STUDIES ON THE PATHOGENESIS OF ACUTE BLOAT IN RUMINANTS.

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INTRODUCTION.

Acute bloat or tympany, to which apparently all ruminants are subject, is defined in various textbooks on animal diseases as a rapid distention of the rumen due to the formation of gases. (Wester (1936) and Hutyra, Marek and Manninger (1938)). The clinical manifestations are described as marked bulging of the left flank, small frequent pulse, frequent respirations, colicy symptoms, groaning and staggering and finally death due to asphyxia.

Broadly speaking, bloat can be divided into two distinct types, namely acute and chronic. Chronic bloat is defined as a persistant or intermittent accumulation of gas in the forestomachs especially after feeding, extending over a considerable period and not dependant on any special feeding regime. It is the result of an interference with the eructation mechanism or elimination of gas. (Wester (1936) and Cole, Huffman, Kleiber, Olson and Schalk (1945).

Hutyra *et al* (1938) do not regard chronic bloat as a disease *per se*, but rather as a symptom of an underlying condition or affection of the forestomachs or oesophagus. Conditions such as compression of the oesophagus by enlarged lymphatic glands, oesophageal diverticula, traumatic reticulitis, extensive peritoneal adhesions interfering with ruminal mortility and atony of the ruminal musculature, dan all give rise to chronic bloat. The primary lesions associated with this type of tympany, are fully dealt with in the literature and require no further elucidation. Furthermore, chronic bloat has a low incidence as it only affects individual animals sporadically. The losses to farmers are therefore not as disastrous as in the case of acute bloat, where a large number of animals may be affected at the same time.

According to Cole *et al* (1945) acute bloat occurs in association with certain feeding regimes such as legume pasturing. This type of bloat has become a problem of major economic importance all over the world in those areas where legumes are cultivated and used as stock feeds. Losses appear to be particularly severe in intensive farming areas, especially amongst valuable dairy animals, due to the fact that these animals are highly fed for production. The ruminant is physiologically adapted to the digestion of roughage, with the result that forced feeding is unnatural to this type of animal and predisposes them not only to bloat, but also to digestive disturbances and various metabolic diseases.

As pointed out by Cole et al (1945) the seriousness of the bloat problem should not only be attributed to actual losses, but other factors such as expensive preventative measures and restrictions on the use of legumes should also be considered.

According to Niborg (cited by Cole et al (1945)) acute bloat became a serious problem from about the middle of the eighteenth century when pasturing on clover became a common practice. It has since been reported from many countries adapted to the cultivation of legumes, such as Canada, Australia, New Zealand, India, Scotland, England, Germany, United States of America and South Africa. (Cole et al (1945)). The increasing incidence of acute bloat has given research on the problem a tremendous impetus. From about the middle of the first half of this century a vast amount of literature relating to bloat has appeared, and although many theories have been advanced, various aspects of the pathogenesis of acute bloat have remained unsettled. The recent review of bloat by Cole et al (1945) actually revealed many of the shortcomings of our present state of knowledge.

It is felt that the material which forms the basis of this study, might prove of some value in elucidating the pathogenesis of this baffling condition, especially as the approach to the problem is from an entirely different angle. Although no new methods of treatment or prevention are suggested, the underlying principles of many of the time-honoured methods are demonstrated.

THE CURRENT THEORIES OF BLOAT.

The more commonly accepted theories of bloat have been fully discussed by Cole et al (1945) in their review. These are summarized below together with more recent contributions to the literature.

1. Bloat due to excessive gas formation.

Most of the older theories regarding the pathogenesis of acute bloat are based on the assumption that readily fermentable and succulent feeds produce excessive amounts of gas when subjected to rapid fermentation in the rumen, especially when large amounts are consumed. This was described as the cause of bloat by workers in various countries (Murray (1909), Gallagher (1921), Viljoen (1922), Kephart (1929), Veech (1937) and the older textbooks on animal diseases (Hutyra, Marek and Manninger (1938) and Wooldridge (1923)).

This theory was disproved when Cole, Mead and Kleiber (1942) and Quin (1943) showed that animals could eructate far more gas than is actually produced in the rumen. Cole et al (1942), Washburn and Brody (1937) and Quin (1943) also found that green lucerne does not stimulate more gas production than lucerne hay. Jacobson, Espe and Cannon (1942) found comparable figures for in vitro gas production of green lucerne and green grass.

To quote from Cole et al (1945): "The evidence points fairly convincingly to the conclusion that excess gas production in the rumen is not the cause of bloat per se. On the contrary, most investigators agree that bloat is due to an upset in the normal mechanism for expelling gas. The evidence at hand does not indicate that bloat - provoking feeds result in greater gas formation than feeds not associated with bloat. The proponents of all other theories agree, however, that the rapid formation of gas associated with eating and the consumption of large amounts

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of feed, with the consequent increased gas production, may be predisposing factors."

2. Bloat due to excessive consumption of dense feeds.

This theory is based on the assumption that the rapid ingestion of large amounts of dense feeds such as succulent legumes, causes a mechanical obstruction to the exit of gas from the rumen by blocking the cardiac orifice. The time-honoured practice of treating bloat by elevating the fore-quarters lent support to this theory. From in vitro observations on the behaviour of fermenting ruminal ingesta, the proponents of this theory (Jacobson, Espe and Cannon (1942)) believed that if large amounts of succulent material are rapidly ingested, this material forms a compact mass in the reticulum and anterior part of the rumen, which tends to depress the stomach, so that the cardiac orifice is shifted to a position below the level of fluid in the rumen. This, together with further bouying up of the ingesta due to gas formation, prevents the escape of gas and leads to bloat.

These investigators support their statements by pointing out that bloat invariably occurs amongst growing and producing animals with voracious appetites; also the prior feeding of hay or grain will prevent overfeeding on succulent feeds and so prevent bloat. According to them, legumes covered with dew or frost are especially dangerous as animals consume dampened legumes faster. They also believe that wet feeds cut down salivary secretion and that a decreased amount saliva in the rumen increases gas formation. Although they found that as much gas is produced per pound of blue grass eaten as per pound of lucerne, they maintain that succulent lucerne is consumed much faster.

According to Cole et al (1945) however, this theory does not explain the occurrence of bloat amongst animals fed grain only or the relief of mildly bloated animals by feeding Sudan grass. As pointed out too by Mead, Cole and Regan (1944) bloat cannot always be correlated with the amount of succulent feed consumed.

3. Bloat due to toxic gases.

According to this theory, toxic gases like carbon monoxide and hydrogen sulfide, which are produced in the rumen from legumes with a high protein content, produce bloat by paralysing the rumen.

Dougherty (1940, 1941 and 1942) found that, by raising the intraruminal pressure with air or other gases common to the rumen, even small amounts of carbon monoxide or hydrogen sulfide present in the rumen are absorbed and cause marked toxic symptoms, rumen paralysis and bloat. The amount of carbon monoxide and hydrogen sulfide present in ruminal gas was also found to increase appreciably after feeding freshly cut clover, and large amounts of hydrogen sulfide were found in ruminal gas and ingesta of animals which died of bloat.

Although Dougherty originally subscribed to this theory he later maintains (personal communication cited by Cole et al (1945)) that toxic gases are not responsible for cessation of ruminal motility and bloat as such, but that they probably play an important part in causing death from bloat, especially hydrogen sulfide, through increased absorption due to high intra-ruminal pressure.

Olson (1944) however believes that hydrogen sulfide is responsible for bloat by paralysing the rumen, as well as for death from bloat, following absorption. Olson (1940) found that carbon monoxide and hydrogen sulfide had no recognisable toxic effects unless accompanied by an increase in intra-ruminal pressure. In 1944 he reported that hydrogen sulfide occurs in large amounts in the ruminal gas of bloated animals. In support of the "toxic gas" theory of bloat, Olson mentions the fact that the protein of legumes is higher in sulphur than the protein of non-legumes and that the leafy parts of legumes, which are usually grazed, contain more sulphur than the stems.

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(Alway (1927) and Painter (1943)). He attempts to explain why bloat occurs on some pastures and not on others, by postulating that if hydrogen sulfide is produced in the rumen from the sulphur of protein in legumes and this in turn depends on the sulphur content of the soil, bloat will occur on pastures with sulphur-rich soil. The increase in the incidence of bloat in times of abnormal rainfall is explained by the assumption that plants, induced to grow rapidly by heavy rainfall, contain more sulphur.

The experimental results of Kleiber, Cole and Mead (1943), who found no significant difference in the amount of hydrogen sulfide in the ruminal gas of bloated and non-bloated animals on lucerne pasture, seems to disprove this theory. Cole et al (1945) however acknowledge the fact that hydrogen sulfide may be a contributing factor in death of animals from bloat.

4. Bloat due to abnormal ruminal flora or fauna.

This theory has been suggested, but there is not sufficient proof that bloat is actually caused by the presence of abnormal micro-organisms or an inbalance of the normal ruminal flora and fauna. In a study of the ruminal organisms of bloated and non-bloated sheep, Koffman (1937) found a decrease in the number of large protozoa in the ingesta of the bloated animals and suggested that this change may have resulted in a greater number of gas producers.

Quin (1943) showed that false yeast cells (Schizosaccharomyces ovis), present in large numbers in the rumen of sheep on a diet of lucerne, are responsible for the oxidative assimilation of plant sugars with the rapid evolution of large amounts of gas, mainly carbon dioxide. Clark (1946) showed a significant correlation between the number of Schizosaccharomyces ovis present in ingesta and the volume of gas evolved.

According to Quin (1943) acute bloat represents an integral part of the normal processes of sugar metabolism in the forestomachs of ruminants. The presence of these characteristic yeast cells is regarded as an important factor in the pathogenesis of acute bloat, but they are not regarded as abnormal inhabitants of the rumen. To control bloat he contends that ruminants should be safeguarded against spells of acute hunger, because starvation leads to a depletion of the glycogen reserves within the yeast cells, with a consequent accentuated phase of oxidative assimilation and gas formation from plant sugars if the animal is subsequently allowed to feed green lucerne. If the energy demands of the yeast cells are however kept satisfied by regular supplementation of carbohydrate rich foods such as grains with lucerne, the sugars in the lucerne will not be metabolised at the same dangerously high speed, with the result that gas and foam production are kept within bounds. Cole et al (1945) believe that Quin's hypothesis may explain frothy bloat, but state that there is no evidence that the sugar content of lucerne, producing this type bloat, is higher than normal.

5. Bloat due lack of coarse roughage in the rumen.

According to this theory, proposed by Cole, Mead and Kleiber (1942), coarse roughage is necessary to elicit the eructation reflex. These workers believe that there is a rough correlation between eructation and rumination, and since it has been shown conclusively by Schalk and Amadon (1928) that rumination depends on stimulation of nerve fibres in the rumen by coarse roughage, they concluded that the eructation reflex is initiated by the same type of stimulus. Conclusive evidence on this point is however lacking.

The theory that the physical condition of the feed is an etiological factor in bloat, is however backed by considerable indirect evidence. Mead, Cole and Regan (1944) showed that the incidence of bloat on a ration of ground hay and grain is much higher than on unground hay and grain. Since the only difference between these two diets is a change in physical nature, the

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physical condition of the feed must obviously have played a role. Mead and Goss (1936) also reported bloat in cattle on a non-roughage diet and McCandlish (1923) encountered bloat when milk was the sole diet for calves.

Cole, Mead and Regan (1943) also showed that bloat can be produced and prevented on the basis of this theory. According to them, bloat can be produced any time of the year and under varying environmental conditions provided the lucerne is young and succulent and free from old hard and dry stems. The pasture should be free from contaminating weeds and grasses and provided with sufficient water to induce rapid growth of the lucerne. The animals themselves should be deprived of all hay and straw prior to pasturing. Under these conditions bloat is attributed to the lack of coarse roughage in the diet, which results in insufficient stimulus for the eructation reflex.

These same workers also conclusively demonstrated that bloat can be prevented by feeding a coarse hay prior to legume pasturing. They found that a coarse hay afforded greater protection than a fine-stemmed leafy hay; Sudan hay proved the best. The hay should also be palatable, otherwise the animals will not eat enough hay to be protected. The preventative action of hay is also explained on the basis of this theory. To lend further proof to their postulate, these authors attribute the action of turpentine in the relief of bloat to stimulation of the eructation reflex by irritation. Clark (1948) however showed that the beneficial effect of turpentine is mainly due to its action on surface tension, thereby breaking froth.

6. <u>Bloat due to frothing of ruminal ingesta</u>.

In his classification of tympany, Wester (1935) distinguished between two distinct types of acute bloat. In the one type, which is caused by the ingestion of young, fresh lucerne, clover or grass, the gas is mixed with the ingesta to

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form a foamy mass. In the other type of acute bloat, which can be caused by mechanical obstruction of the oesophagus, overfeeding or rumen paralysis, the gas is free and lies above the ingesta.

Frothing of ruminal ingesta has been encountered by various workers in cases of acute bloat on green clover (McCandlish (1937), Hudson (1938), Dougherty (1941) and Olson (1942)). Quin (1942, 1943) found that the ingesta of sheep bloated on green lucerne consisted of a strongly foaming, frothy mass. In fact, Amadon (cited by Cole et al) concluded from his experience that most cases of bloat on green legumes are of the frothy type. This type of bloat has also been encountered when feeding lucerne hay (Quin 1942) and Dougherty reported frothy ingesta in three steers that died of bloat on a diet of chopped lucerne hay and grain. Kick, Gerlaugh and Schalk (1937) also believe that frothiness is a factor in bloat of steers fed corn in the feed-lot. Furthermore, the beneficial effect of antifrothing agents in the treatment of acute bloat on green legumes has been reported on by Quin, Austin and Ratcliff (1949) and conclusively demonstrated by Clark (1950). Clark (1948) also demonstrated that the main effect of turpentine in the relief of bloat is due to the breaking of froth.

In spite of all the evidence that this type of bloat occurs, Cole et al (1945) do not appear to be convinced that frothing is actually the cause of bloat. The following is quoted from their review: "Cole and co-workers (unpublished data), on the other hand, have tapped a number of cows bloated on alfalfa pasture without encountering a case in which the free air space was absent. The fact that often no free gas but, rather, frothy ingesta, escapes, when the rumen is tapped is regarded by many as proof that free gas is not present. The cause, conceivably, may be the fact that the free air space is difficult to tap when the rumen is excessively filled. If a free air space exists, it is difficult to understand why frothing would cause bloat. At the moment at which belching occurs there is a dilation of the reticulum and anterior rumen, thus tending to free the cardia for the passage of gas into the oesophagus."

Although they do state that bloat on green legumes may fall into two categories, one in which free gas is present and another in which the gas is incorporated in the ingesta as a frothy mass, they apparently do not attach any significance to frothing as a cause of bloat.

The actual cause of frothing has been attributed to the presence of saponins in lucerne and clover. (McCandlish (1937), Olson (1942) and Quin (1943)). Jacobson (1919) isolated a strongly foaming saponin from alfalfa, but according to Cole et al (1945) attempts to produce bloat by feeding saponins have not been successful.

Wester (1935) describes the pathogenesis of frothy bloat as follows: Very rapid fermentation of succulent feeds leads to a thorough mixing of the food with the gas. This impedes belching and on account of the rise in intraruminal pressure, there is an increase in the tone of the ruminal wall which prevents the regular antiperistaltic movement of the rumen, necessary for eructation. The rumen reacts to the increasing pressure by increasing its motility, which has the effect of further thoroughly mixing the gas and ingesta.

7. Bloat due to inhibition of ruminal motility.

As eructation occurs only when the rumen is in an active state of contraction (Wester (1935), Hofland (1940) and Cole, Mead and Kleiber (1942)), ruminal atony must obviously be a cause of tympany if gas formation is adequate. Various chemical substances, which cause ruminal paralysis, have therefore been incriminated as etiological factors in acute bloat associated with the feeding of legumes.

Dougherty (1942) showed that the intravenous injection of histamine in doses varying from 2 to 5 mgrm. causes complete

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paralysis of the rumen. This observation was subsequently confirmed by Clark (1950). During his studies on gas and ruminal ingesta of bloated animals Dougherty (1942) found large amounts (.9 to 2.4 mgrm.%) of histamine in the ingesta samples of three steers that died of bloat. He also mentions the fact that histamine can increase by feeding high protein diets. Although Dougherty does not believe that histamine by itself is the cause of acute bloat, he suggests that histamine might be a contributory factor.

Quin and van der Wath (1938) showed that the dosing of potassium cyanide to sheep causes ruminal paralysis. Steyn (1934) described tympanites as a symptom of prussic acid poisoning from plants containing cyanogenetic glucosides. (Species of Dimorthotheca and also various members of the family of Gramineae such as species of Aristida, Cynodon and Sorghum have been found to contain prussic acid when wilted). In spite of the fact that Clark and Quin (1945) failed to incriminate hydrocyanic acid as a possible cause of acute bloat, Evans and Evans (1949) believe that this substance is associated with acute bloat on clover. They have isolated hydrocyanic acid from clover juice and demonstrated its presence in the blood of an animal bloated on clover. They found .1 mgrm. hydrocyanic acid per 100 ml. blood in the case of a bloated bullock, whereas two non-bloated heifers on the same pasture showed only .04 mgrm. hydrocyanic acid per 100 ml. blood.

Recently Ferguson, Ashworth and Terry (1949) isolated a muscle-inhibiting compound, identified as a flavone, from lucerne. Although they failed to produce bloat with feeding experiments, they believe that it might have a possible connection with bloat.

All the abovementioned theories have been advanced in an attempt to elucidate the pathogenesis of acute bloat on green legumes or in general on feeds lacking in roughage.

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Bloat occurring under these circumstances is distinct from the well known type of acute bloat, which is associated with the feeding of tubers, caused by obstruction of the oesophagus which mechanically interferes with the escape of free gas.

Inhibition of ruminal motility caused by factors other than those associated with legume feeding, is also a cause of bloat. Wester (1935) mentions extensive peritoneal adhesions and overloading of the rumen, as the cause of free gas tympany, while Begg (1912) believes that the tympany associated with digestive distubances is due to ruminal atony. Wester also mentions poisonous plants as a cause of this type of bloat. Various poisonous plants in South Africa, such as species of Homeria and Moraea (tulip), Urginea and Geigeria etc., have reported to cause bloat in addition to the usual symptoms of poisoning (Steyn (1934)). The possibility of contamination of pastures or baled lucerne hay with these plants should always be considered when investigating outbreaks of acute bloat.

CONDITIONS UNDER WHICH BLOAT OCCURS WITH SPECIAL REFERENCE TO THE OCCURRENCE IN SOUTH AFRICA.

In order to obtain fairly comprehensive data on the occurrence of bloat in this country, questionnaires were sent to veterinarians in the field as well as to experienced farmers. The information so obtained is discussed in conjunction with observations of workers in other countries. For a full summary of the different questionnaires see Appendix I.

1. The distribution of bloat in South Africa.

Apart from sporadic cases of bloat not associated with a special feeding regime, outbreaks of acute bloat apparently occur all over the country, wherever green feed is available or where lucerne hay is fed. Bloat is more common in the intensive farming areas, where lucerne or other lush pastures are grown under irrigation or where the annual rainfall is adequate for the cultivation of these feeds under dryland conditions. According to one veterinarian, bloat is relatively rare amongst cattle and sheep on dryland lucerne in the Western Province but extremely common on lucerne under irrigation (see Appendix I No. 11).

As lucerne is by far the most important greenfeed grown in South Africa the distribution of bloat would correspond closely with that of lucerne. The reader is referred to the publication of Turpin and McKellar (1937) for a map of the Union, showing the distribution of lucerne. According to these workers this feed is grown extensively in the Southern, Eastern and Northern Cape Province and Southern Orange Free State especially on farms bordering the Orange River, and also to a smaller extent in the Southern Transvaal and Natal Midlands. It is therefore cultivated mostly in the drier areas of the country where irrigation is available. In the higher rainfall areas such as along the East Coast the atmosphere is too hot and humid and the soil unsuitable for the cultivation of lucerne. The following statistical data is taken from Turpin and McKellar (1937) to show the area under lucerne in each province in 1930: Cape Province 74267, Natal 1538, Orange Free State 11786 and Transvaal 5864 morgen.

Bloat is seldom reported from the more arid ranching areas of the country because irrigation facilities are usually not available, and greenfeed pastures are therefore not grown to any extent. Cases do however occur, due to the feeding of lucerne hay especially in periods of drought, and due to heavy concentrate feeding of steers during fattening. The experience of a certain rancher at Bandolierskop in the Northern Transvaal is of interest. Due to severe drought in the spring of 1952 veld grazing became depleted, and lucerne hay feeding had to be resorted to. A particular batch of exceptionally good quality leafy hay, grown in the Upington district, caused serious outbreaks of acute bloat in cattle on this farm.

2. The type of animal affected.

According to Cole et al (1945) cattle, sheep and goats and probably all other ruminants are subject to bloat. The relative susceptibility of the different species has however not been determined experimentally. According to McCandlish (1933), dairy cows appear to be more susceptible than beef animals or sheep, and Mead, Cole and Regan (1944) found worse bloat amongst dairy cows than amongst sheep under the same feeding conditions.

Although cattle appear to be the species mainly affected by bloat in South Africa, there is no direct evidence that this is due to a species difference. It is more likely due to the fact that bovines are the predominant species in those areas where legume pasturing is practiced. In fact bloat is just as bad in sheep farming areas if legumes are fed. The experience of one farmer may be quoted as an example. Being a sheep farmer the lucerne pasture is used mainly for the finishing off of lambs before sale with the result that bloat occurs regularly

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amongst his sheep. After the lucerne has been grazed down, his cows are allowed onto the pasture and hardly any cases of bloat are encountered amongst these animals. The reverse is probably true in many of the cattle farming areas. After the bovines have grazed down the pasture and been subjected to bloat, the sheep are allowed to graze the stubble on which bloat is not likely to occur. Apart from this, the best type of pasture which is often bloat provoking, is usually reserved for the particular species or breed of animal which is the main farming concern.

However, the fact must be acknowledge that as a species bovines in general are far less particular and careful in their feeding habits than sheep. Cattle consume their feed much faster and are more inclined to be greedy. This might well account for some difference in the incidence of bloat between the two species.

Replies to the questionnaires nearly all state that high producing dairy cows, with voracious appetites and greedy feeding habits are the animals most commonly subjected to bloat. Of the dairy breeds the Friesland and Jersey appear to be mostly affected. It is felt that this is not due to any specific difference in susceptibility of breeds but that the occurrence of bloat amongst different breeds depends on the preponderance or popularity of a breed in a certain area.

Animals of all ages are apparently equally susceptible. Pregnant animals are sometimes regarded as particularly susceptible. This might be due to an increased appetite or due to individual susceptibility.

It is a wellknown fact that certain animals are more susceptible to bloat than others. This has been described by various workers (Cole, Mead and Regan (1943), Mead, Cole and Regan (1944), Quin 1942 and Clark (1950)). Espe, Jacobson and Cannon (1943) state that dry cows seldom bloat, but that it is the milking cow or growing animal with a large appetite that gorge themselves and bloat. Although Mead, Cole and Regan (1944) acknowledge the fact that the greater susceptibility of lactating cows, as compared with dry cows, may be due to individual differences in food intake caused by greediness, they maintain that there are as yet unexplained variations in individual susceptibility not dependent on the amount of feed consumed.

3. The type of feed on which bloat occurs.

According to Cole et al (1945) bloat has been reported to occur on lucerne, various species of clover, trefoil, peas and cabbabe leaves. Although it is not common to experience bloat in animals on grasses, Taylor (1940) in New Zealand reported that bloat may occur on rye that has been stimulated to grow rapidly, and Ohman (1938) in Australia states that rapidly growing cereals may produce bloat.

Bloat has also been reported on various other feeds. McCandlish (1923) found bloat in a calf on milk as the sole diet. According to Mead and Goss (1936) bloat can occur in animals fed grain only, and Mead, Cole and Regan (1944) showed that bloat can be produced on a ration of finely ground lucerne hay and grain, but not on unground hay and grain. Kick, Gerlaugh and Schalk (1937) found that steers fed concentrates and forage started bloating as soon as the concentrates were increased to about 50% or more of the total ration.

Bloat as a result of obstruction of the oesophagus is wellknown to occur on tubers such as chopped beets and potatoes.

The following green-feeds are reported to cause bloat in South Africa: green lucerne, clover (various species) oats, barley, Italian rye, wheat, cowpeas, chemolier and lush green grass such as Kikuyu (Pennisetum clandestinum). Bloat is also caused by the feeding of good quality leafy lucerne hay especially if the hay is soaked before feeding. Heavy concentrate feeding either alone or in conjunction with lucerne also cause bloat. It is a significant fact that it is usually the exceptionally good quality lucerne hay and the best type of greenfeed that cause bloat. Some of the best lucerne hays are produced on farms bordering the Orange River, especially in the Upington district, and many reports of bloat on lucerne hay coming from this area have been received.

4. The stage of growth and condition of the bloat producing greenfeed.

Cole, Mead and Regan (1943) found that bloat can be produced experimentally if lucerne is in the preflowering stage of growth, crisp and succulent. In order to obtain succulence, sufficient water should be supplied to induce rapid growth.

Many of these observations are confirmed by the replies to the questionnaires. It is mentioned that bloat occurs when the greenfeed is young and very succulent and have grown rapidly under irrigation. The bloat procuding lucerne is reported to grow mostly on heavy, fertile soils, although bloat also occurs on lucerne grown on other soils and even under dryland conditions.

According to one farmer bloat is common on a pasture consisting purely of clover, whereas bloat seldom occurs on a mixed grass-clover pasture. This is in accordance with the findings of Bell and Britton (1939), who found that bloat ceased to be a problem when clover pastures were covered with more than 50% of grasses.

5. The influence of environmental conditions.

It is wellknown that bloat can occur under widely different environmental conditions. In fact Cole, Mead and Regan (1943) showed that bloat can be produced any time of year, and under varying environmental conditions if the lucerne is in the appropriate stage of development. In spite of this it does appear that the incidence of bloat is greater under certain environmental conditions, provided other factors are favourable.

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From observations at the Grootfontein College of Agriculture, Turpin and McKellar (1937) found that frosting and wilting of lucerne are important factors in bloat and that the occurrence of bloat is associated with the moisture content of the plant, the stage of growth and the type of soil it is grown on.

Most veterinarians and farmers state that hot and dry weather, accompanied by hot winds which cause wilting, are conditions which are favourable for the production of bloat on green legumes. Intermittent rain and hot weather probably also cause wilting. Frosted lucerne and lucerne wet with dew or rain are also regarded as dangerous.

In spite of the fact that wetting of legumes by dew or rain is often regarded as an important etiological factor, McIntosh (1937) reported bloat on lucerne during a period of severe drought and Cole, Mead and Regan (1943) found that bloat may occur on legumes free from external moisture. A possible explanation, given by Cole et al (1945), for the occurrence of bloat during periods of severe drought, is that all other plants except the lucerne are killed off by the drought, and due to the scarcity of feed there is a greater tendency to pasture the lucerne while young. They state that the amount of rainfall probably affects the incidence of bloat by controlling the type of plants that will grow. They cite many examples where the incidence of bloat on clover increased tremendously in times of abnormal rainfall and attribute this to the fact that wet weather seems to favour the growth of clover over that of grasses. Apart from the effect of rainfall on the growth of other plants, excessive rainfall will contribute to the succulence of legumes by directly promoting plant growth, and as has been shown by Cole, Mead and Regan (1943) succulence is an important factor in the production of bloat.

Espe, Jacobson and Cannon (1943) believe that external

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moisture such as dew, rain or frost on the plants, directly increase the possibility of bloat by causing the animal to eat and swallow the forage faster, and by cutting down salivary secretion which, according to them, increases the amount of gas formed in the rumen.

Although frost, heat and wind have repeatedly been incriminated as etiological factors, the underlying principles have not yet been satisfactorily explained.

6. The Type of Bloat.

Before one can intelligently discuss acute bloat, one must accept Wester's classification of the condition. He divided acute bloat into two distinct types; in the one type, bloat is due to frothing of the ingesta and in the other free gas is found above the ingesta.

Reports by farmers and veterinarians in this country indicate that acute bloat on legumes is usually of the frothy type. This fact is further substantiated by the successful treatment of most cases of bloat with turpentine or other antifrothing agents. Apart from other causes, cases of free gas tympany have also been reported to occur on legumes, but in the present author's opinion most of these cases are due to frothing in spite of the fact that a certain amount of free gas escapes when a trocar or stomach tube is inserted. This matter will be discussed at length in the chapter dealing with experimental results.

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THE FORMATION OF GASES IN THE RUMEN.

According to Cole, Mead and Kleiber (1942), the composition of the ruminal gases does not vary markedly with different feeds. The following figures are taken from their publication:

Feed	Average CO_2%	Average O_2%	Average CH_4%	Average other gases%
lucerne hay	62.3	2.5	22.4	12.8
green lucerne	68.0	1.6	22.5	7.9
lucerne hay and grain	70.8	1.4	17.1	10.8

They also confirmed the work of Washburn and Brody (1937) who showed that the composition of ruminal gases varies more with the time interval after feeding than with the ration. According to the latter workers, the average carbon dioxide content of ruminal gases for the first five hours after feeding is 65%. This decreases to from 10% to 28% at 15 to 23 hours after feeding. The percentage of methane remains approximately constant, whereas the percentage of oxygen and nitrogen rise as that of carbon dioxide decreases.

The most recent figures by Kleiber, Cole and Mead (1943), on the composition of ruminal gases of cows on lucerne pasture are the following: CO_2 67%; CH_4 26%; N_2 and H_2 7%; H_2S .1% and less than 1% O_2. The composition of ruminal gases of bloated animals, as determined by Olson (cited by Cole, Mead and Kleiber (1942)) apparently does not differ markedly from the normal.

Dougherty (1941 and 1942) found large amounts of hydrogen sulfide (.1 to .7 vols. %) in ruminal gas and ingesta of animals that died of bloat. The hydrogen sulfide content of ruminal ingesta was found to increase with the feeding of bloat provoking feeds, such as good quality lucerne

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hay, green lucerne and clover. Dougherty also reported the presence of carbon monoxide in concentrations up to .17% in ruminal gas of normal animals, but found no correlation between carbon monoxide variations and feed changes.

Olson (1944) also found that carbon monoxide and hydrogen sulfide are present in the ruminal gases of normal animals and that the hydrogen sulfide concentration is greatly increased in cases of bloat. Kleiber, Cole and Mead (1943) however found no significant difference in the hydrogen sulfide content of ruminal gases from bloated and nonbloated animals on the same pasture.

1. The Sources of Carbon Dioxide.

The carbon dioxide in ruminal gas is derived largely from fermentation of carbohydrates, especially sugars. Markoff (1911) found that when sugar was added to fermenting ruminal ingesta in vitro, the rate of carbon dioxide production increased markedly. Quin (1943) showed that large amounts of gas, presumably carbon dioxide, are rapidly formed in the rumen from fermentation or oxidative assimilation of sugars by pseudo yeast cells and iodophylic bacteria. This rapid gas formation does not follow the introduction of starch, cellulose, protein or fats into the rumen. Cole et al (1945) however state that there is an unlimited number of organic substances from which micro-organisms can produce carbon dioxide.

Another source of carbon dioxide in the rumen is from the bicarbonate in swallowed saliva. Cole et al (1945) state that saliva can only be a source of carbon dioxide if the ruminal pH is below 6.9. Since Phillipson (1942) showed that the pH of the ruminal ingesta becomes acid after feeding, due to the formation of organic acids, it is obvious that saliva is a potential source of carbon dioxide.

2. The Sources of Methane.

Wherεas carbon dioxide formation is usually rapid under aerobic conditions, methane production is slow and continuous under anaerobic conditions. Tappeiner (1882) showed that cellulose is a source of methane in the rumen. Kellner and Köhler (1900) however found that not only cellulose but also sugars and starches caused an increase in methane production, when added to a maintenance ration.

The main source of methane appears to be carbohydrates, although Kluyver (1931) suggests that a great variety of organic compounds are capable of producing methane on fermentation.

According to Barker (1936) and van Niel (1943) micro-organisms can reduce carbon dioxide to methane by oxidizing hydrogen or compounds which serve as hydrogen donors. A small amount of methane present in ruminal gas may therefore also be derived from carbon dioxide.

3. The Sources of other Gases.

According to Woods and Clifton (cited by Cole et al (1945)) the source of hydrogen in bacterial fermentations is carbohydrates. The entrance of atmospheric air during the process of swallowing is mentioned by Cole et al (1945) as one of the sources of free nitrogen and oxygen in the rumen. Some oxygen and nitrogen can apparently also diffuse into the rumen from the blood.

Hydrogen sulfide is derived from sulphur containing organic compounds such as proteins which are present in large amounts in the leaves of legumes (Cole et al (1945)).

4. Factors affecting the rate of gasformation.

As already stated excessive gas formation is not the basic cause of acute bloat when the eructation mechanism is normal. Nevertheless the rate of gas formation must obviously play an important role when elimination is inefficient.

Various workers have shown that feeds, which usually cause bloat, do not produce more gas than feeds not usually associated with bloat. (Washburn and Brody (1937), Cole, Mead and Kleiber (1942), Jacobson, Espe and Cannon (1942) and Quin (1943)). In fact Cole, Mead and Kleiber (1942) found that green lucerne forms less gas than lucerne hay and concentrates.

Quin (1942) attribute rapid gas formation shortly after feeding to the presence of sugars in the feed, which is subject to rapid fermentation by pseudo yeast cells. The gas formation reaches its peak within half to one and a half hours and then steadily declines. He states that the quantity of gas evolves during this periods is in direct proportion to the sugar content of the plant. Quin also found that the sugar content of lucerne varies under different conditions and is highest in the afternoon when bloat usually occurs. McAnnally (1943) also showed that gas formation is stimulated by the addition of sugars to fermenting ruminal ingesta. Quin further showed that fermentation and gas formation is slow when the yeast cells in the rumen are destroyed by chemical substances or starvation of the animal. This is in accordance with the findings of Clark (1946) who showed a significant correlation between the number of yeast cells present in ruminal ingesta and the volume of gas evolved.

Jacobson, Espe and Cannon (1942) found that the *in vitro* rate of fermentation of ruminal ingesta was not significantly affected by changes in dilution, temperature and pH in the ranges normally occurring in the rumen, or by sodium chloride in amounts comparable to that which animals could tolerate in their drinking water. Clark (1948) showed that turpentine and certain proprietary coaltar preparations have little or no inhibitory effect on gas formation when added to fermenting ruminal ingesta in therapeutic concentration.

The amount of feed consumed has a decided influence on the rate of gas formation. (Quin (1943), Washburn and Brody (1937) and Cole, Mead and Kleiber (1942)). The latter workers found that elven litres of gas were produced over a five hour period after the consumption of 4 lbs. lucerne hay, whereas 77 litres of gas were produced when 25 lbs. were consumed. This is given as an explanation why greedy feeders and lactating animals are more subject to bloat than poor feeders or dry cows. However as pointed out by Mead, Cole and Regan (1944), the occurrence of bloat cannot always be correlated with the amount of feed consumed.

5. The elimination of Gas from the Rumen.

The main avenue of escape of gas from the rumen is via the oesophagus by means of the specific reflex act of eructation. Wild (1913) concluded that eructation is a normal and absolutely necessary process in ruminants in order to rid the rumen of accumulated gases.

Although bloat has been investigated all over the world, very little is actually known about the eructation reflex and the factors which may affect it. This fact is acknowledged by Clark (1948).

Since the modern conception of bloat is that it is due to faulty elimination and not to excess gas formation, the study of bloat turns largely on a study of the eructation reflex and the factors affecting it. As this forms the basis of the present work, the literature pertaining to this reflex will be fully discussed in the subsequent sections.

