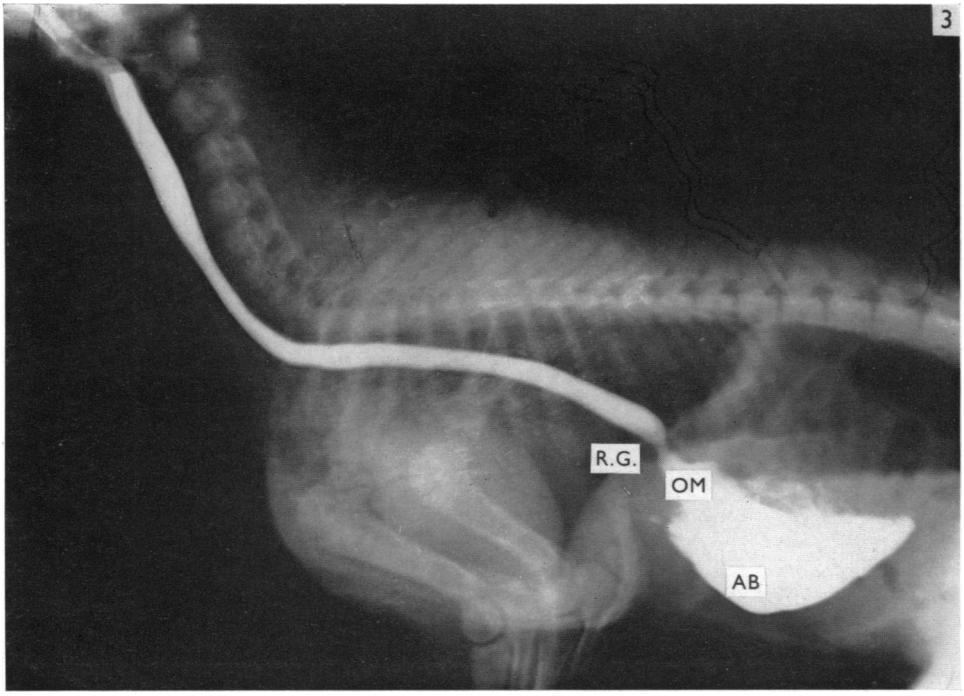
Fig. 6. 175 ml. liquid had been sucked and provides outlines of the reticulum (RE), cranial sac of the rumen (C.S.), the cranial pillar (C.P.), the caudal dorsal blind sac of the rumen (C.D.B.S.), the main ventral rumen (V.R.) and the caudal ventral blind sac (C.V.B.S.).

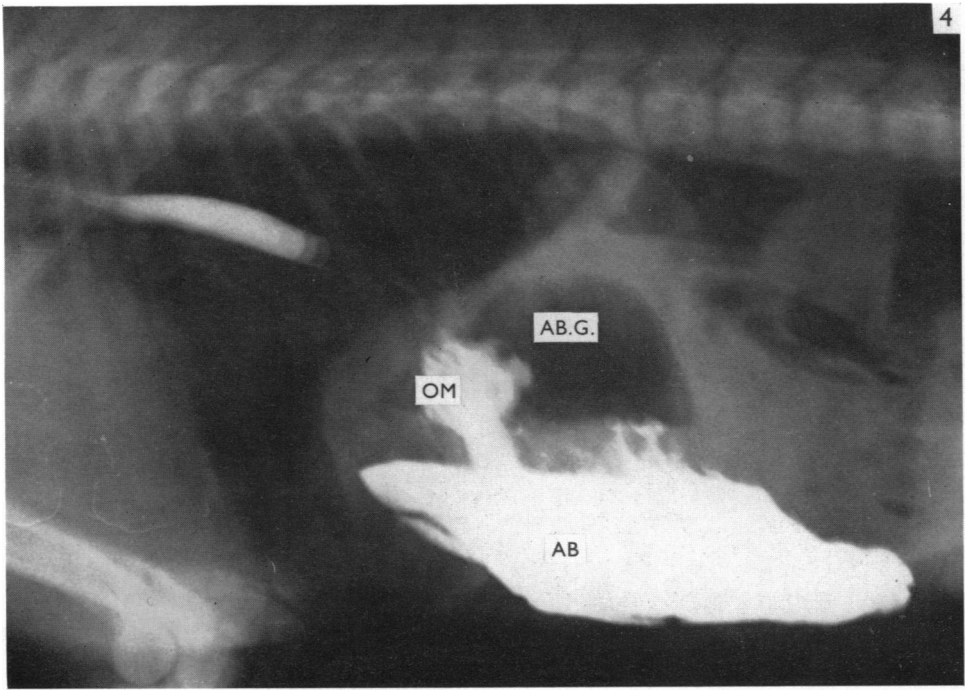
Fig. 7. Six hours after sucking 175 ml., liquid can be seen passing into the abomasum (AB). The loss of layering of contrast medium evident in Fig. 6 is due to the movement of the animal whilst preparations were made for radiography. It appeared to be expecting to be suckled.

