Acta Biol. Par., Curitiba, 10/11; 131 - 156, 1981/1982

OMASUM-PHYSIOLOGICAL FUNCTIONS
OMASUM-FUNÇÕES FISIOLÓGICAS

RECEBIDO EM 13/02/81
APROVADO EM 26/02/81

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INTRODUCTION

The omasum, almost spherical in shape, is the aboral third compartment of the ruminant forestomach. This three chambered proventriculus is deprived of any glandular secretion. The digestion of roughage is processed by bacterial fermentation, mainly in the first two compartments, the rumen and the reticulum. The omasum is a sort of "flood-gate" separating this large "vat" in which bacterial enzymes act from the abomasum where peptic digestion occurs.

It is now known that the four compartments develop during early embryonic life from a spindle-shaped gastric primordium. The rumen and reticulum correspond to the fundus and body of the simple stomach and the omasum to an outgrowth of the lesser curvature (49). An interesting feature is the rapid development of the omasum in the growing ruminant. In calves, the capacity of the omasum increases 60 times between the ages of 10 and 150 days (7).

The size and internal configuration of the omasum are lied to many variations in the different ruminant species. Only small and large domesticated ruminants will be considered here. In adult animals, the ratio of the omasal volume to the total forestomach volume is approximately 2 p. 100 in sheep and 4 p. 100 in cattle.

The most striking feature is the inner structure of the omasal body. The omasal cavity is divided by thin laminae [100 to 140 in cattle according to Lauwers](44) which justify the dif-

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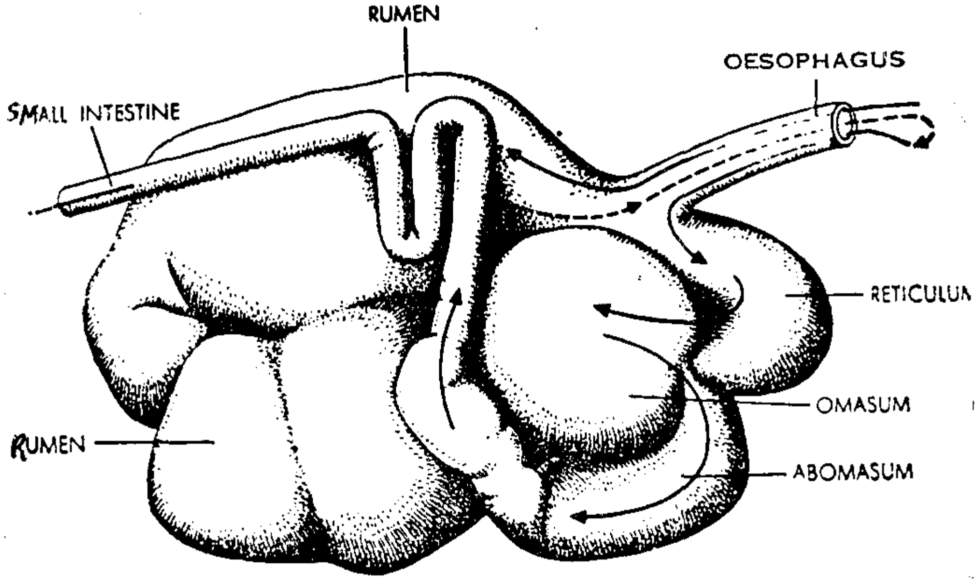

Fig. 1 — **General anatomy of the ruminant stomach** (cattle)
Right lateral view

ferent vernacular names: "manyplies", "psalter", "libro", "librillo", "feuillet". The total surface area of the laminae is large: about 247 ± 84 dm^2 in cattle and 20,1 ± 4,2 dm^2 in sheep (7, 20, 44). The surface area is icreased by 28 p. 100 for the papillae, giving such a total net absorptive surface area as 3.8 m^2 in beef cattle and 5.5 m^2 in dairy cattle (44). This surface area has been estimated to about one-third of the total epithelial area of the forestomach (65). A fine fibrous material is trapped in the interlaminar spaces, very different from the watery suspension in the rumen or the creamy liquid in the abomasum. The average dry matter of the ingesta in the forestomach was reported to be 17.2 p. 100 for the rumen, 13.1 p. 100 for the reticulum and 22.6 p. 100 for the omasum of calves (7).

These features justify the many odd physiological hypothesis of the past. Peyer and Duverney (quoted by Colin, 1853) compared the action of the omasum to that of a wine press (22). Other authors focused on the papillae which are evenly scattered upon the laminae. They were supposed to act as rasps, when the laminae move in a way that grinds the food in between. In fact, a reduction in the size of feed particles inside the omasum has been found and is shown in Table I.

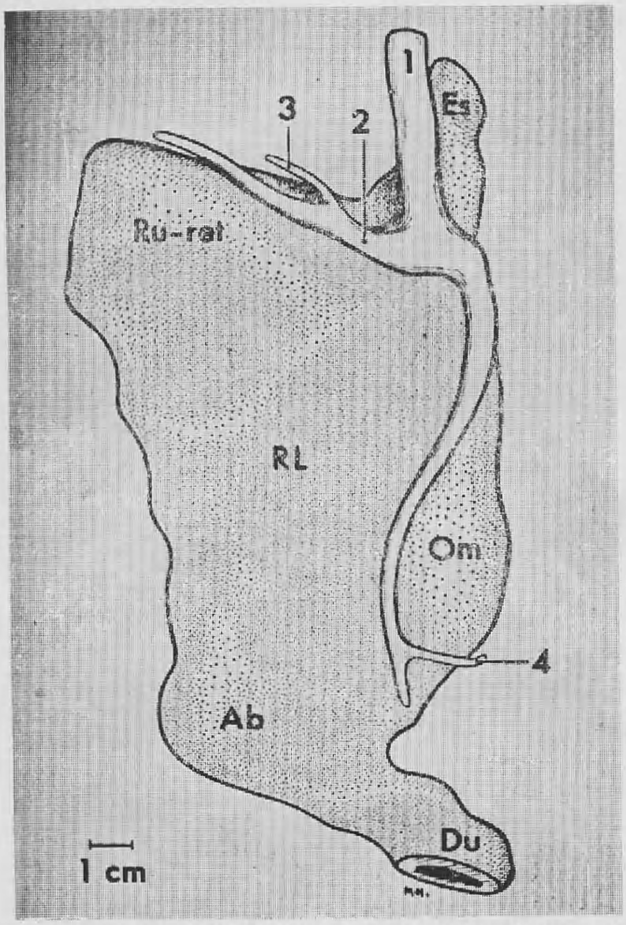

Fig. 2 — **Dorsal view of gastric primordium of a 34 days old bovine embryo** Es, oesophagus; Ru Ret, Rumino-reticulum; RL, depression caused by the dorsal lip of gastric groove; Om, omasal primordium; Ab, abomasum primordium; Du, duodenum; 1, Dorsal vagal trunk; 2, dorsal rumino-reticular branch; 3, branch to future dorsal ruminal sac; 4, omasal branch; from Mc Geady, T.A. & Sack, W.O. **Am. J. Anat.,** New York, **121:** 121-130, 1967. Ref. N.° 49.