Eructation is however not the only method of expelling gas. Large amount of carbon dioxide and possibly also methane, diffuses through the rumen wall into the circulation and are expired. Dougherty (1940) found increased respirations during carbon dioxide insufflation into the rumen. The hypernoea which is noticeable during active fermentation after feeding, is undoubtedly due to stimulation of the respiratory centre by absorbed carbon dioxide. Although the rate of carbon dioxide diffusion is not known, Zuntz et al (cited by Cole et al (1945)) noted that the carbon dioxide-methane ratio of ruminal ingesta fermenting in vitro is from 3:1 to 7:1, whereas gas samples taken directly from the rumen a few hours after feeding had about the same percentage of carbon dioxide as of methane. These differences led them to conclude that large amounts of carbon dioxide are actually transferred to the blood.

Citing the work of Boycott and Damant, Dukes (1942) states that apparently at least ten per cent of the total amount of carbon dioxide in expired air is derived from the alimentary canal.

Since any carbon dioxide which is absorbed into the blood-stream must necessarily affect the CO_2-combining power of the blood, the following relevant experiment was conducted, in order to obtain information on the extent of carbon dioxide transference.

Four Merino sheep with permanent fistulae were used. The fistulae were sealed to ensure minimum leakage of gas. Blood was collected under oil, before and after feeding, for determinations of the CO_2-combining power by Van Slyke's method. Samples of ruminal ingesta were also collected before and after feeding for determination of pH. The animals were fed good quality lucerne hay. The results are given in Table I.

Table I.

Sheep No.	Before feeding		One hour after feeding	
	Ruminal pH.	Alkali Reserve	Ruminal pH.	Alkali Reserve
1	7.0	72	6.35	67
2	6.8	71	6.35	63
3	6.6	71	6.70	63
4	6.7	67	6.25	62

The results show a decided reduction in the CO_2-combining power of the blood one hour after feeding. The change in ruminal pH to the acid side indicates that fermentation was active.

Although absorbed organic acids may be partly responsible for the drop in the alkali reserve of the blood it is felt that it is mainly carbon dioxide which is responsible for this reduction.

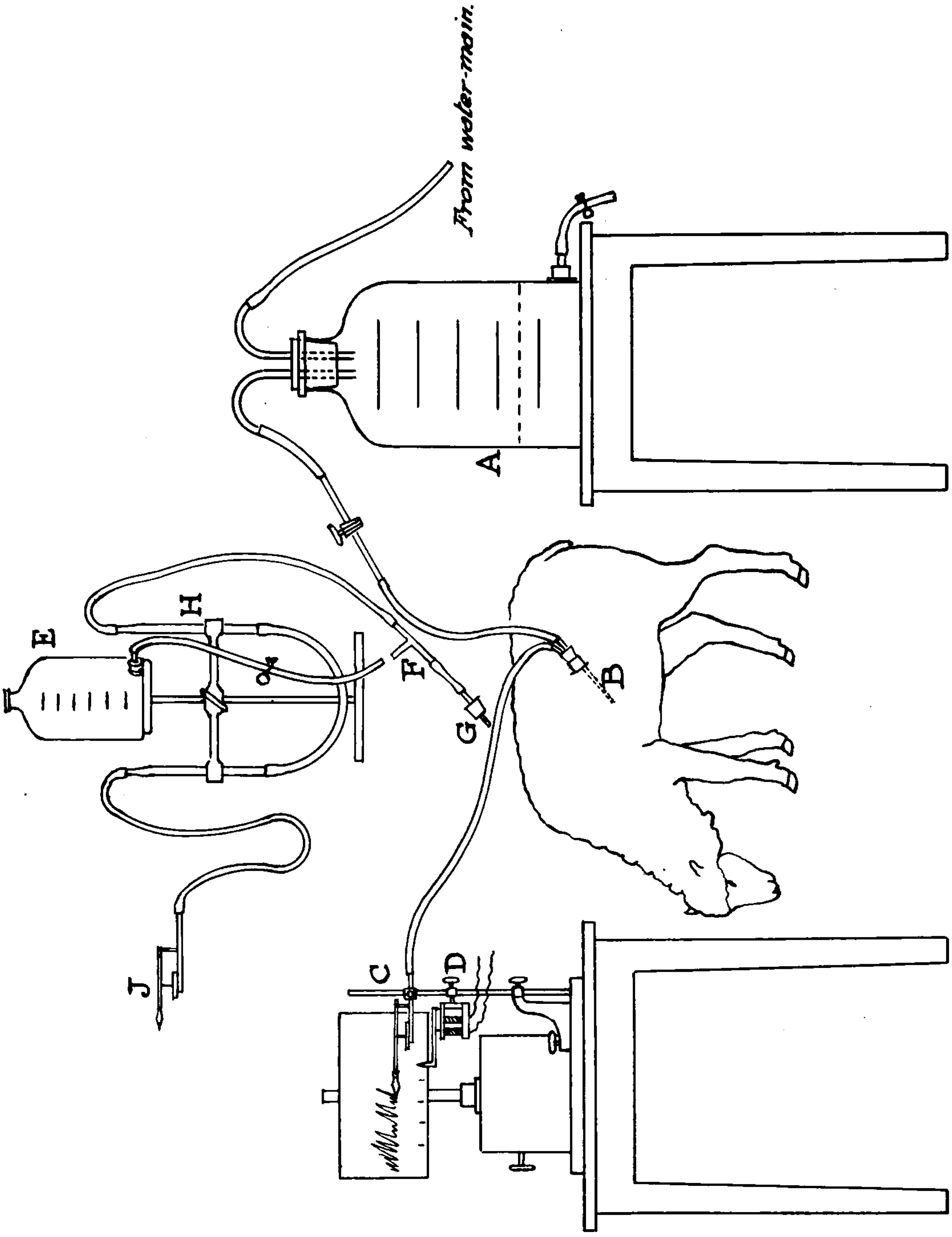

FIG. I.

Apparatus used for forced air insufflation and direct ruminal recording.

In order to prove this statement the following experiment was made: Two of the above-mentioned sheep were starved overnight and blood-samples under oil were then collected for a determination of the alkali reserve.

Twenty litres carbon dioxide was then insufflated into the rumen of each sheep at the rate of one litre per minute. (For a description of the apparatus and technique of insufflation refer to the section dealing with experimental procedures). Eructation was entirely efficient in both animals as ruminal distention failed to occur. Hyperpnoea commenced approximately three minutes after insufflation was started. Blood-samples were again taken during introduction of the last five litres of carbon dioxide.

The results are given in Table 2.

Table 2.

Sheep No.	Before CO_2-insufflation	After insufflation of 15 - 20 litres CO_2.
	Alkali Reserve	Alkali Reserve
1	74	67
2	78	65

The results clearly show that carbon dioxide is absorbed from the rumen and markedly influences the CO_2-combining power of the blood. One can therefore conclude that the reduction in the alkali reserve found after feeding was mainly due to absorbed carbon dioxide.

EXPERIMENTAL PROCEDURES.

The experiments were carried out at the Onderstepoort Veterinary Research Institute. Eight full-grown merino sheep, two adult goats, and two young Friesland-cross bovines, with permanent ruminal fistulae, were used. The sheep were selected at random from a team of fistulae sheep kept at the Institute for a number of years. They were numbered from 1 to 8. In addition to the ordinary rumen fistulae, sheep No. 7 was provided with a caecal fistula and sheep No. 8 with an abomasal fistula. (For a full description of operating techniques see appendix 2.)

During an experimental period the animals were kept in individual under-roof pens where feed and water consumption could be determined, otherwise they were allowed into an open paddock for exercise. Good quality lucerne hay was usually fed _ad. lib._ to these animals except if otherwise stated. In a few of these experiments green lucerne, grown at the station, was either pastured or cut and fed _ad. lib._ Water was constantly available except in a few instances mentioned in the text.

Technique:

Due to the difficulty in reproducing natural bloat without the complication of frothiness, the method of forced air insufflation and direct ruminal recording was used to study the mechanics of the eructation reflex and factors affecting it. A slight modification of the method described by Clark (1950) was used. Fig I illustrates the apparatus.

The air in the 20 litre aspirator bottles (A), was displaced by water from the mains and forced into the ruminal mass through a 9" long gas inlet (B), with a perforated tip, which passed through an airtight cork in the fistula. Another short tube, passing only through the cork sealing the fistula opening, was connected to an ordinary membrane tambour (C), which directly recorded the pressure changes in the rumen in

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general and of the left dorsal sac in particular, on a kymograph. In the sheep and goats air was introduced at the rate of approximately one litre per minute in some cases and one litre per three or four minutes in other cases. Each litre of air was marked by the signal (D). The rate of introduction of air does not appear to affect the issue; the faster rate of introduction being employed on occasion because of the greater ease of evaluating the efficiency of eructation. In the case of the bovines, air was usually introduced at the rate of approximately three litres per minute.

In order to eliminate the complication of frothiness of the ruminal ingesta, when bubbling air through it, a proprietary anti-frothing agent (Cooper and Nephews or I.C.I.) (Clark 1950) was dosed as a routine prior to the introduction of air into the rumen, except in those cases in which frothiness itself was the subject of investigation.

Reticular recordings were obtained by inserting a flexible copper tube (3/16th inch diam.), with a balloon attached to one end into the reticulum, through an extra opening in the ruminal fistula stopper. After some practice it was quite easy to direct the balloon into the reticulum. The animal usually started ruminating when the balloon was in the proper position. The other end of the tube protruding through the fistula cork was connected to one arm of a water manometer. After inflation of the balloon, the other arm of the manometer was connected to a membrane tambour, adjusted to record on a kymograph synchronously with the ruminal recording. Recordings of caecal and abomasal motility were obtained in a similar manner.

The additional apparatus depicted in fig. I, shows the method that was used for recording the abomasum or caecum after distention of the organ with either saline or air. An aspirator bottle (E) was connected directly to the abomasal fistula (G). By means of a T. piece (F) the fistula was also connected to one arm of a water manometer (H). The other arm of the manometer was connected to a tambour which recorded abomasal pressure simultaneously with ruminal pressure. Saline was run by gravity from the aspirator bottle into the abomasum or caecum. If air was used, this was forced in by water pressure in exactly the same way as the rumen was insufflated. During recordings the animals were restrained in specially constructed stocks.

The pH of ruminal and abomasal ingesta were taken with a glass-electrode pH-meter immediately after withdrawal from the animal. The alkali reserve of the blood was determined by the biochemical section using van Slyke's method. The animals were bled from the jugular vein and the blood collected under oil. The operation for abdominal vagotomy performed on the two goats, is described in appendix 2.

In the experiments on froth formation the apparatus depicted in fig. 2 was devised in order to determine the consistency of ruminal ingesta. This consists of a mercury-filled bulb (A), weighing 15.9 grams, attached to a thin rod. A silk thread connects the rod with the scale pan (B) onto which a pointer arm is attached. The thread is passed over two pulleys on a crossbar which is fixed to an ordinary retort stand. A 200 c.c. test tube with an inside diameter exceeding that of the bulb by at least 1 cm. (C) is clamped into position to receive the glass bulb.

With the bulb at the bottom of the test tube and the pointer arm opposite a zero mark (D), the tube is filled with ruminal ingesta. Sufficient weights are then placed on the scale pan to cause the bulb to be drawn through the column of ingesta, the fixed distance of 18.7 cms. (D to E) in approximately three seconds. The consistency index is thus obtained by multiplying the weight required by the actual time taken.

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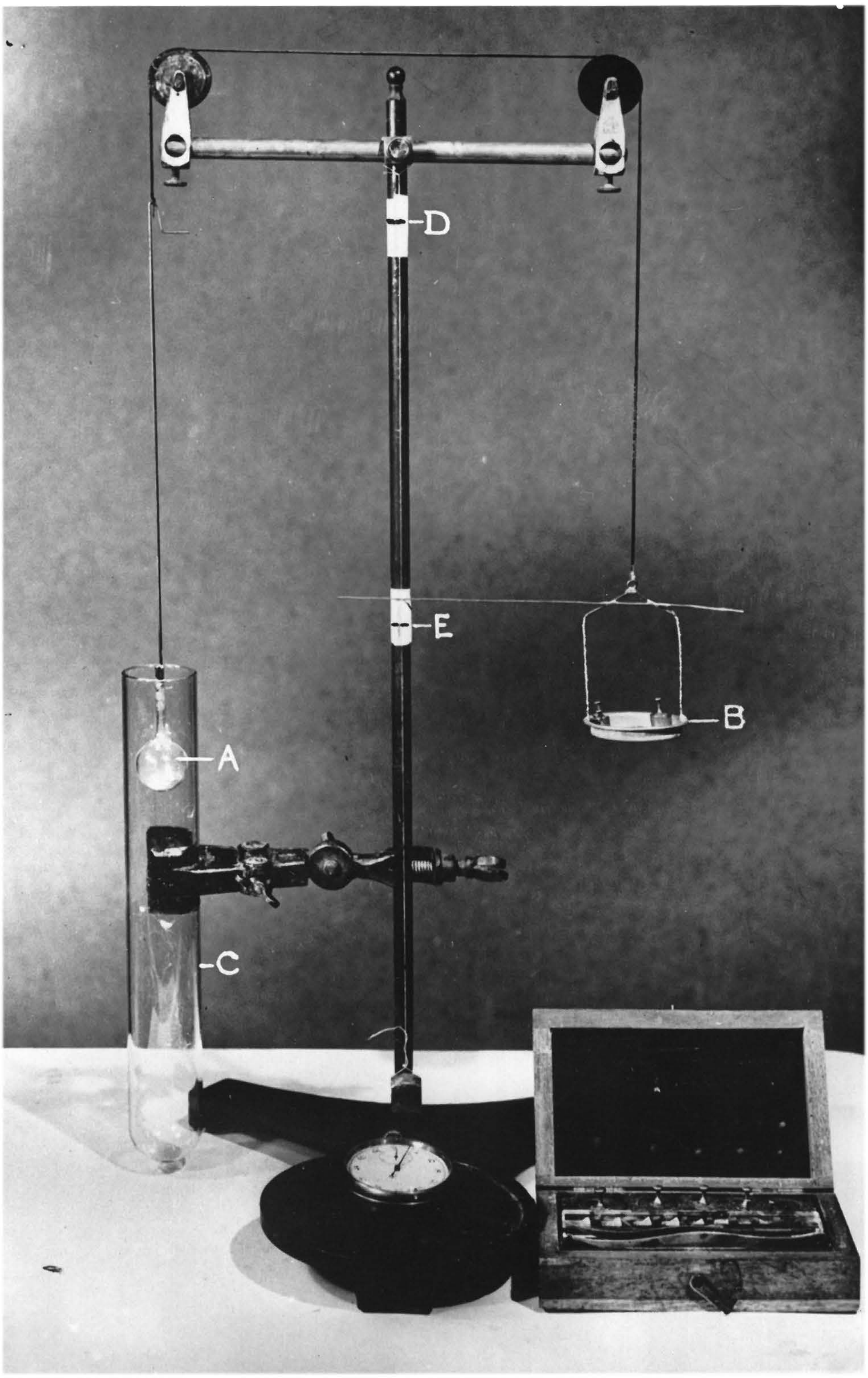


FIG. 2.

Apparatus for determination of the consistency of ruminal ingesta.

There appeared to be no significant difference in the consistency of frothy ingesta before or after the addition of an anti-frothing agent sufficient to break the froth.

For the experiments on frothy bloat the same fistula-sheep, mentioned above, were used. Representative samples of ingesta were removed from the rumen, when required, by means of a hand-operated vacuum pump supplied with a trap. A wide-bore glass tube, connected to the trap by means of rubber tubing, was introduced into the rumen via the fistula and constantly moved about when suction was applied.

For the same experiments on cattle a group of stable-fed bovines, consisting of three Friesland heifers, one Friesland cow, one Hereford heifer and two young Friesland bulls were used. Since the animals were not provided with fistulae, trocarisation was resorted to whenever samples of ruminal ingesta were required for examination. The animals suffered no ill-effects from this procedure, and subsequent clinical examinations showed that ruminal motility was unaffected.

I. THE NORMAL ERUCTATION REFLEX.

THE MECHANICS OF THE REFLEX.

The oesophagus enters the rumino-reticular sac at a level considerably below the dorsal limit of the rumen (Sisson 1938). To quote from Cole et al (1945): "This structural arrangements would appear to offer considerable interference with the freedom of movement of gas to the oesophagus."

The following conditions are, therefore, considered essential before eructation can take place. Gas accumulated in the dorsal sac of the rumen must be moved forward and downwards to reach the cardia. This has been postulated by Amadon (cited by Cole et al, (1945) and Clark (1948)). The second essential factor is that the cardia must be patent and clear of any obstructing ingesta. Thirdly, the oesophagus must be patent and relaxed for the free passage of gas. It is evident, therefore, that eructation is an active and co-ordinated reflex, mainly involving the ruminal musculature.

(A) Eructation in relation to ruminal motility.

Most investigators (Wester (1935); Hofland (1940); Dougherty (1942); Cole, Mead and Kleiber (1942); Mead, Cole and Regan (1944); Cole et al (1945); Clark (1948) and Evans and Evans (1949)) have associated eructation with active rumen motility, in the absence of which eructation is suspended. The cycle of ruminal contractions has been studied by Czepa and Stigler (1926), Magee (1932) and Phillipson (1939) by means of X-rays. Wester (cited by Czepa and Stigler (1926)) and Schalk and Amadon (1928) have recorded ruminal motility through permanent ruminal fistulae. The main outcome of these extensive investigations in relation to the present study, is that ruminal contractions can be divided into two types: (1) A backward moving cycle of contractions, involving a two-stage contraction of the reticulum, immediately followed by a contraction of the left dorsal and right ventral sacs, and then a pause of varying length; (2) a forward moving ruminal contraction starting at the posterior dorsal blind sac, followed by another pause of varying length.

Wester (1935) and Hofland (1940) have reported from their observations that eructation occurs in conjunction with a return movement or antipersistaltic wave which follows on the backward rumen contraction.

In order to confirm the observations of Wester and Hofland on the direction of the two types of rumen contractions, the following variation of the method described, was employed. Two flexible tubes, with balloons attached to the ends, were inserted through two holes in the pressure stopper sealing the fistula opening. One balloon was directed to the region of the cardia and the other to the posterior part of the left dorsal sac of the rumen. Each balloon was connected to a recording tambour. The usual gas inlet with its connections was passed through a third opening in the fistula stopper. Air was introduced into the rumen at the rate of one litre per three minutes, in order to recognise the ruminal contraction at which eructation occurs. This can be readily identified as a marked drop in intraruminal pressure coinciding with a specific rumen contraction.

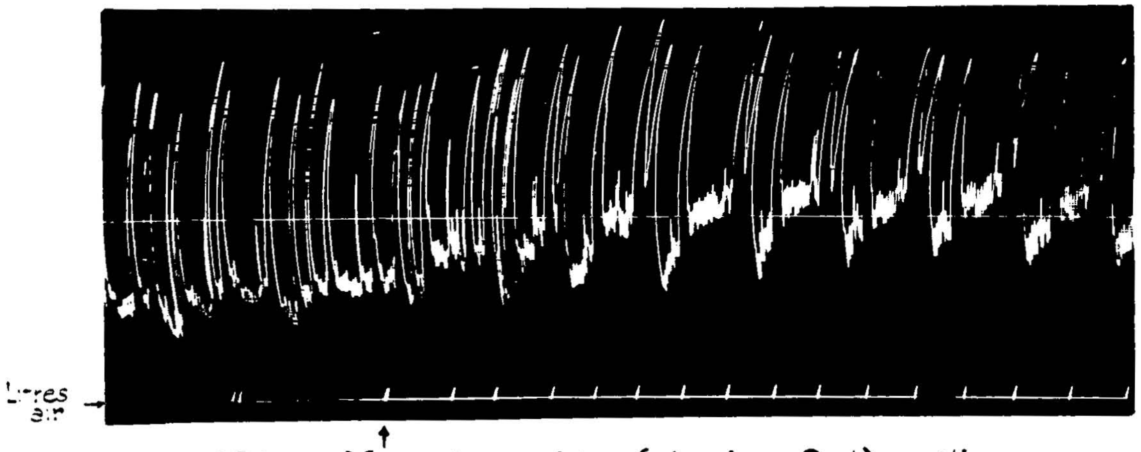
By observing and comparing the time at which the anterior balloon responded to pressure changes in relation to the response of the posterior balloon, it was found that, with the ordinary rumen contraction, the anterior balloon responded before the posterior, whilst with the rumen contraction which coincides with eructation, the posterior balloon responded before the anterior. This indicates that the eructation contraction moves from behind forwards with the object of moving the gas bubble in the dorsal sac forward and downwards towards the cardia. The ordinary rumen contraction, essential for the mixing of the ingesta, is a wave in the opposite direction. Tracings of normal eructation in sheep and cattle are presented in Figs. 3 and 4. Eructation results in a sharp drop in intraruminal pressure and occurs at the height of each eructation contraction, which frequently follows immediately on a backward contraction. Phillipson (1939) has observed that ruminal contractions follow a definite rhythm in relation to reticular contractions and that the rhythm can change from one type to another, without any apparent reason. It is evident from the tracings that not every backward contraction is followed by an eructation movement. These may occur after every backward movement (1:1 rhythm) or after every alternate one (2:1 rhythm). It is also evident from the tracings that this rhythm can change as a result of a pressure stimulus. This will be discussed in the part dealing with the initiation of the reflex. The varying rhythm of ruminal contractions, mentioned by Phillipson, would therefore depend on the presence or absence of eructation contractions.

The interval between the backward and forward rumen contractions is variable. In most cases the eructation contraction follows within 10 to 15 seconds after a backward contraction, although intervals of up to 60 seconds were recorded on occasions.

(B) <u>The Role of the cardiac orifice</u>.

Although Cole <u>et al</u> (1945) have suggested the failure of a hypothetical cardiac sphincter to relax as a possible cause of bloat, there is no anatomical or histological evidence of a true sphincter of the cardiac orifice. Aggazzotti (1910) believed that the orifice was normally relaxed because, when a sheep was placed on its back with the head downwards, some ruminal contents leaked into the mouth at each inspiration. On the other hand, Stigler (1931) palpated the cardia and found it usually closed. In the present author's opinion the cardia is kept closed, not so much by tonic contraction of its own musculature, but more by external pressure exerted

Normal Eructation in the Bovine on a Non-roughage diet

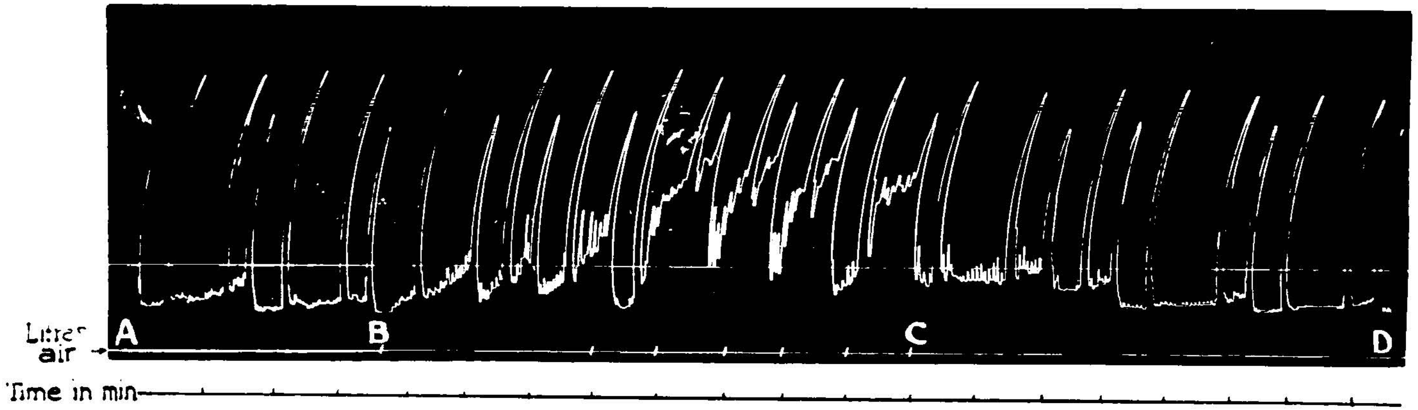


Note : Normal motility (rhythm 2:1) with regurgitation and efficient eructation

Fig. 4

FIG. 3.

Normal Eructation in Sheep.



A-B : Normal motility ; rhythm 2:1 B-C : Introduction of air ; rhythm 1:1
C-D : Return to normal ; rhythm 2:1

by surrounding organs on the orifice itself and on the abdominal portion of the oesophagus. This would explain the partial patency when the animal was inverted, noted by Aggazzotti.

In their review Cole et al (1945) state that in Wester's opinion the opening of the oesophagus depends on the strength of the ruminal contraction, more particularly on the contraction of the "transverse folds". The review also states that Amadon and Detweiler palpated the cardia at the moment of eructation when they found it widely dilated and funnel-shaped. They concluded this was due to muscular contraction, but the muscles involved are not stated. Active dilation of the cardia could only be brought about by muscles surrounding the orifice, i.e. rumen musculature.

As Wester's original publication is not available, it is difficult to understand what is meant by the "transverse folds". In the present author's opinion the cardiac orifice is pulled open at the moment of eructation by contraction of the medial and lateral pillars of the rumino - reticular fold. These are described by Sisson (1938) as follows: "The lateral part of the fold fades out an inch or two lateral to and behind the cardia. The medial part of the fold ends just behind the reticular groove and about three inches below the level of the cardia". As will be seen a shortening of these pillars would tend to pull the cardia open to the 'funnel shape' described above.

A strong contraction of these pillars of the rumino-reticular fold, with the object of dilating the cardia, is considered an integral part of the forward eructation roll of the rumen and occurs at the moment the free gas is over the cardiac orifice.

From clinical observations, Clark (1950) postulated that excess ruminal pressure interfered mechanically with the act of eructation. Nichols (1951) found that when gas was introduced into a rumen already overloaded with fluid, belching took place for a time and then failed. He remarks that further investigations are required into the motility of the rumen under such conditions. The present author considers that the overloading interfered with the efficiency of eructation (vide infra) and that the rising pressure ultimately caused mechanical closure of the cardia. Tracings made from animals with excessive ruminal pressure and failure of eructation have clearly shown that the eructation contractions of the rumen are still powerful and regular. Similarly, clinical examination of animals with acute bloat has proved the rumen to be highly active. Wester (cited by Cole _et al_ 1945) noted that there is hyper-motility of the rumen in the early stages of acute bloat.

During numerous insufflation experiments it has been noted that, under a given set of conditions, eructation efficiency is inversely proportional to intraruminal pressure. A study of the anatomical relations of the cardiac region suggests an explanation of this interference. It is suggested that, with a high intraruminal pressure, the anterior dorsal sac bulges over and presses on the cardiac orifice and abdominal portion of the oesophagus, thus causing a mechanical closure. This pressure will be counteracted by the pull of the ruminal folds described above. The efficiency of the cardiac dilation will, therefore, depend on the relation between intraruminal pressure and the strength of the ruminal contractions.

(C) _The role of the reticulum in the eructation reflex._

The importance of the reticulum in the complex eructation reflex has not yet been fully assessed. It has been mentioned that the second requisite factor for eructation is that the cardia must be freed of obstructing ingesta. In a normally full rumen the level of ingesta lies above the cardiac orifice. (Magee 1932). The X-ray photographs reproduced in fig. 5 was taken from a sheep with a normally full rumen after feeding. A barium filled rubber tube was introduced into the rumen to mark the entrance of the oesophagus. As can be seen the cardiac orifice lies well below the level of ingesta in the rumen. For efficient eructation to take place some mechanism must come into play which lowers the level of fluid in the anterior rumen below that of the cardia. Amadon (cited by Cole et al 1945) has reported that the dilation of the reticulum which accompanies ruminal contraction, lowers the fluid level in the anterior rumen, so that the cardiac orifice is unobstructed for the free passage of gas. The present author is in full agreement with this view. The simultaneous recording of ruminal and reticular contractions, illustrated in fig. 6, clearly shows the dilatation which accompanies eructation. The importance of this dilatation in lowering the fluid level and permitting efficient eructation will become evident when dealing with the factors affecting the eructation reflex.

In order further to confirm this hypothesis, sheep No. 13 was deprived of a functioning reticulum by operative invagination and suturing of the organ, thus obliterating the lumen. Before the operation eructation and ruminal motility were found to be normal on a full rumen after feeding. The degree of rumen filling was roughly determined by the removal of 3½ litres of fluid rumen contents.

Food and water consumption was very low after the operation and the rumen was obviously relatively empty when recordings were taken on the sixth post-operative day. The degree of rumen filling was again roughly determined by the removal of 2½ litres of fluid. Eructation efficiency was then found to be normal. Replacement of the 2½ litres ruminal contents reduced the efficiency of eructation slightly, but the further addition of one litre of water markedly interfered

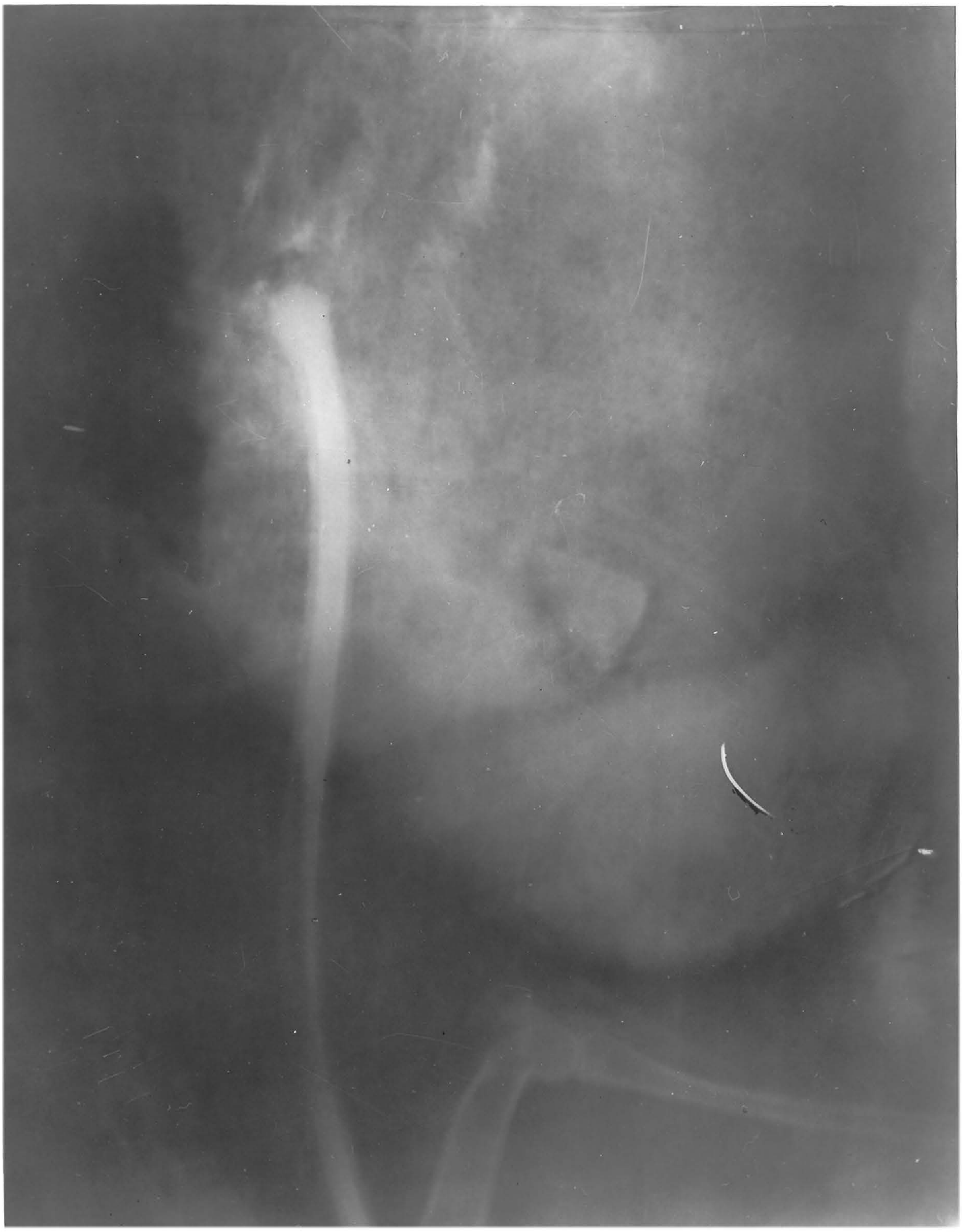


FIG. 5(a).

