Physiological Aspects of the Omasum and Abomasum

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Within the last two decades much attention has been focused on the clinical disorders of the bovine abomasum, and emphasis has been justifiably placed on the diagnosis and treatment of these conditions. Clinicians interested in disorders of the abomasum frequently feel the need to know about this structure from a physiological point of view. This review, admittedly incomplete, is designed to help re-acquaint the clinician with some of the physiological aspects of the abomasum and the omasum. A subsequent paper will attempt to interpret and relate this research information to certain clinical disorders of the abomasum.

Much of the information available on the physiology of the abomasum has been obtained from experiments with sheep; this by necessity will be cited. However, because of the possibility of physiological differences between species of ruminants, it is well to remember that A. T. Phillipson (34) has contended that "it is never wise to assume that different species of ruminants are the same." Further, it has been pointed out (5) that the abomasum is comparable to the stomach of monogastric animals. In this light, Hill (26) has stated that a "strict comparison" of the abomasum with the stomach of other animals is not justified because of the nature of the food entering the abomasum and its immediate introduction to large volumes of acid juice.

In order to more fully appreciate the events which occur in the abomasum, it is appropriate to consider briefly what occurs to the ingesta in the omasum and the nature of its introduction into the abomasum.

The Omasum

The ingesta presented to the omasum has been subjected in the rumen and reticulum to extensive bacterial and protozoal alterations. Although in the mature ruminant reticular fluid can pass directly into the abomasum (11,21), there is evidence that the omasum does produce an overall change in the character and composition of the ingesta (27). What are some of these alterations?

Stevens, *et al.* (44), with experiments in dairy cattle, have suggested that the omasum serves as a two-stage pump. The first stage, consisting of contractions of the omasal canal corresponding in time to contractions of the rumen, draws reticular contents into the omasal canal and pumps the more fluid portion into the body of the omasum. The second stage of the pump, expressing the contents from the body of the omasum into the abomasum by contractions of the body, was thought to be initiated by the omasal leaves. Becker, *et al.* (9), have indicated that at least one of the functions of the omasum is to reduce the size of the particles that pass through it.

Absorption

Hill (27) noted that workers, as early as 1910, had the impression that water was absorbed by the omasum. In view of the more recent evidence (29), it appears that this impression is fact. In a series of experiments with cows and using polyethylene glycol as a marker, Hyden (29) was able to show that 60-70% of the water entering the omasum was absorbed. This amounts to about 100 liters per day and, interestingly, appears to be similar to the volume of gastric juice added in the abomasum (29). Other investigators (21) have made similar observations in sheep. Oyaert and Bouchaert (32) observed that the amount of water absorbed by the omasum was dependent upon the molar concentration of the contents. These workers (32) also showed that carbon dioxide, sodium, potassium, and ammonia seemed to be absorbed by the omasum. Hill (27) has noted that Ebman and Sperber found that the concentration of bicarbonate was greatly reduced in the omasum. Also, it has been shown (13,21) that short-chain fatty acids are absorbed from the omasum. In sheep, this may amount to nearly 70% of the fatty acids entering the omasum. However, an appreciable amount of short-chain fatty acids enter the abomasum (13).

Flow of Ingesta

The outflow of digesta from the omasum, having a pH of about six, is continuous and dependent upon contractions of the reticulum (8,27). Phillipson and Ash (36) have noted that the volume of both the ruminal and the abomasal contents influence the rate of outflow. Apparently, not only the quantity of food in the rumen but the degree to which it is fermented influences the volume of omasal outflow; highly fermentable rations, probably as the result of reduction in dry-matter content, leave the omasum at a rate slower than diets which are not so readily fermented (36). Ash (7) has shown experimentally in sheep that the introduction of food into the rumen enhanced omasal outflow, but this response was temporarily abolished by the rapid introduction of omasal contents into the abomasum. Perhaps of clinical significance is the work of Titchen (46) who demonstrated, in sheep and goats, that distension of the omasal canal was followed by increased force and frequently of reticular contractions. However, distension of the abomasum and manipulation of the pylorus inhibited reticular contractions. It is of interest to note that an increase in the amplitude and frequency of reticular contractions has been observed when acetic, butyric, or lactic acids were introduced into the abomasum.

