15 Function of the Ruminant Forestomach

Understanding rumen function requires an understanding of the anatomy and physiology of the gastrointestinal tract, subjects so extensive as to merit books in their own right. The development of ruminant function in the young animal, the control of rumen fermentation, and the effect of diet involve an intimate integration of digestive physiology and nutrition. Students are referred to the extensive background literature on these subjects (Church, 1988; Tsuda et al., 1991). This chapter on rumen function must necessarily provide a synopsis.

Rumination is, literally, chewing of the cud, an activity limited to true ruminants and the tylopods. Foregut fermentation in nonruminants does not involve regurgitation or chewing of food. The discussion in this chapter is limited to the true ruminants; nonruminant herbivores are discussed in Chapter 5.

15.1 Development

The infant ruminant is functionally a monogastric animal with all the usual dietary requirements for vitamins and amino acids characteristic of nonruminants. Calves, and most likely the young of other ruminant species, lack sucrase and secrete limited amounts of amylase, and so are unable to use sucrose and starch. Thus milk replacers must be based upon glucose or lactose. The infant depends on its mother's milk until the development of ruminant fermentation allows digestion of carbohydrates other than glucose and lactose. The ability of the lower tract to utilize starch develops later.

The blood sugar concentration of infant ruminants is similar to that of nonruminants. As the animal grows, this level declines to the adult level and the rumen attains and develops fermentation. The two processes do not seem to be interdependent, as blood sugar declines even when the development of ruminant function is prevented.

At birth the rumen is essentially undeveloped and forms only a small proportion of the total stomach (Table 15.1). The increase in relative size of the reticulorumen rises from 25–35% at birth to 62–80% in the adult. At the same time the lower digestive tract is proportionally diminished (Section 17.2). Rumen development depends on access to a fibrous diet and inoculation by rumen bacteria. Specifically, rumen wall development depends on stimulation by volatile fatty acids (VFA), whose production requires the requisite bacteria and substrate.

If calves are maintained on a milk diet, rumen development can be greatly retarded. Leakage of milk into the rumen promotes a lactic acid type of fermentation with little VFA production. Suckled milk is bypassed to the abomasum via esophageal groove closure. This reflex is elicited by suckling and other stimuli. It has been possible to train lambs to retain this ability into adulthood (Ørskov et al., 1970). This function seems to be retained in adult selector ruminants (Hofmann, 1989).

In adults, the reticulorumen is the largest stomach compartment (Table 15.1). The omasum in sheep, goats, and many African antelope is relatively smaller than in cattle (Hofmann, 1973). The omasum seems more significant in reports of tissue weight because the amount of tissue per unit volume is much larger relative to that of the reticulorumen because of its internal structure.

R. G. Warner and W. P. Flatt (1965) elucidated the mechanisms that stimulate rumen development. Placing sponges or some other coarse material that simulates hay in the rumen of calves has no effect on development, which is characterized by the proliferation of the rumen wall and the development of papillae (Figure 15.1). Development *can* be elicited by placing dilute buffered solutions of VFAs in the organ. Butyrate is more effective in this regard than propionate, followed by acetate. This order is the same as that in which the acids are known to be metabolized by the rumen epithelium. The rate of VFA absorption is markedly influenced by rumen development. This difference is probably a function of both VFA concentrations and epithelial surface area.

Table 15.1. Stomach compartment sizes in young and adult ruminants

	Body weight	Reticulorumen		Omasum		Abomasum	
	(kg)	(g)	(%)[a]	(g)	(%)[a]	(g)	(%)[a]
Cattle							
Birth	24	95	35	40	14	140	51
Adult	325	4540	62	1800	24	1030	14
Deer							
Birth	4	9	25	2	6	25	69
Adult	67	1010	80	102	8	145	12
Sheep							
Birth	6	19	32	5	8	36	60
Adult	62	919	73	119	9	226	18

Source: Adapted from Lyford, 1988.
[a]Percentage of the total stomach.

15.1.1 Inoculation

Young ruminants probably acquire rumen bacteria mainly through feed and interanimal contact. Anaerobic bacteria similar to those found in the rumen occur in nature, particularly in manure and soil. Despite the sensitivity of many rumen organisms to temperature and oxygen, they can be transferred via saliva and feed from one animal to another and escape down the digestive tract to inoculate the lower tract of ruminants and nonruminants alike. Inoculation probably depends on the survival of only a few cells. It is not possible to prevent the ultimate development of the rumen or intestinal fermentation merely by isolating an animal, although isolated calves may not develop the correct protozoa. Some years ago there was a flurry of studies on rumen inoculation as a method of hastening rumen development; however, no consistent advantage of inoculation was ever established.