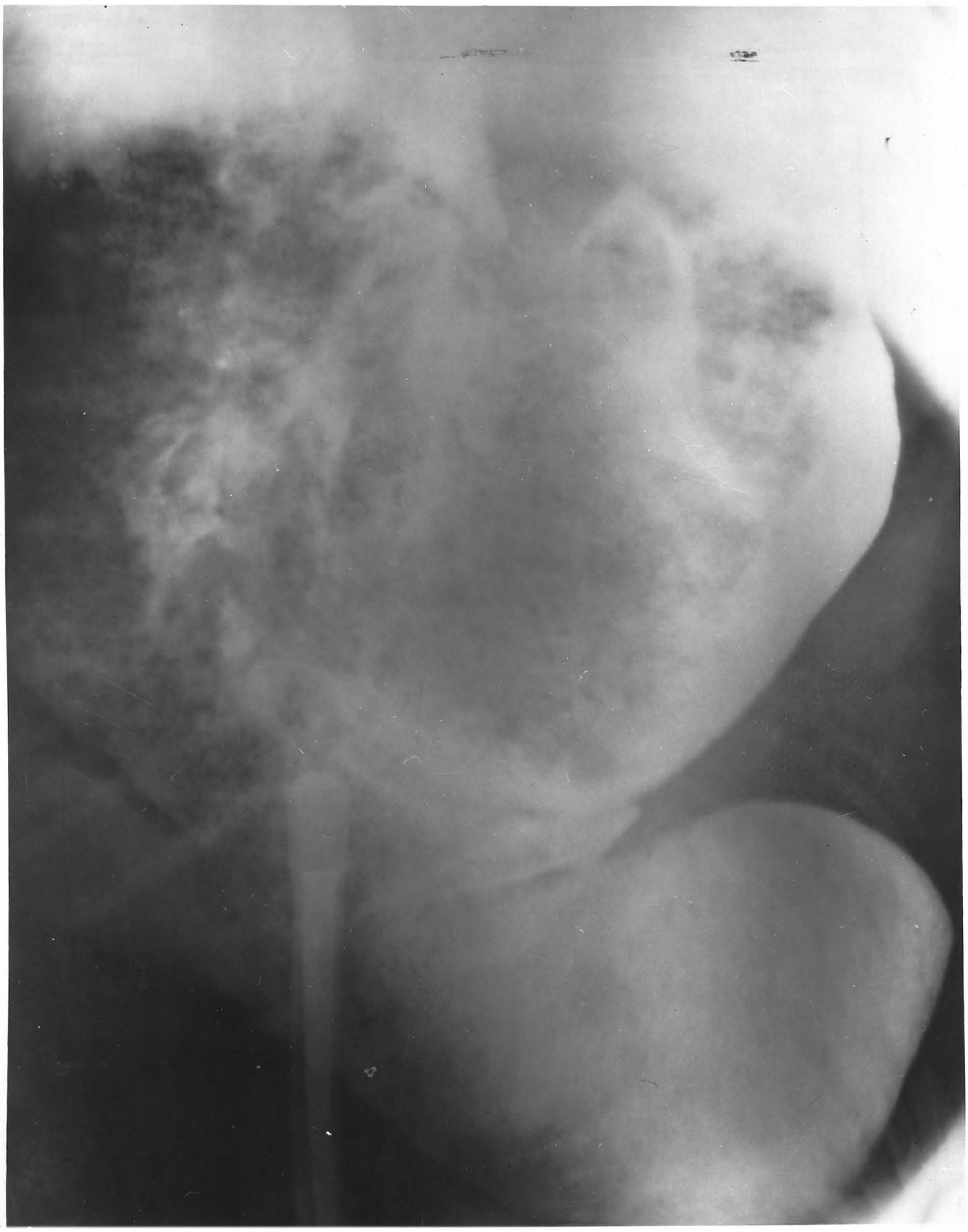
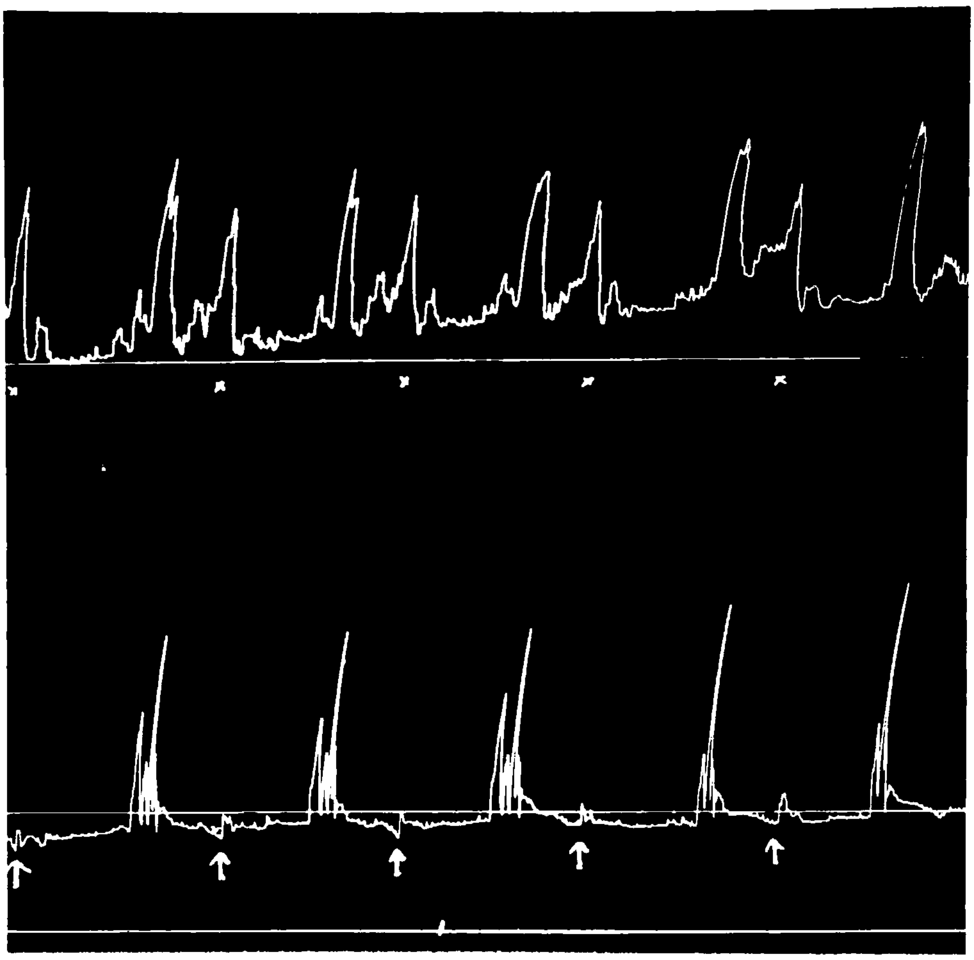


FIG. 5(b).

The Rôle of the Reticulum in the Eructation reflex

A

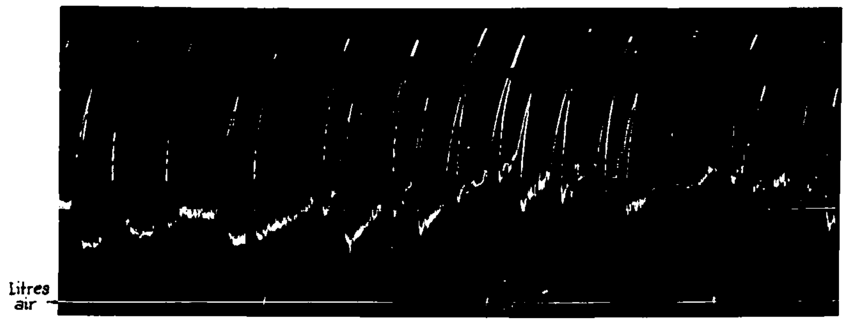
B



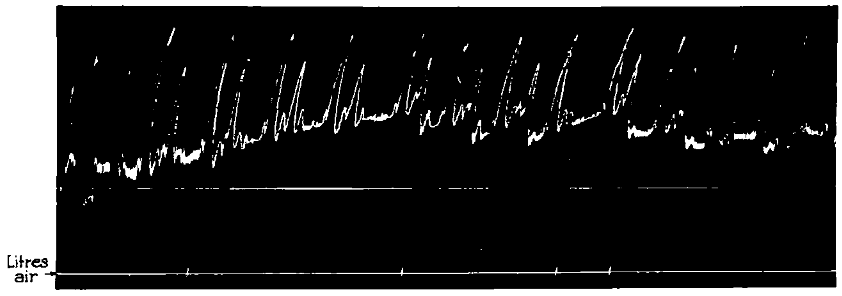
A : Ruminal Motility . x = eructation contraction
B : Reticular Motility . ↑ = dilatation of reticulum coinciding with eructation

FIG. x.

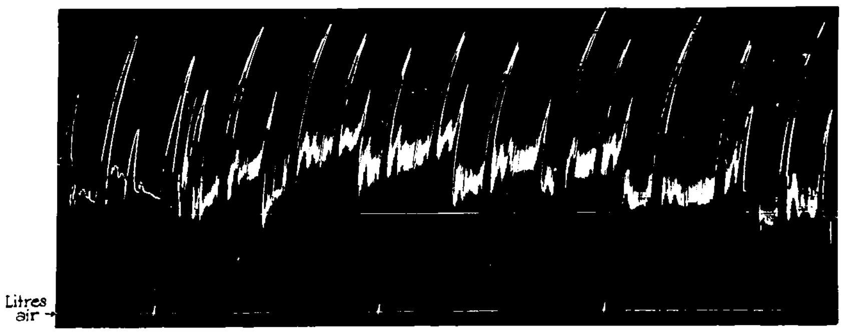
The Effect of Rumen Filling and Posture on Eructation Efficiency in Sheep.



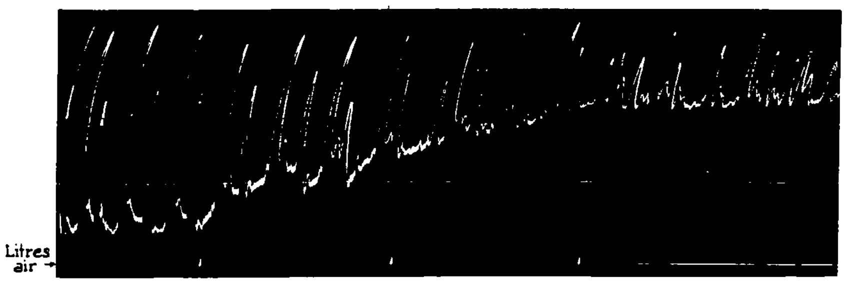
Normal Efficient Eructation.



Interference with Eructation by the addition of 2 litres water to the rumen.



Eructation Efficiency improved by raising forequarters.



Eructation Efficiency markedly reduced by raising hindquarters.

FIG. 8.

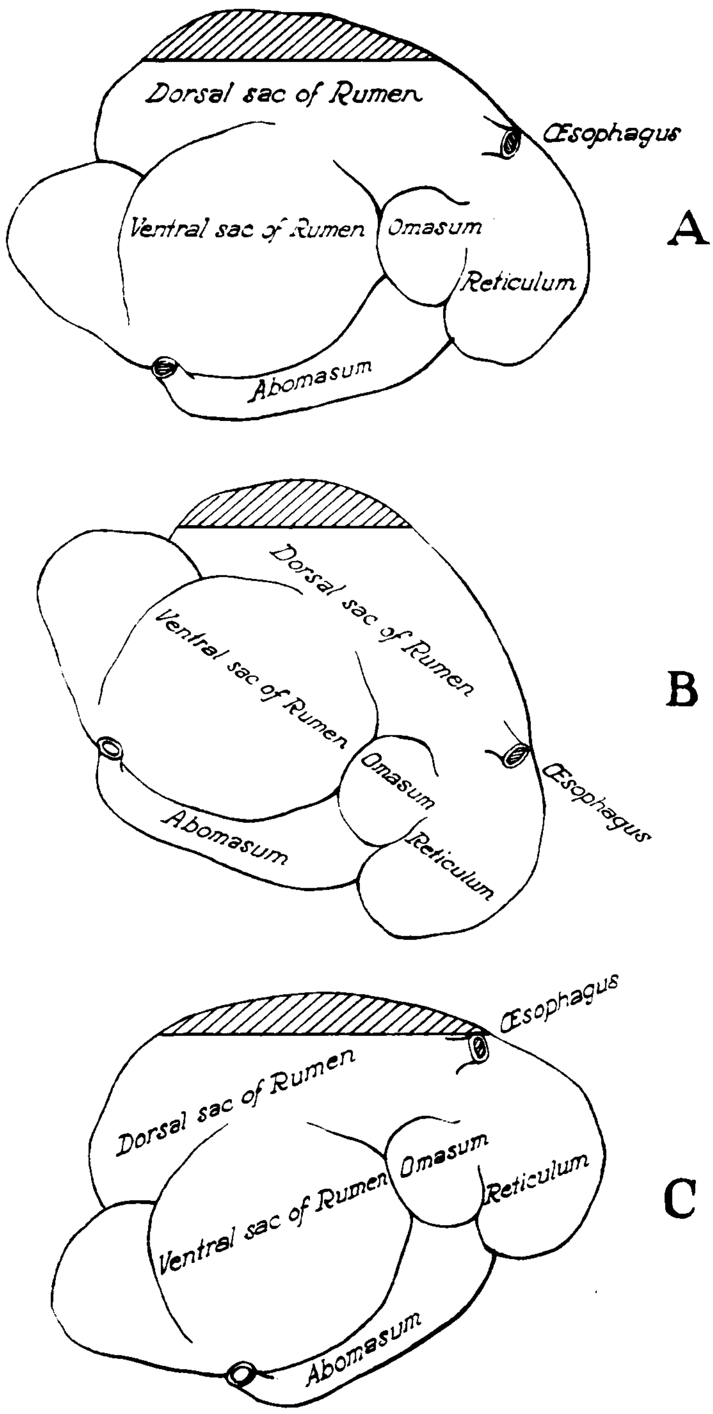

Dorsal sac of Rumen
Œsophagus
Ventral sac of Rumen
Omasum
Reticulum
Abomasum
A
Dorsal sac of Rumen
Ventral sac of Rumen
Omasum
Œsophagus
Reticulum
Abomasum
B
Œsophagus
Dorsal sac of Rumen
Omasum
Ventral sac of Rumen
Reticulum
Abomasum
C

FIG. 7.

with the reflex. It would thus appear that, at approximately the same degree of rumen filling (3½ litres), eructation efficiency was markedly reduced in the absence of a functional reticulum.

The animal also appeared to be more than normally susceptible to elevation of the hindquarters. Raising the hindquarters 15° resulted in marked interference with eructation efficiency, whereas normal sheep with approximately the same degree of rumen filling show no effect on 15° elevation. The effects of posture will be discussed later.

(D) The initiation of the reflex.

According to Cole et al (1945) eructation is a reflex rather than a voluntary act because involuntary muscles are involved in the process. Being considered as a reflex, one must necessarily think in terms of a reflex arc, consisting of receptors, nerves, the co-ordinating centre and the efferent motor nerves, which has been shown to be the vagi. (Ellenberger (cited by Cole et al (1945)), Mangold and Klein (1927) and Hoflund (1940)).

Wester observed that eructation could occur in an animal with an open ruminal fistula, thus concluding that an increase in intraruminal pressure is not essential to initiate the reflex. Stålfors (1926), however, believed that gas pressure is an important stimulus for the reflex and postulated that pressure may be exerted in certain parts of the rumen in spite of an open fistula.

Hoflund (1940) observed that the eructation contractions became irregular and reduced in rate on starvation, but during active fermentation, after feeding, they became regular with extra eructations at intervals.

Dougherty (1942) showed that by increasing intraruminal pressure by the insufflation of various gases, especially oxygen, ruminal motility was markedly stimulated even after total paralysis caused by atropine. Nichols (1951) also reported that insufflation of the rumen increased belching.

During experiments with the artificial introduction of air into sheep, it has constantly been observed that an increase in intraruminal pressure stimulates eructation contractions. After a period of fasting, a ruminal rhythm of two to four backward contractions to every one forward eructation contraction was often observed. The introduction of air under these conditions markedly changed the rhythm of ruminal contractions, bringing more regular eructation movements into play, often with extra eructations interposed. A rhythm of 2:1 to 4:1 has often been observed to change to a rhythm of 1:1 or even 1:2 on introduction of air. The same effect is produced by feeding. An animal exhibiting a rhythm of 2:1 before feeding will show a rhythm of 1:1 and 1:2 after feeding, i.e. during active fermentation. This is most pronounced after feeding green lucerne or lucerne hay which are known to produce large amounts of gas.

Bovines can handle far greater amounts of air at a faster rate than sheep. It has been found that bovines usually exhibit a 2:1 rhythm, even during air insufflation. The rhythm has been noticed to change, however, in some cases, to 1:1 if intraruminal pressure rose above atmospheric.

In experiments on sheep which will be described later, a total paralysis of the rumen was brought about by dosing either sodium carbonate or potassium cyanide. Introduction of air into the rumen caused an increase in intra ruminal pressure which stimulated the eructation reflex so that forward eructation contractions reappeared rhythmically although backward rumen contractions remained inhibited. The rate of these eructation contractions was observed to be markedly increased especially if eructation was inefficient with consequent sustained high intraruminal pressure.

The tracing presented in Fig. 3 shows the change of rhythm from 2:1 before insufflation (A to B) to 1:1 during insufflation (B to C) with return to the original 2:1 rhythm after the introduction of air was stopped (C to D).

The suggestion of Stålfors (1926) that pressure in any part of the rumen may initiate the reflex, suggested that receptors in the posterior dorsal blind sac might be more sensitive to pressure stimuli than those elsewhere in the rumen, since it is here that the forward moving eructation contraction has its origin.

Observations on the effect of posture of the animal have strengthened this theory. A ruminal rhythm of 2:1 changed to 1:1 during air insufflation with the animal standing level. With the forequarters raised it remained at 2:1 in spite of air insufflation. In this position pressure was being exerted mainly in the anterior dorsal part of the rumen. With the hindquarters raised pressure was exerted mainly in the posterior sac and the rhythm changed to 1:1 with very frequent extra eructation contractions. (The tracings presented in Fig. 8 illustrate these results.)

It would therefore appear that an increase in intra-ruminal pressure, especially in the posterior dorsal blind sac, is the main stimulus for the eructation reflex. The increased rate of ruminal contractions caused by oxygen insufflation, reported by Dougherty (1940), was presumably caused by an increase in the rate of eructation contractions.

Mead, Cole and Regan (1944)advanced the theory that the presence of coarse irritating material in the rumen provided the stimulus for the eructation reflex and that the absence of such material leads to defective eructation and bloat. Cole, Mead and Regan (1943) also reported the existence of a rough correlation between rumination and eructation and postulated that both acts were apparently initiated by the same stimulus.

Although the "physical deficiency" theory of the cause of bloat is backed by considerable evidence from clinical trials, these authors have failed to prove that the eructation reflex itself is stimulated by coarse roughage or that it is inhibited by the absence of such material. Their suggestion that turpentine relieves bloat by stimulating eructation, due to its irritant action, cannot be accepted. The administration of turpentine has no stimulating action on the eructation reflex, but, as shown by Clark (1948), the beneficial effect of this drug is due to the breaking of the froth by its surface tension action.

In order to test the "physical deficiency" theory, one of the bovines was placed on a ration consisting solely of freshly-cut tops of young lucerne. Despite the complete absence of coarse material in this feed there was no adverse effect on the efficiency of eructation. The tracing shown in Fig. 4 was made after the animal had been on the purely succulent diet for one month. As will be seen, eructation was entirely efficient. Ruminal motility and rumination persisted throughout. By chance the animal was actually ruminating during the experiment recorded in Fig. 4. Regurgitation took place immediately before a backward ruminal movement, and was accompanied by a sudden sharp rise in intraruminal pressure presumably caused by the extra contraction of the reticulum known to accompany regurgitation. At various times the experimental sheep were placed on a diet of young green lucerne for extended periods, but, apart from mechanical factors, such as frothing, interfering with the efficiency of eructation, the reflex mechanism itself was never found to be inhibited.

During the insufflation experiments on sheep it has frequently been found that the experimental animals could ruminate normally, even though showing a completely inefficient eructation mechanism. This has been found on various occasions, both when inefficiency of eructation was associated with the degree of ruminal filling, and during total paralysis of the rumen due to atropine.

These observations indicate that there is no common stimulus for, or correlation between, the two totally different acts of regurgitation and eructation. Rumination can occur independently of ruminal or reticular contractions, whereas eructation is entirely dependent on active ruminal and reticular motility. The presence or absence of coarse roughage in the rumen does not appear to affect the eructation reflex nor apparently is it the stimulus for its initiation.

As already stated, pressure by gas is considered by the present author to be the main stimulus for the eructation reflex.

INDIVIDUAL VARIATIONS AMONGST ANIMALS.

It is a well-known fact that certain idividual animals in a herd may bloat repeatedly, whilst others, kept under similar conditions, are less affected. In an outbreak of bloat on lucerne pasture, one rarely finds all the animals bloated. This individual difference in susceptibility has been observed by Cole, Mead and Regan (1943) and Clark (1950). Knapp Baker and Phillips (1943) have described variations in the occurrence of bloat in the steer progeny of beef bulls, and suggest that these variations are due to a difference in the level of nervous reaction amongst the different animals. They have found a significant difference in the number of steers showing excessive bloat between the progeny of various bulls and also a highly significant difference between progeny groups.

Mead, Cole and Regan (1944) suggested that individual differences are due to a change in rumen activity brought about by feeding concentrates.

During the series of experiments on the eructation reflex, the eight sheep used as experimental animals showed marked differences in their ability to eructate. Some sheep consistently showed low-grade efficiency while other were very efficient throughout. A third group could be classified as

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medium. (See Appendix IIB). This individual variation can be satisfactorily explained by assuming a difference in the level of nervous reaction of each animal. As the stimulus for eructation appears to be gas pressure, any given pressure would thus produce a varied response in eructation contractions depending on the threshold of nervous reaction. These variations would also apply to the effective opening of the cardia by the contraction of the pillars of the rumino-reticular fold in conjunction with the eructation contraction. The efficiency of eructation is also dependent on reticular activity to clear the cardia, so that any variation in effective reticular activity could also account for individual differences in susceptibility.

The significance of reflex salivation in relation to froth formation and acute bloat in ruminants will be dealt with later. It will be shown that reflex salivation, which is stimulated by coarse material in the rumen, obviates froth formation and bloat. The amount of saliva secreted, therefore also depends on the degree of nervous reaction of individual animals and is an important factor together with the rate of feeding and feeding habits in general, in determining individual susceptibility to bloat.

As the whole eructation reflex and its efficient functioning depends on innate nervous and muscular reactions, it is probable that defects in the mechanism can be hereditary. The work of Knapp and his associates, quoted above, is evidence of the truth of this assertion. Evidence of a hereditary tendency to bloat has also been reported in this country, particularly amongst a certain pedigree Friesland herd. (McFarlane personal communication). See also Appendix IA No. 7 and IIIA). For obvious reasons, however, details of the breeding records could not be obtained for publication. Acute bloat is merely an expression of the fact that the eructation ability of the individual animal has failed under the prevailing circumstances

While we must continue our endeavour to eliminate the factors which render eructation more difficult, a natural corollary is to breed cattle with innately efficient reflexes.

II. FACTORS AFFECTING THE EFFICIENCY OF THE ERUCTATION REFLEX.

A. MECHANICAL.

(1) Obstruction of the Oesophagus.

As the main avenue of escape of gas from the rumen is via the oesophagus, any obstruction of this organ will naturally interfere mechanically with the eructation of free gas. Outbreaks of acute bloat may follow the feeding of chopped tubers, such as beets and potatoes. (Cole et al) (1945). The usual sites at which such tubers become lodged in the oesophagus are the entrance to the thoracic cavity and at the point where the oesophagus passes through the diaphragm. Apart from the fact that enlarged mediastinal lymphatic glands can cause chronic bloat by compression of the oesophagus, slight enlargement of these glands would favour obstruction by tubers.

As such conditions are well-known and have no direct effect on the reflex as such, they do not require any further discussion.

(2) Frothing of Ruminal Ingesta.

Wester (1935) divided bloat into two types. In the one free gas is present in the dorsal sac of the rumen whereas in the other the gas is entrapped throughout the ingesta as a froth, thus preventing eructation. In 1943 Quin discussed the question of frothing and suggested saponins in the plant as a cause. Clark (1948, 1950) suggested the use of surface tension agents in order to free the gas. Quin, Austin and Ratcliff (1949) described successful clinical trials with such preparations.

The formation of froth in this type of bloat interferes mechanically with both the eructation and the absorption of gas. Eructation is interfered with in the same manner as overfilling of the rumen, which will be described later.

By adding an anti-frothing agent to a measured amount of frothy ingesta, the degree of actual frothing can be determined. It was found that frothing can increase the total volume of the ruminal contents by anything up to 100%. The rising-up of the ingesta in the form of a froth not only increases the distance between the free gas and the cardia which progressively encumbers eructation, but also diminishes the amount of free gas which can be eliminated through absorption.

The basic cause of frothy bloat which is related to reflex salivation, is dealt with in section III.

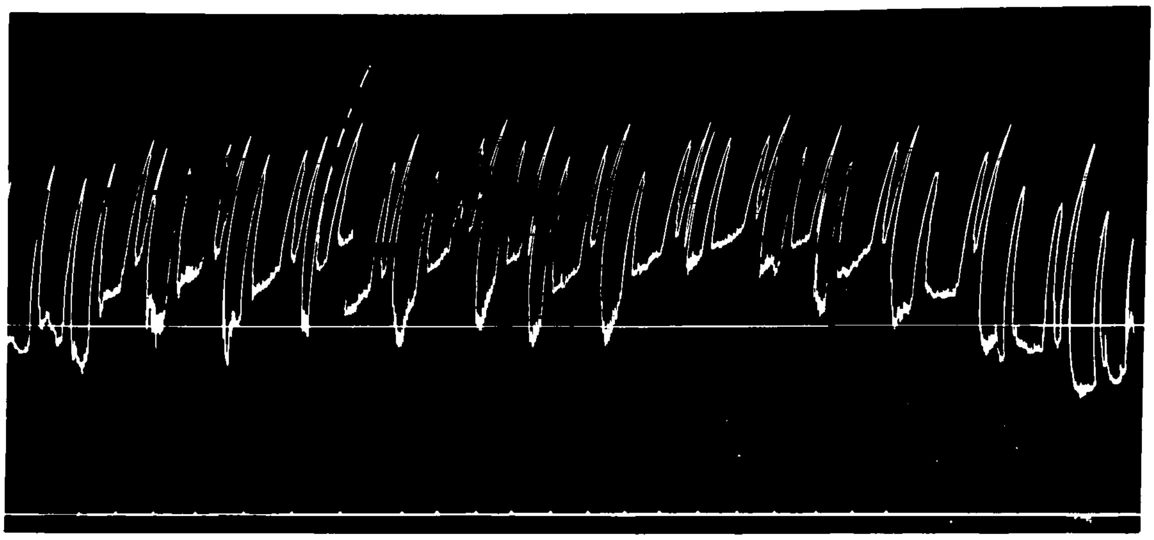
(3) The degree of filling of the Rumen and Posture.

As already described, the fundamental requisite for eructation is the movement of the free gas forwards and downwards to the cardia. This is accomplished by both the forward wave of contraction of the rumen and the relaxation of the reticulum. As the amount of fluid present in the rumen will determine the distance between the free gas and the cardia, the degree of filling will obviously play an important role in eructation. Elevation of the fore- or hindquarters also influences the relative positions of the free gas and the cardia as demonstrated in Fig. 7.

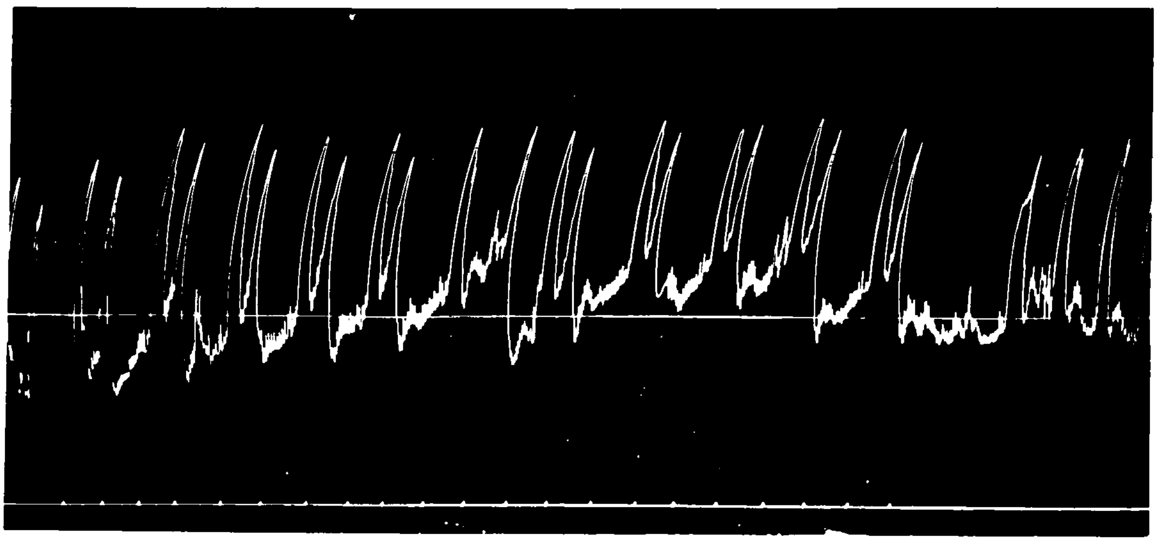
Although Quin (1943) could not demonstrate any effect on the eructation of artificially introduced gas by filling the rumen and elevating the hindquarters, Dougherty (1940) has shown that by pumping water into the rumen and elevating the hindquarters of the animal so that the fluid level is well above the cardia, belching of introduced air is markedly interfered with.

The following relevant experiment, of which tracings are presented in Fig. 8, was conducted. Air was introduced at the rate of one litre per three minutes into one of the experimental sheep, three hours after feeding on a ration of 500 grams of lucerne hay and grass hay ad lib. with available water.

The Effect of Volume of Ingesta on Eructation Efficiency in the Bovine.



Normal Eructation. (2-1 Rhythm)



Increased Efficiency (1-1 Rhythm) after removal of 8 litres ingesta.

FIG. 2.

The rumen was regarded as normally full at the start of the experiment.

A recording of normal efficient eructation was obtained and is shown in the top tracing. Two litres of water were then added to the rumen, the effect of which is shown in the second tracing. Eructation efficiency was interfered with as can be seen from the rise in pressure and protracted recovery after air insufflation was stopped. The effect of 28° elevation of the forequarters is shown in the third tracing. It is evident that, in spite of an unaltered degree of rumen filling, eructation efficiency was markedly improved. The initial ruminal pressure, though slightly higher as a result of elevation, was not increased by air insufflation. The drop in intraruminal pressure coinciding with eructation contractions is well illustrated. The bottom tracing shows the effect of 28° elevation of the hindquarters. Eructation efficiency was markedly reduced compared with when the animal was standing on the level.

The effect of the degree of filling of the rumen on eructation and rumination was clearly shown by the following observations. On a particular occasion one of the experimental sheep showed complete inability to eructate introduced air despite the presence of normal ruminal motility. During this period the animal was ruminating regularly. After removal of three litres of ingesta from the rumen, rumination ceased but eructation was found to be entirely efficient. Replacement of the ingesta caused resumption of rumination while inefficient eructation reappeared.

Similar results were obtained from one of the bovines as illustrated in Fig. 9.

In view of the fact that the degree of filling of the rumen had been shown to play such an important part in the efficiency of eructation, it was decided to investigate the influence of water and food intake on the pathogenesis of bloat.

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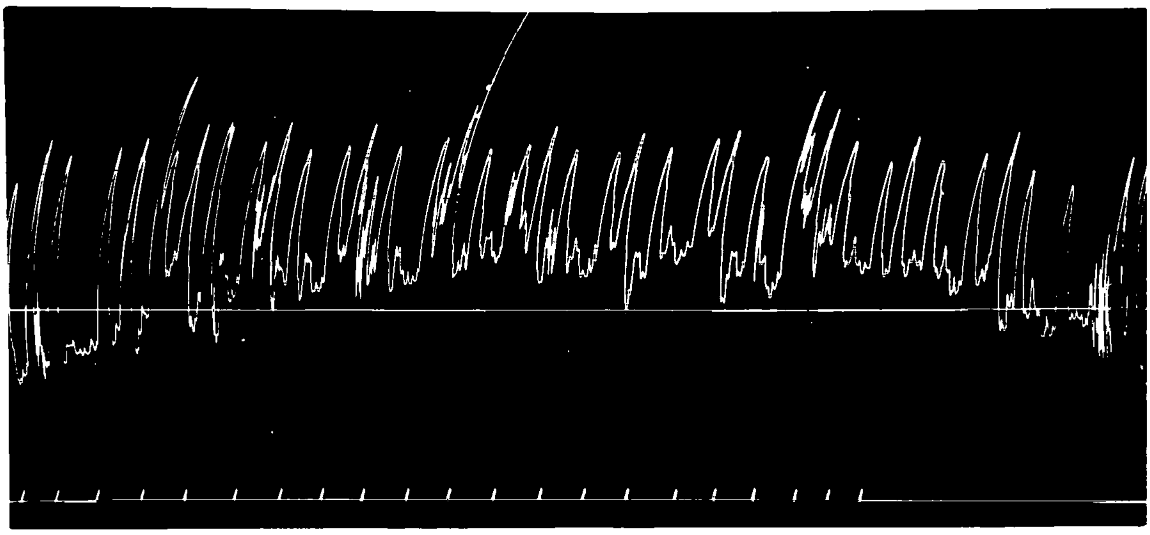
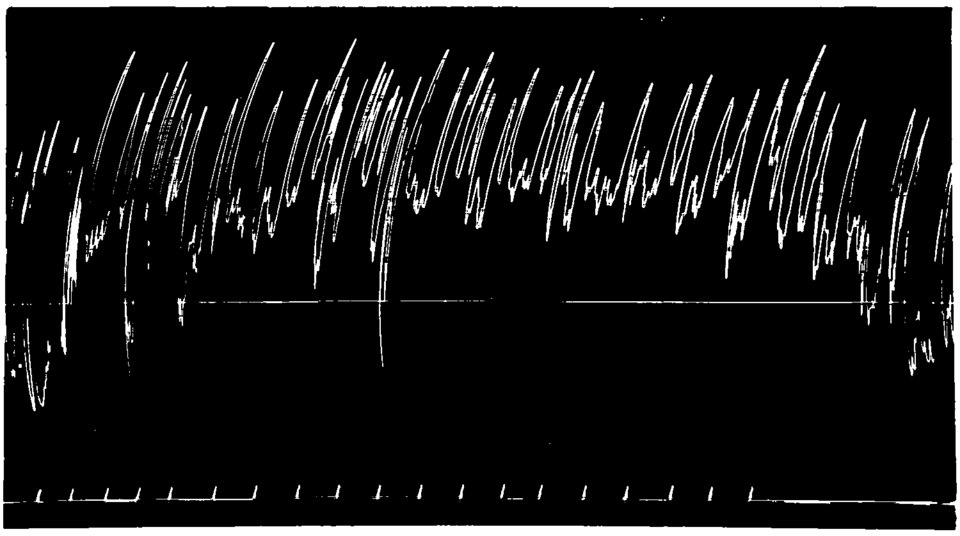
The Effect of Volume of Ingesta on Eructation Efficiency in the Bovine.



Decreased Efficiency after introduction of 12 litres water.



Failure of Eructation after introduction of further 8 litres of water.

FIG. 9 (cont.)

In one trial all six experimental sheep were deprived of water for 24 hours but given lucerne hay ad lib. up to the time of recording. The eructation efficiency of each animal was then determined after which both water and food were made available for a period of two hours, the consumption being recorded. The ability of the animals to eructate introduced air was then again tested. The efficiency of the reflex was found to have decreased in all six cases and the degree of decrease was proportional to the combined food and water intake. (See Appendix 2C).

These results indicate that the time of watering might play an important rile in the pathogenesis of spontaneous bloat. In several trials groups of normal cattle and sheep were deprived of water for 24 hours. Half of the animals were then offered water ad lib. before the whole group were turned out onto lucerne pasture. The incidence and severity of bloat was considerably higher amongst the watered groups than amongst the controls. (See Appendix 2D and E).

Watering immediately before pasturing may therefore render the animals more susceptible to bloat, especially if water has not been available for some time previously. The well-known association between rapid greedy feeding and hoven may also, in many cases, be attributable to overloading, although as pointed out by Mead et al (1944) the incidence of bloat cannot always be correlated with the consumption of feed.

B. THE EFFECT OF ALKALOSIS.

Clark and Lombard (1951) showed that the administration of alkali, whether dosed into the rumen or injected intravenously, caused ruminal paralysis. This effect was shown to be of central origin and presumably due to alkalosis. Consequently it was decided to investigate the effect of alkalosis on the eructation reflex.

By giving graded doses of sodium carbonate per ruminal fistula it was found that the two types of ruminal movements were not equally affected. (See Appendix 2F and G). The backward moving contraction was reduced in strength first and could even be entirely inhibited, while the eructation contraction still persisted at almost normal strength. Under such conditions, however, the animals were found to be particularly susceptible to overfilling, probably due to paralysis of the reticulum. Even when the eructation contractions were completely inhibited by large doses, they tended to reappear when the intra-ruminal pressure was raised by air insufflation.

In their work, Clark and Lombard showed that after dosing alkali, ruminal paralysis persisted for several hours after the pH of the ruminal ingesta had returned to normal. They postulated that this was due to a continued upset in the acid-base ratio of the blood. Similarly it was found that the decreased efficiency of eructation persisted despite a recovery of the pH of the ingesta. In order to prove that this was due to a residual alkalosis, the CO_2-combining power of the blood was followed throughout the experiment. (See Appendix II#). As shown in the graph (Fig. 10) the average eructation efficiency of the six sheep (as rated on an arbitrary scale) showed a remarkable inverse correlation to the average CO_2-combining power of the blood. It will be noted that these two factors took 72 hours to return to normal, although the reaction of the rumen was again acid within 24 hours. Probably owing to the numerous other factors affecting eructation, the inverse relationship between eructation efficiency and the alkali reserve of the blood in the case of individual sheep was not always exact. The tracings in Figs. 11 and 12 are given as illustrations of the effects of alkalosis on sheep and cattle respectively.

C. <u>THE EFFECTS OF ABDOMINAL VAGOTOMY</u>.

As far back as 1883 Ellenberger (cited by Cole *et al*

The Effect of Artificial Alkalinity on the Eructation Efficiency.

In Sheep.