Ash (8) has observed, directly, the manner in which ingesta leaves the omasum in sheep and has described it as:

1. "oozes and trickles of a few ml. of fluid devoid of solid matter, and often occurring about the time of reticular contraction."
2. "gushes of 10-20 ml. containing appreciable amounts of finely divided plant material and occurring at irregular intervals but between cycles of reticular contractions."
3. "the slow extrusion and washing through of lumps of relatively solid food."

Hence, we can visualize the omasum as a grinder and an extractor preparing and modifying the ingesta from the rumen-reticulum for continuous introduction into the abomasum.

The Abomasum

In 1950, the first reports (10,19) of left displacement of the abomasum (L.D.A.) in the dairy cow were published. Initially, this disorder was considered a rarity. However, the condition was soon being described with increasing frequency from many areas of the world. As recognition of the problem grew, emphasis was placed on diagnosis and treatment. More recently, the emphasis has been on attempting to define the factors associated with the production of L.D.A., as well as other dilative disorders of the abomasum. Pinsent, *et al.* (37), are of the opinion that atony of the abomasum must be considered an essential prerequisite for the occurrence of L.D.A.

Abomasal Motility

Habel (22) has reported that abomasal motility is rather primitive and relatively simple. The body of the abomasum shows little movement (11,27) with the exception of an occasional peristaltic wave (27) or "small localized ripples" on the ventral surface (11). These "ripples" and any stronger contractions of the body were thought to be the result of contractions of the reticulum (11,27). Svendsen (45) simultaneously examined the motility of the proximal and distal segments of the abomasum in cattle. Although strong contractions were recorded near the pylorus, he found that there did not seem to be a relationship between contractions of the forestomach and motility of the abomasal segments examined. His data failed to demonstrate the passage of peristaltic contractions over the entire length of the abomasum. However, Svendsen (45) did demonstrate that when rumen fluid obtained from a cow on a high grain ration or solutions containing relatively high levels of volatile fatty acids (V.F.A.) were placed into the abomasum, a reduction in the frequency of abomasal contractions occurred.

Vagotomy and the Abomasum. Of the four compartments of the ruminant stomach, the abomasum appears to possess the greatest degree of intrinsic control over its movements (27). It is the only compartment which contains both a myenteric and a submucosal plexus (27). Duncan (16) made the assumption that the motility of the abomasum is not necessarily dependent on vagal connections. She (16) found in experiments with lambs and calves that abomasal activity after total denervation was sufficient to empty the organ but at a much reduced rate. However, Duncan (16) noted that the pylorus remained empty when the body of the abomasum became distended; she concluded that the residual motility of the denervated abomasum was insufficient to elevate intra-abomasal pressure to the level necessary to produce normal emptying. Habel (22) has extensively reviewed the results of vagotomy, by various workers, on motility of the ruminant stomach and has included his observations as well. He reported that the results of ventral vagotomy have not been uniform in the hands of different investigators. According to Habel, (22) Mangold and Klein demonstrated in sheep that ventral vagotomy caused distension of the omasum and abomasum, probably as the result of pylorospasm from unopposed sympathetic impulses. Hoflund noted similar consequences from ventral vagotomy; however, Habel (22) has pointed out that Hoflund specifically stated that the dilatation of the abomasum was in the body of the abomasum and that atony had occurred and not pylorospasm. Duncan (16) observed no effect on gastric motility from the sectioning of the splanchnic nerves. Thus, "unopposed sympathetic stimulation of sphincters" was not the case of distension (22). Hoflund, according to Habel (22), demonstrated that sectioning of the ventral trunk at the cardia and the dorsal trunk on the omasum caused fatal atony and distension of the abomasum. In contrast, Habel (22) found that neither dorsal nor ventral vagotomy caused serious disability to any of the compartments of the stomach in sheep. Total vagotomy caused distension of the rumen and reticulum but no abomasal abnormality was noted (22).