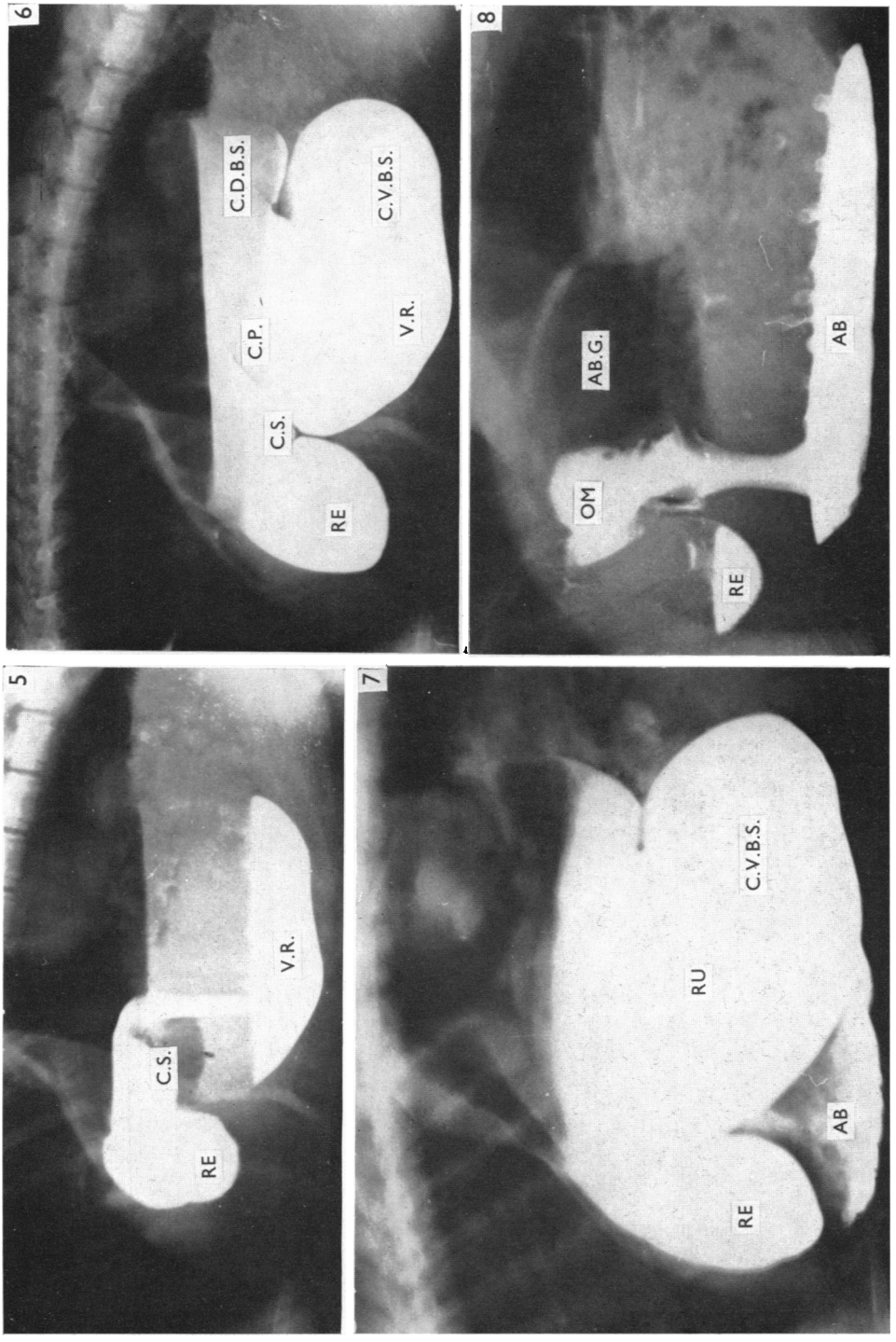
Fig. 8. The mixed destination of liquid in a lamb 22 days old when it was sucking 300 sec after being given atropine (800 $\mu$g/kg). Some contrast material has entered the reticulum (RE); most is passing ventrally via the omasum (OM) into the abomasum (AB) which has a distinct gas cap (AB.G.).


1
S
P.A.
R.G.
OM.
AB.
RU.G.
AB.G.


2
P.A.
R.G.
OM
AB
AB.G.
PYL.


3
R.G.
OM
AB


4
AB.G.
OM
AB


6
C.D.B.S.
C.P.
C.S.
RE
C.V.B.S.
V.R.
8
AB.G.
OM
RE
AB
5
C.S.
RE
V.R.
7
RU
C.V.B.S.
RE
AB