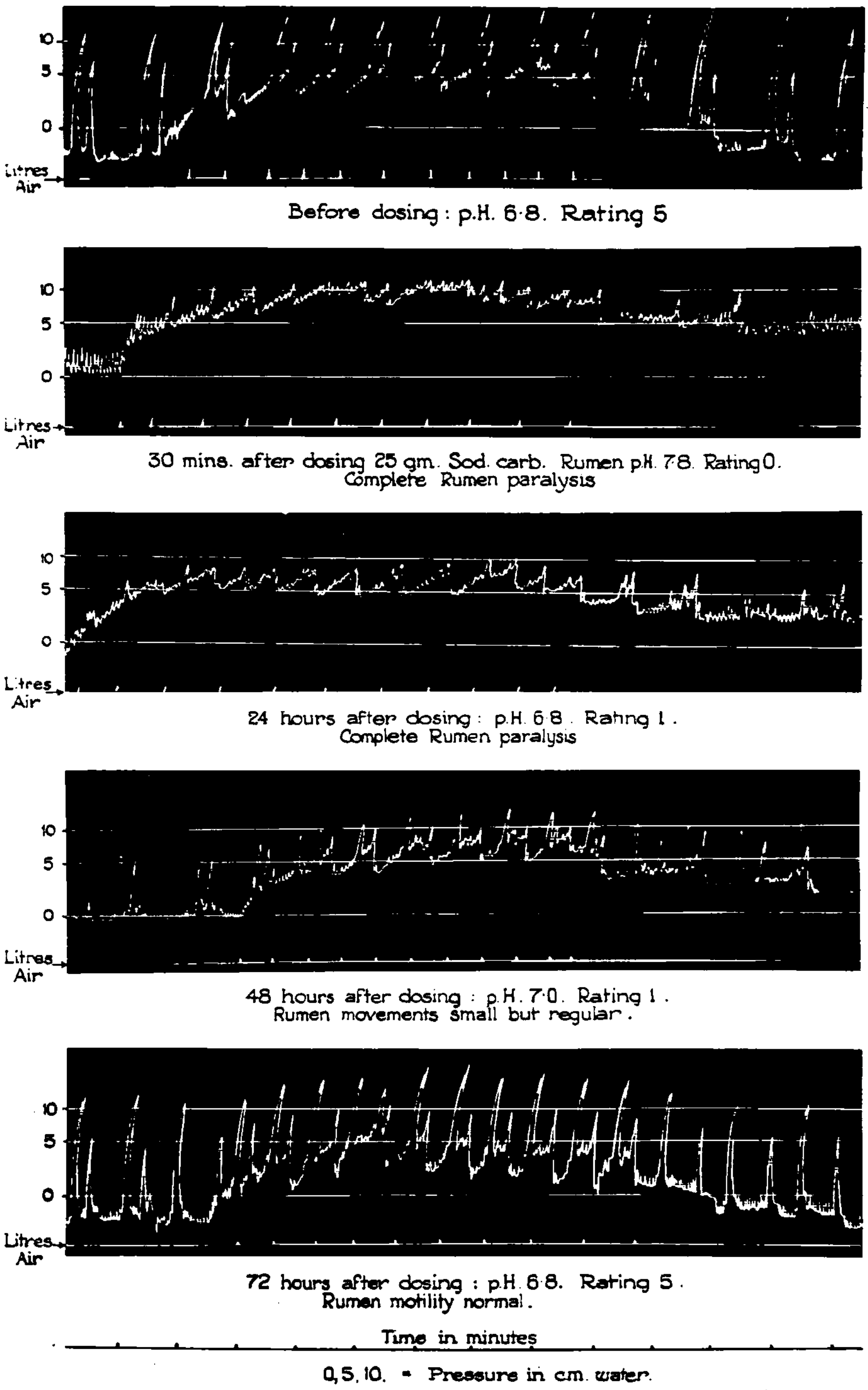
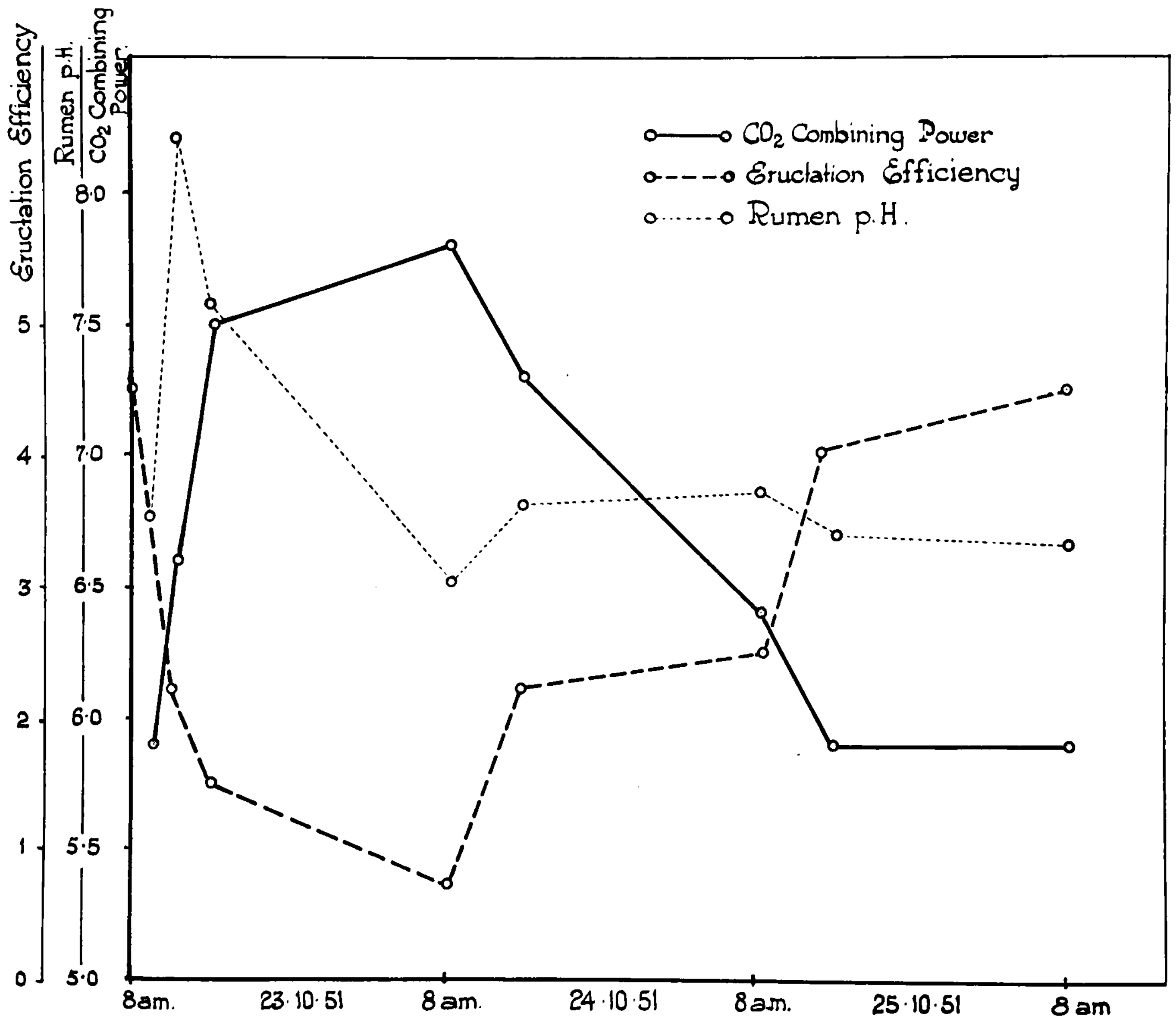


FIG. 12.

Fig. 10.

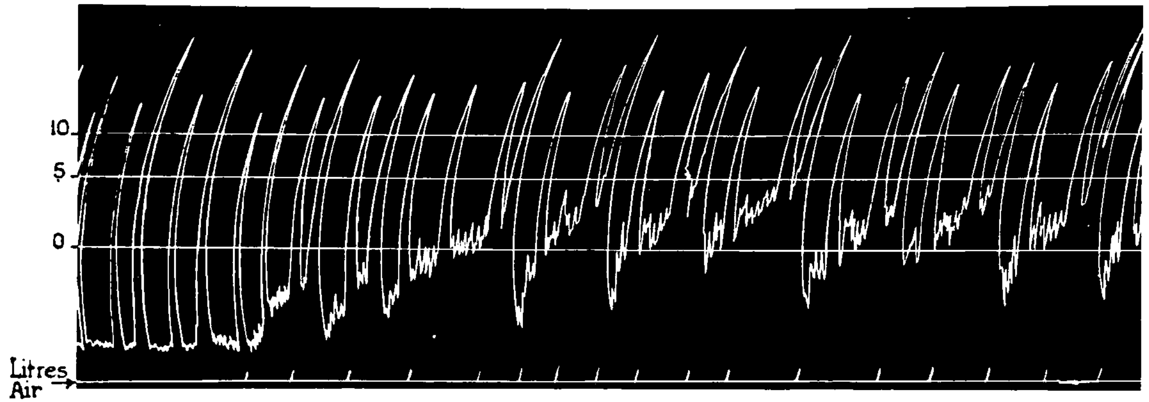


Eructation Efficiency
Rumen p.H.
CO2 Combining Power
CO2 Combining Power
Eructation Efficiency
Rumen p.H.
8·0
7·5
7·0
6·5
6·0
5·5
5·0
5
4
3
2
1
0
8am.
23·10·51
8 am.
24·10·51
8am.
25·10·51
8 am

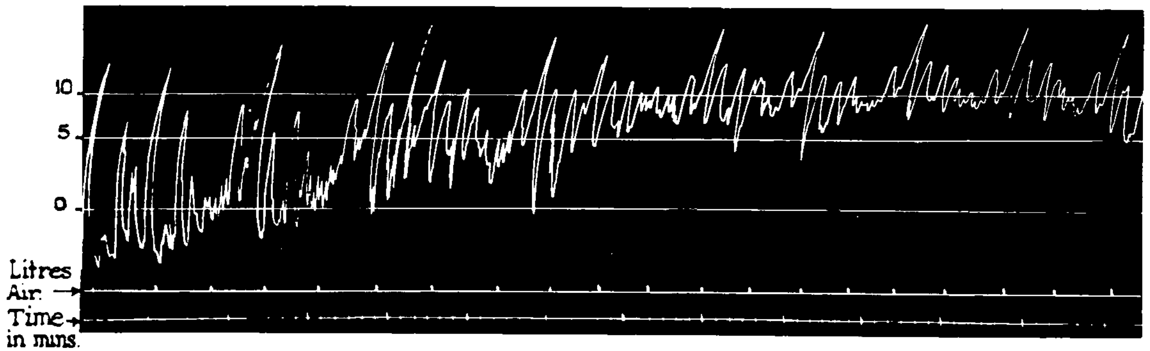
Fig. 13.

The Effect of Artificial Alkalinity on the Eructation Efficiency.

In the Bovine.



Normal Eructation on mixed diet.



Interference with eructation caused by dosing 150 gm. Sod. carb.. Rumen p.H. 6·9.

0, 5, 10, = Pressure in cm. water.

(1945)) demonstrated that chronic tympany could be produced by section of both vagus nerves in the region of the neck. It is now well-known that the vagi are the motor nerves to the entire alimentary tract. Mangold and Klein (1927) studied the effects of left- and right-sided abdominal vagotomy on the behaviour of the ruminant forestomachs. They showed that the cutting of both these branches at the level of the cardia abolished eructation. Bloat was, however, never encountered where only one of the branches was cut, owing probably to the lack of specificity in the distribution of these nerves, or to the type of feed on which the animals were fed. According to these authors the left dorsal branch of the vagus innervates mainly the rumen but also sends a few fibres to the reticulum. The right ventral branch mainly supplies the reticulum, omasum and abomasum, with a few fibres to the rumen. Crossover fibres connect these two nerves proximal to the cardia.

Hoflund (1940) confirmed the work of Mangold and Klein, and showed that pyloric stenosis with abomasal distension resulted from damage to the right ventral branch of the vagus and other collateral fibres supplying this area. He further showed that this condition can arise spontaneously as a result of traumatic reticulitis and peritonitis involving damage to these nerves.

In order to study the effect of section of the abdominal branches of the vagus nerve on the eructation reflex, two adult goats with permanent ruminal fistulae were used. In goat No. 1 the right ventral branch of the vagus was cut at the level of the cardia, approximately one inch of the nerve being removed. In the case of goat No. 2 a similar operation was performed on the left dorsal branch. Recordings of the eructation of artificially introduced air had been made prior to vagotomy and both animals had been found to be normal in all respects. Similar observations were made periodically from two days after the operation. The animals were fed on lucerne hay ad lib and their food and water consumption, together with the amount of faeces passed, were determined daily. (See Appendix 2J). The following are the main observations on the two animals over a period of one month.

Goat No. 1 (right ventral branch severed). For the first eight days after the operation both types of ruminal contractions were found to be almost doubled in strength. Normal rumination was observed on the eighth post-operative day. From this time onwards it was noticed that the backward moving contractions decreased progressively in strength and rate, while the eructation contractions remained exceptionally strong throughout. The diminution in the strength of the backward contractions can be ascribed to abomasal distention (vide infra).

On the ninth day the animal showed clinical bloat, the ruminal ingesta was frothy but a certain amount of free gas escaped on opening the fistula. On the 12th to 22nd day the animal showed continous bloat, the rumen being filled with a frothy slimy mass of ingesta of a light colour, in spite of the food consisting of good quality lucerne hay. This disappearance of chlorophyl was an indication of the length of time the ingesta had remained in the rumen.

Food and water consumption was very low and dropped progressively during the month to almost nil. The amount of faeces passed was likewise minimal, being frequently less than ten grams per day towards the end of the period. Eructation efficiency, as determined by air insufflation, was markedly reduced to the 12th day after which a progressive improvement was noticed. From the 22nd day eructation was normal but could be markedly reduced by the addition of two litres of water to the rumen. The improvement in eructation efficiency was probably due to a gradual reduction in the volume of ruminal contents.

The animal was finally destroyed one month after the operation. The rumen was found to be relatively empty containing a total of three litres watery, straw-coloured ingesta. The abomasum was enormously distended and occupied the major portion of the abdominal cavity, as shown in the photograph reproduced in Fig. 13.

The abomosal contents weighed six kilograms and contained coarse particles resembling normal ruminal ingesta. The intestines were practically empty and distended with gas.

Section of the right ventral branch of the vagus, therefore, did not affect the forward contraction of the rumen, nor eructation, provided the rumen was relatively empty. The paralysis of the reticulum, however, rendered the animal particularly susceptible to over-filling. This is further evidence of the role of the reticulum in clearing the cardia for the free passage of gas.

The bloat that was encountered in this case was due to froth formation in the rumen, which was already particularly susceptible to over-filling. As will be shown later the formation of froth was due to diminished reflex salivation on account of cutting the afferent fibres of the reflex in the one vagus.

<u>Goat No. 2</u> (left dorsal branch severed). Both types of ruminal contractions were markedly reduced in strength for the first 20 days. From then on progressive recovery took place. Food and water consumption were practically normal and spontaneous bloat never occurred. Rumination was observed on the twelfth post-operative day.

The eructation efficiency was markedly reduced for the first 20 days, but later improved parallel to the recovery in the strength of the ruminal contractions.

After destruction the abdominal organs appeared normal, the rumen containing 5½ litres of ingesta.

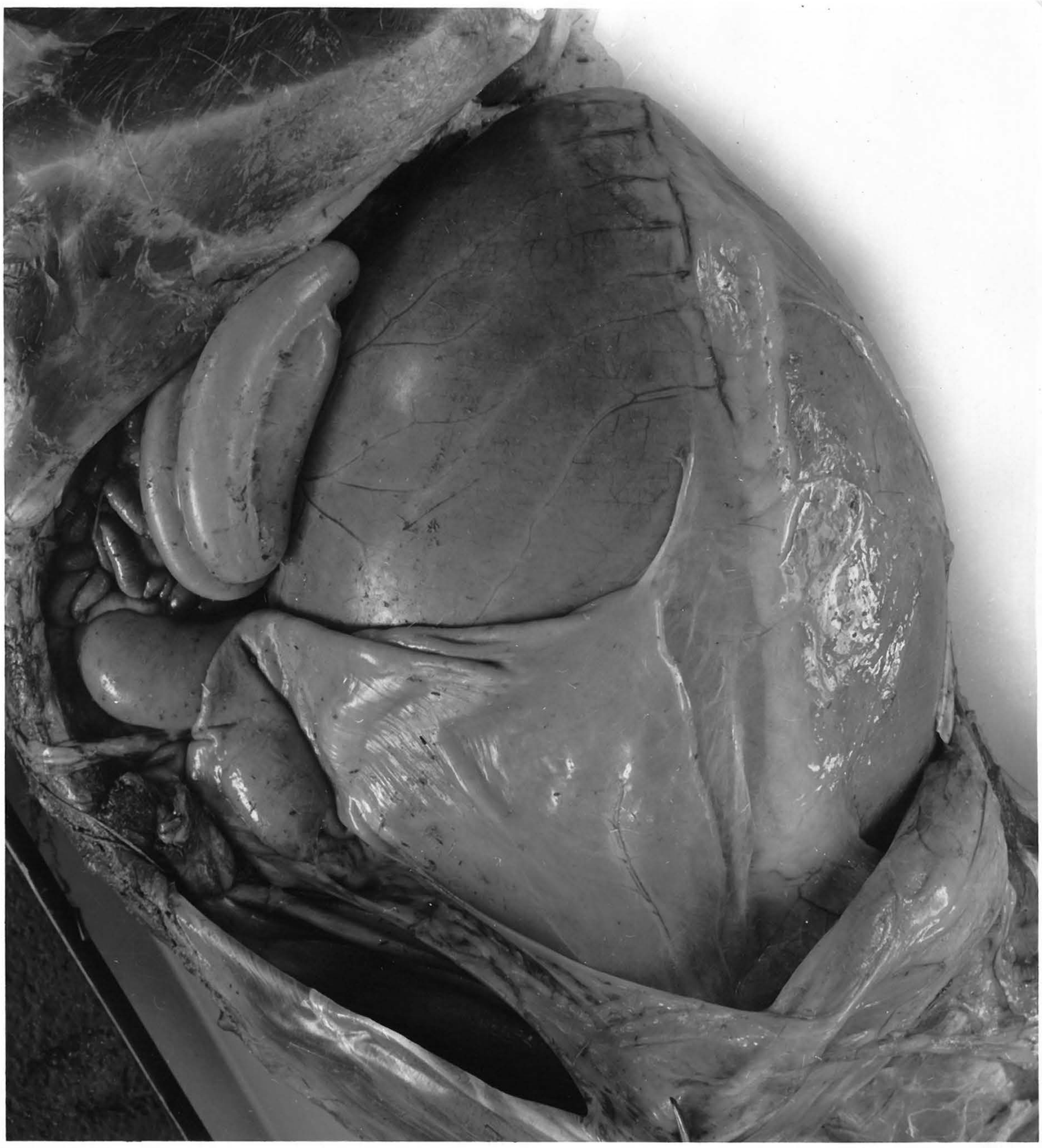


FIG. 13.

Section of the left dorsal branch of the vagus, therefore, did not cause complete ruminal paralysis due to the presence of fibres from the right ventral branch already described. The eructation efficiency was found to correspond with the strength of the ruminal contractions. The gradual improvement can only be ascribed to the adaptation of the ruminal musculature to a diminished nerve supply. Reflex salivation was apparently not markedly diminished in this case because froth formation was not encountered.

D. REFLEX INHIBITION FROM THE POSTERIOR DIGESTIVE TRACT.

(1) The Abomasum.

Wester (1935) considered the motility of the forestomachs to be largely dependent on the state of the abomasum. Conditions such as abomasitis, distention, sand impaction, etc. were said to cause reflex ruminal paresis and tympany.

Phillipson (1939) showed conclusively that distention of the abomasum, either by the introduction of warm saline or by the insertion and inflation of a balloon, inhibited reticular contractions and markedly influenced the character and rhythm of the ruminal motility.

The effect of abomasal distension on the eructation reflex was studied in the following manner:

The experimental sheep with both ruminal and abomasal fistulae was used. Ruminal pressure during air insufflation was recorded in the usual manner. Abomasal distention was brought about by the introduction of either air or warm saline by means of the apparatus depicted in Fig. 1 and described under experimental technique.

It was found that distension of the abomasum, with either fluid or air, caused inhibition of the backward ruminal contractions. This inhibition was proportional to the degree of distension. Even severe distension, however, did not inhibit the forward-moving contractions of the rumen, although eructation was rended less efficient depending on the degree of filling of the rumen. Referring to Fig. 14, tracing 2, it will be seen that the backward contractions were entirely inhibited, the only movements being those related to eructation. As the rumen was relatively empty, the expulsion of gas was entirely efficient. The addition of two litres of water to the rumen (tracing 3), however, completely prevented eructation. After drainage of the abomasum eructation was efficient again in spite of filling of the rumen. (See also Appendix IIK).

These findings confirm the statement of Phillipson quoted above, namely that abomasal distension causes reticular paralysis. As already shown reticular motility is of paramount importance in eructation when the rumen is relatively full. The hyper-sensitivity of the animal to overfilling of the rumen, when the abomasum was distended, can therefore, be ascribed to reticular paralysis.

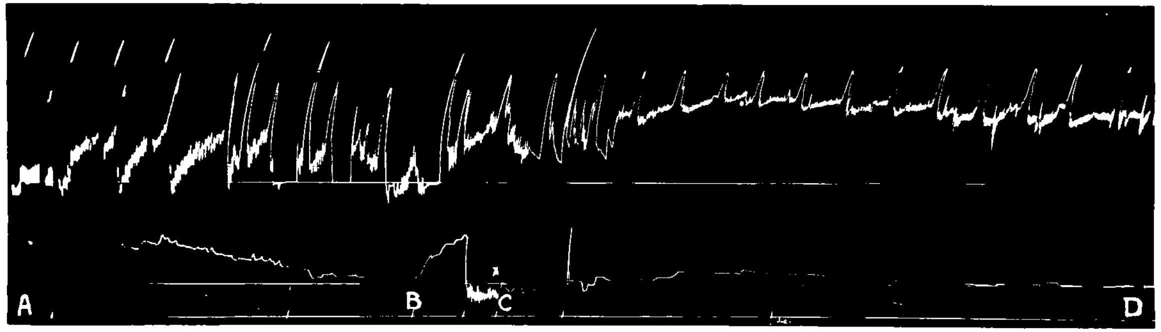
The recordings of the abomasal pressure revealed that the introduction of even two litres of air caused only a transitory rise in intra-abomasal pressure, the organ apparently losing tone to accommodate the new volume (Fig. 15). The effects of abomasal distension, however, persisted for up to 1½ hours.

When the abomasum had been distended with saline, drainage was followed by almost immediate recovery of ruminal motility. On the other hand, removal of the abomasal fistula stopper after air had been introduced, did not at once restore eructation efficiency. As the fistula was inserted near the pyloris, the air was probably trapped in the fundus.

The presence of a gas bubble in the fundus of the abomasum has been a constant feature in the X-ray observations of Czepa and Stigler (1926), Magee (1932) and Phillipson (1939). An increase in the size of the bubble was noted when fluid passed directly in bulk to the abomasum. Stålfors (1926) showed that young succulent grass can pass to the abomasum

FIG. 15.

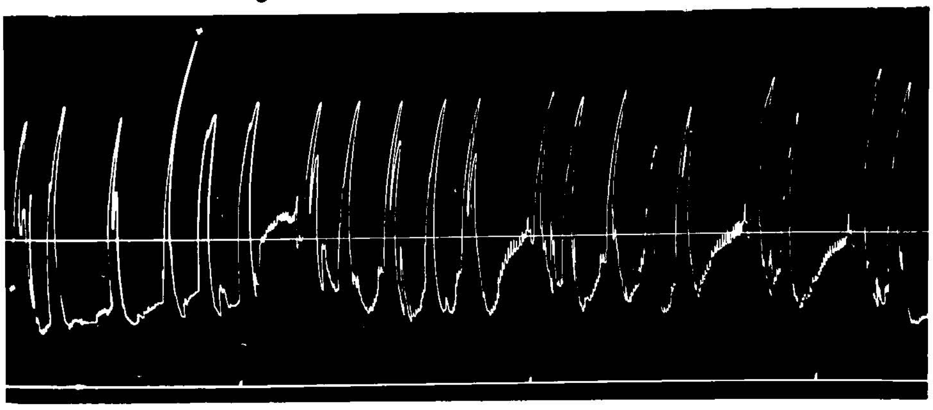
The Effect of Abomasal Distention on Eructation Efficiency in Sheep.



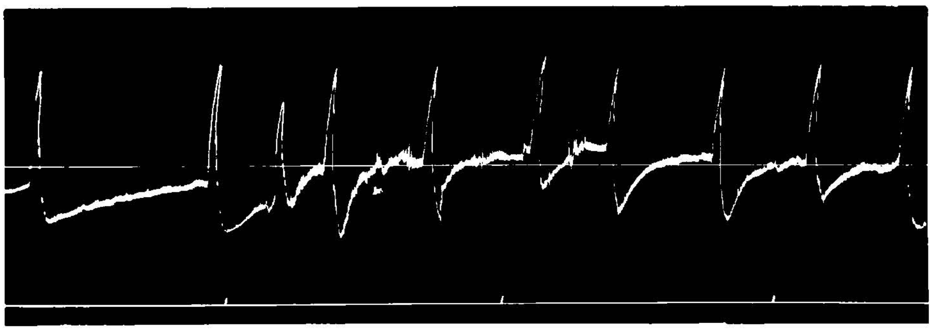
Top: Rumen Recording: A-B Normal Eructation.
C-D Interference with eructation after introduction of 2 litres air into abomasum at B-C.

Bottom: Abomasal Recording: B-C. 2 litres air introduced into abomasum.

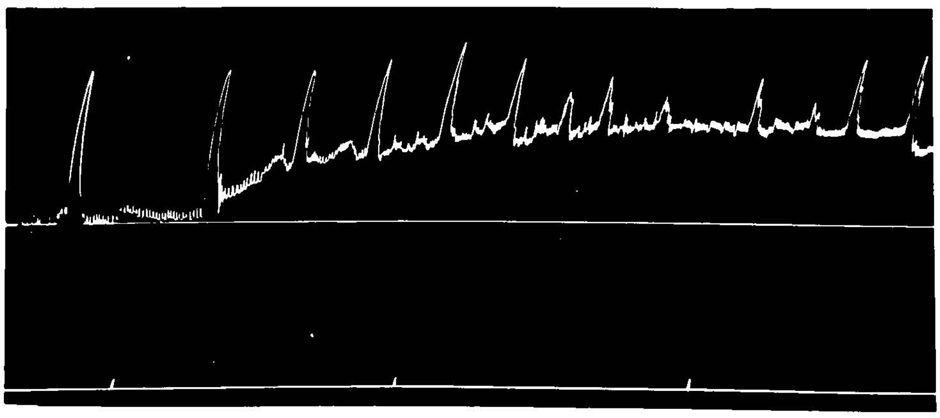
The Relation between Abomasal Distention and Degree of Rumen Filling on the Eructation Efficiency in sheep.



Normal Eructation - Abomasum not distended. Rumen relatively empty.



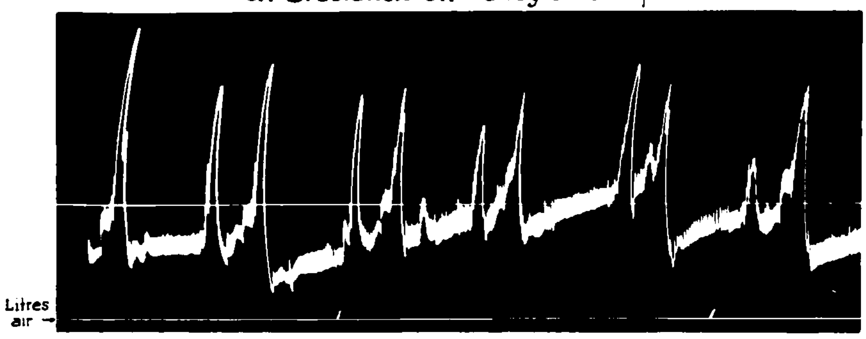
Eructation after Abomasal Distention - Rumen relatively empty.



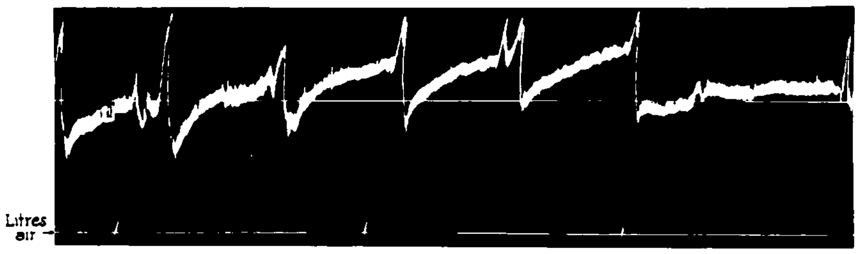
Interference with Eructation after addition of 2 litres water to rumen. Abomasum distended.

FIG. 14.

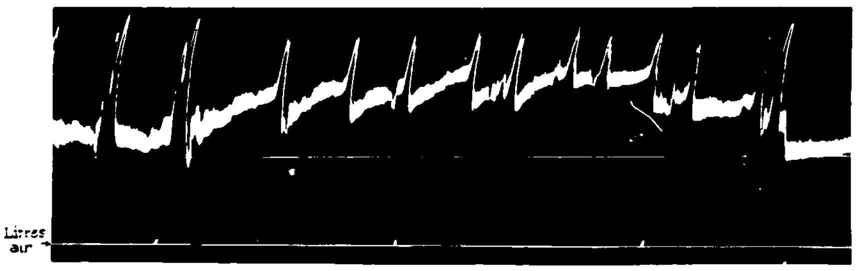
The Effect of Distention of the Posterior Digestive Tract on Eructation Efficiency in Sheep.



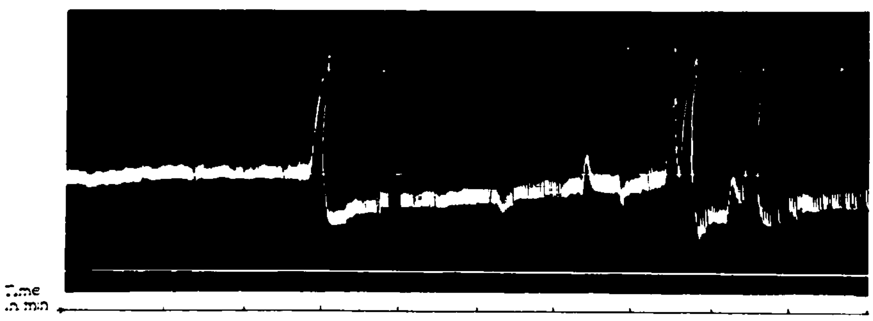
Normal eructation and rumen motility. Caecum not distended. Rumen relatively empty.



Effect of caecal distention. Abolition of backward contraction. Forward contraction still present with efficient eructation. Rumen relatively empty.



Inefficient eructation after addition of 2 litres water to rumen. Caecum still distended.



Inhibition of rumen contraction due to caecal distention in the absence of intraruminal pressure.

FIG. 16.

within 20 minutes after ingestion. Any distension of the abomasum, whether caused by gas formation or overloading with ingesta will, therefore, result in inhibition of the reticulum with consequent impairment of eructation.

Gas formation in the abomasum depends on the rate of passage of ingesta from the rumen to the abomasum and also the difference in pH of ruminal and abomasal ingesta. Reflex inhibition of ruminal motility could be brought about in a sheep if 100 c.c. or more ruminal ingesta of pH 7.2 is injected into the abomasum with a pH of 2, whereas a similar amount of ingesta of the same pH as the abomasum had no effect. In vitro studies also showed that the greater the difference in pH between ruminal and abomasal contents the larger the volume of gas evolved chemically. (See Appendix III). Phillipson (1952) has shown that the rate of passage of ruminal ingesta to the abomasum is dependent on the physical state of the ingesta. Concentrate feeds will therefore tend to pass through rapidly.

(2) The Caecum.

The animal with both the caecal and ruminal fistulae was used to determine the effect of caecal distension on eructation. The method was as described for the abomasal experiments. As shown in Fig. 16 the effects of caecal distension were identical with those found in abomasal distension.

When air was introduced into the caecum there was no escape of gas on subsequent removal of the fistula stopper, although the inhibition of the reticulum was still present. The air had presumably been moved into other regions of the intestinal tract from whence it exerted its effect.

Stålfors (1926) recorded cases of bloat in which rectal examination revealed gas formation and distension of the intestinal tract in conjunction with ruminal tympany.

E. THE EFFECT OF DRUGS INFLUENCING RUMINAL MOTILITY.

(1) Those causing Hypomotility.

(a) Prussic acid.

Quin and van der Wath (1938) showed that small doses of prussic acid caused complete,though transitory paralysis of all ruminal movements. In 1949 Evans and Evans reported ruminal paralysis caused by clover juice and claimed that prussic acid was the active principle. The association between prussic acid and bloat has been the subject of considerable controversy for many years.

In the present series of experiments it was found that small doses of potassium cyanide inhibited the reticulum and backward moving contractions of the rumen. Introduced air could thus be eructated proved the rumen was not overfilled. The possible reason why Clark and Quin (1945) failed to produce bloat by dosing potassium cyanide and introducing air into the rumen is that the degree of ruminal filling of their sheep, which were starved prior to the experiment, was not sufficient. Larger doses caused complete inhibition of all motility and eructation, but at this stage the animals exhibited hyperpnoea and other symptoms of acute prussic acid poisoning. Fig. 17 illustrates these reactions.

It would, therefore, appear that subclinical poisoning with prussic acid could only cause bloat in conjunction with overfilling or other complications.

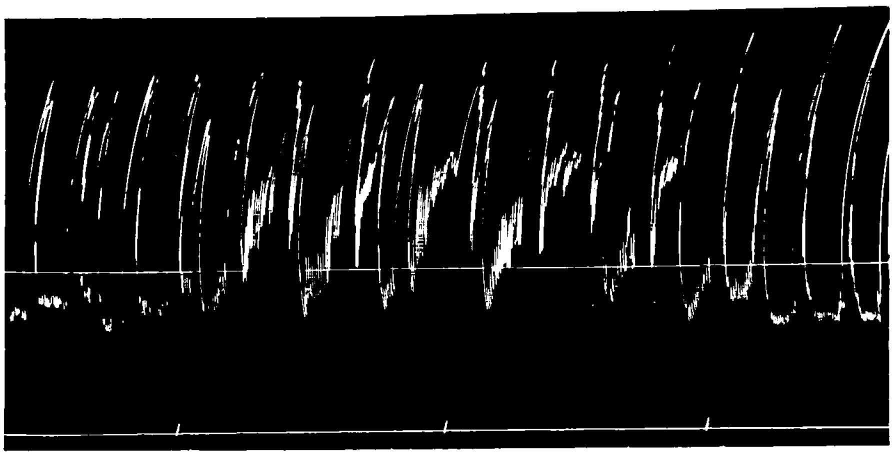
(b) Atropine.

Atropine is well-known to cause ruminal paralysis through blocking of the parasympathetic nerve endings of the vagus.