Abomasal Motility and Chemical Agents. The effects of various chemical agents on abomasal motility has been investigated by several workers. Singleton (40) studied the effects of duodenal contents on abomasal motility by introducing various solutions into the duodenum of goats. He found that solutions of hydrochloric acid (0.01N) having a pH of 2.1, proteins or their breakdown products in 2% solution or suspension, 5 ml. of a 50% emulsion of fat, or strong solutions (20-30%) of glucose produced varying degrees of abomasal inhibition. Emulsions of fat, usually following a short latent period, always produced inhibition of abomasal motility. Duncan (17) demonstrated that the independent intravenous injection of 1.0-10.0 mg. of acetycholine chloride, or the subcutaneous injection of 10-20 mg. of atrophine sulfate, in sheep, produced a cessation of activity of all parts of the stomach. The effects of the atropine were often more pronounced in the abomasum (17). The effects of histamine on the musculature of the abomasum both have been studied *in vivo* (17,28) and *in vitro* (17,39). Duncan (17) found that the intravenous injection of histamine acid phosphate in doses of 0.1 - 0.5 mg. caused an inhibition of all gastric movements. Hill (28) described what occurred to abomasal motility, in sheep, when four mg. of histamine acid phosphate was injected subcutaneously. The abomasum "became completely quiescent 60 to 75 minutes after the injection of histamine . . . and it was not until 75 to 80 minutes later that abomasal contractions began again." Both Duncan (17) and Sanford (39) demonstrated that solutions of histamine, in varying concentrations, produced relaxation of isolated muscle strips from the abomasum. It is of interest to point out that Hill (24), who induced hypoglycemia in sheep by the intravenous injection of insulin, demonstrated an abomasal inhibitory period of 30 to 40 minutes; however, when blood glucose levels fell to about 20 mg. per 100 ml. of blood, abomasal contractions occurred having, graphically, a greater height than those observed during the control period.

Abomasal Secretion

Hill (28) has stated that "the most characteristic feature of the abomasum in the adult ruminant is the continuous nature of its secretory activity . . . ." Hence, the digesta present in the abomasum, despite the frequent introduction of material having a relatively high pH, "are always of high acitity" (28). The abomasum of the cow probably secretes between 30 (25) and 100 l. (29) of gastric juice per day (28,35). This volume of gastric juice is necessary in order to deal with the continuous introduction of digesta into the abomasum (27). It would appear that the acidity and the electrolyte composition of the gastric juice in the abomasum are similar to that found in the stomach of other animals (25,27). According to Brouwer (14), von Weerden found in cattle that the juice of abomasal contents nearly always proved to be slightly hypotonic in comparison to blood. Maximal hydrogen ion concentrations, after feeding, in sheep, of 124 mEq./l. (4) to 140 mEq./l. (27,28) have been reported. von Weerden, as cited by Brouwer (14), felt that the osmotic pressure of the gastric juice was due to the content of sodium, potassium, magnesium, calcium, phosphorus and chloride. Ash (4) showed that the concentration of potassium increased and those of sodium and calcium decreased with increasing acidity. Garton (20) found that there were similar concentrations of phosphorous and magnesium in abomasal and ruminal fluids of sheep. However, there was a higher percentage of soluble calcium in the abomasal fluid than in the rumen fluid, probably due to the decreased pH in the abomasum (20). The concentration of chloride, the chief anion in gastric juice (4,27), appears to be relatively constant under conditions of frequent food intake (27). However, it would appear that the concentration of this electrolyte does increase with increasing volumes of more acid secretion (4). Abomasal secretion seems to contain little, if any, fatty acids; the pH within the abomasum, 1.5 to 3.0, is due to the hydrochloric acid content of the gastric juice (3).

Stimulation of Secretion. Factors which stimulate abomasal secretion have been described in several reports (5,6,25,28). Ash (4) could not demonstrate a marked correlation between hourly secretory rates and feeding when sheep were fed *ad. libitum*. However, fluctuations in abomasal secretory flow were observed when the animals were fed only every 12 hours (4). Fasting in sheep has caused a reduced secretory rate; but gastric juice of high acidity could still be collected (4). Hill (25) has suggested that the most important stimulus of gastric secretion, in sheep, was the passage of ingesta into the abomasum. Ash (5) demonstrated that the prevention of outflow from the abomasum did not retard acid secretion until the acidity of the abomasal contents reached a pH of two. Ash (6) later reported that distension of the abomasum by a saline-filled rubber condom stimulated acid secretion; but Hill (25) noted that moderate distension of the pyloric region provoked variable secretory responses. However, if abomasal outflow was inhibited by duodenal distension, acid secretion by the abomasum immediately stopped (25). Ash (5) concluded that inflow to the abomasum, acid secretion and outflow of digesta are normally integrated and that the acidity of the abomasal contents is an important factor in the control of abomasal secretion. Hill (25) induced hypoglycemia with insulin and observed an increase in volume and acidity of abomasal secretion coinciding with declining blood sugar levels.