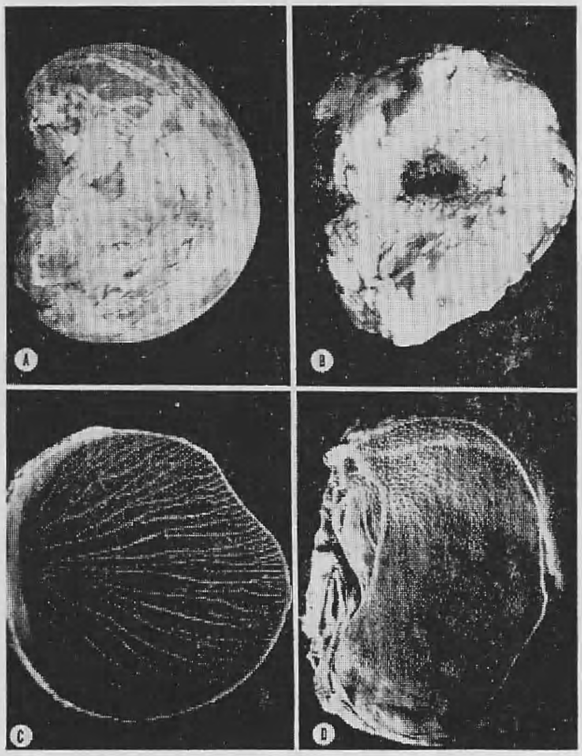

Fig. 3 — **General anatomy of the bovine omasum**
A — external shape
B — reticulo-omasal orifice, partly occluded by anterior insertions of primary laminae
C — horizontal cross-section showing four orders of laminae with ingesta in between
D — horny papillae on the first order laminae
from Becker, R.D.; Marshall, S.P.; Dix Arnold, P.T. **J. Dairy Sci.,** Lancaster, Pa., **46:** 835-839, 1963. Ref. N.° 7.

Compartment	diameter of air — dry particles				
	Above 5 mm	5 to 3 mm	3 to 2 mm	2 to 1 mm	Under 1 mm
	percentage by weight of air-dry particles				
Rumen	2,54	9,55	20,12	35,14	32,65
Reticulum	2,35	8,50	17,94	33,95	37,26
Omasum					
Upper portion	0,13	0,83	5,95	25,73	67,36
Lower portion	0,09	0,65	5,88	25,40	67,98
Abomasum *	0,65	2,48	7,39	24,58	64,70

* Enzymatic digestion removes substantial proportions of smaller particles. Also, some fine particles go into solution, and slightly increased moisture contents may swell some particles larger.

TABLE I — Proportion of weighed air-dry particles of different sizes in ingesta from stomach compartments of 68 dairy calves between 30 and 227 days old. (quoted from BECKER, **et alii** (7).

For many years, physiologists did not understand how ingesta could enter the deep interlaminar spaces because the omasal canal was thought to be a nearly horizontal groove forming the floor of the organ. Accurate anatomical studies and radiographic pictures have definitely shown that the omasal canal is nearly vertical (8, 30, 31, 54). Consequently, the ingesta flowing into the omasal atrium will flood the free edge of the laminae.

Omasal physiology has been previously reviewed (13, 55, 65). Since 1969, several important papers have greatly improved our knowledge.

1 — Omasal motor functions

The motor activity of the omasum has been controversial for many years. Three mains anatomical difficulties are encountered in the exploration of mechanical or physical events in the omasum. Firstly, the organ is deeply situated under the liver and the diaphragm, at the level of the ninth and tenth right ribs in sheep and goats. Secondly, the cavity is almost filled with the laminae so it is not easy to insert the usual pressure recording devices and difficult to effect visual or tactile inspection.

X — ray pictures gave but little information. Nevertheless, Benzie and Phillipson published clear pictures showing displacements as well as changes in shape (8). Akester and Titchen demonstrated in sheep that the floor of the reticulum is raised to the level of the reticulo-omasal orifice during the second phase of reticular contraction (3).

Manual insertion of recording devices into the omasum through rumen fistulae is rather easy in cattle (66), much more difficult on smaller ruminant (52).

A better access to the omasal cavity on conscious sheep and goats was achieved by chronic fistulation of the omasal body (11, 70). An alternative procedure for the study of the two omasal orifices is provided by chronic fistulae of the upper or lower compartments: reticulum or abomasum (12, 14).

Whatsoever, the classical manometric method using large rubber baloons placed in the omasum had been used in most of the earlier works (15, 64, 69). Owing to the small size of the omasal lumen and the presence of the laminae, the baloon can only record gross pressure changes in the omasal canal. The only sound results of these rough experiments are two:

a — the omasum displays some slow strong tonic contractions which are not always correlated with the rythmic rumino-reticular cycle.

b — each reticular contraction is correlated with a sudden pressure drop inside the omasal cavity.

Wester, had already published some data suggesting that the canal and the body of the omasum did not behave the same way (69). Obviously, the conventional large balloon method was no more satisfying for further studies.

Stevens **et alii** (66) used open-tipped catheters connected to pressure transducers on cattle. Ohga **et alii** (52) succeeded in placing up to four small recording balloons at one time in different locations of the sheep omasum. However these techniques are reliable only if the location of the catheter or balloon is very accurate. This is hard to prove in a small contracting organ. Better results could be achieved by using strain-gauges