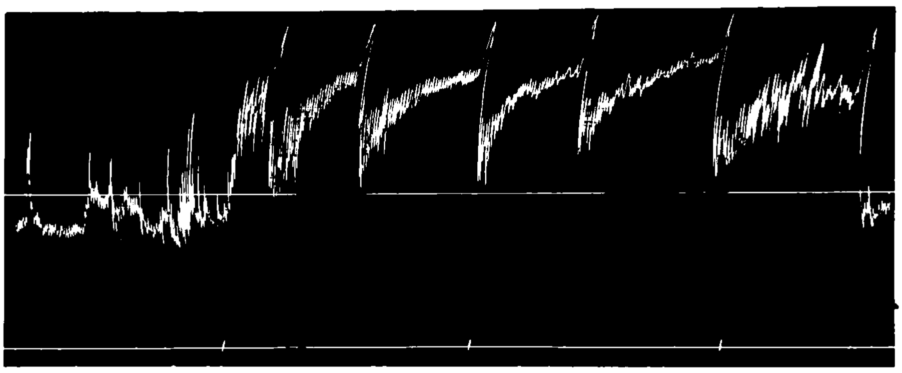
It was found that even small doses of atropine which did not cause complete ruminal paralysis resulted in complete inhibition of the eructation reflex. This is illustrated in Fig. 18.

As many poisonous plants are known to contain atropine, their presence in the pasture or hay might well result in outbreaks of acute bloat.

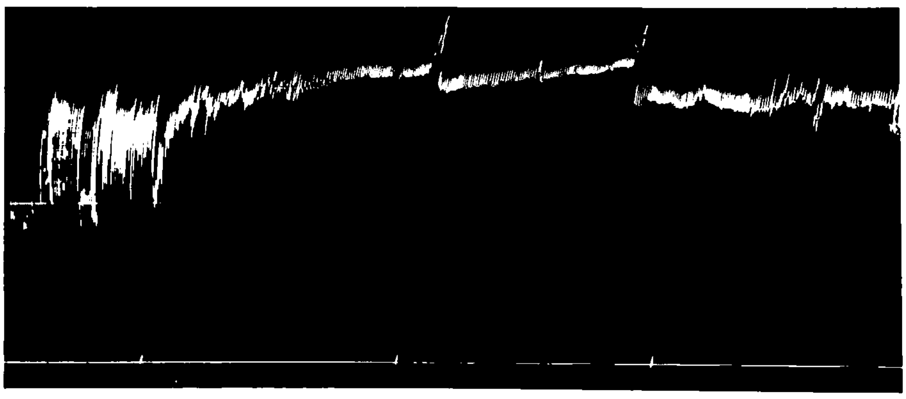
The Effect of K.C.N. on Eructation Efficiency in sheep.



Normal Eructation.



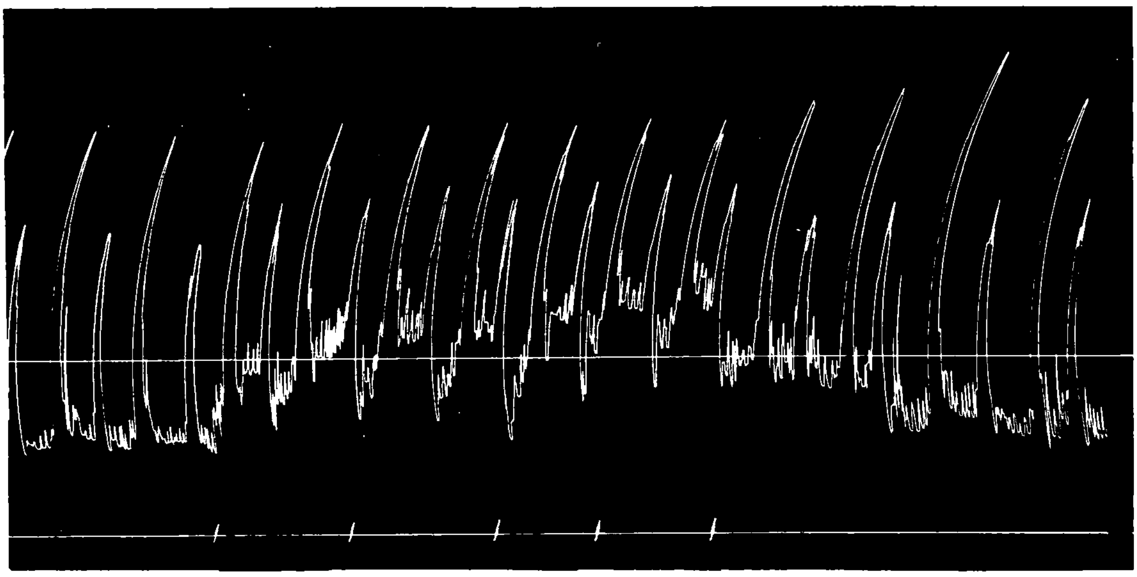
Eructation 5 mins. after dosing 150 mgm. KCN.



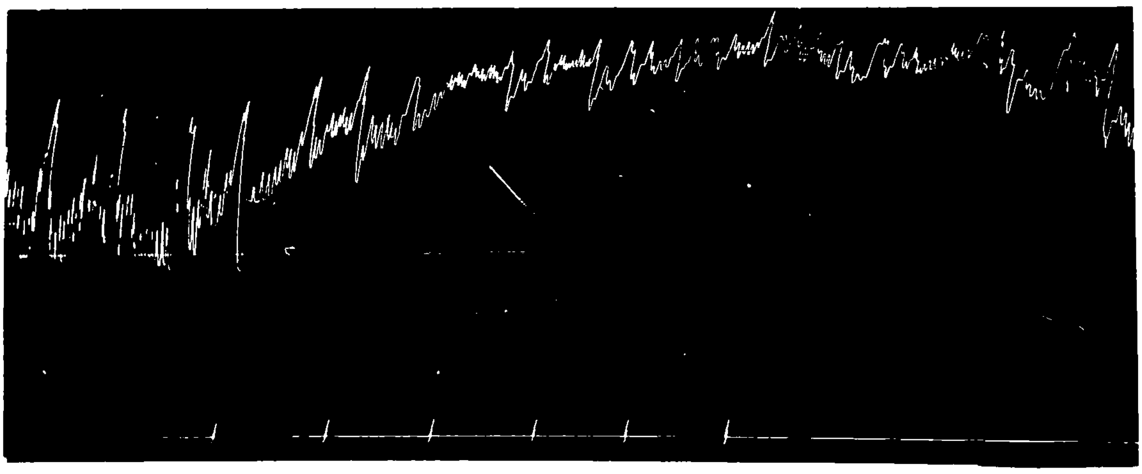
Interference with Eructation 5 mins. after dosing another 50 mgm. KCN. (Total dosage 200 mgm. KCN.)

FIG. 17.

The Effect of Atropine on Eructation Efficiency in Sheep.



Normal Eructation



Interference with Eructation 20 mins. after Subcutaneous injection of 30 mgm. atropine sulph.

FIG. 18.

(c) Histamine.

In 1942 Dougherty showed that the intravenous injection of histamine caused ruminal paralysis and suggested this as a possible factor in the etiology of acute bloat. Furthermore, large amount of histamine (.9 to 2.4 mgms. per 100 c.c.) were found in the ruminal ingesta of steers that had died of bloat. The histamine content of the ruminal ingesta was found to be increased on a high protein diet.

As shown in Fig. 19 the intravenous injection of 2 mgms. of histamine into a sheep completely inhibited all ruminal movements and eructation.

Clark (unpublished report) dosed up to 250 mgms. histamine into the rumen with no effect on ruminal motility. This would indicate that under certain conditions the histaminase activity of the ruminal contents is exceedingly high. On the other hand, the presence of free histamine in ruminal ingesta, found by Dougherty, would indicate that this is not always so.

(d) Adrenalin.

It has been shown by Dougherty (1942) that adrenalin causes marked depression both in strength and speed of ruminal contractions in cattle.

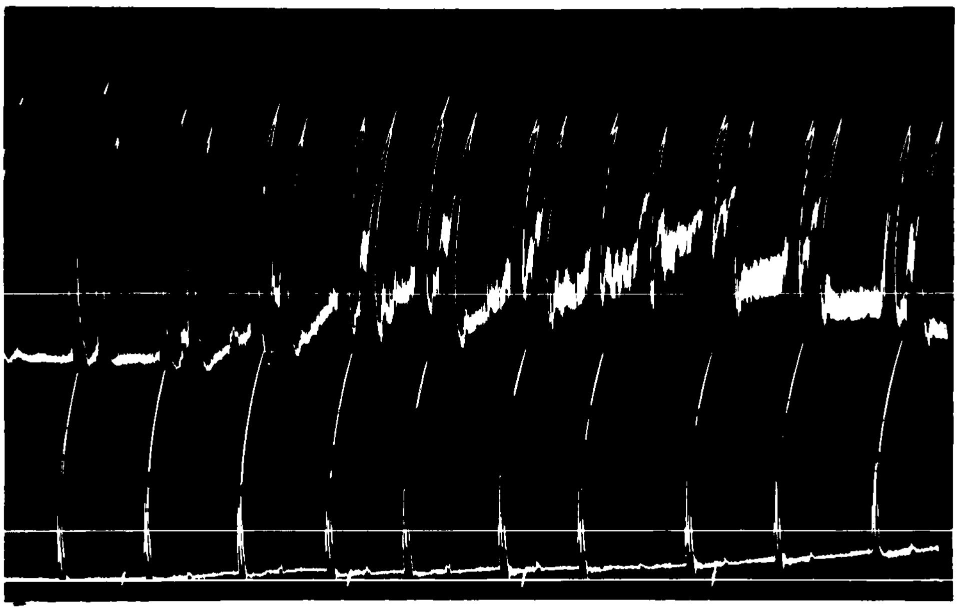
In the present series of experiments the intravenous injection of 1 c.c. adrenalin hydrochloride (1:1000) into sheep was found to cause varying degrees of depression and even total paralysis of rumino-reticular activity, lasting for at least 30 minutes. Susceptibility to adrenalin appeared to be very variable even in the same animal. Eructation was inefficient during the period of depression of ruminal motility. This is illustrated in Fig. 20.

From this finding it would be logical to assume that the liberation of adrenalin during excitement would tend to inhibit the eructation reflex and so contribute to the occurrence of bloat in conjunction with other factors. This would

The Effect of Adrenaline
on Eructation Efficiency in Sheep

A

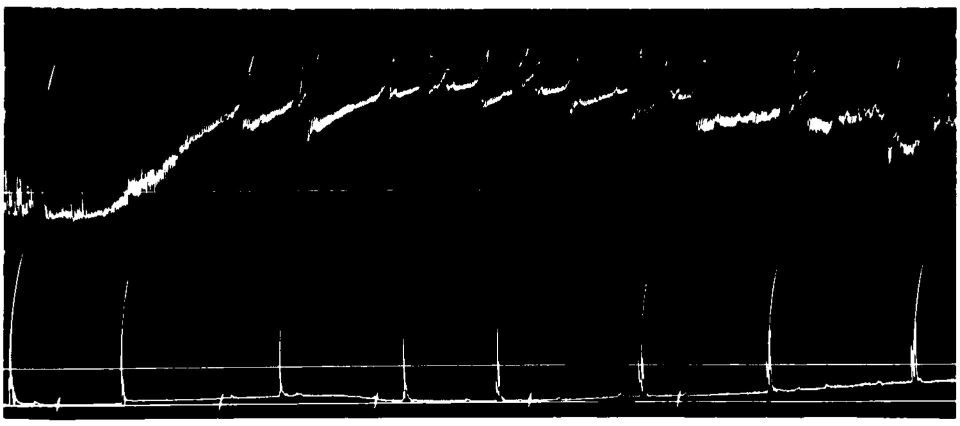
B



Normal Eructation
A : Ruminal Motility . B : Reticular Motility .

A

B

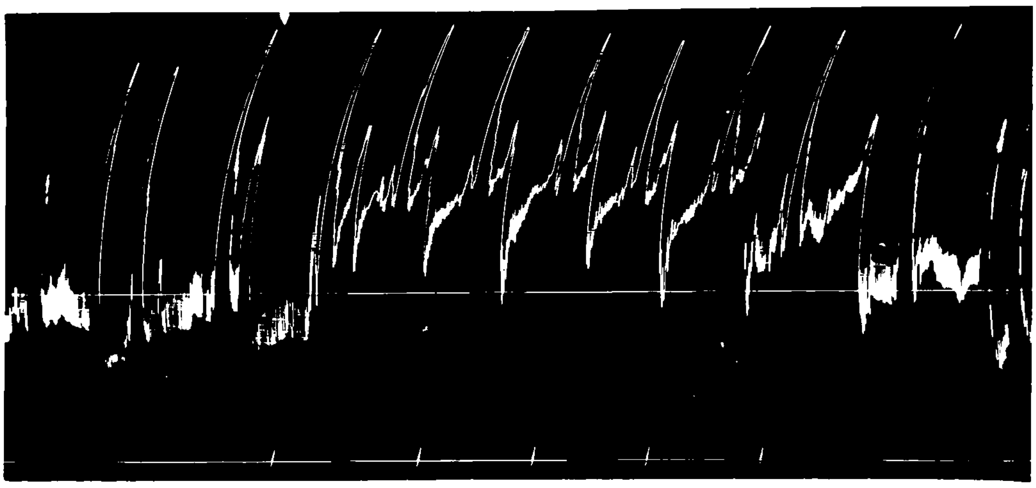


Eructation after 1c.c. Adrenaline hydrochloride
(1 : 1000) injected intravenously .

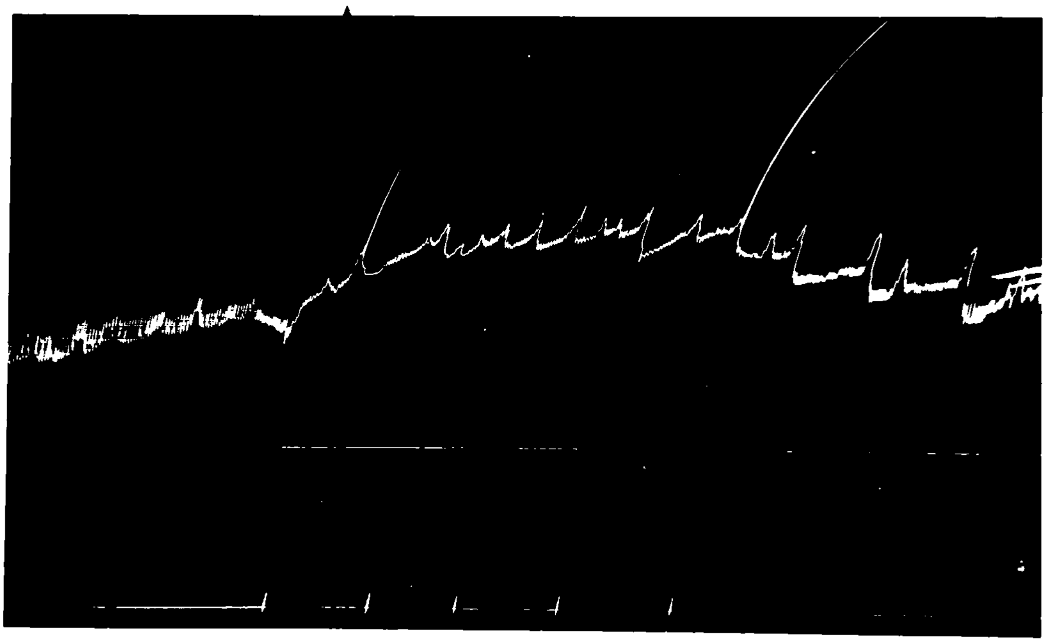
A : Rumen motility : note inefficient eructation .
B : Reticular Motility : note temporary inhibition and recovery coinciding with return of eructation efficiency

FIG. 20.

The Effect of Histamine on Eructation Efficiency in sheep.



Normal Eructation



Interference with Eructation after intravenous injection of 2mgm. Histamine.

FIG. 19.

be a parallel to the well-established inhibition of the "milk let-down reflex" under similar conditions and also caused by adrenalin.

(2) Those causing Hyper-motility.

(a) Carbamylcholine chloride (Carbachol).

The use of carbachol for the treatment of bloat has frequently been advocated, In the author's opion this is an exceedingly dangerous procedure if only because of the inhibition of an already embarrassed circulation.

Duncan (1951) showed that carbamylcholine chloride causes complete inhibition of the reticulum apart from increased tone and frequency of ruminal contractions. This has subsequently been confirmed by the present author. The tracings reproduced in Fig. 21 show the effect of carbachol on rumino-reticular motility. As can be seen, reticular contractions are completely inhibited. The mixing movements of the rumen (marked M on the tracings) are increased in rate but actually reduced in strength, whereas the eructation contractions (marked E) remain unaffected.

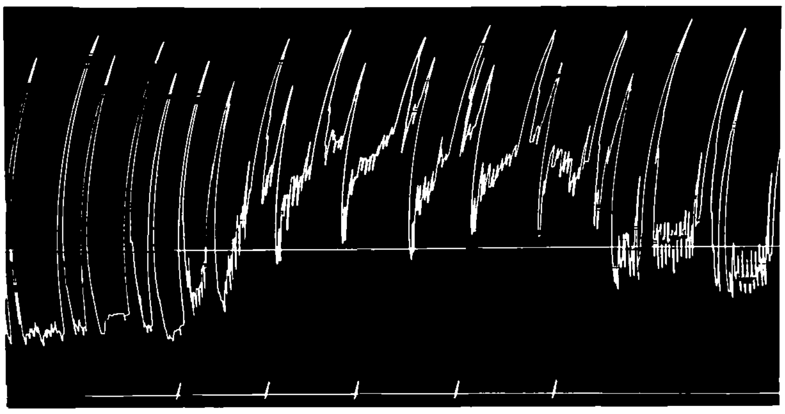
As shown in Fig. 22 even small doses of carbachol cause spasm of the ruminal musculature and interference with eructation. This effect frequently leads to spontaneous bloating. Acute bloat has been seen to occur in cattle following the administration of carbachol in the dosage recommended by the makers. (Clark personal observations). The interference with eructation is largely due to the inhibition of the reticulum and the spastic contractions of the rumen. This results in abolition of the co-ordinated movements required for eructation.

On these grounds the use of carbamylcholine in acute bloat would appear to be completely contra-indicated.

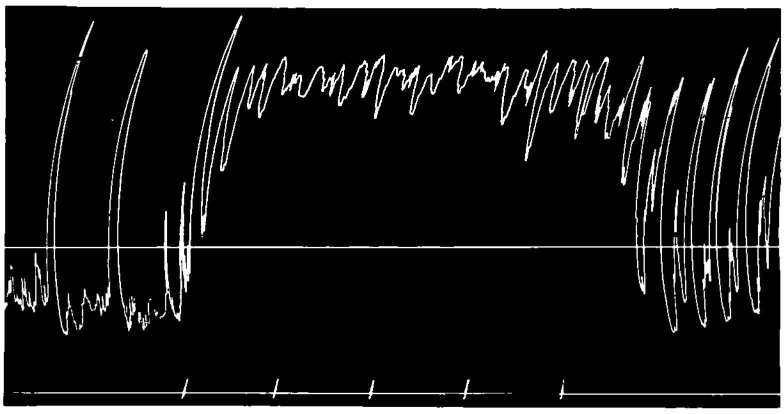
(b) Veratrine.

Wester (1935) recommended the use of veratrine as a ruminatoric and Schmidt (1933) recommended it's use in cases

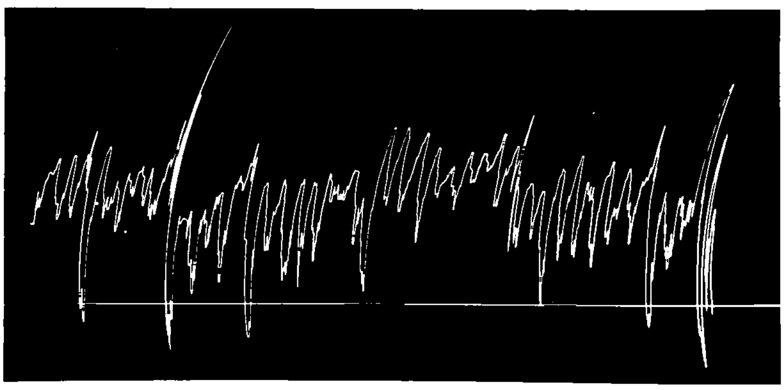
The Effect of Carbachol on Eructation Efficiency in Sheep.



Normal Eructation.



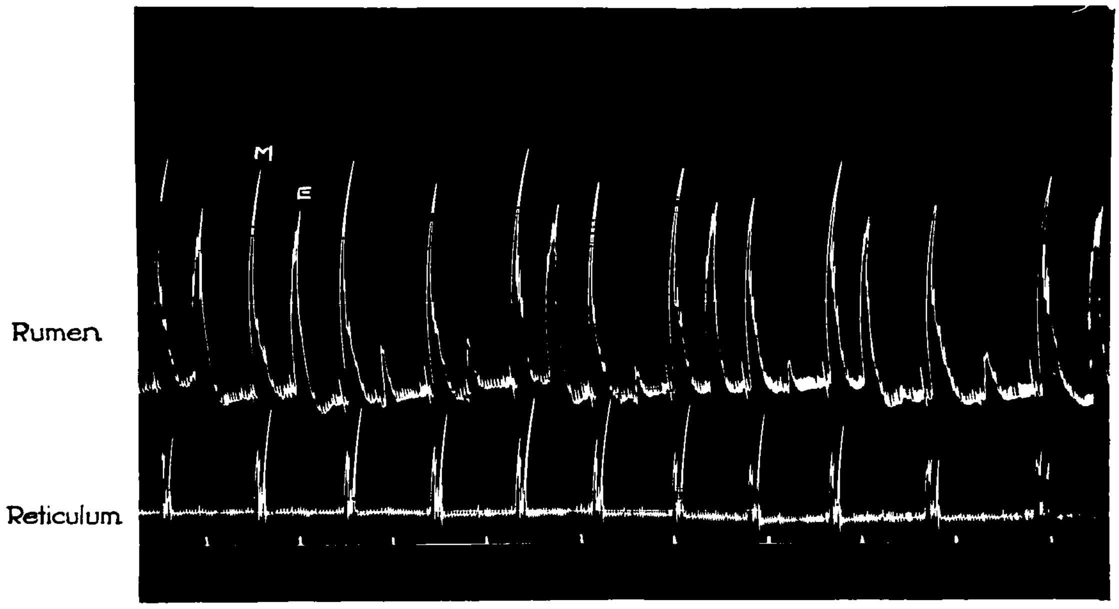
Interference with eructation 30 mins. after subcutaneous injection of 1mgm. Carbachol.



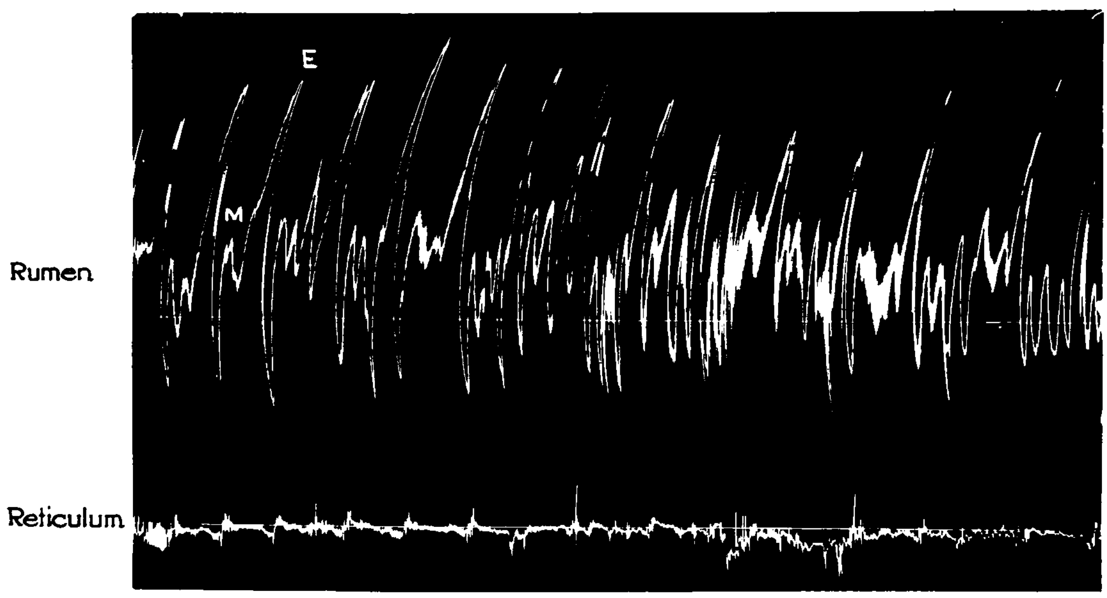
Spontaneous rise in intra-ruminal pressure, and interference with eructation 40 mins. after subcutaneous injection of 1mgm. Carbachol.

FIG. 22.

THE EFFECT OF CARBAMYLCHOLINE CHLORIDE ON RUMINO-RETICULAR MOTILITY IN THE SHEEP.



Normal Motility.



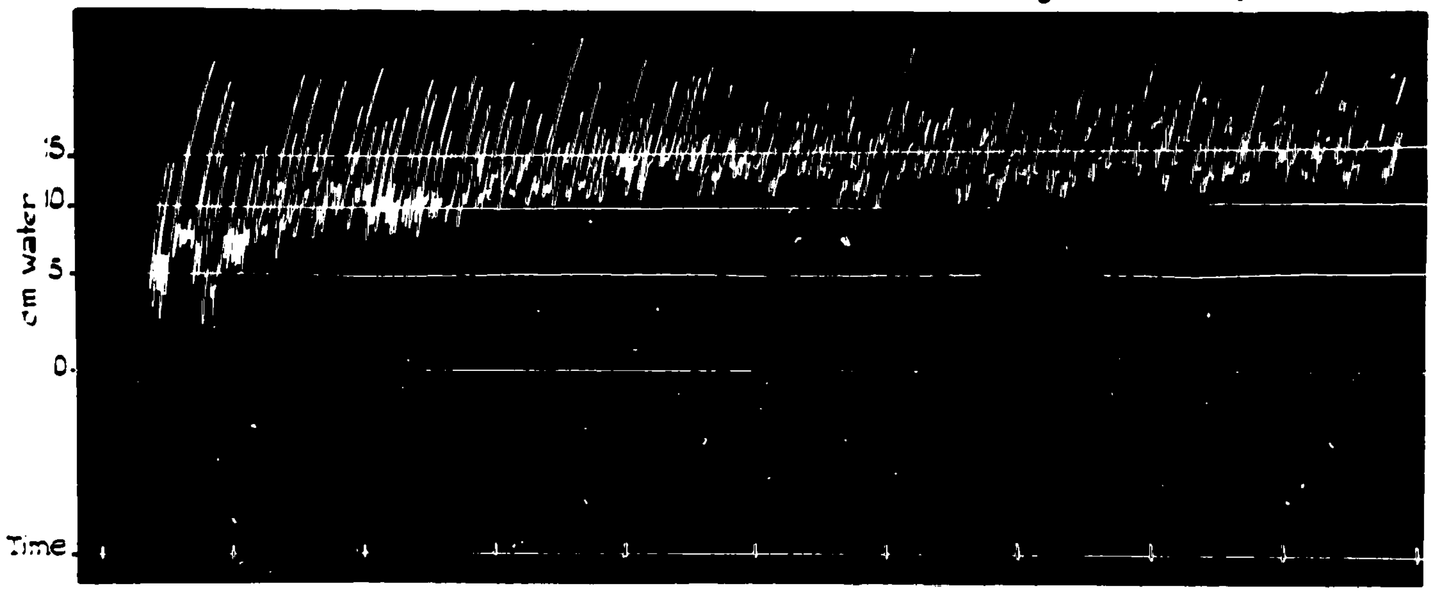
5 minutes after 1 mgm. Carbachol subcut.

Note : Inhibition of reticular contractions .

FIG. 21.

FIG. 23.

The Effect of Veratrine on Eructation Efficiency in Sheep.



Spontaneous bloat after intravenous injection of 10mgm. Veratrine hydrochloride.
Rumen full

of over-filling of the rumen, tympanites and foreign body obstruction of the oesophagus in cattle.

In the present series of experiments it was found that the intravenous injection of 10 mgms. veratrine hydrochloride into a sheep caused acute ruminal spasms and spontaneous bloat. (See Fig. 23). Doses of 5 mgms. resulted in ruminal spasm and interferences with eructation in spite of the fact that reticular motility was not inhibited. Smaller doses had no visible effect.

The use of veratrine in bloat, especially with an overloaded rumen, must therefore be condemned.

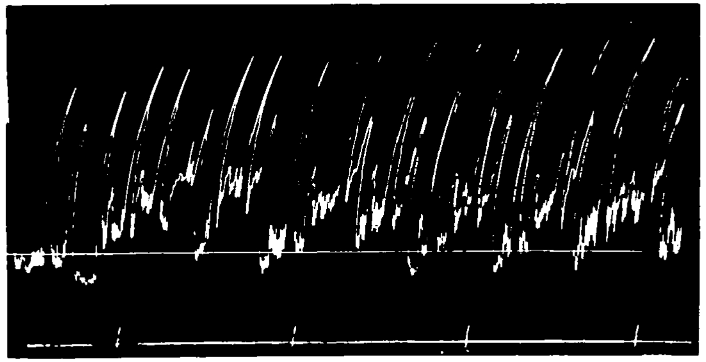
NOTE.

Experiments have shown that the eructation reflex itself is not affected by temperature changes in the rumen brought about by the introduction of iced water. The reflex was also unaffected by the forced introduction of a mixture of air plus 60% Carbon dioxide and 1% hydrogen sulfide.

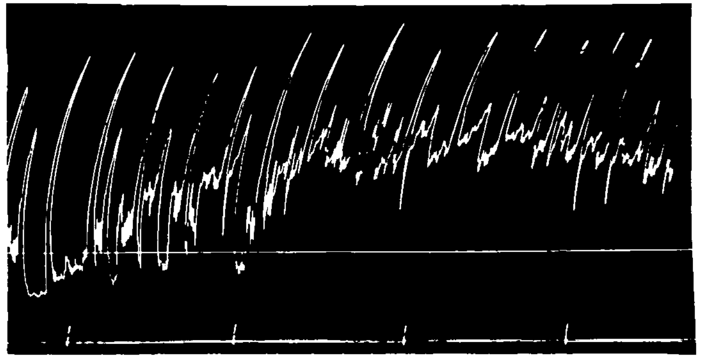
Fig. 2

THE EFFECT OF CONSISTENCY OF THE RUMINAL INGESTA ON GAS RETENTION

I : Ruminal Ingesta 'thick' and 'glutinous'. Consistency Index 42.

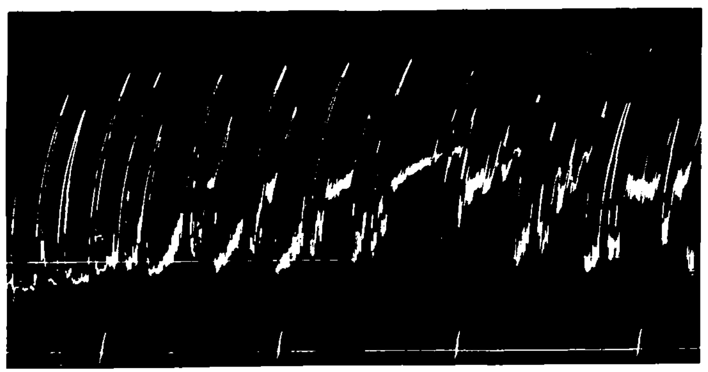


Normal eructation of free air introduced above the ruminal mass.

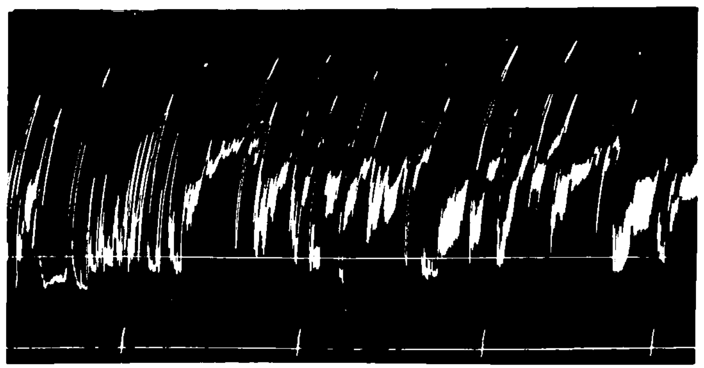


Interference with eructation due to retention of air introduced deeply into the ruminal mass.

II : Ruminal Ingesta watery. Consistency Index 9.



Normal eructation of free air introduced above the ruminal mass.



Normal eructation due to free escape of air introduced deeply into the ruminal mass.

III. THE SIGNIFICANCE OF REFLEX SALIVATION IN RELATION TO FROTH FORMATION AND ACUTE BLOAT IN RUMINANTS.

The successful use of surface tension agents in the treatment of acute bloat, (Clark (1950) and Quin, Austin and Rattclif (1949)) - has confirmed the importance of frothiness of ruminal ingesta in this condition, a subject of much controversy in the past. In their discussion on frothy bloat Cole, Huffman, Kleiber, Olson and Schalk (1945) do not appear to be convinced of its validity. Various workers, Weaver ([illegible]), McCandlish (1937), Dougherty (1942), Olson (1942), Quin (1943) and Clark (1948) on the other hand, have reported the existence of frothy ruminal ingesta in cases of bloat on green legumes. Kick, Gerlaugh and Schalk (1937) also believe that frothiness is the factor responsible for bloat in cattle fed corn in the feed-lot.

McCandlish (1937) supported by Olson (1942) and Quin (1943) incriminated saponins in lucerne as being responsible for frothing. It is difficult, however, to explain all the manifestations of acute frothy bloat on the basis of the saponin theory, with the result that the pathogenesis of this condition has remained unsettled.

Clark and Weiss (1952) have recently demonstrated the existence of a salivary reflex initiated by mechanical stimulation of the mucous membrane of the fore-stomachs. The significance of this reflex in relation to froth formation and bloat is described in this section.

Method:

Six Merino sheep with permanent ruminal fistulae were each given 4000 grams freshly cut green lucerne daily, and the following data were collected over the experimental period:- The consistency of the ruminal ingesta of each sheep before feeding; the degree of bloat and the type and consistency of the ruminal ingesta two hours after feeding.

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The type of lucerne fed daily and its origin was also noted.

Results:

I. The relation between consistency of ruminal ingesta and the occurrence of frothiness and bloat.

The ruminal ingesta of sheep fed exclusively on green lucerne has a tendency to foam, but the type of foam formed was found to be directly dependent on the consistency of the ingesta. When the ruminal content was watery, the gas-bubbles rose freely to the surface to form a layer of unstable free foam on the top. As the consistency increased there was a greater tendency for the gas-bubbles to become entrapped in the thick viscid material, causing the ingesta to rise up into a frothy mass.

The data on one of the sheep, collected over a period of 19 days are given in Table 3. Similar results were obtained from the other experimental animals. (See Appendix IIM). A summary of the results is given in Table 4. The degree of bloat was rated arbitrarily but it should be mentioned that it is extremely difficult to determine the exact degree of bloat in sheep with fistulae as some leakage of gas invariably takes place. Under normal circumstances the degree of bloat would have been much greater than that actually encountered.

Table 3.

The relation between consistency of ruminal ingesta and the occurrence of frothy bloat as determined by the physical condition of green lucerne. (Details of one individual sheep).

Type of Lucerne	Days	Before feeding: consistency index	After feeding: consistency index	After feeding: Type of ingesta	After feeding: Degree of Bloat
Flowering stalky small leaves	1	21.6	7.2	Watery with small amount of free foam on top	Nil
	2	31.2	7.5		Nil
	3	30.6	5.8		Nil
	4	45.0	7.8		Nil
	5	35.2	6.0		Nil
	6	-	9.3		Nil
	7	24.0	9.0		Nil

Table 3 (cont.)