Ash (6) studied the effect of introducing rumen fluid into the abomasum of sheep on acid secretion by this organ. He observed in all trials an increase in acid output which reached a maximum 45 to 90 minutes after the infusions of rumen fluid were given. Hill (25) was of the opinion that fermentation products in the rumen might act as stimulants to gastric secretion. He (25) showed that the introduction of acetic acid into the rumen caused an increase in the volume of abomasal secretion; proprionic and butyric acids also stimulated abomasal secretion but to a lesser extent. Hill (25) believed that the secretagogue effect of the fatty acids was mediated after they had been absorbed from the rumen and was not due to direct stimulation of the gastric glands. Ash (6) introduced into the abomasum buffered solutions of differing composition and observed that acid secretion was enhanced when fatty acids were present and that the degree of stimulation appeared to depend upon the concentration of fatty acids in the solution. He felt that the amount of acid secreted by the abomasum during normal feeding was influenced by the fatty acid concentration of abomasal contents and that these (VFA) might cause the release of gastric hormones.

Gastrin, the hormonal stimulant of gastric secretion (1), induces the release of both water and acid (28) from the fundic area. Gastrin seems to essentially effect the release of histamine at the parietal cells (1,28) and histamine in turn stimulates the flow of gastric juice (1).

Hill (28) investigated the secretory response of the abomasum to the parenteral administration of histamine. He found that the abomasum is very responsive to histamine and will secrete large amounts of "highly acid juice" within 15 to 30 minutes after injection. At the peak of secretory activity, the abomasum becomes completely quiescent (28), so far as motor activity is concerned.

Inhibition of Abomasal Secretion. Inhibition of abomasal secretory activity may arise from intragastric mechanisms such as an inhibition of gastrin release because of excess acidity of the abomasal contents (28). However, inhibition of abomasal secretion may also come from the duodenum and the liberation of enterogastrone stimulated by the presence of fat (28). Hill (28) has pointed out that normally dietary fats in the ruminant are hydrolyzed before they reach the duodenum; and since fatty acids inhibit gastric secretion more than triglycerides, it is very important to ascertain what level of dietary fat can be fed before inhibition of motility and secretion occurs. Unpublished work cited by Hill (28) indicates that 5% palm oil in the diet did not affect acidity or flow from the abomasum, whereas 10% palm oil produced some reduction in flow of ingesta. Yet, 5% tallow in the diet produced an increase flow from the abomasum.

Ash (6) has shown that infusions into the duodenum of saline-hydrochloric acid solutions produced a marked inhibition of abomasal secretion. Parenterally administered atropine and adrenaline also abolished abomasal secretory activity (6). Distension of the duodenum has been shown (5) to inhibit acid secretion by the abomasum.

Hill (28) summarized abomasal secretory function by stating that the volume and acidity of the secretion produced by the abomasum is influenced by the amount and composition of the material which enters the abomasum and by the relative degree to which various inhibitory mechanisms from the abomasum and duodenum participate.

In sheep, the quantity of ingesta passing to the duodenum is variable (23,31,33), but may be in the order of 8.5 to 12 l. daily (36). Harrison and Hill (23) have observed that when the frequency of feeding is increased in sheep from one to three times daily there occurred a marked increase in volume of ingesta leaving the abomasum. Phillipson (33) found that a grain ration increased the abomasal outflow in sheep. Phillipson and Ash (36) speculated that this effect could be due to greater secretion of saliva and gastric juice. The pattern of flow to the duodenum is elevated during feeding, but after feeding it subsides, decreases to a low point, and then increases before the next feeding (36). It is felt (36) that the volume of ingesta in the duodenum inhibits outflow from the abomasum and as material accumulates in the abomasum, omasal outflow is retarded. The acidity of abomasal contents entering the duodenum is high (31); and although apparently influenced by the diet (31), it varies within comparatively narrow limits (6). The pH values are usually between two and three (6,36). It would appear that the neutralizing capacities of duodenal secretions, in sheep at least, are insufficient to deal with acid contents leaving the abomasum (23). Magee (30) has pointed out that abomasal contents are apparently not neutralized until they are beyond the common bile duct. Singleton (41,42) using electromagnetic measurement methods, has shown that food enters the duodenum in gushes, but that a portion of the food entering the duodenum is returned to the abomasum. In goats 40% of the ingesta entering the duodenum is returned to the abomasum, while in sheep about 5% returns (42).