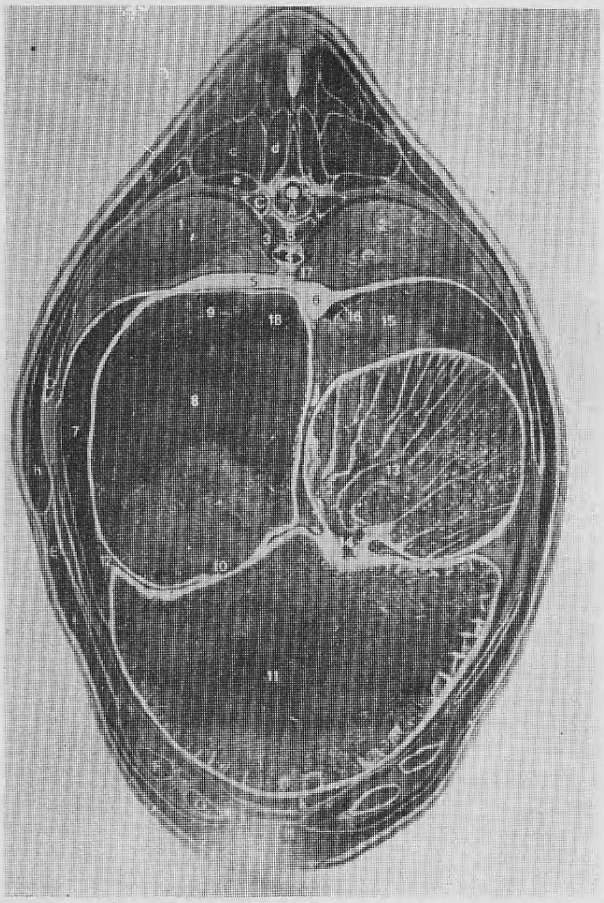

Fig. 4 — **Cross section of the body at the level of the 8th dorsal vertebra (cattle).**
1 and 2, lungs; 5 and 6, crus diaphragmae; 8, atrium ruminis; 10, rumino-reticular fold; 11, reticulum; 13, omasum; 14, omasal canal; 15, liver.
from Pavaux, Cl.; Gouffe, D; Biraben, J.P. **Contribution icomographique à la connaissance de la topographie viscérale des bovins.** Edouard Privat, 14 rue Idrac, Toulouse, 1968. Ref. N.° 54

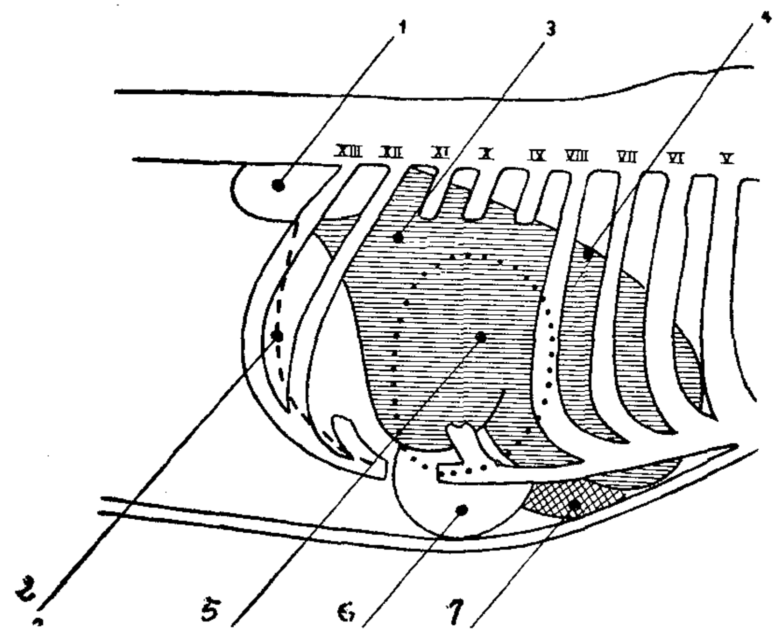

Fig. 5 — **Right lateral projectioin of the omasum in the goat**
1, kidney; 3, liver covering the omasum; 4, cranial limit of the phrenic dome; 2, costal insertion line of the diaphragm; 5, omasal projection (dotted line); 6, abomasum; 7, reticulum.
from Bost, J. **J. Physiol.**, Paris, **49:** 56-59, 1957, Ref. **11.**

(19, 24) or micro-balloons (19) sewn to the omasal walls. By accurate location of permanent electrodes a detailed analysis of the electromyographic correlations of the muscular contraction was made available (38, 48, 62).

Thus we can give now a rather complete account of the movements of the different parts of the omasum.

1 — 1. **Omasal canal**

The omasal canal (also called omasal groove), is a short groove, 5 to 10 cm long in sheep, corresponding to the lesser curvature, which extends from the reticulo-omasal orifice to the omaso-abomasal orifice. The direction of this groove is nearly vertical on the standing animal and it faces the free edge of the laminae. The reader should be reminded that the reticulo-omasal orifice is connected to the cardia by another canal, the oesophageal groove.

Pressure events in the omasal canal are correlated to the cyclic movements of the reticulo-rumen. According to Sellers and Stevens, in cattle, a small increase of pressure is associated to the first reticular contraction, then a small decrease to the second reticular contraction. This second reticular contraction is immediately followed by a much larger pressure increase in the omasal canal which must be a genuine contraction of the canal itself. Whenever a secondary ruminal contraction occurs, but only then, a second contraction of lesser amplitude is recorded (65). Similar results were recorded in goats (24): relaxation of the canal occurs during the reticular movement; a contraction always follows immediately the second peak of the reticular activity. Here too, another contraction can be seen at the time of a secondary motor cycle of the rumen, when present.

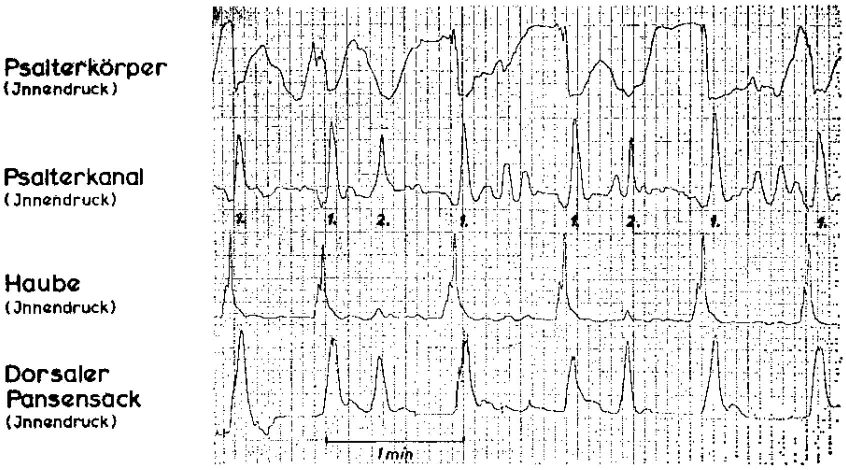

Fig. 6 — **Omasal motility (pressure records with micro-balloons)**
See from top to bottom: pressure variations in the omasal body, omasal canal, reticulum, dorsal sac of the rumen. During each reticular cycle, the omasal canal contracts once or twice together with the dorsal sac of the rumen (1 and 2: primary and secondary contractions).
Sudden omasal body relaxation is conspicuous at each reticular contraction.
from Ehrlein, H.J. & Hill, H. **Zbl. Vet. Med. A.**, Berlim, **16:** 573-596, 1969. Ref. N.° 24.