Type of Lucerne	Days	Before feeding: consistency index	After feeding: consistency index	After feeding: Type of ingesta	After feeding: Degree of Bloat
Crisp succulent pre-bloom with large leaves	8	50.0	33.6	Large amount of intermixed tenacious froth.	Severe
	9	38.4	50.0		Marked
	10	62.5	39.1		Marked
	11	45.0	66.0		Marked
	12	45.0	15.0	Watery with free foam on top	Nil
	13	70.0	45.0	Large amount of intermixed tenacious froth	Marked
	14	38.5	60.0		Marked
	15	70.0	75.0		Marked
	16	60.0	69.0		Marked
Stalky etc.	17	75.0	10.0	Watery with free foam on top	Nil
Crisp succulent etc.	18	66.0	45.0	Large amount of intermixed tenacious froth	Marked
	19	36.0	90.0		Marked

Table 4.

The relation between consistency of ruminal ingesta and the occurrence of frothy bloat as determined by the physical condition of green lucerne. (Summary of results).

Days	Type of Lucerne	Number of sheep used	Number of sheep showing frothy bloat	Average consistency of ingesta: Before Feeding	2 Hrs. after feeding: Bloated sheep	2 Hrs. after feeding: non-bloated sheep
1	Flowering stage stalky with small sparse leaves.	6	0	46.3	-	7.3
2		6	0	43	-	7.6
3		6	0	44.1	-	5.7
4		6	0	50.3	-	8.2
5		5	0	37.4	-	8.2
6		5	0	38.8	-	7.6
7	Old hard stems present	4	0	42	-	14.3

62/...

Table 4 (cont.)

Days	Type of Lucerne	Number of sheep used	Number of sheep showing frothy bloat	Average consistency of ingesta: Before feeding	2 Hrs. after feeding: Bloated sheep	2 Hrs. after feeding: Non-bloated sheep
8		6	5	68	63.9	9.0
9	Pre-flo-	6	5	36.6	92.8	14.0
10	wering	6	4	50	63.8	14.8
11	stage,	6	5	67.5	119.8	12.5
12	crisp	6	4	67.3	50.2	16.5
13	succulent	6	5	64.3	80.4	12.5
14	with lar-	6	5	43.5	55.1	13.0
15	ge leaves	6	6	94.6	97.6	-
16	Old dry stems absent.	6	6	66.8	68.8	-
17	stalky etc.	6	0	69	-	12.1
18	succulent etc.	3	3	97.1	47.5	-

These results clearly show that whenever the ruminal ingesta was thick and viscid, with a high consistency index after feeding, frothing was marked and bloat occurred. Animals with a watery ingesta and a low consistency index did not bloat.

To show how frothing of ruminal ingesta, with a high consistency index, interferes mechanically with eructation, air was introduced artificially into the rumen of one sheep by the method described previously. Air was first introduced above the ruminal mass by passing the air inlet only just through the fistula stopper, in order to ascertain whether eructation could take place normally. The air inlet was then pushed deeply into the ruminal contents and air again introduced at the same rate. This procedure was followed in the same sheep when the ingesta had a consistency index of 42 and again two hours after feeding when the ingesta was reduced to a watery consistency with an index of 9.

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The tracings reproduced in Fig. 24 show the results. With the ingesta viscid and thick, tracing A shows that free air can be eructated efficiently, but when the air was bubbled through the ruminal mass there was marked interference with eructation as shown in tracing B. Dougherty (1941) also found, during one air-insufflation experiment on a cow, that it took much less air to increase the intraruminal pressure when the air was forced through the ruminal mass by an extension on the pressure plug, than when air was forced into the top part of the ruminal cavity. Eructation was also more difficult. This was undoubtedly due to the ingesta rising up into a frothy mass. This has the same effect as over-filling of the rumen by increasing the distance between the free gas and the cardia, thus mechanically interfering with eructation. On the other hand tracings D and C show that no such interference with eructation took place when air was bubbled through watery ingesta.

II. <u>Variations in consistency of ruminal ingesta and the effect of the type of lucerne</u>.

Clark and Weiss (1952) have recently demonstrated a salivary reflex in sheep and goats initiated by mechanical stimulation of the cardiac region of the fore-stomachs, causing a four-to-five-fold increase in salivary flow.

It is evident from the data in Tables 3 and 4 that the ruminal ingesta of the sheep on green lucerne showed marked variations before and after feeding. The ingesta invariably had a high consistency index before feeding. This may be explained by the absence of sufficient coarse material in the rumen to stimulate a continuous reflex salivary secretion.

The consistency of the ruminal ingesta and the occurrence of frothy bloat after feedings, was shown to be influenced by the type of lucerne fed. It was found that bloat, caused by frothing of thick, viscid ruminal ingesta, occurred immediately on feeding succulent, leafy lucerne in the pre-flowering stage of growth. When mature stalky lucerne was fed, the ruminal ingesta immediately reverted to a watery consistency even in the absence of available drinking water, and bloat ceased to occur. The conclusion is justified that the rapid reduction in consistency of the ruminal ingesta after feeding stalky lucerne, was due to reflex stimulation of salivary secretion initiated in the fore-stomachs by the physical character of the feed. It was also noted that ingestion of this type of lucerne was slow, with the result that proportionately more saliva is secreted per given weight of food.

The occurrence of bloat on the succulent lucerne is ascribed to the lack of coarse material and consequent diminished reflex salivary secretion. The rapid rate of feeding observed in the case of this type of lucerne, contributed by causing a proportionately smaller amount of saliva to be secreted per given weight of feed.

The consistency of the ruminal ingesta therefore increased and, if gas-formation was adequate, the ingesta rose up into a tenacious frothy mass.

In order to prove further that the presence of coarse material in the rumen is the main stimulus for the copious salivary secretion encountered, 120 grams chopped grass hay was introduced directly through the fistula into the rumen of one sheep. The consistency index of the ingesta before introduction was 150; one hour later it was reduced to 12 despite the absence of drinking water. This undoudtedly proved that the reflex is far more important in controlling the consistency of the ruminal contents than reflexes initiated by the sense of taste, or the acts of chewing and swallowing.

Cole, Mead and Regan (1943) showed that bloat could be prevented by feeding coarse hay prior to lucerne pasturing.

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It was therefore decided to determine whether this protective action is due to reflex stimulation of salivary secretion. The sheep were divided into two groups of three each and fed succulent green lucerne. Each animal in Group I received in addition 400 grams chopped grass hay well mixed with the lucerne. The results are given in Table 5.

Table 5.

Days	Group 1-3 sheep fed succulent lucerne plus 400 grams grass hay mixed: Average consistency index of ruminal ingesta: Before feeding	Group 1: Average consistency index of ruminal ingesta: 2 Hrs. after feeding	Group 1: Number of sheep showing frothy bloat	Group 2-3 sheep fed succulent lucerne only: Average consistency index of ruminal ingesta: Before feeding	Group 2: Average consistency index of ruminal ingesta: 2 Hrs. after feeding	Group 2: Number of sheep showing frothy bloat
1	65.8	10.5	Nil	74.5	47.5	3
2	31.8	9.0	Nil	52.5	48.0	3
3	30.0	15.0	Nil	46.8	32.0	3

It can be seen that bloat did not occur in those sheep receiving grass hay in addition to lucerne and that the consistency index of their ruminal ingesta was low compared to the group receiving succulent lucerne only. In the latter group bloat occurred daily. In another experiment the sheep were given a choice of succulent lucerne and grass hay. This practice, however, did not prevent bloat completely, as the sheep did not eat any hay until a certain degree of bloat had developed. The consistency of ingesta was reduced and the bloat subsided within an hour of the animal taking the hay. As soon as distention of the rumen took place, the sheep refused to take further lucerne and showed preference for the coarse hay. This indicates a natural tendency to supply the roughage required to maintain reflex salivation and prevent bloat.

An example of the marked difference between the two types of lucerne used during the experiment is shown in Fig. 25.

FIG. 25.

Fig. 3

Showing the Difference between the Two Types of Lucerne used in the Experiment.

Specimen of the Succulent Bloat-producing Lucerne.

Specimen of the Stalky Lucerne on which Bloat could not be produced.

A specimen of the bloat-provoking lucerne is shown on the left. This was in the pre-flowering stage, approximately 18" high and exceptionally succulent and crisp with large, closely packed leaves. Contaminating weeds and old dry stems were absent. B shows a specimen of the lucerne on which bloat could not be produced. This was in the flowering stage approximately 12" to 15" high and stalky, with small sparse leaves. A fair amount of old, hard, dry stems was present. A noteworthy fact is that the succulent lucerne grew on heavy fertile soil, which retains moisture well. The stalky lucerne grew on light, sandy loam which is well drained. Both lands were irrigated regularly. It appears to be quite obvious that these factors influence the growth of lucerne and directly determine its bloat provoking potentiality.

In order to prove that frothy bloat in cattle on a non-roughage diet is associated with the consistency of the ruminal ingesta, the seven stall-fed bovines, mentioned before were used. These animals were all non-producing and varied in ages from 15 months to 4 years.

They were first fed a non-roughage diet on which bloat started to occur after two days in some of the animals. The animals were left until bloat was marked before the trocar was inserted to obtain ruminal ingesta for examination. It was noticed that, in all the bloated animals, a certain amount of free gas escaped from the canula before frothy ingesta started to exude.

The following feeding regime was followed with the non-roughage diet:

8 a.m. Freshly cut succulent green lucerne ad lib.

3 p.m. 6 to 7 lbs. dairy meal consisting of crushed yellow maize 65%, lucerne meal 10%, monkeynut meal 10%, bone meal 3½%, salt 1% and mineral mixture ½%.

Towards the end of the experiment the green lucerne became unsuitable with the result that the following change in the feeding regime had to be made:

8 a.m. Dairy meal 7 lbs. per animal.

3 p.m. Soaked good quality leafy lucerne hay ad lib.

For the roughage diet in the case of bovines Nos. 2, 3 and 4 the latter feeding regime was also used with the exception that coarse stalky green lucerne or hay was fed instead of the soaked hay. In the case of bovines Nos. 6 and 7 grass hay was fed ad lib throughout the day. The results are given in table 6.

Bovine No. 5 actually died of bloat after feeding the non-roughage diet for a week. Digestive disturbances was evident on post mortem examination.

The results show that bloat in bovines on a non-roughage diet is of the frothy type and is associated with thick, tenacious ruminal ingesta of a high consistency index. On a diet containing adequate roughage bloat does not occur and the ingesta becomes watery. These results are comparable with those obtained with sheep and can also be explained on the basis of reflex salivation.

The results also show the marked individual variation in susceptibility to bloat amongst the different bovines in the group. Animal No. 1 bloated repeatedly on the non-roughage diet whereas bovines No. 2, 6 and 7 failed to bloat on this type of diet.

Table 6.

Type of diet	Bovine No.	Bloated: Consistency of ruminal ingesta	Bloated: Type of ingesta	Non-bloated: Consistency of ruminal ingesta	Non-bloated: Type of ingesta
a) Nonroughage green lucerne and dairy mixture	1	60.0	Thick tenacious and frothy	-	-
		39.6		-	-
		54.0		-	-
	3	68.0	"	-	-
	4	66.0	"	-	-
	5	39.0	"	-	-
	7	-	-	16.8	watery
Dairy mixture and soaked lucerne hay	1	117.0	"	-	-
	2	-	-	14.0	watery
b) Roughage stalky green lucerne and dairy mixture	1	-	-	14.0	watery
	2	-	-	22.5	"
	3	-	-	14.0	"
	4	-	-	8.0	"
Dairy mixture and coarse lucerne hay	2	-	-	8.0	"
	3	-	-	8.0	"
	4	-	-	10.0	"
Grass hay only	6	-	-	7.2	"
	7	-	-	9.0	"

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DISCUSSION AND CONCLUSIONS.

It has been shown that eructation is a complex, co-ordinated reflex involving the rumen, reticulum, cardiac orifice and oesophagus. The role played by the fore-stomachs is to bring the free gas forward and downwards to the cardia.

Frothing of the ingesta reduces the amount of free gas present and so interferes mechanically with eructation. In the absence of frothing the efficiency of eructation at any given moment will, therefore, be determined by the balance between the efficiency of the rumino-reticular mechanism, on the one hand, and the relative positions of the gas and the cardia, on the other. The rumino-reticular mechanism has been shown to be influenced by various factors. The relative positions of the gas and the cardia depend on the degree of filling of the rumen and the posture of the animal, with frothing as an additional complication. The ability of the animal to clear the cardia for the free escape of gas via the oesophagus is the most important part of the rumino-reticular mechanism determining the efficiency of eructation, and has been shown to be influenced by mechanical factors such as over-filling and frothing, chemical and nervous factors.

Bloat is, therefore, an expression of an adverse balance between the efficiency of the eructation mechanism and the factors militating against it. In other words, if the efficiency of the reflex is kept constant, bloat may occur through over-filling or frothiness or a combination of the two. When the rumen is excessively filled, a lesser degree of frothing will be required to produce bloat. With a reflex impaired by any of these factors a correspondingly lesser degree of over-filling or frothiness may result in bloat. It is, therefore, apparent that bloat can occur under widely varying conditions and its appearance will more often

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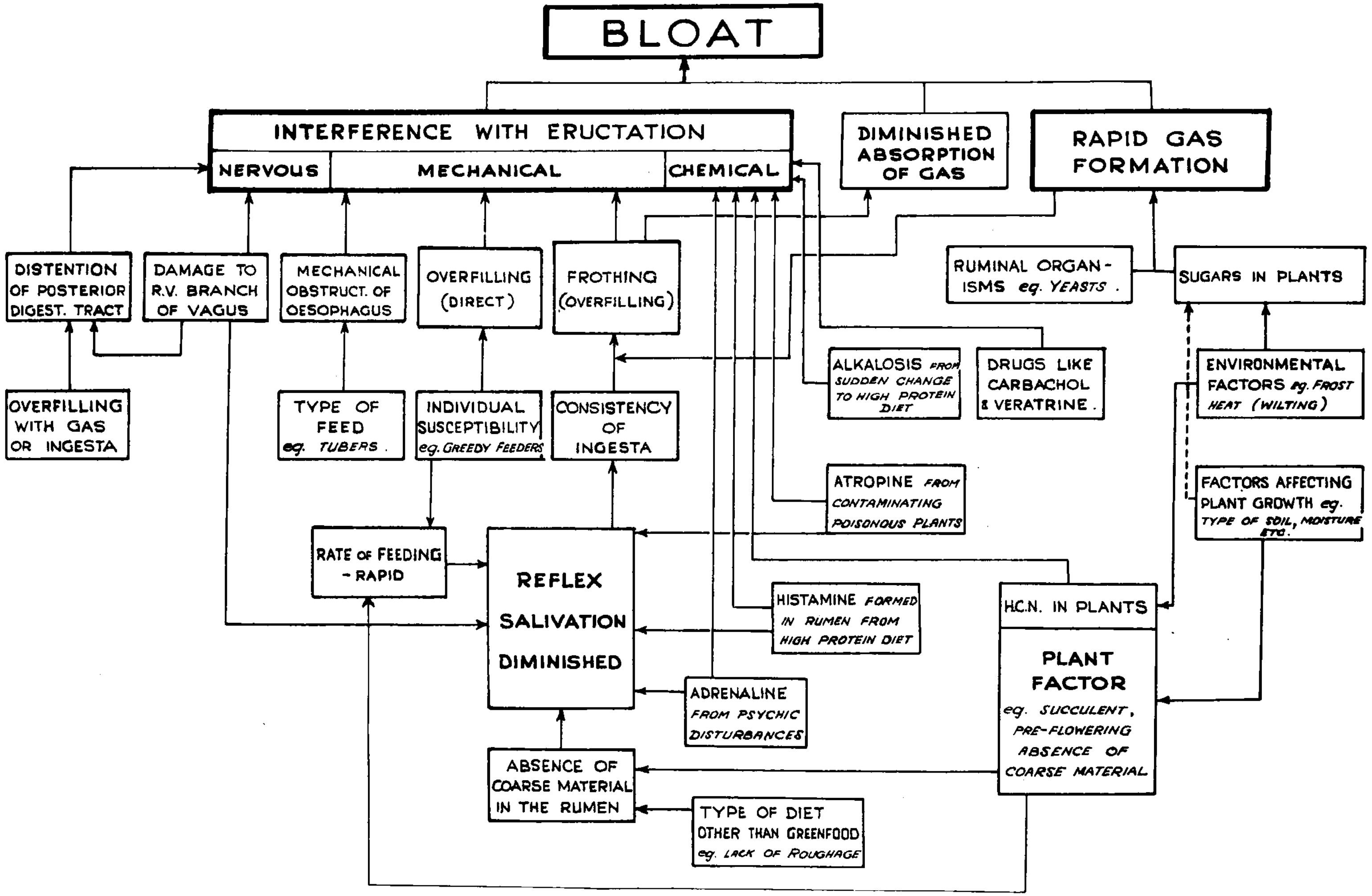
BLOAT
INTERFERENCE WITH ERUCTATION
NERVOUS
MECHANICAL
CHEMICAL
DIMINISHED ABSORPTION OF GAS
RAPID GAS FORMATION
DISTENTION OF POSTERIOR DIGEST. TRACT
DAMAGE TO R.V. BRANCH OF VAGUS
MECHANICAL OBSTRUCT. OF OESOPHAGUS
OVERFILLING (DIRECT)
FROTHING (OVERFILLING)
RUMINAL ORGANISMS eg. YEASTS.
SUGARS IN PLANTS
OVERFILLING WITH GAS OR INGESTA
TYPE OF FEED eg. TUBERS.
INDIVIDUAL SUSCEPTIBILITY eg. GREEDY FEEDERS
CONSISTENCY OF INGESTA
ALKALOSIS FROM SUDDEN CHANGE TO HIGH PROTEIN DIET
DRUGS LIKE CARBACHOL & VERATRINE.
ENVIRONMENTAL FACTORS eg. FROST HEAT (WILTING)
ATROPINE FROM CONTAMINATING POISONOUS PLANTS
FACTORS AFFECTING PLANT GROWTH eg. TYPE OF SOIL, MOISTURE ETC.
RATE OF FEEDING - RAPID
REFLEX SALIVATION DIMINISHED
HISTAMINE FORMED IN RUMEN FROM HIGH PROTEIN DIET
H.C.N. IN PLANTS
PLANT FACTOR eg. SUCCULENT, PRE-FLOWERING ABSENCE OF COARSE MATERIAL
ADRENALINE FROM PSYCHIC DISTURBANCES
ABSENCE OF COARSE MATERIAL IN THE RUMEN
TYPE OF DIET OTHER THAN GREENFOOD eg. LACK OF ROUGHAGE

depend on a combination of contributing or supplementing circumstances than on any single factor acting alone.

A schematic representation of the different factors which may contribute towards acute bloat is given in Fig. 26.

The experimental results clearly show that frothing of ruminal ingesta is the main cause of bloat in sheep on green lucerne, acting in the same manner as over-filling of the rumen, by mechanically interfering with eructation. In fact, there is convincing evidence, not only in the literature but also in the reports from farmers and veterinarians, (See Appendix I) that most cases of bloat on green feeds are of the frothy type. Cole et al (cited by Cole, Huffman, Kleiber, Olson and Schalk) (1945), however, claim that they have tapped a number of cows, bloated on lucerne pasture, without encountering a single case in which the free air space was absent. Taking these observations into account, Cole et al (1945) find it difficult to understand how frothing could cause bloat when a free air space exists. In the present author's opinion it is merely a matter of degree of frothing. In most of the cases of frothy bloat produced during the experiment, free gas escaped from the fistulae on opening. Only in a few cases did the ingesta froth to such an extent as to fill the whole rumen and exude from the fistulae on removal of the stopper.

Cole, Mead and Regan (1943) have shown conclusively that the feeding of coarse hay prior to lucerne pasturing prevents bloat; and the experiments of Mead, Cole and Regan (1944) proved that the incidence of bloat was much higher in cattle fed ground hay and grain, than in those fed unground hay and grain. These workers attributed the protective action of hay to their theory that coarse material is necessary to elicit the eructation reflex. The present author has shown previously that the physical state of the ruminal contents does not appear to affect the eructation reflex directly. The results now obtained, clearly show that the protective action of hay is due to reflex stimulation of salivary secretion, thus reducing the consistency of the ruminal ingesta and obviating froth formation.

Bell and Britton (1939) found that bloat was a serious problem on pastures with a pure stand or a very high percentage of clover, whereas it ceased to be a problem on certain pastures covered with more than fifty per cent of grasses. These findings can be explained on the basis of reflex salivation. A pure stand of succulent clover does not provide adequate stimulus for reflex salivary secretion, whereas grasses, especially the coarse-stemmed varieties, provide sufficient stimulus to prevent bloat. Mixing grasses with legumes, therefore, appears to be a feasible method of preventing bloat but, as pointed out by Cole et al (1945), the difficulty is to maintain a proper balance at all times.

Perhaps the greatest single factor responsible for the failure to elucidate the pathogenesis of bloat has been the difficulty encountered in reproducing the natural condition. Cole, Mead and Regan (1943), however, showed that certain essential conditions are necessary before bloat can be expected to occur. These are briefly summarized as follows:-

(1) The lucerne should be in an appropriate stage of development, e.g. crisp and succulent to allow for rapid feeding.

(2) Animals should be deprived of all hay and straw and the lucerne itself should be free of grasses, weeds and old, dry tough stems.

(3) The lucerne should have been provided with sufficient water to induce rapid growth.

(4) The green-feed should be fed as fresh as possible and not older than 24 hours. Dried alfalfa tops failed to produce bloat.

These observations are confirmed by the experimental results recorded above. Contrary to the interpretation of those authors, however, who ascribe the bloat-provoking

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capacity of this type of lucerne to a lack of sufficient coarse material to initiate the eructation reflex, it is maintained that the physical condition of the lucerne has a direct bearing on the occurrence of bloat through its action on reflex salivation. The rate of feeding of succulent lucerne appears to be an important factor. In accordance with reports by other workers (Mead, Cole and Regan (1944)) the occurrence of bloat could not be correlated directly with the amount of lucerne consumed. In the present trials (Appendix IIM) in many cases of bloat, the amount of lucerne eaten was actually less than that consumed by non-bloated sheep. Apart from individual differences amongst the sheep, a difference in the rate of feeding of the two types of lucerne was, however, noted. The amount of succulent lucerne consumed over a given period of time was much greater than the amount of stalky lucerne over the same period.

Apart from green-feed, frothy bloat can occur on any diet lacking in roughage. This has been proved by the experiments on cattle detailed above. The feeding of good quality leafy lucerne hay, especially if soaked in water beforehand, caused frothy bloat in several cases. due to the lack of sufficient roughage to stimulate the salivary reflex. Kick, Gerlaugh and Schalk (1937) reported frothy bloat in steer during the finishing-off period. Bloat started to occur soon after the amount of concentrates in the ration exceeded the amount of roughage. The cases of bloat in cattle on a non-roughage diet, which has been reported by Mead and Goss (1936) can also be explained on the same basis.

In the present author's opinion the presence of saponins in lucerne is also not the cause of bloat <u>per se</u>, but that it merely contributes towards the colloidal state of the ingesta favourable for foaming. Daily mechanical shaking of samples of expressed lucerne juice over a period

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of months, under different metereological conditions, showed no significant variations in the amount of foam produced daily.

Frothy bloat on green legumes frequently occurs in association with direct over-filling of the rumen. As pointed out by various workers, (Cole, Mead and Regan (1943), Mead, Cole and Regan (1944), Quin (1942) Clark (1950), Espe Jacobson and Cannon (1943), acute bloat is common amongst those animals with large appetites or greedy feeding habits. It is common experience that some cases of bloat cannot be relieved by anti-frothing agents only, but require other measures, such as elevation of the fore-quarters of the animal, in order to facilitate elimination of the gas.

The tracings presented in Fig. 27 show actual recordings of cases of frothy bloat in sheep on green lucerne. Both were injected intraruminally with anti-frothing agents immediately before recording, carefully avoiding escape of free gas via the fistula. In the one case, breaking of the froth resulted in efficient eructations which decreased intra-ruminal pressure. This was, therefore, a case of uncomplicated frothy bloat. In the other case, eructation remained inefficient despite the anti-frothing agent. Removal of 1700 c.c. ruminal ingesta improved eructation efficiency on artificial introduction of air. It proved that this was a case of frothy bloat complicated by direct over-filling. Although direct over-filling is dependent on the amount of feed consumed, froth formation is dependent on the nature of the feed. This is probably the reason why the occurrence of bloat cannot always be correlated with the amount of food and water consumed.

The occurrence of frothy bloat does not always depend solely on the type of feed, but contributory factors may play a role. Referring to Fig. 26, it can be seen that the liberation of adrenalin during psychic disturbances not only affects

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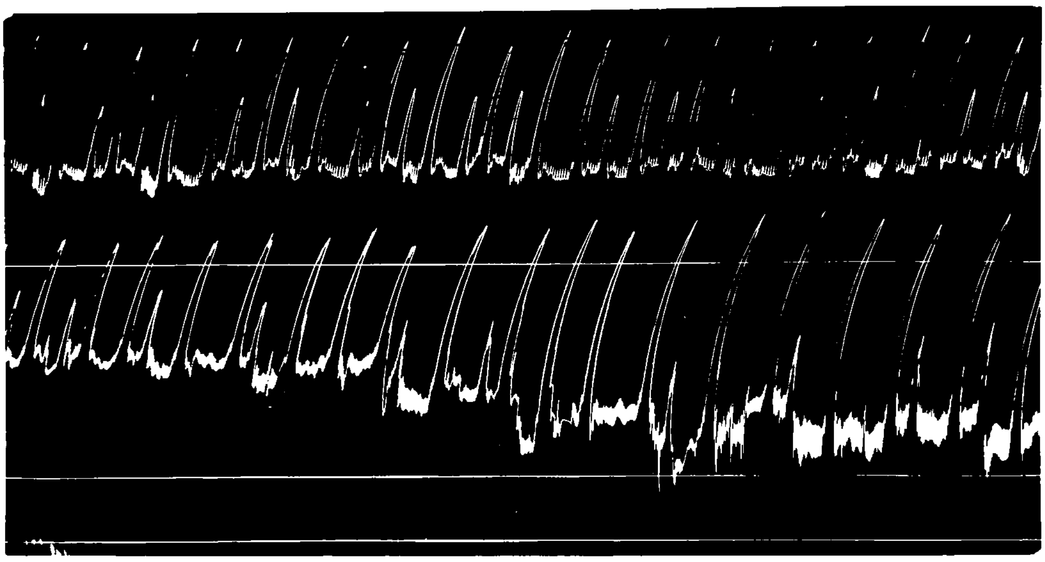
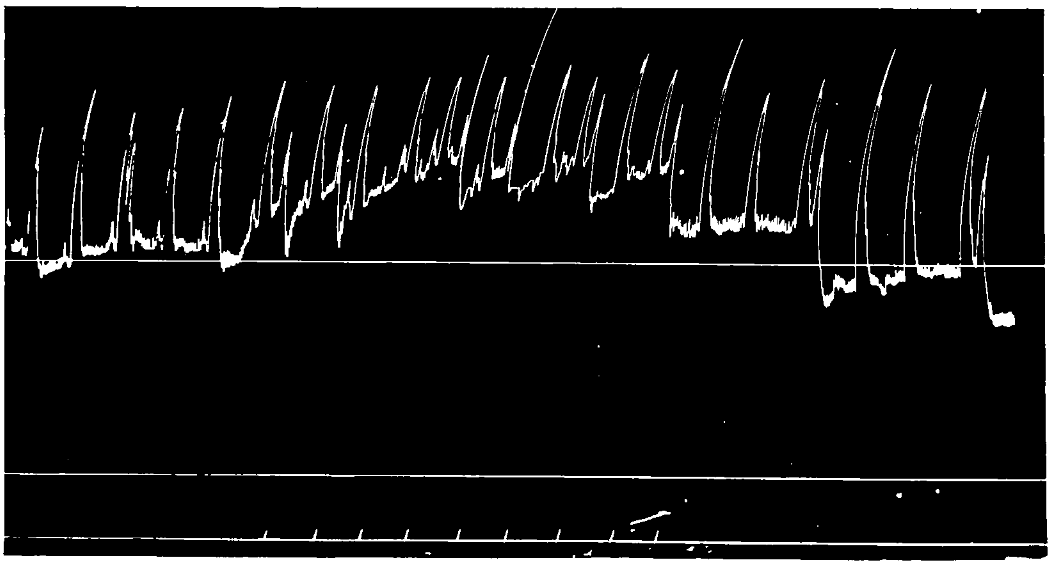
Spontaneous Bloat in Fistula. Sheep fed Frosted Green Lucerne.



Top. Sheep No. 6 : Inability to eructate after anti-frothing agent. (Rumen p.H. 6·1)
Bottom. Sheep No. 3 : Spontaneous recovery after anti-frothing agent. (Rumen p.H. 6·3.)



Sheep 6 : Normal eructation of artificially introduced air following removal of 1700 cc. ingesta. (Rumen p.H. 6·1)

Fig. 27.

the eructation reflex directly, but also diminishes reflex salivation, with consequent froth formation and further interference with the efficient elimination of gas. A striking example of the role that psychic disturbances can play in the pathogenesis of acute bloat has been encountered. Amongst a particular herd (See Appendix III), of high-producing dairy cows, sporadic cases of frothy bloat occurred daily. These animals were fed chopped and wetted good quality lucerne hay in addition to their high-production ration. During a certain period a mass outbreak of frothy bloat occurred amongst the herd, coinciding with the change-over from hand to machine milking. The bloat responded to treatment with anti-frothing agents. There was no change in feed or feeding routine, and careful investigation could reveal no possible reason for the large-scale outbreak of bloat other than that inevitable disturbance of the animals, which was simultaneously reflected in a sharp drop in milk yield.

Although the present author does not regard histamine formation in the rumen as a common contributory factor in the pathogenesis of acute bloat on legumes, due to the histaminase activity of ruminal ingesta, it is felt that histamine may under certain conditions play a role. Apart from the direct effect on the eructation reflex, histamine will also tend to diminish reflex salivation and therefore cause froth formation.

By making use of the method described by Clark and Weiss (1952) it has been shown that the intravenous injection of 2 mgm. histamine into a goat decreased the resting salivary flow of both parotids from 92 to 24 drops per minute. Atropine has the same effect, so that the ingestion of poisonous plants, which contain this principle, may also lead to frothy bloat.

Damage to the vagi nerves may similarly result in sporadic cases of acute bloat. This type of lesion, how-

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ever, usually tends to produce chronic bloat. Hoflund (1940) has described bloat in natural and experimental cases of interference with the nerve sypply to the fore-stomachs.

The frothy bloat encountered in the one experimental goat mentioned before, resulted from cutting the afferent nerve supply necessary for eructation, as well as the afferent fibres of the salivary reflex.

Although hydrocyanic acid has been proved to be present in clover (Evans and Evans (1949)) and various poisonous plants (Steyn (1934)), it has not been possible to isolate hydrocyanic acid from lucerne. Steyn (personal communication), however, states that he has isolated large amounts of hydrocyanic acid from lucerne under certain environmental conditions and van der Walt (1944) found 2 mgm. hydrocyanic acid per 100 grams of the fresh plant material in a certain sample of lucerne.

Although the present author has failed to demonstrate the presence of hydrocyanic acid in the cases of frothy bloat produced, it is nevertheless felt that hydrocyanic acid may be an important contributory factor under certain conditions. A point which should receive due consideration is the possibility of contamination of green-feed pastures or baled hay by other plants, already mentioned, which contain cyanogenetic glucosides or toxic principles which cause inhibition of ruminal motility.

Wetting of legumes has frequently been mentioned as an etiological factor, although, as pointed out by Cole et al (1945), bloat also occurs in the absence of those conditions. Espe, Jacobson and Cannon (1943) believe that wetting of legumes results in an increased rate of consumption of the feed, and decreased salivation. These factors have been shown to be important in the pathogenesis of frothy bloat.

The relation between rainfall and bloat has been fully discussed by Cole et al (1945) in their review.

It is evident that climatic conditions, which favour plant growth, determine its succulence and therefore its bloat-producing ability.

Environmental conditions, such as frost or heat, which cause wilting have frequently been mentioned as etiological factors. The physiological reaction of most plants to adverse conditions, such as frosting or wilting, is to hydrolyse starches to sugars. According to Henrici (1949) frost and drought cause a decrease in starch values and an increase in sugar values of the aerial parts of lucerne. This occurs through hydrolysis and translocation of starch, which takes place rapidly at low temperatures especially during the night. Both Quin (1942) and McAnnally (1943) found that gas formation is increased by the addition of sugars to fermenting ruminal ingesta, and Quin (1943) showed that the occurrence of bloat can be correlated with increased sugar values in lucerne.

Although Mead, Cole and Regan (1944) showed that bloat can be produced under varying environmental conditions, provided the lucerne is in the appropriate condition and stage of development, the present author is of the opinion that environmental conditions, such as frost and drought, can increase the incidience of bloat by causing an elevation of the sugar content of the plants. If other etiological factors are favourable, the increased gas production, resulting from fermentation of these sugars, will accentuate froth formation and the possibility of bloat.

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SUMMARY.

The eructation reflex in sheep and cattle, and factors affecting it, have been studied mainly by the method of forced air insufflation and direct recording of intraruminal pressure.

I. THE NORMAL ERUCTATION REFLEX.

(1) Eructation is a complex, co-ordinated reflex involving the rumen, reticulum, cardiac orifice and the oesophagus. It consists essentially in the movement of free gas from the dorsal rumen, forwards and downwards to the cardia.

This is accomplished by:-

(a) A forward wave of contraction of the ruminal musculature (as distinct from the usual backward cycle of contractions).

(b) Opening of the cardiac orifice which, it is argued, is brought about by the contraction of the lateral and medial pillars of the rumino-reticular fold.

(c) The clearing of the cardia of fluid ingesta effected by relaxation of the reticulum.

The importance of this phase depends on the degree of filling of the rumen.

The main stimulus for eructation is gas pressure in the posterior dorsal sac of the rumen.

(2) From variations found amongst the individual experimental animals it is argued that the efficiency of the reflex may depend on hereditary factors.

II. FACTORS AFFECTING THE EFFICIENCY OF THE ERUCTATION REFLEX.

The factors affecting the reflex discussed are:-

(1) Mechanical.

(a) Obstruction of the oesophagus.

(b) Frothing of the ingesta.

(c) The degree of filling of the rumen and posture.

Over-filling of the rumen was found to hinder eructation by increasing the distance between the free gas and cardiac orifice. Elevation of the hind-quarters

had a similar effect, while elevation of the fore-quarters mitigated the effects of over-filling. Animals with a non-functioning reticulum were found to be particularly susceptible to over-filling.

(2) Alkalosis.

In the absence of other factors, the efficiency of eructation was found to vary inversely with the degree of alkalosis as determined by the CO_2-combining power of the blood. This was mainly due to reticular paralysis.

(3) Abdominal Vagotomy.

Section of the right ventral branch of the vagus caused abomasal distension and chronic tympany, again mainly due to inhibition of reticular activity. Section of the left dorsal branch diminished the strength of ruminal contractions and eructation efficiency for the first three weeks with subsequent partial recovery.

(4) Reflex inhibition from the Posterior Digestive Tract.

Distension of either the abomasum and caecum reduced the eructation efficiency again by inhibition of the reticulum.

(5) The effect of Drugs influencing Ruminal Motility.

(a) Hypomotility.

(i) Small doses of prussic acid inhibited the reticulum and backward movement of the rumen with consequent inefficiency of eructation. Larger doses cause complete paralysis and abolition of the reflex.

(ii) Atropine and histamine were found to inhibit the reflex completely, even before a total paralysis of the rumen was brought about.

(b) Hypermotility.