The concept of manual inoculation emerged from the notion that rumen malfunction might be caused by a defect in the microbial population. Rumen populations tend to be similar in animals on a given diet, although many microbe species may occur in relatively small numbers, and any of these may respond to a dietary change. The presence or absence of a certain organism is determined by its access to favorable

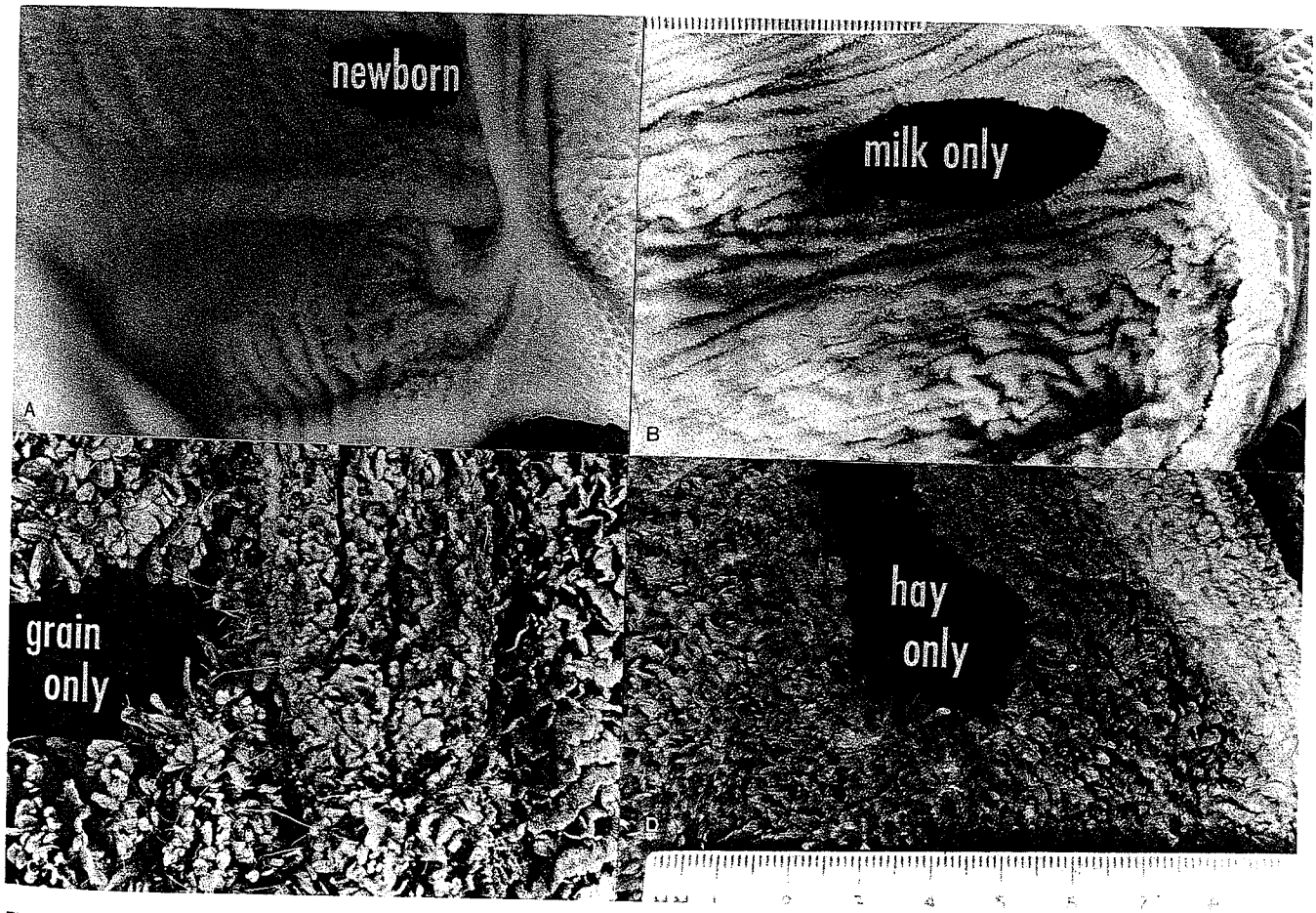

Figure 15.1. Photographs of rumen wall showing the ventralmost portion of the cranial dorsal sac just caudal to the reticuloruminal fold. The reticuloruminal fold and reticulum are visible in the righthand portion of each picture. (A) Newborn. (B) Milk-fed to 13 weeks. (C) Grain-fed to 13 weeks. (D) Hay-fed to 13 weeks. (Photos courtesy of R. G. Warner; see also R. G. Warner and Flatt, 1965.)

growth conditions (Hungate, 1966). Existing bacteria can adapt or mutate to accommodate a new substrate and changes in rumen conditions. The normal adaptation period is about one to two weeks. Evidence that inoculation can have a positive effect does exist. For example, in the case of abrupt dietary change from hay to concentrate, rumen adjustment is facilitated by inoculation with rumen contents from an animal already on the diet. Another example is the case of fasted ruminants in which the microbial population may be diminished. Inoculation at the time of refeeding may establish a normal rumen pattern more quickly than in uninoculated animals.