1 — 2. **Omasal body**

The pressure curves recorded from the interlaminar spaces near the greater curvature are quite different. They display slow and potent contractions, which reach usually their peak during the phases of reticular relaxation. These are obviously similar to the pressure waves previously recorded by the old conventional balloon technique. Such an agreement is also found on the sudden pressure drop which occurs during each reticular contraction (66). The exact timing of this pressure drop was clearly established in goats (24). There is no doubt that it occurs at the second peak of the reticular contraction during each reticulo-ruminal cycle.

The elaborate method used by Ohga **et alii.** (52) had given interesting additional data on sheep. Two types of tonic contractions of the omasal body were described: the one which correlates with each reticulo-ruminal cycle, which is most frequent in the oral part and body of the omasum, and the other which may last during two or more cycles and which is mainly apparent in the aboral part of the organ. The above mentioned pressure drop during the reticular contraction is refered to as a "sudden relaxation", followed by a period of rest then a gradual increase of tone until the next reticular contraction. For the first time, the time relationships of the pressure waves in the different parts of the omasum were emphasized: "simultaneous recording in the various parts of the omasum, however, showed that the contraction of the omasum started at the upper pole and was conducted to the lower pole, and that at last the organ contracted in total" (52). Ehrlein and Hill (24) could also demonstrate that the wave of contraction proceeds slowly from the oral to the aboral part. This is a very important point as a clue to the long unanswered question of the progression of digesta towards the omaso-abomasal orifice. A special type of contraction of the lower pole was also seen on the records in goats (24). This part of the omasum contracts independently from the rest of the body, sometimes rythmically.

These particulars have been studied thorougly by Ruckebusch and co-workers, owing to electromyographic techniques (20, 21). Pressure records, from micro-balloons inserted in the interlaminar spaces near the omasal wall, were in good relation with the bursts of potentials recorded from electrodes placed close to them (21). Accordingly, these bursts of potentials can be assumed as the electrical equivalent of local mechanical activity. The orderly progression of the contraction was stated as follows in sheep: starting from the parietal wall, the contraction spreads onto the greater curvature and later onto the visceral wall. The activity is initiated during the rest period of the reticulum and travels from the oral to the aboral pole at an

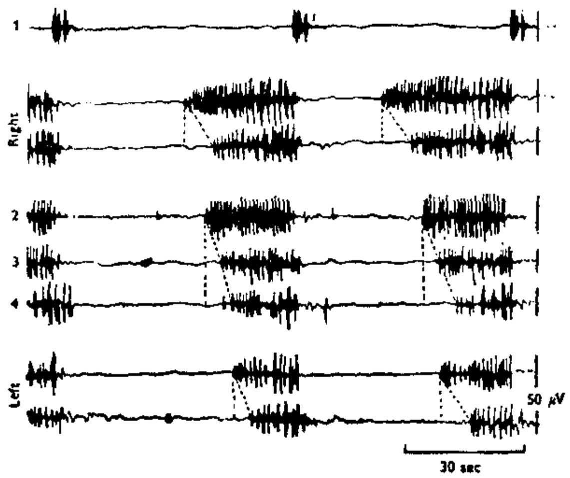

Fig. 7 — **Electromyographic correlations of the omasal body motility**
1, reticular electromyogram; right surface of the omasum; 2, 3, 4, greater curvature; left surface, From top to bottom, electrodes are placed 3 cm apart, from oral to aboral parts.
The electrical activity starts from the right wall, spreads onto the greater curvature and then onto the left surface, in the oral-aboral direction.
from Bueno, L. & Ruckebusch, Y. **J. Physiol.**, London, **238**:295-312, 1974. Ref. N.° 21.

approximate speed of 1 cm/s (21). Any electrical activity vanishes at once at the onset of the next reticular contraction (21). This observation provides an important clue for the omasal pressure drop at the beginning of the reticulo-ruminal cycle. Obviously, the old mechanical explanation of the reticular contraction pulling the omasal wall can be excluded. There must be some sort of active inhibition of the omasal muscles. According to Bueno and Ruckebusch, this pattern of activity is quite regular in sheep during any reticulo-ruminal cycle in the upper two-thirds of the organ, whereas the whole omasal body in cattle contracts independently from the reticulorumen (21). Other authors did find a greater variability in goats and even in sheep especially during feeding periods (15, 24).

X — ray examinations do not show any noticeable change in the surface area of the omasum while contracting. This fact and other direct observations led to the idea that the contraction of the omasal body is nearly isometric (24). The opposite would be surprising, owing to the fact that the omasal cavity is nearly filled with the laminae.

1 — 3. **Laminae**

In spite of the presence of smooth muscle inside the laminae, their motility was still questionable a few years ago.

We now have three sorts of evidence of their movements:

a — motion pictures of the opened omasum on well -oxygenated, halothane anesthetized goats. The film shows slow wavelike movements of the free edge of the laminae at the rate of 2 to 3/mn (71).

b — isometric myographic records of isolated strips of laminae. Small contractions (2/mn approximately) can be recorded in vitro in a well oxygenated Tyrode solution modified by addition of sodium acetate (61).

c — Electromyographic records on conscious sheep demonstrate the existence of bursts of potentials in the laminae at the rate of 2 to 3/mn. No relationship can be seen between this activity an that of the omasal body. Sometimes the laminae do not display any potentials for periods as long as 30 to 40 mn (21, 61).

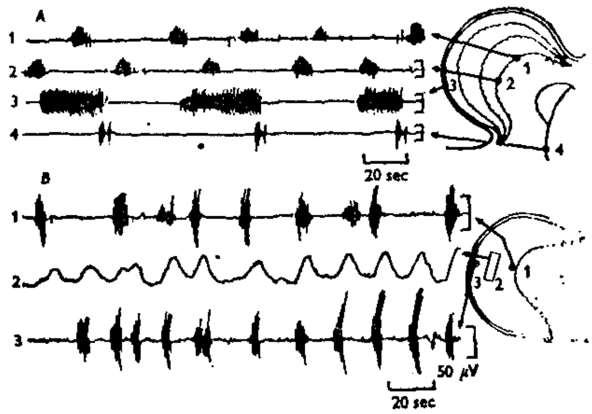

Fig. 8 — **Motility of the laminae**
A — Bursts of spikes recorded from two points (1 and 2) 4 cm apart on the edge of a lamina
They discharge quite independently from the omasal body (3) and the reticulum (4)
B — 1, electrical activity of the edge of a lamina; 2, record from a strain-gauge placed on the lamina (mechanical activity); 3, electrical activity of the base of the same lamina.
from Bueno, L. & Ruckebusch, Y. **J. Physiol., London, 238:** 295-312, 1974. Ref. N.° 21.

The mechanical effects of these movements are not very conspicuous. They may possibly stiffen the free edge of the laminae, thus allowing better access of the digesta into the inter-laminar spaces.