(i) Carbamylcholine interferes with eructation by causing paralysis of the reticulum and small inco-ordinated mixing movements of the rumen.

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(ii) Veratrine also causes spastic contractions of the rumen and reticulum and so abolishes the rhythmic contractions necessary for eructation.

III. THE SIGNIFICANCE OF REFLEX SALIVATION IN RELATION TO FROTH FORMATION AND ACUTE BLOAT IN RUMINANTS.

(1) Frothing of ruminal ingesta is the main cause of bloat in sheep on green lucerne.

(2) It was found that the formation of froth is dependent on the consistency of the ruminal ingesta, which in turn is influenced by reflex salivary secretion.

(3) Reflex salivary secretion is largely stimulated by the presence of coarse material in the fore-stomachs, and the amount of saliva secreted therefore depends on the physical condition of the feed. The explanation for the protective action of hay is based on this finding.

(4) The condition and type of lucerne fed has a direct bearing on the occurrence of bloat.

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LITERATURE.

Aggazzotti, A. (1910). Beiträge zur Kentniss der Rumination. *Pflügers Arch. f. d. ges. Physiol.* No. 133, pp. 201-224.

Alway, F.J. (1927). Detection of Sulfur-deficiency of Soils by means of Plants. *First Internat. Congress of Soil Science*, 3, pp. 590-618.

Barker, H.A. (1936). Studies upon the Methane Producing Bacteria. *Arch. f. Mikrobiol.*, Vol. 7, pp. 404-419.

Begg, H. (1912). Tympanites in Bovines. *Vet. J.*, Vol. 68, pp. 442-458.

Bell, W.B. and Britton, J. (1939). Losses of Lambs and Cattle on Ladino Clover Pastures. *Mimeo. Col. Agr., Univ. of Calif.*, 17 p.

Clark, R. (1946). The Significance of Schizosaccharomyces ovis in fermentation and gas production in the fore-stomachs of ruminant animals. *S.A. Jl. of Sc.* Vol. XLII, pp. 154-155.

Clark, R. (1948). The effect of some commonly used anti-fermentatives on the *in vitro* formation of gas in ruminal ingesta and its bearing on the pathogenesis of bloat. *Onderstepoort Jl.* Vol. 23, Nos. 1-2, p. 389.

Clark, R. (1950). The use of antifrothing agents in the treatment of acute bloat. *J.S.A. Vet. Med. Ass.* Vol. 21, No. 4, pp. 173-178.

Clark, R. (1950). The paralytic action of histamine on the ruminal musculature. *J.S.A. Vet. Med. Ass.* Vol. 21, No. 1, pp. 13-17.

Clark, R. and Lombard, W.A. (1951). Studies on the alimentary tract of the merino sheep in South Africa XXII. The effect of the pH of the ruminal contents on ruminal motility. *Onderstepoort Jl.*, Vol. 25, No. 1, p. 79.

Clark, R. and Quin, J.I. (1945). Studies on the alimentary tract of merino sheep in South Africa. XIII. The role of prussic acid in the etiology of acute bloat. Onderstepoort Jl. Vol. 20, No. 2, pp. 209-212.

Clark, R. and Weiss, K.E. (1952). Reflex salivation in sheep and goats initiated by mechanical stimulation of the cardiac area of the forestomachs. *Jl. S.A. Vet. Med. Ass.* Vol. 23, No. 3, pp. 163-165.

Cole, H.H., Huffman, C.F., Kleiber, M., Olson, T.M. and Schalk A.F. (1945). A review of bloat in ruminants. *Jl. An. Sci.* Vol. 4, No. 3, pp. 183-236.

Cole, H.H., Mead, S.W. and Kleiber, M. (1942). Bloat in cattle. *Calif. Agr. Exp. Sta. Bull.*, 662.

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Cole, H.H., Mead S.W. and Regan, W.M. (1943). Production and prevention of bloat in cattle on alfalfa pasture. Jl. An. Sci. Vol. 2, No. 4, pp. 285-294.

Czepa, A. and Stigler, R. (1926). Der Wiederkäuermagen im Röntgenbild I. Pflügers Archiv. für des ges. Phys. Band 212.

Dougherty, R.W. (1940). Physiological studies of induced and natural bloat in dairy cattle. J.A.V.M.A. Vol. 96, pp. 43-46.

Dougherty, R.W. (1941). Further investigations of rumen gases and bloat in ruminants. J.A.V.M.A. Vol. 99, pp. 110-114.

Dougherty, R.W. (1942). Analysis of gas and ingesta of bloated cattle. Am J. Vet. Res. Vol. 3, No. 9, pp. 401-402.

Dougherty, R.W. (1942). A study of drugs affecting the motility of the bovine rumen. Cornell Vet. Vol. 32, pp. 269-280.

Dukes, H.H. (1942). The physiology of domestic animals. 5th. ed. p. 189. Comstock Publ. Co., Ithaca, N.Y.

Ducan, D.L. (1951). Effect of some choline esters upon the rumen and reticulum of sheep. Jl. Phys. Vol. 115 p. 75.

Espe, D., Jacobson, N.I. and Cannon, C.Y. (1943). Why do cows bloat? Holstein Friesian World, Vol. 40, p. 1020.

Evans, W.C. and Evans, E.T. Rees. (1949). Relation of a clover juice factor causing paralysis of smooth muscle to bloat in ruminants. Nature, Vol. 163, p. 373.

Ferguson, W.S., Ashworth, De B. and Terry, R.A. (1949). Nature of a muscle-inhibiting compound in lucerne and its possible connection with bloat in cattle. Nature, Vol. 163, No. 4146.

Gallagher, B.A. (1921). Diseases of sheep. U.S.D.A. Farmers' Bull. 1155.

Hoflund, S. (1940). Untersuchungen über Störungen in den Funktionen der Wiederkäuermagen, durch Schädigungen des N. Vagus verursacht. Svensk. Vet. Tidskr., Vol. 45, Sup. No. 15, 322p.

Henrici, M. (1949). The carbohydrate content of lucerne under different meteorological and physiological conditions. Onderstepoort Jl. Vol. 22, No. 2, p. 373.

Henrici, M. (1952). Comparative study of the content of starch and sugars of Tribulus terrestris, Lucerne, some Gramineae and Pentzia incana under different meteorological, edaphic and physiological conditions. Onderstepoort Jl. of Vet. Res. Vol. 25 No. 3, p. 45.

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Hudson, R. (1938). Clover tympany in cattle. Vet. Jl. Vol. 94, pp. 429-430.

Hutyra, F., Marek, J. and Manninger, R. (1938). Special pathology and therapeutics of the diseases of domestic animals. 4th ed. Vol. 2, pp. 72-78. Bailliere, Tindall and Cox, London.

Jacobson, C.A. (1919). Alfalfa Saponin. Alfalfa investigations VII. Am. Chem. Soc. J. Vol. 41, Part 1, pp. 640-648.

Jacobson, D.L., Espe, D. and Cannon, C.Y. (1942). Factors modifying the rate of fermentation of ingesta and their possible relation to bloat in dairy cattle. J. Dairy Sc. Vol. 25, pp. 785-799.

Kellner, O. and Kohler, A. (1900). Untersuchungen über den Stoffund Energie Umsatz der erwachsenen Rindes bei Erhaltungs- und Produktionsfutter. Landw. Vers. Sta., Vol. 53, pp. 1-474.

Kephart, L.W. (1929) Do cattle bloat on sweet clover? Wallaces' Farmer. Vol. 54, p. 727.

Kick, C.H., Gerlaugh, P. and Schalk, A.F. (1937). Some factors affecting the length of time whole corn kernels are retained in the rumens of steers. Am. Soc. An. Prod. Proc. Nov. 26-28, pp. 95-97.

Kleiber, M., Cole, H.H. and Mead, S.W. (1943). Bloat in cattle and composition of ruminal gasses. J. Dairy Sc. Vol. 26, pp. 929-933.

Kluyver, A.J. (1931). The chemical activities of micro-organisms. Univ. of London Press, 1939, 109p.

Knapp, B., Baker, A.L. and Phillips, R.W. (1943). Variations in the occurrence of bloat in the steer progeny of beef bulls. J. An. Sci. Vol. 2, pp. 221-225.

Koffman, M. (1937). Connection between protozoa of the rumen and tympany. (Abstr.) Vet. Bull. Vol. 7, p. 592.

Magee, H.E. (1932). Observations on digestion in the ruminant. J. Exp. Biol. Vol. 9, pp. 409-426.

Mangold, E. and Klein, W. (1927). Bewegungen und Innervation des Wiederkäuermagens. Georg Thieme, Leipzig.

Markoff, I. (1911). Untersuchungen über die Gärungs-prozesse bei der Verdauung der Wiederkäuer. Biochem. Ztschr., Vol. 34, pp. 211-232.

McAnally, R.A. (1943). Studies on the alimentary tract of merino sheep in South Africa X. Notes on the digestion of some sugars in the rumen of sheep. Onderstepoort Jl. Vol. 18, pp. 131-138.

McCandlish, A.C. (1923). Studies in the growth and nutrition of dairy calves. V. Milk as the sole ration for calves. J. Dairy Sci. Vol. 6 pp. 54-66.

McCandlish, A.C. (1937). Hoven or bloat in dairy cattle. XI. Milchwirtschaftlicher Weltkongress. Berlin, I pp. 410-412.

McCandlish, A.C. and O'Brien, D.G. (1933). Hoven or bloat in dairy cattle. West of Scot. Col. Agr. Bull. 127.

McIntosh, R.A. (1937). Tympany in cattle with special reference to its occurrence while grazing on alfalfa pasturage. Canad. J. Comp. Med. Vol. I, pp. 23-25.

Mead, S.W., Cole, H.H. and Regan, W.M. (1944). Further studies on bloat J. Dairy Sci. Vol. 27. pp. 779-791.

Mead, S.W. and Goss, H. (1936). Some results of eigth years of investigation concerning the role of roughage in the diet of ruminants. (Abstract). J. Dairy Sci. Vol. 19, p. 465.

Murray, A.J. (1909). Diseases of the stomach and bowels of cattle. U.S.D.A. Bureau Anim. Indus. Cir. 68 (rev.).

Nichols, R.E. (1951). A note on eructation in sheep as related to rumen fluid level and gas insufflation. Am. J. Vet. Res. Vol. 12, No. 44, p. 199.

Niel, C.B. van. (1943). Biochemical problems of the chemo-autotrophic bacteria. Phys. Rev., Vol. 23, pp. 338-354.

Ohman, A.F.S. (1938). Bloat in cattle. Queensland Agr. J. Vol. 50, pp. 350-351.

Olson, T.M. (1940). Bloat in dairy cattle. J. Dairy Sci., Vol. 23, pp. 343-353.

Olson, T.M. (1942). Ruminal gases in normal and bloated animals. (Abstract). J. Dairy Sci. Vol. 25, pp. 684-685.

Olson, T.M. (1944). Bloat in dairy cattle. Results of recent investigations. S.Dak. Agr. Sta. Cir. 52.

Painter, E.P. (1943). Sulfur in forages. N. Dak. Agr. Exp. Sta. Bimo. Bull. Vol. 5, pp. 20-22.

Phillipson, A.T. (1939). The movements of the pouches of the stomach of sheep. Quart. J. Exp. Phys., Vol. 29, pp. 395-415.

Phillipson, A.T. (1942). The fluctuation of pH and organic acids in the rumen of the sheep. J. Exp. Biol. Vol. 19, pp. 186-198.

Phillipson, A.T. (1952). The passage of digestibles from the abomasum of sheep and the composition thereof. J. Phys. Vol. 116, No. 1, pp.

Quin, J.I. (1942). Bloating in Ruminants. Its development and control. Farming in South Africa, Vol. 17, pp. 757-760.

Quin, J.I. (1943). Studies on the alimentary tract of merino sheep in South Africa VII. Fermentation in the fore-stomachs of sheep. Onderstepoort Jl. Vol. 18. pp. 91-112.

Quin, J.I. (1943). Studies on the alimentary tracts of merino sheep in South Africa VIII. The pathogenesis of acute Tympanites (Bloat). Onderstepoort Jl. Vol. 18, pp. 113-118.

Quin, A.H., Austin, J.A. and Ratcliff (1949). A new approach to the treatment of bloat in ruminants. J. Am. Vet. Med. Ass. Vol. 114, No. 866, p. 313.

Quin, J.I. and van der Wath, J.G. (1938). Studies on the alimentary tract of merino sheep in South Africa V. The motility of the rumen under various conditions. Onderstepoort Jl. Vol. II, No. 2, p. 361.

Quin, J.I. and van der Wath, J.G. and Myburgh, S. (1938). Studies on the alimentary tract of merino sheep in South Africa. IV. Description of experimental technique. Onderstepoort Jl. Vol. II, pp. 341-360.

Schalk, A.F. and Amadon, R.S. (1928). Physiology of the ruminant stomach. (Bovine). Study of the dynamic factors. N. Dak. Agr. Exp. Sta. Bull. 216, pp. 1-64.

Schmidt, W. (1933). Beiträge zur Injektionstherapie der Pansenüberfüllung, Tympanitis und Schlundverstopfung des Rindes. Tierärztl. Rundschau, Vol. 39, pp. 867-871.

Sisson, S. and Grossman, J.D. (1938). The anatomy of the domestic animals. W.B. Saunders Co., Philadelphia and London.

Stålfors, H. (1926). Beiträge zur Kenntnis der Physiologie der Wiederkäuermägen III. Ructus und Pansengasdruck. Arch. f. Wissensch. u. prakt. Tierh., Vol. 54. pp. 527-530.

Steyn, D.G. (1934). The toxicology of plants in South Africa. Central News Agency Ltd., South Africa.

Stigler, R. (1931). Der Mechanismus der Rumination. Arch. f. Tierernähr. u. Tierzucht. Vol. 4, pp. 613-694.

Tappeiner, H. (1882). Über Celluloseverdauung. Deutsche Chem. Ber. 15, pp. 999-1002.

Taylor, C.R. (1940). Bloat can be reduced. New Zealand J. Agr., Vol. 60, pp. 247-250.

Turpin, H.W. and McKellar, D.H. (1937). Lusern in Suid Afrika. Pamflet No. 170. Unie van Suid Afrika Dept. van Landbou en Bosbou. (Uitbreidings No. 13). Staatsdrukker, Pretoria.

van der Walt, S.J. (1944). Some aspects of the toxicology of hydrocyanic acid in ruminants. Onderstepoort Jl. Vol. 19, Nos. 1 and 2, pp. 79-160.

Veech, E.C. (1937) Hoven in cows. Agr. Gaz. N.S. Wales, Vol. 48, pp. 105-107.

Viljoen, P.R. (1922). Acute tympanites or Hoven in cattle. J. Dept. Agr., South Africa, Vol. 5, pp. 346-348

Washburn, L.E. and Brody, S. (1937). Growth and development with special reference to the domestic animals. XLII. Methane, hydrogen and carbon dioxide production in the digestive tract of ruminants in relation to the respiratory exchange. Mo. Agr. Exp. Sta. Res. Bull. 263.

Wester, J. (1935). Orgaanziekten by de grote huisdieren, J. van Boeckhoven, Utrecht and Amsterdam.

Wild, H. (1913). Über den Vorgang des Rülpsens (Ructus) bei den Wiederkäuern und über dessen Klinische Bedeutung. Diss., Giessen.

Wooldridge, G.H. (1923). (Ed.) Encyclopaedia of Veterinary Medicine Surgery and Obstetrics. Vol. I (Veterinary Medicine). Henry Frowde and Hodder and Stoughton, London.

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APPENDIX I.

(B) FARMERS.

No.	Farming area	Species, breed and type of animal	Type of feed and conditions	Irrigated or dry land	Type of soil	Environmental conditions	Effect of watering	Individual susceptibility and feeding habits	Type of bloat	Treatment
1	Lady Grey	Bovines	Very succulent and young green oats and rye	Both	Heavy fertile soil	Hot and dry	-	Yes, greedy feeders	Frothy	Turpentine
2	Worcester	Dairy cows	Green lucerne very succulent and young	Both	Any soil	Frost, drought and heat	-	Yes, greedy feeders	Frothy	Antifrothing agents (oils etc).
3	Donkerpoort O.F.S.	Dairy breeds Frieslands, Jersey and Africanders	Green lucerne preflowring and succulent	Irrigated	Heavy black soil	Frost wet with dew or rain, hot (wilting)	-	Yes, greedy feeders and hungry animals	Frothy	Turpentine
4	Norvals Pont (Orange River)	Sheep (Dorper) cows seldom bloat because never allowed onto pasture until grazed down by sheep	Green lucerne preflowering very succulent and leafy. Danger of bloat diminshes as lucerne matures when in full bloom very few cases	Irrigated	Rich sandy silt on banks of river. Dark heavy vlei soil. Bloat more common on lucerne growing on latter soil	Frost and wind	Always on hand	-	Frothy	Antifrothing agents. (~~mielaid~~ (mustard)
5	Boshoff	Cattle and sheep	Green legumes (lucerne) very young and succulent	Irrigated	Loamy soil	Heat (wilting)	Dangerous if given water after pasturing	Yes, greedy feeders	Frothy	Antifrothing agents (paraffin)
6	Ventersdorp	High producing dairy cows	Young and succulent green lucerne	-	-	-	Free access	Yes, young greedy animals	Frothy	Antifrothing agent (old oil)
7	Barkley East	Dairy cows	Very succulent green lucerne and wheat. Bloat depends on succulence of plant	Dry land	Sandy loam and clay	-	-	Yes, greedy feeders	Frothy	Antifrothing agent (Kerol)
8	Barkley East	Jersey cows and sheep	Green lucerne succulent any stage of growth	Irrigated	Loam especially on river banks	Frost and heat	-	Yes definite evidence of hereditary tendency to bloat in Jersey cows	Frothy	Antifrothing agents (Turpentine, o: oil etc.)

No	Farming area	Species, breed and type of animal	Type of feed and conditions	Irrigated or dry land	Type of soil	Environmental conditions	Effect of watering	Individual susceptibility and feeding habits	Type of bloat	Treatment
9	Kroonstad	Cattle	Young succulent green lucerne 12-15" high	Irrigated	Heavy vlei soil	Frost if lucerne is succulent	-	-	Frothy	Antifrothing agents (old oil etc.)
10	Koppies	Cattle	Young succulent green lucerne and lucerne hay	Irrigated	Heavy black turf soil	Frost, drought and heat	-	Yes, greedy rapid feeders	Frothy	Antifrothing agents (turpentine or oil)
11	Ficksburg	Frieslands and Jerseys. Dairy cows	Young succulent clover 4-6" high, dry lucerne hay	Irrigated	Sandy loam small portion clayey	Frost and heat especially mid day heat	Animals bloated when they were first allowed water	Yes, animals with big appetites and rapid feeders	Frothy	Turpentine in milk; as preventative feed roughage prior to pasturing. Allowed mixed grass clover pasture before pasturing pure clover.

yield by many of the cows. At the time of the visit the cows were becoming used to the milking machine, milk production was returning to normal and the incidence and severity of bloat was declining.

(C) <u>Report on Investigations into the Occurrence of Bloat on the farm Brakfontein, Irene</u>.

<u>Owner: S. Baard</u>.

<u>History</u>: Over a period of ten days the owner has had six sporadic cases of bloat amongst his dairy herd, consisting of fairly high-grade Friesland cows. Bloat started to occur approximately four days after changing over from veld-grass to grazing on an old mealie land with abundant green cow-peas (Vignia Sinensis) between the stubble.

<u>Feeding Regime</u>:

(1) Animals sleep in bare camp.

(2) Brought in at 4 a.m. into stable for milking.

Fed: Green, cut cow-peas (cut previous afternoon),, approximately 10 lbs. per cow. (Approximately ½ ton for 50 to 60 cows over 24 hours).

N.B. These cow-peas have a large percentage of green pods and are very succulent. The animals are next given a 50.50 mixture of a proprietary concentrate and mealie-meal (3 lbs. for each gallon of milk produced), and two lbs. of chopped mealie stalks and leaves.

(3) The animals are let out at approximately 6.30 a.m. and have the opportunity to drink water. They are then allowed to graze on the lands, where an abundance of green cow-peas with pods are available. They graze until noon, when they are taken to water which is available in the camp. After watering they graze again until 2 p.m. when they come back to the stable for the same routine, commencing at 2.30 p.m.

<u>Observations</u>:

(1) The large type of animal, producing over four gallons of milk, was mostly affected. Thus heavy producers and heavily fed animals (over 12 lbs. concentrates).
Friesland cows.

(2) Bloat was of the frothy type, possibly complicat by over-filling, because not all the cases responded to treatment with anti-frothing agents, and bloat usually occurred *after* drinking a fill of water at twelve noon. Most cases occurred between 1 and 2 p.m. In the cases of bloat examined the ruminal ingesta was a frothy, glutinous mass with a low fibre content.

(3) There is evidence by the veterinarian in charge, that one of the bloated animals showed gaseous distention of the small and large intestines on opening immediately after death.

(4) *Feeding Habits*: It was noticed that the out cow-peas, fed in the stable, were consumed greedily, especiall by the large type of animal. Approximately 10 lbs. being consumed in half-an-hour.

Conclusions:

The main cause of bloat in this case was over-feeding of a diet with a low fibre content, which leads to frothiness. Direct over-filling was a possible contributory factor.

(D) *Report on the Occurrence of Bloat at the Krugersdorp Sewage Farm*.

(Observations made by Veterinarian in charge,
Dr. U. Von Backström).

The Municipal Sewage Farm is divided into plots of approximately 150 acres each, on which Italian Rye is grown under irrigation. The plots are irrigated daily with large amounts of sewage water (approximately two million gallons water per 150 acres per 24 hours; equivalent to 200 inches rainfall annually). Under these conditions the Italian Rye, which is naturally prolific, grows luxuriantly and is extremely succulent. The grazing is hired by various dairy farmers in the vicinity, and one particular farmer has had severe losses from bloat. Out of a total of 150 cows, 46 died over a period of 14 months.

Stock: The animals are all very good quality high-producing Friesland cows.

Feeding Regime:

Each animal is fed 6-8 lbs. of concentrates and a liberal amount of dampened lucerne hay twice daily, during milking. No roughage is supplied. After milking, the animals are allowed into a bare camp for watering, and then out onto the rye pasture immediately adjacent, until the next milking, when the procedure is repeated. Observations indicate that the animals do not drink water in the camp, but prefer the sewage water with a high chloride content, running in the irrigation furrows. Because the pasture was adjacent to the stables, there was no opportunity to graze the veld while moving to and from the pasture.

Observations on the Occurrence of Bloat:

(1) The bloat was of the frothy type and was treated successfully with anti-frothing agents.

(2) Some of the plots lie on a slope with very sandy soil. The stand of rye on these plots is less luxuriant than on the richer, loamy soil on the level. Most of the cases of bloat has been observed to occur on the latter plots of succulent rye.

(3) The rye is not allowed to seed, but is cut or grazed regularly. Most cases of bloat occur when cattle graze on a full stand of rye. Hardly any bloat occurs when the rye is first cut down, and the cattle allowed to graze on the stubble.

(4) It appears that bloat is worse during the winter months. This is explained by the fact that during winter the other grasses and weeds die off, and a practically pure stand of rye prevails. During the summer months the rye pastures are contaminated by weeds and grasses which will prevent bloat by virtue of their ability to stimulate reflex salivation. It was noticed that the cows keep the coarse grasses on the edges of the plots, and along the irrigation furrows, closely cropped.

(5) Environmental factors seemed to play a role. The incidence of bloat increased after severe frost.

(6) When advised to feed teff hay before pasturing, the incidence of bloat was markedly reduced.

(7) Individual animals were observed to bloat repeatedly.

(8) Although other dairy farmers in the vicinity also used the grazing, hardly any cases of bloat occurred amongst their animals. The obvious reasons are the following:-

(a) The particular herd subjected to bloat, had access to the best plots with the most luxuriant stand of rye. The other farmers usually preferred to pasture their animals on the rye-stubble after cutting, especially in winter. A full stand of rye was only used as pasture in summer, when there was adequate veld grazing, or contaminating coarse grasses, amongst the rye to supply roughage. These animals also had veld grazing available at night, as well as ample opportunity to graze while being moved to and from the pasture, over a distance of 3 to 4 miles.

Conclusions:

The bloat, which was of the frothy type, was due to a lack of roughage in the diet of the animals belonging to one particular farmer. The other herds in the vicinity had access to sufficient roughage to prevent bloat.

APPENDIX I.

(A) VETERINARIANS.

Summary of Questionaires submitted to veterinarians in the field.

No.	Area.	Species and breed of animals.	Type of animal.	Do individual animals bloat repeatedly and feeding habits.	Type of feed and condition of feed.	Environmental Conditions.	Effect of watering.	Type of Bloat usually encountered.	Treatment and Prevention of Bloat.
1	Calvinia.	Jersey, Friesland.	Any.	Yes. Greedy and hungry.	Lush, succulent green-feeds, e.g. lucerne and wild clover. Leafy lucerne hay.	Wilting and frosting.	-	Frothy.	Turpentine, raising fore-quarters, massage, stomach-tube and trocar. Feed fibrous material prior to lucerne as preventative.
2	Middelburg C.P.	Jersey, Friesland, Africander.	Milking cows.	-	Green lucerne and lucerne hay.	Hot, dry weather.	-	Mostly frothy.	Bland oil or Turpentine.
3	Oudtshoorn.	Jersey.	Milking cows, especially if pregnant.	Yes rapid feeding	Green-feed, lucerne.	Wilting, heavy dew.	After pasturing, causes rapid bloat	Frothy.	Turpentine or anti-frothing agents.
4	Swellendam.	Bovines and sheep.	Milking cows.	Yes Greedy feeders.	Green lucerne, clover, wheat barley and oats.	Warm weather wilting.	-	Frothy.	Turpentine
5	Paarl.	Bovines.	Milking cows, especially pregnant animals.	-	Heavy, concentrate feeding.	-	Increases incidence of bloat.	Frothy.	Turpentine or anti-frothing agents.
6	Somerset West.	Friesland.	Milking cows, especially pregnant animals.	Yes.	Lucerne hay and concentrates.	-	-	Frothy.	Turpentine, elevation of fore-quarters, massage; trocar, if necessary.
7	Queenstown.	Frieslands mostly (predominant in area).	Milking cows, especially pregnant animals.	Yes. Hereditary tendency in 3 pedigree jersey cows	Green lucerne (dry land).	Hot, dry conditions (wilting).	-	Usually free gas, but also frothing.	-
8	Queenstown.	Friesland and Jersey.	Milking cows high producers.	-	Green lucerne and oats.	Warm weather wilting.	-	Frothy.	Turpentine.

No.	Area.	Species and breed of animals.	Type of animal.	Do individual animals bloat repeatedly and feeding habits.	Type of feed and condition of feed	Environmental Conditions.	Effect of watering.	Type of Bloat usually encountered.	Treatment and Prevention of Bloat.
9	Cedara	Frieslands.	Milking cows.	-	Green lucerne and clover, very leafy lucerne hay. The best type of non-stalky lucerne the most dangerous.	Frosted and wilted, hot, windy days.	-	Frothy.	Turpentine.
10	Middelburg C.P.	Jersey, Friesland, Africander.	Mostly milking cows.	-	Green lucerne, oats and barley, lucerne hay.	Hot dry weather, (wilting).	-	Mostly frothy	Turpentine or bland oil and elevation of fore-quarters.
11	Vredendal Oudtshoorn.	-	-	Yes.	Young succulent green lucerne and clover under irrigation. Bloat rare on dryland lucerne in W.P.	Wilted, or wet with rain or dew.	After pasturing dangerous.	Frothy.	Turpentine or anti-frothing agents.
12	Port Elizabeth.	Frieslands.	Milking cows, high producers	-	Green lucerne.	Hot weather.	-	Frothy.	Turpentine.
13	Greytown.	Jerseys and Frieslands.	Milking cows high producers	-	Green clover.	Hot dry weather after rain (wilting).	-	Frothy,	Turpentine.
14	Pietermaritzburg.	Friesland predominant in area.	Lactating cows because they are allowed onto the best pastures.	Yes Greedy feeders.	Lush pastures, such as kikuyu grass and chemolier.	Intermittent rain and hot weather (wilting.)	Cases occur especially after watering.	Frothy.	Anti-fermentatives, Trocar or Ruminotomy.
15	Robertson.	-	-	-	Green lucerne.	Dry windy conditions.	-	Frothy.	Turpentine or anti-frothing agents and elevation of fore-quarters.
16	Piet Retief.	Dairy breeds Jersey and Friesland.	Milking cows (predominant class of animal).	Greedy, hungry animals.	Green lucerne and lush kikuyu grass.	Hot weather.	-	Frothy.	Turpentine or anti-frothing agents.
17	Johannesburg.	Dairy breeds	Milking cows.	-	Over-eating concentrates.	-	-	Frothy.	-

No.	Area.	Species and breed of animals.	Type of animal.	Do individual animals bloat repeatedly and feeding habits.	Type of feed and condition of feed	Environmental Conditions.	Effect of watering.	Type of Bloat usually encountered.	Treatment and Prevention of Bloat.
18	Pretoria.	Dairy breeds	Milking cows, (predominant class of animal.	-	Green lucerne or other legumes and lush grass.	Warm sun, following rapid growth of plants.	-	Frothy.	Turpentine or anti-frothing agents.
19	Pretoria.	Dairy breeds Frieslands.	Lactating cows.	Greedy feeders.	Green lucerne, lucerne hay and concentrates.	Hot, humid conditions.	-	Frothy.	Turpentine or anti-frothing agents. Feed coarse hay and cut down concentrates.
20	Krugersdorp.	Friesland, Jersey.	Milking cows, high producers especially if pregnant.	Yes Greedy feeders.	Green lucerne, and lush Italian Rye.	Rain or dew and hot sun (wilting).	Watering after pasturing wilted legumes dangerous.	Frothy.	Turpentine. Feeding of roughage as preventative.
21	Pietersburg.	Dairy breeds Friesland.	Milking cows.	Yes. Greedy feeders.	Green lucerne, lucerne meal.	Cloudy, warm and humid.	Watering before or after feeding, dangerous.	Frothy.	Turpentine.
22	Klerksdorp.	Friesland and Jersey.	Milking cows.	Yes. Greedy feeders.	Young, green lucerne and rye.	Frosted or wilted.	Watering before or after feeding, dangerous.	Frothy.	Turpentine and elevation of front quarters.
23	Vryburg.	Dairy breeds	Lactating cows, high producers which are forced-fed	Yes. Greedy feeders.	Wilted, green legumes.	Those factors causing wilting	Increases danger of bloat.	Frothy, but also free gas.	Turpentine.
24	?	Jersey and Friesland.	Lactating cows.	Greedy feeders.	Green lucerne.	Hot weather, with warm winds (wilting).	-	Frothy.	Turpentine or anti-frothing agents.

APPENDIX II.

(A) OPERATIVE TECHNIQUE.

(a) The operation for creating a ruminal fistula:

The operative technique is similar to that described by Quin, v.d. Wath and Myburgh (1938).

The animals are starved for 24 hours prior to the operation and before anaesthetising with chloral hydrate (1 c.c. per lbs. body weight of a 10% solution), the skin over the left flank is clipped and shaved. This area is washed with soap and water after the anaesthetic has been administered, cleaned with ether, and Cetavlon (I.C.I.) or Zepheran applied as an antiseptic. Full aseptic precautions are taken throughout the operation.

An incision is made in the skin of the left flank, approximately 5 cms. behind and parallel to the last rib. Blunt dissection is used to separate the muscle layers. The rumen is drawn out through the laporotomy wound, freed of ingesta and a bowel forceps, guarded with rubber tubing on both jaws, is applied to the rumen. A relatively non-vascular part of the ruminal wall is selected and an oval purse-string suture is made using No. 1 catgut on a small, curved, round needle. An incision is made in the centre of the sutured area and the flange of the previously boiled fistula tube of ebonite with attached rubber tubing, is passed through the slit. The lips of the incision are inverted and the purse-string suture tightened. If invagination is incomplete, a second purse-string suture is applied. Sulphanilamide powder is then applied to the visceral peritoneum round the fistula. It is felt that this ensures firm adhesion between the visceral and parietal peritoneum after the tube has been drawn into position. A stab wound is next made through the skin, muscles and peritoneum at a point high up in the angle between the last rib and transverse processes of the lumber vertebrae, and at least 1½ to 2 inches away from the laparotomy wound. A pair of long artery forceps is passed through the stab wound, and the rubber connection to the fistula is gripped, and the tube and fistula are drawn through the stab wound as far as possible by gently incising the opening until the tube slips through. If the stab wound opening has become too large, a single interrupted suture, using No. 2 catgut, is applied to the skin close to the fistula. The laparotomy wound is closed by suturing the peritoneum and muscular layers separately with a continous suture of No. 1 catgut. The skin incision is closed with an interrupted mattress suture of No. 2 catgut and collodion-iodoform used as a dressing. The rubber tube attached to the fistula is closed with a tight-fitting cork and a collar of cotton-wool is tied tightly round the fistula, in order to ensure that the visceral and parietal peritoneum is kept in contact, and to prevent the fistula from slipping into the rumen after healing has taken place. The wounds usually heal by first intention. After-treatment consists in cleaning and re-placing the cotton-wool collar round the fistula once a week.

In the case of the bovines, the same operative technique is employed, with the exception that the operation is performed under paravertebral anaesthesia, using a 2% novocain solution, with the animal standing, instead of general chloral hydrate anaesthesia. The same type of ebonite fistula is used for bovines, but these should preferably be provided with a ridge on the tube approximately 2 inches above the flange, behind which a wire clip can be fixed. The clip will prevent the fistula from falling into the rumen. A cotton-wool collar is not considered necessary in the bovine.

(b) <u>The operations for abomasal and caecal fistulae.</u>

Essentially the same operative technique and material are used as described above. The incision for the abomasal fistula is made approximately two inches from and parallel to the costal arch on the right ventral side of the animal, starting about six inches posterior to the xyphoid cartilage. The stab wound through which the fistula is pulled, is made two inches to the right of the mid-ventral line. The fistula is inserted near the pyloric end of the abomasum. The stab wound for the caecal fistula is made in the centre of the right flank of the animal, approximately three inches ventral to the transverse processes of the lumber vertebrae. The laparotomy wound is made about two inches behind and parallel to the last rib.

(c) The operation for abdominal vagotomy.

This operation has been described by Hoflund (1940).

The animals are starved for 48 hours and anaesthetised with chloral hydrate in the manner described above. The operation site, comprising the ventral side of the animal posterior to the xyphoid cartilage, is prepared in the usual manner. Strict aseptic precautions are taken throughout. An incision, approximately six inches long, is made about one inch to the right of the mid-ventral line, extending from immediately behind the xyphoid cartilage. The hand of the operator is inserted through the incision and a hook, with a string attached, is applied to the reticulum. By exerting traction on the string an assistant pulls the reticulum to one side in order to clear the cardiac area. With blunt dissection the operator isolates whichever branch of the vagus (right ventral or left dorsal) is required. A long silk thread is tied round the nerve, and the nerve is cleared for a distance of about one inch. With a pair of blunt scissors about one inch of the nerve is excised. By visual inspection the operator makes absolutely sure that the nerve is actually severed. The laparotomy wound is closed in the manner described previously.

APPENDIX III.

REPORTS ON INVESTIGATIONS OF OUTBREAKS OF ACUTE BLOAT.

(A) Report on the occurrence of bloat at Isis Estates, 5th July 1951.

Isis Estates has a large herd of pure-bred Frieslands, kept for milk production and pedigree breeding.

Strict records are kept by Dr. McFarlane, the veterinarian in charge of the farm. Bloat is a serious problem at Isis Estates, a few cases occurring almost daily.

The animals are forced-fed for production.

Feeding Regime:

Cows sleep overnight in bare paddock.