Absorption from the Abomasum

Hill (27) was of the opinion that it was unlikely that absorption of food breakdown products occurred in the abomasum. However, Phillipson and Ash (36) recently pointed out that because the fatty acid concentration of ingesta leaving the abomasum is usually one-fifth to one-tenth the rumen concentration—too great a reduction to be attributed to dilution—absorption must occur from the abomasum. Apparently glucose can be absorbed from the abomasum (47), and the abomasum can utilize glucose, but not lactic acid for energy and lipogenesis (12). Hyden (29) has shown in the cow that 37% to 66% of the water leaving the rumen was absorbed in the abomasum. Care and Van't Klooster (15) could not demonstrate a net absorption of magnesium from the abomasum of sheep. It is of interest to note that frequently more nitrogen leaves the abomasum then enters it (36). Mucus and enzymes secreted by the abomasum as well as bacterial protoplasm may contribute to this nitrogen content (36).

Abomasal Flora

It is usually assumed that rumen protozoa and bacteria are destroyed in the acid environment of the abomasum (27), with the digestion of microbial protein resulting. To an extent, this is true (27,38). Rumen protozoa are destroyed in the abomasum (27,38); however, Pounden, *et al.* (38), have concluded that the fate of rumen bacteria varied between "the extremes of complete destruction in the abomasum to passage" through the entire digestive tract of cattle. Recently, Smith (43) culturally examined portions of the gastrointestinal tract of cattle and sheep. In cattle, Streptococci and Bacteriodes organisms were cultured in large numbers from the rumen but could not be recovered from abomasal contents; however, *E. coli* and Lactobacilli were recovered from the abomasum but in reduced numbers (43). In contrast, in sheep Streptococci were isolated from both the rumen and abomasum, as were *E. coli* and Lactobacilli—all in reduced numbers (43). However, *Clostridium welchii* was found in the abomasum, but not the rumen; and Bacteriodes were not isolated from either site (43). It is worthwhile to note that in the cow, Smith (43) cultured from the caecum all organisms, with the exception of Bacteriodes, that were found in the rumen. These findings indicate that bacterial cells can successfully survive the environment of the abomasum.

The association of diseases of the abomasum with parturition and the onset of lactation has been well documented. In this light, it is of interest to note the work of Fell, *et al.* (18), who investigated the morphology and nitrogen content of the gastrointestinal tract of sheep. These workers (18) found that the wall of the "alimentary canal" fluctuated in weight and total nitrogen content during pregnancy; however, during lactation both the weight and nitrogen content rapidly and progressively increased, reaching a peak at weaning and then declining rapidly. Histologically, during advanced pregnancy the abomasal mucosa was reduced in height, slightly edematous and heavily infiltrated with globule leukocytes. By 19 to 31 days of lactation, definite hypertrophy of the mucosa were observed and showed both enlargement of epithelial cells and parietal cell hyperplasia. By the 39th to 51st day following weaning, the mucosa "presented a clear picture of regression and atrophy" containing many vacuolated and degenerating cells separated from each other by edema and numerous globule-leukocytes (18). The significance of these findings are not known (18).

Summary and Considerations

The abomasum can be envisioned as a structure having a somewhat primitive contractile pattern and the capability of secreting large volumes of acid fluid. In addition, it may have the capacity of absorbing a portion of the chemical products resulting from rumen fermentation. Both the secretory activity and the motility patterns of the abomasum can be apparently altered by the nature of the ingesta presented to it. Are these physiological aspects relevant when clinical disorders of the bovine abomasum are considered? Perhaps they are very relevant. A subsequent paper will attempt to relate research information to certain clinical disorders of the abomasum and to speculate on possible pathophysiologic processes involved.

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