1 — 4. Reticulo-omasal orifice (R — O orifice)

Borgatti **et alii.**, Stevens **et alii.** stated that the orifice is open during most part of the relaxation period of the reticulum, but closes immediately after the peak of the second reticular contraction for a few seconds (10, 66). According to Ohga **et alii.** the orifice is open during the whole duration of the reticular contraction and closed, except for a very short time, during the reticular relaxation (52). Moreover, during the closure periods, they recorded small rythmic movements of the orifice whose frequency was much higher than that of the reticular contractions (52). A wide funnel-like opening of the reticulo-omasal orifice was observed by Ehrlein and Hill (24). Later, Newhook and Titchen gave a better description of the fast rythmic contractions (rate: 6/mn) (51).

The most direct investigation was made by Bueno and Ruckebusch (21). They used the impedance bridge technique with four small clips attached to the edges of the orifice. They too recorded (in conscious sheep) alternating small movements of dilatation and closure (amplitude 2 to 5 mm) at the rate of 8/mn. The orifice opens during the reticular contraction, reaches its widest diameter (15mm) during the second stage of this contraction, and closes soon after (0,5 to 0,75 s). The mean diameter is approximately 5 to 7 mm during the stage of reticular rest (21).

1 — 5. Omaso-abomasal orifice (O — A orifice)

This orifice is much wider than the R — O one and its closing mechanism is still questionable. In goats, continuous recording of the pH inside the omasal canal provided no evidence of any backflow of abomasal contents (24). However, the O — A orifice is limited by two mucosal folds which may act as a valve, providing thus a passive closure against backflow.

Movements and closure have been detected by palpation in calves: the orifice often stays dilated for extended periods. Then it closes either for 10 — 15 s. during each reticular cycle or for longer periods which may include more than one reticulo-

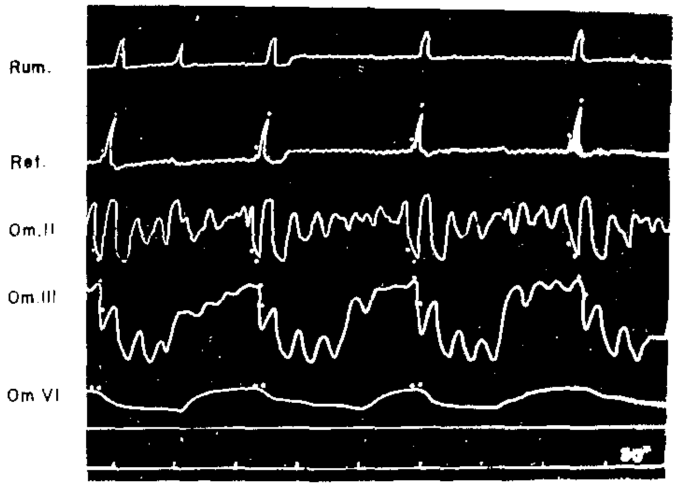

Fig. 9 — **Pressure records in various parts of the omasum (microballoons).** Rum., Rumen; Ret., reticulum, Om II, mid-part of the omasal canal; Om III, lower part of the omasal canal; Om IV, lower pole of the omasal body.
Fast contractions of the R-O orifice can be seen on Om II, as well as the relaxation of the omasal canal during the reticular contraction. The R-O fast contractions are superimposed to the large contractions of the omasal body on Om III.
from Ohga, A.; Ota, Y.; Nakazato, Y. **Jap. J. Vet. Sci.**, Tokyo, **27**: 151-160, 1965. Ref. N.° 52.

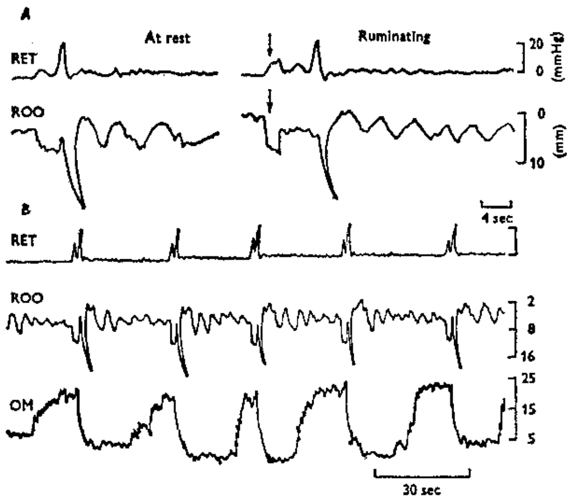

Fig. 10 — **Movements of the R-O orifice (impedance bridge method).**
Ret, reticular pressure; Roo, reticulo-omasal orifice diameter; Om, omasal body pressure.
from Bueno, L. & Ruckebusch Y. **J. Physiol.**, London, **238:** 295-312, 1974. Ref. N.° 21.

omasal cycle (66). It was suggested that the independent contractions of the lower part of the omasal body may provide the closing mechanism. This can be tentatively explained by the presence of special muscular bundles which originate from the omasal pillar (24).

The records of the diameter variations of the O — A orifice in conscious sheep, (impedance bridge technique) are not quite conclusive (19).

2 — Regulation of the omasal motor functions

2 — 1. Vagal innervation

It is well known that the omasum is innervated by several different branches of the vagus nerve. Some of them are common to the reticulum and the oral part of the omasum (32, 45). New experimental data should be explained by a different type of vagal innervation for the omasal canal and the omasal body.

The effects of a double vagal section had been studied on sheep by Duncan, since 1953 (23). Any cyclic motility of the rumen and reticulum disappears, whilst the abomasal motility is unaffected. Zaluckn, in 1972, demonstrated that such a section did not disturb noticeably the omasal motility (35). The fast movements (6/mn) of the R — O orifice too, are not suppressed by a double vagal cut as well as by the injection of atropine or ganglioplegic drugs (51).

Other experiments were soon in agreement with these data (9, 19, 21). After a thoracic section of both dorsal and ventral vagal trunks in conscious sheep, two types of motor activity can still be recorded from the omasum:

— the unaffected regular small contractions of the R — O orifice at an approximate rate of 6/mn.

— large contractions of the omasal body, whose rate is slightly faster than in normal animals (1 to 1.4/mn).

On the contrary, the large opening movements of the R — O orifice disappear (9).

The movements of the laminae are unaffected either by vagal stimulation or by vagal section (21, 71).

The conclusion is, that in opposition to the reticulum and the rumen, the fast rythmic movements of the R — O orifice and the slower contractions of the omasal body are not initiated by the vagal efferent innervation.

The role of the vagus on the omasum is probably limited to:

a — the cyclic inhibition of the tonus of the muscles surrounding the R — O orifice.

b — the inhibitory effect on the contractions of the omasal body which is most obvious at the peak of the reticular contraction.

c — the stimulation of the contraction of the omasal canal which follows each reticular contraction (This point needs further experiments to be fully established).