3 a.m.: Brought into stable and fed chopped, soaked lucerne hay. After this they are given dairy meal, and milked. Water is constantly available to each cow. After milking, the cows go to grazing.

9 a.m.: Cows to paddock with teff hay available. Rest from half-an-hour to one hour.

10 a.m.: Cows into stable, fed and milked as before. To grazing.

3 p.m.: As before again.

Lucerne: Good quality lucerne hay, all obtained baled from Upington, in fairly large consignments.

Dairy Meal: Mixture of yellow mealie-meal, 54%; Bran, 15%; Coarse germ meal, 6%; Monkeynut meal, 9%; Sunflower, 5%; Maize bran, 4%; Mineral mixture, 3%; and Molasses up to 2%.

Grazing: Grazing is either oatlands or veld, as available.

Occurrence of Bloat:-

Cases of bloat occur almost daily, mostly between 3 a.m. and 10 a.m. milkings. Cases have, however, been seen to occur within a few minutes after the 10 a.m. stable feed. There is decided evidence of individual susceptibility, as certain cows definitely tend to bloat repeatedly. There is

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also the impression that many of these habitual bloaters are from the same breeding line. This indicates hereditary susceptibility to bloat, but, for obvious reasons, these breeding records are not available for publication. It was noticed that the cows usually affected are the best fed, heavy producers and the greedy feeders. According to McFarlane, it appears that the greater the moisture content of the soaked lucerne, the greater the danger of bloat. Shutting off the individual water supply to each cow, and using a common trough, increased bloating. This may have been due to the cows drinking large amounts at once.

Type of Bloat and Treatment:-

Most of the cases of bloat were due to frothing of the ingesta. This conclusion was drawn from direct observations of ruminal ingesta, and the beneficial effect of treatment of the cases with anti-frothing agents, such as turpentine or Avlinox (ICI). Cases that would not respond to these measures, were walked up a rise, which immediately facilitated belching. This proves that some cases at least were complicated by direct over-filling.

Conclusion:-

The frothy bloat in this instance is attributed to the feeding of large amounts of feed lacking in roughage. Apart from the dairy meal which is entirely devoid of fibre, the lucerne hay was deprived of its coarse character by chopping and wetting. The oatland grazing itself was also lacking in roughage, and, although the veld grazing at times should have been coarse enough to prevent bloat, some animals must obviously have consumed insufficient amounts to afford protection. This was probably the result of heavy stable feeding, which further contributed towards bloat by causing a relative over-filling of the rumen. It is significant that most cases of bloat occurred after the 3 a.m. milking, when the cows had not had any grazing since the previous evening.

(B) Report on severe outbreak of bloat at Isis Estates 24th January 1952.

McFarlane reported numerous cases of bloat as from 24/1/52. The feeding and general routine had remained as described in the report of 5/7/51, and only occasional cases of bloat had occurred in the interim. On the 23rd and 24th the cows were for the first time milked mechanically in a newly-installed unit. The feeding remained as before. On the 24th there were thirty cases of bloat of varying severity and one death. Further large scale outbreaks occurred on subsequent days, and on the morning of the 26th there were six moderate cases of bloat. The bloat occurred very rapidly within twenty minutes of feeding lucerne which had been previously soaked in water, and before the dairy meal was fed.

Bloat was of the frothy type in most cases. In spite of the fact that some free gas escaped from a few animals after trocarization, it is believed that some degree of frothing was present. Bloat was most common at the 3 a.m. milking, i.e. when the cows had not had any grazing since the previous day. Animals which received a small ration of lucerne and had not been introduced to the milking machine, had not shown any bloat.

Treatment:

McFarlane reported excellent results with I.C.I's anti-frothing agent Avlinox. It was further found that spraying the lucerne with a one-in-ten dilution of Avlinox greatly reduced the incidence of bloat.

Conclusion:

In the light of the evidence, the conclusion is justified that the wide-spread bloating was associated with the introduction of mechanical milking. The psychic upset must have resulted in the production of adrenalin, which affects both reflex salivation and the eructation reflex. This caused large-scale outbreaks of bloat in these animals, already particularly susceptible to bloat as a result of the specific feeding regime. The upset was also reflected in a reduced milk

(B) THE INDIVIDUAL VARIATIONS IN ERUCTATION EFFICIENCY AMONGST SIX OF THE EXPERIMENTAL SHEEP, AS RECORDED AT VARIOUS INTERVALS:

Date.	ERUCTATION EFFICIENCY. Sheep Nos.					
	1	2	3	4	5	6
24/1/51	-	-	-	-	-	4
26/1/51	-	-	4	-	-	4
30/1/51	-	-	4	-	-	4
7/2/51	-	-	3	-	-	4
26/2/51	-	-	4	-	-	4
12/3/51	-	-	-	-	-	4
19/3/51	0	-	-	-	2	-
23/3/51	0	2	1	-	-	-
27/3/51	-	-	1	1	-	2
29/3/51	-	-	4	0	1	-
11/4/51	0	1	4	2	2	2
20/4/51	0	1	-	-	-	-
10/5/51	1	4	4	2	2	2
15/5/51	1	3	3	3	2	5
16/5/51	1	1	3	3	3	4
17/5/51	2	3	5	2	3	3
23/5/51	3	3	-	3	2	4
28/5/51	-	-	2	-	-	4
29/5/51	0	3	1	1	2	5
4/6/51	2	4	3	4	3	4
6/6/51	2	4	5	4	5	5

Conclusion: It appears that there is a marked individual variation in eructation efficiency between the different sheep in the group, as well as a marked variation in individual animals themselves. Frothing did not play a role, as each animal was given an anti-frothing agent before recording.

(C) THE EFFECT OF THE DEGREE OF RUMINAL FILLING ON ERUCTATION EFFICIENCY.

Six of the experimental sheep were used. Water was removed for 24 hours prior to the experiment, but lucerne hay was available up to the time of recording. A recording of eructation efficiency, which was rated arbitrarily, was obtained from each sheep by using the method of forced air insufflation. Frothing of the ingesta was prevented by dosing an anti-

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frothing agent before recording. The sheep were then watered and fed lucerne hay _ad lib._ for a period of 2 hours. Food and water consumption were then taken and a recording of eructation efficiency made. The results are given below:-

Note: E.E. - rating of eructation efficiency.

Date 6/6/51	Sheep No. 1 Consumption			Sheep No. 2 Consumption			Sheep No. 3 Consumption		
Time:	Lucerne hay	Water	E.E.	Lucerne hay	Water	E.E.	Lucerne hay	Water	E.E.
11a.m.			2			4			5
2p.m.	380 grams	2540 c.c.	1	310 grams	2700 c.c.	3	440 grams	3820 c.c.	2
3p.m.						*1			

Date 6/6/51	Sheep No. 4 Consumption			Sheep No. 5 Consumption			Sheep No. 6 Consumption		
Time:	Lucerne hay	Water	E.E.	Lucerne hay	Water	E.E.	Lucerne hay	Water	E.E.
11a.m.			4			5			5
2p.m.	420 grams	2780 c.c.	3	430 grams	3120 c.c.	3	530 grams	3480 c.c.	1
3p.m.			*1						

*Sheep Nos. 2 and 4 each dosed with 1500 c.c. water into the rumen in order to further increase the volume of the ruminal contents.

Conclusion: It is evident that the reduction in eructation efficiency coincides with the combined food and water intake.

(D) THE EFFECT OF WATERING ON THE INCIDENCE OF BLOAT IN CATTLE.

Six bovines of the Africander type, approximately 2 years old, were divided into two equal groups. They were fed on a basic ration of good quality lucerne hay. Food and water were removed from both groups on 3 p.m., 11/7/51. On 12/7/51 at 8.30 a.m. group I was given water, while group II remained without. At 12.30 p.m. both groups were given succulent green lucerne _ad lib_. The animals did not take the lucerne at first, but on 8 a.m., 13/7/51, it was noticed that they must have consumed a large amount over-night. The results are given below:-

Date	Group receiving water prior to green lucerne.		Group without water prior to green lucerne.	
	Bovine No.	Degree of bloat.	Bovine No.	Degree of bloat.
(a) 12/7/51	4348	Full only	4377	Nil
	4293	Markedly bloated	4281	Nil
	4340	Full only	4443	Nil
(b) 17/7/51	4377	Full only	4348	Nil
	4281	Slightly bloated	4293	Nil
	4443	Full only	4340	Nil
(c) 20/7/51	4348	Slightly bloated	4377	Nil
	4293	Nil	4281	Nil
	4340	Nil	4443	Nil

In order to exclude individual susceptibility, the groups were changed round on 17/7/51, the animals previously in group 2 receiving water prior to lucerne feeding. The results are given in table (b).

The original experiment was repeated again on 20/1/51. The results are given in Table (c). In the last two experiments the bovines immediately took to the lucerne, and bloat was evident at 3 p.m. the same afternoon.

Conclusion: The incidence of bloat was greater amongst the animals which received water immediately prior to green lucerne.

(E) THE EFFECT OF WATERING ON THE INCIDENCE OF BLOAT IN 14 SHEEP AND ONE BOVINE.

Fourteen non-fistulae sheep and one bovine were used for this experiment. The sheep were divided into two equal groups, and the bovine was placed with one of these groups.

One of the groups was given lucerne hay and water up to 8 a.m. in the morning of 12/6/51, while the other group received only lucerne hay, water being withheld for 16 hours.

At 8 a.m. on 12/6/51, the latter group was allowed to drink water before both groups were put onto frosted green lucerne pasture. The results are given in Table (a).

Table (a).

Date.	Group I: hay and water up to the time of pasturing.		Group II: water withheld for 16 hours; allowed to drink water immediately prior to lucerne pasturing.	
	Animal No.	Degree of Bloat	Animal No.	Degree of Bloat.
12/6/51	81643	Nil	81159	Slight
	79815	Nil	81160	Marked
	79904	Full only	69725	Slight
	79833	Full only	81141	Moderate
	81131	Moderate	82430	Moderate
	81133	Nil	80085	Slight
	81156	Moderate	81151	Nil
			Bovine no number	Marked

On 14/6/51 the experiment was repeated, with the exception that in this case lucerne hay and water were withheld from both groups for 16 hours. The group of animals given water prior to pasturing in the previous experiment, were allowed onto the pasture without drinking water. The other group, which had previously had water and food available constantly, were now dosed with three litres of water each before allowing them onto the same frosted green lucerne pasture. See Table (b) for the results.

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Table (b).

Date.	Group I: Food and water withheld for 16 hours. Dosed three litres water prior to pasturing.		Group II: Food and water withheld for 16 hours prior to pasturing; no water given.	
	Animal No.	Degree of Bloat	Animal No.	Degree of Bloat.
14/6/51	81643	Slight	81159	Nil
	79815	Slight	81160	Moderate
	79904	Marked	69725	Nil
	79833	Slight	81141	Slight
	81131	Marked	82430	Nil
	81133	Moderate	80085	Nil
	81156	Marked	81151	Nil
			Bovine no number	Nil

Conclusion: It appears that the incidence of bloat is greater in those groups receiving water before pasturing green lucerne. The lucerne was in the appropriate stage of growth and very succulent. By chance, the pasture actually had severe frost during the night preceding both experiments.

(F) <u>THE EFFECT OF DOSING SODIUM CARBONATE ON THE EFFICIENCY OF ERUCTATION, RUMINAL pH AND MOTILITY, AND THE ALKALI RESERVE OF THE BLOOD OF SHEEP</u>. (Detailed data).

Note: E.E. rating of eructation efficiency.

		Sheep No. 2.			
Date.	Time.	pH	CO_2	E.E.	Rumen Motility.
23/10/51	9.30 a.m.	6.9	61	4	Normal
	10 a.m.	Dosed 36 gram sodium carbonate.			
	10.30 a.m.	8.2			1 contraction per 5 minutes
	11.15 a.m.	8.4	59	2	Forward and backward contractions weak.
	2.15 p.m.	7.2	72	1	Both types of contraction weak
24/10/51	8.30 a.m.	6.5	76	0	Both types of contraction weak

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Sheep No. 2.

Date.	Time.	pH	CO_2	E.E.	Rumen Motility.
	2.15 p.m.	6.8	75	4	Increased rate of eructation contraction on air insufflation.
25/10/51	8.30 a.m.	6.8	68	1	Very weak contractions especially backward. Reduced rate. Contractions strong. Animal ruminating.
	2.15 p.m.	6.6	61	4	Contractions strong, animal ruminating.
26/10/51	8.30 a.m.	6.8	63	4	Contractions regular and strong. Increased rate on insufflation.

Sheep No. 3.

Date.	Time.	pH	CO_2	E.E.	Rumen Motility.
23/10/51	8.30 a.m.	6.7	62	4	Normal
	10 a.m.	Dosed			35 grams sodium carbonate
	10.30 a.m.	8.2			Nil
	11.15 a.m.	8.2	65	1	During air insufflation regular; inefficient eructation contractions.
	2.15 p.m.	7.3	77	0	Reduced rate of eructation.
24/10/51	8.30 a.m.	6.5	80	0	Reduced rate of eructation
	2.15 p.m.	6.9	79	0	Reduced rate of eructation.
25/10/51	8.30 a.m.	7.0	54	4	Both types of contraction normal rate.
	2.15 p.m.	6.6	56	4	Contractions strong; animal ruminating.
26/10/51	8.30 a.m.	6.7	61	5	Contractions strong, increased rate on insufflation.

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		Sheep No. 6.			
Date.	Time.	pH	CO_2	E.M.	Rumen Motility.
23/10/51	9.30 a.m.	6.7	59	5	Normal
	10 a.m.	Dosed			30 grams sodium carbonate
	10.30 a.m.	7.7			Nil
	11.15 a.m.	7.0	71	2	Nil, regular inefficient eructation contractions during air insufflation.
	2.15 p.m.	7.1	77	2	Only regular eructation contractions after insufflation.
24/10/51	8.30 a.m.	6.5	74	0	Both types of contractions very weak.
	2.15 p.m.	6.8	66	2	Both types of contractions weak; increased rate on insufflation.
25/10/51	8.30 a.m.	6.9	65	0	Both types of contractions weak; increased rate on insufflation.
	2.15 p.m.	6.8	57	3	Contractions strong; increased rate.
26/10/51	8.30 a.m.	6.8	50	4	Contractions strong and regular; increased rate on insufflation.

		Sheep No. 7.			
Date.	Time.	pH	CO_2	E.M.	Rumen Motility.
23/10/51	9.30 a.m.	6.8	53	5	Normal
	10 a.m.	Dosed			30 grams sodium carbonate.
	10.30 a.m.	[illegible].3			1 eructation contraction per 5 minutes.
	11.15 a.m.	9.2	69	4	Only regular efficient eructation contractions
	2.15 p.m.	8.7	73	3	Only eructation contractions reduced rate regular
24/10/51	8.30 a.m.	6.6	80	3	Only eructation contractions reduced rate regular
	2.15 p.m.	6.[illegible]	73	3	Only eructation contractions reduced rate regular

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Date.	Time.	pH	CO_2	E.E.	Rumen Motility
					S h e e p N o. 7 (cont.)
25/10/51	8.30 a.m.	6.7	63	5	Both types of contractions strong.
	2.15 p.m.	6.6	63	5	Both types of contractions strong.
26/10/51	8 a.m.	6.4	58	5	Both types of contractions regular and strong. Increased rate of and even extra eructation contractions.

(G) THE DURATION OF THE EFFECT OF ARTIFICIALLY INDUCED ALKALOSIS ON THE ERUCTATION EFFICIENCY IN SHEEP.

Six of the experimental sheep were used. Tracings of eructation efficiency were first obtained before each sheep was dosed with 25 grams sodium carbonate. Recordings of eructation efficiency were then made at various intervals. Ruminal pH was also determined before dosing and at each recording.

The results are given below:-

Date	Time	1		2		3		4		5		6	
		pH	E.E	pH	E.E	pH	E.E	pH	E.E	pH	E.E	pH	E.E.
17/5/51	9 a.m	7.0	2	6.9	3	6.8	5	6.8	2	6.9	3	6.7	3
	9.30 a.m	D o s e d		s o d i u m				c a r b o n a t e					
	10 a.m	8.5	1	8.3	0	7.8	0	8.6	0	7.2	0	7.1	0
18/5/51	9 a.m	6.9	0	6.9	2	6.8	1	7.0	2	7.0	0	6.7	3
	2 p.m	6.8	0	7.0	1	6.9	0	6.9	2	6.9	0	7.0	2
19/5/51	9 a.m	7.2	0	7.1	2	7.0	1	6.9	1	7.0	3	6.8	-
20/5/51	9 a.m	7.0	1	6.7	-	6.8	5	6.7	-	6.7	-	6.4	-

Conclusion: Although the ruminal pH returned to the normal range within 24 hours, the residual alkalosis inhibited ruminal motility, and, consequently the eructation reflex for periods up to 72 hours.

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(J) Consumption of lucerne hay and water and amount of faeces passed daily by two goats on which abdominal vagotomy was performed. Data collected from the 4th post-operative day

Date.	Goat No. 1.			Goat No. 2.		
	Lucerne hay grams.	Water ml.	Faeces grams.	Lucerne hay grams.	Water ml.	Faeces grams.
2/11/51	350	-	-	280	-	-
3/11/51	290	-	-	220	-	-
4/11/51	230	-	-	460	-	-
5/11/51	190	-	90	310	-	400
6/11/51	210	-	180	440	-	490
7/11/51	220	-	100	580	-	390
8/11/51	50	-	10	410	-	420
9/11/51	180	-	50	400	-	330
10/11/51	250	-	25	520	-	490
11/11/51	270	-	35	510	-	440
12/11/51	130	-	20	670	-	30
13/11/51	130	-	10	560	-	150
14/11/51	160	-	5	370	-	130
15/11/51	340	-	10	250	-	200
16/11/51	100	-	10	450	-	170
17/11/51	250	-	5	280	-	450
18/11/51	130	-	15	330	-	190
19/11/51	130	1140	10	390	1140	120
20/11/51	30	1400	5	480	1250	215
21/11/51	0	340	10	500	1660	220
22/11/51	120	660	5	600	1520	25
23/11/51	10	560	80	330	960	260
24/11/51	150	860	90	750	1960	290
25/11/51	220	700	40	790	1480	340
26/11/51	120	860	40	730	1360	440
27/11/51	250	440	10	420	820	160
28/11/51	50	1080	10	410	2060	70

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(K) THE EFFECT OF ABOMASAL DISTENSION AND THE DEGREE OF RUMINAL FILLING ON THE EFFICIENCY OF ERUCTATION.

Date: 3/10/51. Sheep No. 8 with both ruminal and abomasal fistulae was used. The animal was fed on 500 grams lucerne hay and grass hay ad lib., before the experiment. The rumen was first emptied as far as possible with the vacuum pump, two litres of fluid ingesta being removed. The abomasum was also drained. A recording of eructation efficiency was then made and arbitrarily rated. Throughout the experiment air was introduced into the rumen at the rate of 1 litre per 3 minutes. Water was then added to the rumen in measured amount and a recording of eructation efficiency made each time. See table below for the results.

Seven litres of fluid was again removed from the rumen and 200 c.c. ingesta from the abomasum. The abomasum was then filled with 2 litres warm saline, and the procedure again repeated.

Progressive Ruminal Filling.

	Amount of water introduced into rumen in c.c.								
	0	500	1500	2500	3500	4500	5500	6500	7500
Eructation efficiency; (abomasum drained).	5	5	5	5	5	4	3	3	0
Eructation efficiency; (abomasum distended with 2 litres saline.	5	5	2	0	-	-	-	-	-

The results show that eructation efficiency is impaired at a much lower level of ruminal filling when the abomasum is distended, than when that organ is empty. It is concluded that this effect is due to the inhibition of the reticulum and mixing movements of the rumen, which is caused by abomasal distension.

(L) (a) *In vitro* gas formation by mixing ruminal and abomasal ingesta.

In order to show that gas formation in the abomasum is dependent on a chemical reaction between free acid and in the abomasum and alkali in the ruminal ingesta entering it, the following experiments were conducted:

The sheep provided with an abomasal fistula, was fed on lucerne hay *ad lib*. At different times samples of abomasal and ruminal ingesta were collected. The pH of each sample was determined immediately after withdrawal, whereupon 50 ml. abomasal ingesta was placed in an Ehrlenmayer flask. A control flask containing 50 ml. distilled water was also prepared. Both flasks were arranged in a waterbath at 38°C provided with a mechanical shaker. 50 ml. of ruminal ingesta was then added to each flask and each flask then immediately connected to a water manometer with an adjustable arm so that the volume of gas evolved could be read at atmospheric pressure every five minutes for a period of half an hour. The flasks were continously shaken during this period. The results are given in the table below:

Date	Rumen pH	Abomasal pH.	Total amount of gas in 30 min. ruminal and abomasal ingesta.	Total amount of gas in 30 min. ruminal ingesta and dist. water control
19/12/51	5.9	3.0	45.0	10.0
21/12/51	6.2	3.2	33.5	11.25
21/12/51	6.4	2.4	35.25	4.75
24/12/51	7.4	2.8	55.75	5.5
27/12/51	6.4	2.4	40.0	11.75
27/12/51	6.5	3.0	49.75	10.75
29/12/51	6.9	2.7	62.0	16.25
7/ 1/52	6.6	2.3	70.5	28.5
7/ 1/52	5.1	2.4	53.5	28.0
9/ 1/52	7.0	2.8	61.0	18.5
9/ 1/52	7.0	2.5	89.0	29.25

15/...

The results show that the amount of gas formed depends on the difference in pH between the ruminal and abomasal ingesta. Since experiments have shown that biological fermentation cannot take place at the pH usually found in the abomasum, it is justified to conclude that gas formation in the abomasum is essentially due to a chemical reaction.

(b) Gas formation in the abomasum _in vivo_ experiment.

The sheep with the abomasal and ruminal fistulas fed on lucerne hay _ad lib_ was used. A recording of normal eructation was obtained by the method described in the text. Reticular motility was simultaneously recorded with a balloon.

The pH of the abomasal ingesta was 2.0 and of the ruminal ingesta 5.4; 200 cc. of the latter was adjusted to pH 7.2 in vitro by adding sodium carbonate. This amount of ruminal ingesta was then injected into the abomasum during recording. There was an immediate reduction in strength and rate of reticular and ruminal contractions and eructation efficiency was markedly reduced. When 200 cc. of abomasal ingesta from another sheep adjusted to the same pH as that of the experimental sheep was injected into the abomasum no such effect was observed. On another occasion 100 cc. ruminal ingesta of pH 7.5 was injected into the abomasum with pH 2.2 and similar though less marked results were obtained.

The results show that ruminal and reticular motility and consequently eructation efficiency, are markedly effected by chemical gas formation in the abomasum, especially when large amounts of ruminal ingesta suddenly enter the abomasum and when the difference in pH of the ingesta is great.

(M) Data of individual sheep showing consistency index of ruminal ingesta before and after feeding, type of ingesta, degree of bloat and consumption of green lucerne and water. The type of lucerne fed during the different periods are as follows:

Period 25/6/52 to 2/7/52 - mature stalky green lucerne with small leaves.

Period 3/7/52 to 15/7/52 - young crisp and succulent green lucerne.

Day 16/7/52 - mature stalky green lucerne.

Period 17/7/52 to 24/7/52 - young, crisp and succulent green lucerne.

Sheep No. 4.

Date.	Before feeding.	After Feeding (2 hours).			Consumption.	
	Consistency index.	Consistency index.	Type of ingesta.	Degree of bloat.	Lucerne grams.	Water ml.
25/6/52	48.0	6.8	Watery	Nil	3200	0
26/6/52	27.0	8.1	"	"	3520	20
27/6/52	30.0	5.6	"	"	3670	0
28/6/52	39.0	7.5	"	"	3430	80
30/6/52	37.7	9.0	"	"	3630	0
1/7/52	42.0	6.0	"	"	3530	0
2/7/52	60.0	15.0	"	"	-	-
4/7/52	21.0	20.0	Thick tenatious frothy	Marked	3580	0
5/7/52	19.2	21.0	"	Slight	3110	0
7/7/52	34.5	14.5	Watery	Nil	3000	100
8/7/52	60.0	12.5	"	"	3680	0
9/7/52	33.6	24.0	Frothy etc.	Slight	3910	20
10/7/52	19.2	30.0	"	"	3760	40
11/7/52	14.0	24.0	"	"	4380	0
12/7/52	66.0	25.0	"	"	4710	0

Sheep No. 4 (cont.)

Date	Before feeding.	After feeding (2 hours).			Consumption.	
	Consistency index.	Consistency index.	Type of ingesta.	Degree of bloat.	Lucerne grams.	Water ml.
15/7/52	55.0	21.0	Frothy etc.	Moderate	4730	180
16/7/52	81.0	12.5	Watery	Nil	3500	-
17/7/52	75.0	37.5	Frothy etc.	Slight	3530	0
18/7/52	45.0	36.5	"	Moderate	3790	80
19/7/52	42.5	36.5	"	Slight	3880	220
21/7/52	60.0	30.0	"	"	3870	-
22/7/52	17.5	12.0	Watery	Nil	3460	-
23/7/52	14.0	10.0	"	"	3300	-
24/7/52	60.0	20.0	Frothy etc.	Moderate	3820	-

Sheep No. 2.

Date	Before feeding.	After feeding (2 hours).			Consumption.	
	Consistency index	Consistency index	Type of ingesta	Degree of bloat.	Lucerne grams.	Water ml.
25/6/52	21.6	7.2	Watery	Nil	2900	0
26/6/52	31.2	7.5	"	"	3240	0
27/6/52	30.8	5.2	"	"	3040	100
28/6/52	45	7.8	"	"	3200	0
30/6/52	35.2	6	"	"	3610	0
1/7/52	-	9.3	"	"	2930	0
2/7/52	24.0	9.0	"	"	4450	0
4/7/52	50.0	33.6	Thick tenacious frothy	Severe	3850	0
5/7/52	38.4	50.0	"	Marked	3480	0
7/7/52	62.5	39.1	"	"	3860	200
8/7/52	45.0	66.0	"	"	3660	40
9/7/52	45.0	15	Watery	Nil	3940	40

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Sheep No. 2 (cont.)

Date.	Before feeding.	After feeding (2 hours).			Consumption.	
	Consistency index.	Consistency index.	Type of ingesta	Degree of bloat.	Lucerne grams.	Water ml.
10/7/52	70.0	45.0	Thick tenacious frothy	Marked	4090	40
11/7/52	36.5	60.0	"	"	3950	40
12/7/52	70.0	75.0	"	"	4350	20
15/7/52	60.0	69.0	"	"	3800	160
16/7/52	75.0	10.0	Watery	Nil	2450	220
17/7/52	86.0	45.0	Thick tenacious frothy	Marked	3630	0
18/7/52	36.0	90.0	"	"	3830	60
19/7/52	48.0	45.0	"	Slight	3550	40
21/7/52	60.0	37.5	"	"	2850	-
22/7/52	51.0	67.5	"	Moderate	2620	-
23/7/52	30.0	60.0	"	"	2650	-
24/7/52	84.0	60.0	"	Marked	3370	-

Sheep No. 3.

Date	Before feeding.	After feeding (2 hours)			Consumption.	
	Consistency index	Consistency index	Type of ingesta	Degree of bloat.	Lucerne grams.	Water ml.
25/6/52	90.6	6.0	Watery	Nil	1910	300
26/6/52	62.5	7.2	"	"	1740	20
27/6/52	47.6	5.0	"	"	1920	0
28/6/52	66.0	6.0	"	"	1910	60

Sheep No. 3 withdrawn from experiment - attempted operation for salivary fistulae.

Sheep No. 9. (substituted).

Date.	Before feeding.	After feeding (2 hours)			Consumption.	
	Consistency index.	Consistency index.	Type of ingesta.	Degree of bloat.	Lucerne grams.	Water ml.
4/7/52	-	116.0	Frothy etc.	Severe	-	-
5/7/52	51.0	159.0	"	Marked	2050	-
7/7/52	115.0	145.2	"	"	1110	400
8/7/52	150.0	380.0	"	Severe	1010	20
9/7/52	195.0	111.0	"	Slight	1500	60
10/7/52	171.0	210.0	"	Marked	1[illegible]30	100
11/7/52	75.0	104.0	"	"	1410	200
12/7/52	276.0	334.0	"	"	1750	20
15/7/52	150.0	180.0	"	Severe	15[illegible]0	200
16/7/52	150.0	12.0	Watery	Nil	430	-
17/7/52	161.0	30.0	Frothy etc.	Slight	[illegible]	-
18/7/52	156.0	90.0	"	Moderate	1060	-
19/7/52	130.0	86.2	"	Slight	690	-
21/7/52	41.0	60.0	"	"	1610	-
22/7/52	70.0	84.0	"	"	1620	-
23/7/52	45.0	45.0	"	"	2570	-
24/7/52	29.0	21.5	"	Moderate	3110	-
25/7/52	30.0	90.0	"	"	-	-
26/7/52	45.0	66.0	"	Marked	-	-

Sheep No. 5.

Date.	Before feeding.	After feeding (2 hours).			Consumption.	
	Consistency index.	Consistency index.	Type of ingesta.	Degree of bloat.	Lucerne grams.	Water ml.
25/6/52	54.0	9.6	Watery	Nil	3000	0
26/6/52	69.0	8.4	"	"	3520	0
27/6/52	62.5	6.0	"	"	3680	0
28/6/52	61.6	6.2	"	"	3680	0
30/6/52	46.0	6.4	"	"	3630	0

Sheep No. 5 (cont.).

Date.	Before feeding.	After feeding (2 hours).			Consumption.	
	Consistency index.	Consistency index.	Type of ingesta.	Degree of bloat.	Lucerne grams.	Water ml.
1/7/52	20.0	6.4	Watery	Nil	3500	0
2/7/52	53.0	19.2	"	"	4240	0
4/7/52	57.0	9.0	"	"	3030	0
5/7/52	45.0	14.0	"	"	3350	0
7/7/52	36.4	15.0	"	"	3430	0
8/7/52	54.0	31.0	Frothy etc.	Marked	1940	0
9/7/52	63.0	21.0	"	Slight	3390	0
10/7/52	56.0	75.0	"	Marked	3320	0
11/7/52	50.0	57.5	"	"	3700	0
12/7/52	47.5	42.0	"	Moderate	4100	0
15/7/52	66.0	17.5	Watery	"	3940	0
16/7/52	52.0	14.0	"	Nil	1980	0
17/7/52	82.5	60.0	Frothy etc.	Marked	2960	0
18/7/52	75.6	18.0	Watery	Moderate	3700	0
19/7/52	50.0	15.0	"	Slight	3610	0
21/7/52	48.0	105.0	Frothy etc.	Marked	1790	0
22/7/52	126.0	17.5	Watery	Nil	3700	0
23/7/52	36.0	15.0	"	"	3890	0
24/7/52	90.0	15.0	"	"	3980	0

Sheep No. 6.

Date.	Before feeding.	After feeding (2 hours).			Consumption.	
	Consistency index.	Consistency index.	Type of ingesta.	Degree of bloat.	Lucerne grams.	Water ml.
25/6/52	27.0	7.5	Watery	Nil	2810	0
26/6/52	37.5	7.8	"	"	3000	0
27/6/52	39.0	6.2	"	"	2970	0
28/6/52	39.0	9.6	"	"	3110	0
30/6/52	27.0	12.0	"	"	3620	0

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Sheep No. 6 (cont.).

Date.	Before feeding.	After Feeding (2 hours)			Consumption.	
	Consisten-cy index	Consisten-cy index	Type of ingesta	Degree of bloat.	Lucerne grams.	Water ml.
1/7/52	24.0	8.1	Watery	Nil	3100	0
2/7/52	24.0	20.0	Slight-ly frothy	Slight	3000	0
4/7/52	45.9	69.0	Frothy etc.	Marked	1260	0
5/7/52	22.4	84.0	"	Slight	290	0
7/7/52	25.0	40.0	"	"	3260	0
8/7/52	60.0	51.0	"	"	3000	0
9/7/52	30.0	45.0	"	"	4000	0
10/7/52	25.0	42.0	"	"	3400	0
11/7/52	25.0	30.0	"	"	3940	0
12/7/52	30.0	45.0	"	"	4300	0
15/7/52	35.0	75.0	"	Moderate	4400	0
16/7/52	41.6	12.0	Watery	Nil	3590	0
17/7/52	50.0	15.0	"	"	3680	0
18/7/52	48.0	11.2	"	"	3410	0
19/7/52	36.0	20.0	Slight-ly frothy	Full	3540	0
21/7/52	36.0	62.5	Frothy etc.	Slight	3650	0
22/7/52	70.0	75.0	"	"	3830	0
23/7/52	30.0	36.0	"	"	3730	0
24/7/52	30.0	42.0	"	"	3750	0

Sheep No. 8.

Date.	Before feeding.	After feeding (2 hours)			Consumption.	
	Consisten-cy index	Consisten-cy index	Type of ingesta	Degree of bloat.	Lucerne grams.	Water ml.
25/6/52	36.0	6.6	Watery	Nil	2680	0
26/6/52	30.0	6.4	"	"	3180	0
27/6/52	54.0	6.4	"	"	3420	0

Sheep No. 8 (cont.).

Date.	Before feeding.	After feeding (2 hours).			Consumption.	
	Consistency index.	Consistency index	Type of ingesta	Degree of bloat.	Lucerne grams	Water ml.
28/6/52	51.0	12.0	Watery	Nil	2740	0
30/6/52	42.0	7.6	"	"	3630	0
1/7/52	23.4	8.4	"	"	3260	0
2/7/52	60.0	14.0	"	"	3820	0
4/7/52	54.0	81.0	Frothy etc.	Severe	2480	0
5/7/52	45.0	149.5	"	Marked	1330	0
7/7/52	26.0	30.8	"	"	1320	0
8/7/52	36.0	21.0	"	"	2850	0
9/7/52	36.0	18.0	Watery	Nil	2950	0
10/7/52	45.0	12.5	"	"	2250	0
11/7/52	30.0	13.0	"	"	1600	0
12/7/52	78.4	16.0	"	Slight	3050	0
15/7/52	35.0	50.0	Frothy etc.	"	2770	0
16/7/52	45.0	12.0	Watery	Nil	1910	0
17/7/52	87.5	10.5	"	"	2650	0
18/7/52	30.0	9.0	"	"	2770	0
19/7/52	40.6	15.0	"	"	3270	0
21/7/52	62.5	25.0	Slightly frothy	Full	2620	0
22/7/52	50.0	36.0	Frothy etc.	Slight	2920	0
23/7/52	33.6	17.5	Watery	Nil	2980	0
24/7/52	45.0	12.0	"	"	2960	0

(X) THE OCCURRENCE OF FROTHY BLOAT AMONGST THE EXPERIMENTAL FISTULA SHEEP.

Six of the fistula sheep were fed succulent green lucerne ad lib. 18 days prior to the 23rd, June 1951. Heavy frost occurred during this time. On the 23rd. it was reported that the fistula sheep were bloating.

Sheep No.	Degree of bloat	Condition of ingesta	Consumption of green lucerne up to time of bloat.
1	Slight	Frothy and tenacious	-
2	Full only	"	-
3	Markedly	Very frothy and tenacious	840 grams
4	"	"	-
5	"	"	-
6	"	"	1780 grams.

Sheep Nos. 3 and 6 were recorded. The tracings are discussed in the text.

Sheep No. 3 showed spontaneous recovery after administration of an anti-frothing agent, which proves it to be a case of uncomplicated frothy bloat. Sheep No. 6 failed to recover spontaneously after breaking of the froth. This case was proved to be complicated by over-filling. The consumption of green lucerne by each of the two animals is evidence in favour of the fact that over-filling of the rumen is sometimes a contributory factor in frothy bloat.