These facts do not exclude the possibility of vagally mediated reflexes which may affect the tonus of the omasal wall.

2 — 2. Reflex responses initiated form various parts of the stomach

The moderate distension of the various compartments may modify the motor activity of the omasum. These effects are most conspicuous on the omasal canal (24). According to others, they

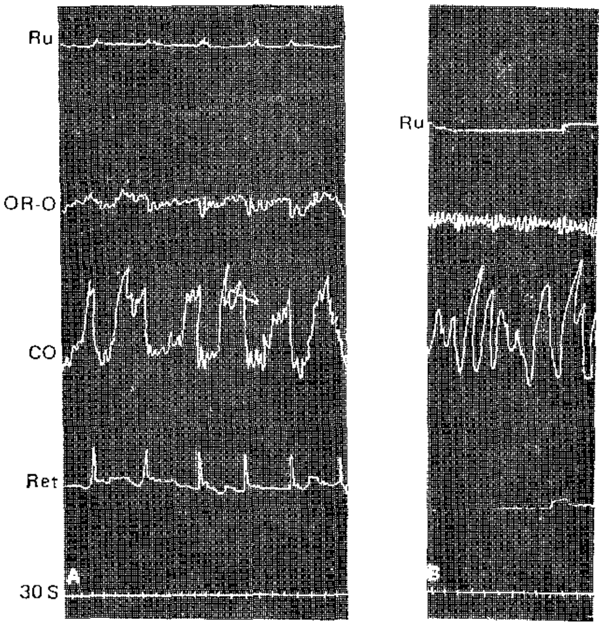

Fig. 11 — **Effects of a double intra-thoracic section of vagal trunks on the omasal movements**
(pressure records with small rubber balloons)
A — normal activity
B — 24 hours after double vagotomy
Ru, rumen; Oro, reticulo-omasal orifice; Co, omasal canal; Ret, reticulum.
In B, omasal activity contrasts with total standstill of the rumen and the reticulum.
Boinvin, R. & Bost, J., unpublished record (from the Author).

may also affect the omasal body but the responses are different in the large and small ruminant (19).

Distensions of the reticulum, the R — O orifice and the abomasum are mainly inhibitory. Distensions of rumen and the omasum itself seem to stimulate the omasal activity (19).

Omasal distension is also strongly inhibitory to the reticulum (16).

2 — 3 Food intake and humoral factores

During feeding, the frequency of the contractions of the omasal canal increases at the same rate as the reticular contractions (24, 52, 63). The effects of the nature of the diet, rumination and water deprivation were investigated (19).

Omasal motility is stimulated by intra-venous pentagastrin, while the rumen and the reticulum are completely inhibited (60).

Short chain fatty acids and lactic acid injected in the rumen, the duodenum or the omasum itself can modify omasal motility (19).

3 — The omasum as a regulator of the flow of ingeste from the reticulo-rumen to the abomasum

Two questions have to be answered: how does the omasum fill from the reticulo-rumen? and how does the omasum empty into the abomasum?

3 — 1 Omasal inflow

This flow depends obviously on the opening of the reticulo-omasal orifice, the pressure inside the reticulum (reticular contraction) and the relaxation of the omasum (omasal aspiration)-

Direct measurements of flow through the R — O orifice have been done by different methods:

a — Pitot tubes inside the omasal canal, close to the orifice (66).

b — detection by a thermistance of the flow of a cold solution infused in the reticulum (24).

c — ultrasonic probes inside the omasal canal, close to R — O orifice (19, 62).

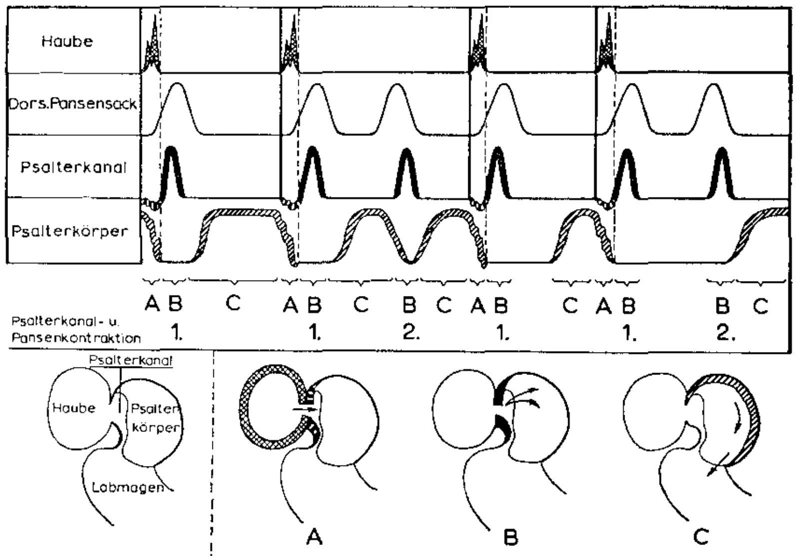

Fig. 12 — **Diagrammatic figuration of the omasal motility, correlated with the reticulo-ruminal cycle according to Ehrlein and Hill.**
Haube, reticulum; dors. pansensack, dorsal sac of the rumen; psalterkanal, omasal canal; psalterkörper, omasal body. The lower part figures the transit of digesta: A, inflow of digesta in the omasal canal during the reticular contraction; B, digesta are forced into the interlaminar spaces by contraction of the omasal canal; C, digesta are squeezed out and slowly pushed into the abomasum (labmagen) by the orderly progression of the omasal body activity.
from Ehrlein, H.J. & Hill, H. **Zbl. Vet. Med. A.**, Berlim, **16:** 573-596, 1969. Ref. N.° 24.

The data collected on cattle, goats and sheep are in agreement. Digesta flow from the reticulum into the omasum during the second stage of the reticular contraction i.e. when the pressure is highest in the reticulum, the R — O orifice open, the omasal canal and the omasal body relaxed. The digesta are then forced into the interlaminar spaces by the contraction of the omasal canal, provided that the omasal body was relaxed, which is the rule.

Evidence was brought of occasional backflow from the omasum to the reticulum in calves and goats (24, 66). It occured during contractions of the omasal body and was also recorded (Pitot tube) during the first reticular contraction or the extracontraction of rumination (66).

Quantitative estimations were obtained with markers (polyethylene glycol for instance). In sheep, mean flow was estimated to 400 ml/h and total flow to 5.8 to 18.0 l/24 h (37, 53).

In goats, figures between 100 and 380 ml/h have been reported (28). In the cow, the total amount of fluid flowing through the R — O orifice during 24 hours decreased from 215 to 59 as the amount of dry matter ingested varied from 14 to 3 kg per day (56). There was a direct relationship between the flow of fluid and the amount of dry matter ingested. The higher the proportion of coarse fodder in the diet, the larger the reticular-omasal flow. Variations of saliva secretion with different diets are thought to be responsible of these large differences (56).

3 — 2. **Omasal outflow**

The mechanism of omasal emptying into the abomasum is not perfectly understood yet.

According to some observations made on omaso-abomasal reentrant fistulated sheep, the flow of material could be recorded at any stage of the reticular cycle but was most frequent soon after the total relaxation of the reticulum (4, 5, 17). The omasal canal contraction could possibly be responsible for this flow. Lumps of solid food which may originate from the interlaminar spaces are probably squeezed out by contractions of the omasal body. The present knowledge of the oral-aboral progression of the omasal tonic contraction provides a clue on the propulsion towards the O — A orifice. However the movements of the digesta between the leaves and throughout the omasum have not been investigated since Badawy **et alii.** who were unable to reach any clearcut conclusion (6).

Omaso-abomasal flow increased during feeding either hay, oats or ground hay. The ratio of the number of outflows recorded to the number of reticular contractions usually decreased during feeding. That is to say the well-known increase in frequency of the reticular contractions was not paralleled by a similar speeding of omasal evacuation (17). Quantitative data obtained by this method on the volume of ingesta passed through the O — A orifice of sheep per hour, (130 to 346 ml (55) or 250 to 300 ml (47) are in good agreement with indirect measurements (300 ml) (37). Recent studies on sheep with ultrasonic probes suggest a more regular pattern of outflow on some records (19). But the data are too scarce for drawing conclusions.

A regular backflow of milk from the abomasum into the reticulum had been described in young kids (67). In adult goats such a backflow did not occur except when abomasum was overfilled. More recently, no evidence of any abomasal flow into the omasum was ever found in adult goats (24).

4 — Bacterial metabolism in the omasum

The observation of a low pH value (5.1 to 5.8) in the omasal contents of deer (57) and sheep (43) led to the interesting hypothesis that bacterial growth would be inhibted, without impairment of cellulase activity. Hence, the omasum could be the site of a production of cellobiose and glucose. This low pH value could be the result of the controversial abomasal backflow.

According to more recent data, the omasal pH in sheep and cattle is near to neutral and production rates of soluble sugars in incubated omasal contents under anaerobic conditions are very low (58). In cattle, the rate of methane production in vitro is the same for omasal digesta as it is for ruminal digesta (58). Thus, in domesticated animals, there is no evidence for a diminished fermentation rate in the omasum. Conversely, this organ may serve as "an additional retention mechanism for the coarse food particles which subsequently are subjected to further fermentation" (58).

5 — Omasal absorptive functions

The large surface area of the epithelial lining of the laminae and the low water percentage of omasal ingesta have suggested that this part of the forestomach may be a privileged site of absorption. Vascularisation and the ultra-structure of the dense capillary network in the laminae are also liable to absorptive function.

5 — 1 Absorption of volatile fatty acids (VFA).

According to Hornicke this absorption had been overestimated on the basis of determinations made on slaughtered animals (35). For instance, it had been calculated that 77 p. 100 of the VFA's entering the omasum were absorbed (6). Conversely, in vivo, the concentration of VFA's falls by 22 p. 100 only (39). We have good evidence that 87 p. 100 of the VFA's which are released in the rumen are readily absorbed by the rumen wall. Later on, 12.5 p. 100 of the total production would be absorbed by the omasum, leaving but the remaining 0.5 p. 100 to enter the abomasum (50). Whatever the physiological extent of this absorption, direct injection of labeled butyrate and acetate in the omasum of anesthetized calves have demonstrated the passage into omasal venous blood (40).

According to a new technique, the rate of VFA's absorption through omasal laminae is approximately twice slower than through the rumen wall (1). A fairly high carbonic anhydrase activity has been found in the forestomach papillae. The omasal wall activity was reported to be about twice the rumen activity. It was suggested that this enzyme might enhance the absorption of VFA's by providing exchangeable intra-cellular bicarbonate ions (2). As in the rumen, butyrate is partly metabolized in the omasal wall, with formation of β-hydroxy-butyrate and also lactate, which pass into the blood (40).

5 — 2 Absorption of water and electrolytes

Earlier estimations of water absorption have been reviewed (35, 36, 46). Quantitative data are very scattered (Table II). According to Masson and Phillipson, the daily omasal absorption in sheep would amount approximately to 3 liters (46).

Raynaud and Bost measured the absorption of distilled water on anesthetized sheep and goats, with polyethylene glycol as a reference substance. In sheep weighting 31 to 35 kg, net water absorption ranged from 42 to 81 ml per hour. Total daily water absorption would then vary between 1, 020 and 1, 910 ml (59). However, these experiments did not give a true picutre of water fluxes through the omasal wall: water may surely flow in both directions as it was demonstrated later by Engelhardt in the rumen wall (25). Moreover, these experiments were quite unphysiological: general anesthesia was used; the transit of ingesta was suppressed and the osmotic pressure of the omasal contents was much lowered.

The effect of osmotic pressure was demonstrated in sheep where a net flux of 50 to 60 ml/h was recorded with distilled water but only 20 ml/h with isotonic saline (53). A rate of 40 ml/h for the net absorption of tritiated water was found in sheep, with a solution of 270 m Osm/l. Between 310 and 330 m Osm/l, net absorption is zero, though the magnitude of fluxes in opposite directions is still of about 60 ml /h. When the osmolarity was decreased from 270 to 50 m Osm/l, water diffusion from

Animal species	Number of animals	Method	Reference substance	Water absorption per cent	VFA's	Authors
Sheep		slaughtered	dry-matter	35	59	BOYNE **et alii** 1956
—		—	lignin	33-64	50-69	GRAY **et alii** 1954
—	7	—	dry-matter	41		GARTON 1951
—	6	—	—	47		BADAWAY **et alii** 1958b
—	7	—	—	48-55*		BADAWAY **et alii** 1958c
—	8	—	—	43*		BADAWAY **et alii** 1958c
—	6	—	lignin		76	BADAWAY **et alii** 1958b
—		in vivo	PEG	33-66		HYDEN 1961
—		omasal cannula	—	8-17		OYAERT **et alii** 1958b
Cattle	6	slaughtered	dry-matter	21		JOHNSTON **et alii** 1961
—	6	—	chromium oxyde		60	JOHNSTON **et alii** 1961

* with reference to the content of the reticulum.

TABLE II — Collected data on the absorption of water and volatile fatty acids from the omasum. [quoted from Hornicke (1964), Litterature references will be found in the original article] (35).

the omasal contents to the blood increased from 95 to 177 ml/h (19). No evidence had been found of such an effect on the ruminal epithelium (26). Such an adaptation of the omasal resorption of water may regulate the osmolarity of digesta flowing into the abomasum.

In conscious goats, with permanent omaso-abomasal re-entrant fistulas, no evidence could be found of a net water absorption during omasal transit of digesta (41, 42).

More recently, attention focused on the ionic movements through isolated sheets of rumen epithelium or omasal laminae (29, 34): Na^+ ions are actively transported and the transfer mechanism is sensitive to ouabain. Some differences between ruminal and omasal absorption could result of an active chloride transport from the blood into the omasum (27).

Hormonal control of ionic and water movements through the omasal wall has been suggested but the data were too scarce to be conclusive (18).

5 — 3. Deprivation of omasal laminae

In spite of the above-mentioned data, it is still difficult to assess the physiological significance of the omasal absorptive function. It depends on the time of retention of the digesta in the omasal cavity. The nearly vertical position of the short omasal canal suggests a rapid outflow of the liquid part of the digesta entering through the R — O orifice. Then, only the more solid fraction trapped in the interlaminar spaces would be liable to significant absorption. We still need quantitative information on this possible partition of digesta flowing through the R — O orifice.

The total deprivation of the omasum could afford an estimation of its physiological importance in ruminant digestion. According to former observations, young goats fitted with a chronic omasal by-pass obtained by the opening of large reticulo-abomasal or rumino-abomasal fistulae, retained normal growth and good health (68). A new approach was the surgical ablation of a large number of omasal laminae in kids or in adult sheep (19, 20, 33). Growth retardation was observed in kids. The adult sheep were studies for 3 to 4 months post-operatively. No change in feeding behaviour and no weight loss were observed. The estimated laminal surface lost varied between 40 and 45 p 100 of the total omasal inner surface. With a diet of coarse feed, but not with grass, the reticulo-omasal flow was increased. Total concentration of VFA's in the abomasal contents increased by 75 to 95 p 100.

RESUMO

A complexa atividade motora do omaso de ruminantes é, hoje, bem conhecida. O orifício retículo-omasal, cuja motilidade é coordenada com o ciclo motor do retículo-rumem, regula o fluxo de conteúdo a partir desta vasta cuba de fermentação. A contração do canal do omaso projeta seu conteúdo sobre as lâminas. Em conseqüência, o líquido rúmino-reticular é filtrado, de modo que as partículas alimentares maiores ficam retidas nos espaços inter-laminares. As contrações possantes do corpo do omaso, provavelmente, expremem o conteúdo inter-laminar fazendo a remoção do líquido que embebe este conteúdo; desta forma fica assegurado o trânsito lento da fração sólida em direção ao orifício omaso-abomasal. Geralmente, no ruminante adulto, um mecanismo de fechamento deste orifício impede o refluxo do conteúdo abomasl.

Os estímulos mecânicos do canal omasal e a distensão moderada do corpo do omaso podem desencadear estículos aferentes que reforçam a atividade dos neurônios bulbares éxcito-motores do retículo-rumem.

A motilidade deste compartimento terminal dos pré-estômagos não é, inteiramente, comandada pela inervação motora vagal: os movimentos rápidos do orifício retículo-omasal e das lâminas, assim como as contrações do corpo do omaso, não são modificados quando a inervação vagal é suprimida.

Demonstrou-se que o omaso é capaz de absorver ácidos graxos voláteis e ions sódio sem que, entretanto, tal função pareça essencial. A importância da absorção de água foi, sem dúvida, exagerada de vez que se demonstrou, hoje, estar esta absorção sujeita a consideráveis variações, dependendo da osmolaridade do conteúdo digestivo.

Palavras chave: omaso; pré-estômago; digestão; ruminantes.

SUMMARY

The elaborate motor activity of the omasum of ruminants in now clearly understood. The reticulo-omasal orifice, whose motility is integrated to the cyclic pattern of the reticulo-rumen, regulates the outflow of digesta from this large "fermentation

vat". The contraction of the omasal canal floods the laminae with digesta. Consequently, the reticular fluid is sifted, as the larger particles are trapped in the interlaminar spaces. The strong movements of the omasal body probably squeeze the contents and provide a slow transit of solid material to the omaso-abomasal orifice. Usually, in the adult ruminant, the closing mechanism of this orifice prevents backflow from the abomasum.

Mechanical stimuli of the omasal canal and moderate distension of the omasal body can induce afferent impulses which stimulate the rumino-reticular motor neurons in the medulla.

The motility of this aboral compartment of the forestomach is not wholly controlled by vagal motor innervation: the fast movements of the reticulo-omasal orifice and of the laminae, as well as the contractions of the omasal body are not affected by vagal denervation.

The absorption of volatile fatty acids and sodium ions is conspicuous but probably not essential. Water absorption had surely been overestimated; its rate is lied to considerable variations according to the osmolarity of the digesta.
Kek-words: omasum; forestomach; ruminants; digestion.

RESUME

L'activité motrice complexe de l'omasum des ruminants est aujourd'hui bien connue. L'écoulement du contenu de la vaste cuve à fermentation constituée par le réticulo-rumen est réglé par l'orifice réticulo-omasal, dont l'activité est coordonnée avec le cycle moteur de ces deux compartiments. La contraction du canal omasal projette son contenu sur les lames. Le liquide rumino-réticulaire est ainsi filtré, car les grosses particules alimentaires sont retenues dans les espaces interlaminaires. Les contractions puissantes du corps de l'omasum ont sans doute pour effet d'exprimer le liquide qui imbibe le contenu interlaminaire; elles assurent aussi le lent transit de la fraction solide vers l'orifice omaso-abomasal. En règle générale, chez le ruminant adulte, un dispositif d'occlusion de cet orifice empêche le reflux du contenu abomasal.

Les stimulations mécaniques du canal omasal et la distension modérée du corps de l'omasum peuvent déclencher des influx sensitifs qui renforcent l'activité des neurones bulbaires excito-moteurs du réticulo-rumen.

La motricité de ce compartiment terminal des pré-estomacs n'est pas entièrement commandée par l'innervation motrice vagale: les mouvements rapides de l'orifice réticulo-omasal et des lames, de même que les contractions du corps de l'omasum, ne sont pas modifiés par la suppression de l'innervation vagale.

La fonction d'absorption des acides gras et des ions sodium a été démontrée mais elle ne joue sans doute pas un rôle physiologique essentiel. L'importance de l'absorption d'eau avait été certainement surestimée; son intensité est sujette à des variations considérables en fonction de l'osmolarité du contenu digestif.

Mots clés: omasum; pré-estomacs; digestion; ruminants.

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