An additional question concerns the probability of differences among microbial populations in widely dispersed animals. Hungate (1966) summarized the evidence for the presence and absence of certain protozoa in New Zealand ruminants. Differences among flora in the digestive tracts of various herbivore species also occur, but many such differences may be accounted for on the basis of different habitats and dietary characteristics of the species (Chapter 16).

15.2 Anatomy

In popular parlance, ruminants are given credit for having four stomachs. In reality they have but one, which is divided into several compartments, the exact number depending on the species. The true ruminants, including sheep, cattle, goats, deer, and antelope, have four compartments. The tylopods—camels, llamas, and related species, often considered pseudoruminants —have a three-compartmented stomach, the omasum being absent.

Figure 15.2 shows the lateral and medial surfaces of the ruminant stomach. The four compartments, in the order of general discussion, are the rumen, reticulum, omasum, and abomasum. The rumen and reticulum, often considered a single organ (reticulorumen), are separated by the reticuloruminal fold. The separation is only partial; free exchange of contents is still possible. It is in these two sacs that the major portion of fermentative activity and absorption of nutrients occurs. The reticular fold is probably an important sorting device for heavier matter that has sunk to the bottom of the rumen. Whole corn and items of high specific gravity (mostly foreign objects) land predominantly in the cranial sac of the rumen. The cranial pillar prevents their passage into the rest of the rumen. At the time of the next cycle, cranial sac contraction dumps them into the reticulum, where they remain due to the reticuloruminal fold.

The total stomach occupies approximately three quarters of the abdominal cavity, from the seventh or eighth rib caudally to the pelvis. It occupies much of the left half of the cavity but extends over the median plane to the right. Its dorsal surface is suspended from the sublumbar muscles and by peritoneal and connective tissue.

Pillars divide the rumen into discrete sacs. During contraction (shortening) of these pillars, sacs become

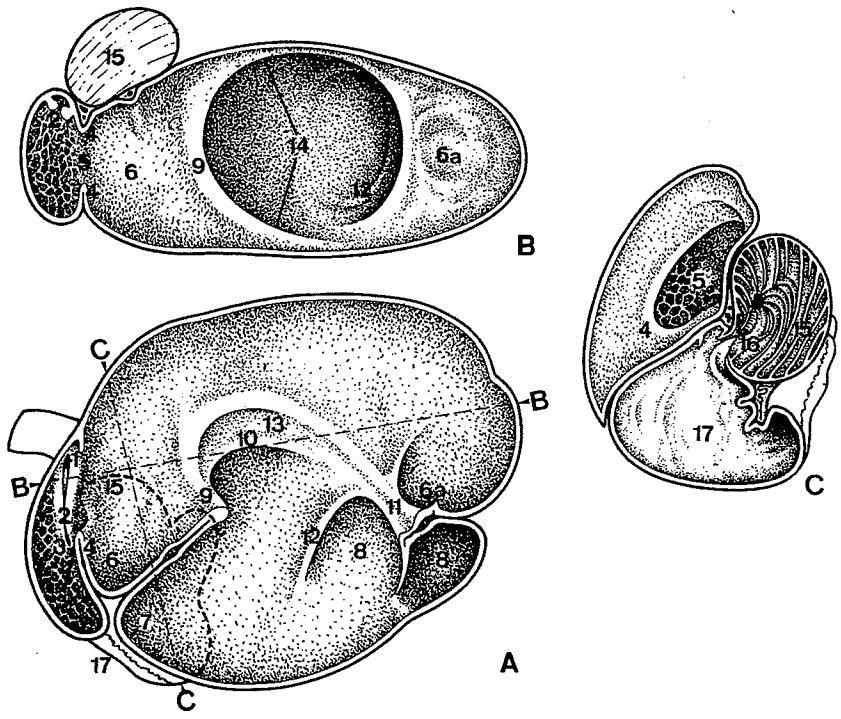

Figure 15.2. The ruminant stomach (from Hofmann, 1988). (A) Longitudinal section, left side. (B) Horizontal section along axis B–B in (A). (C) Transverse section along plane C–C in (A). Structures and compartments are as follows: (1) cardia, (2) reticulo-omasal groove, (2a) reticulum, (3) reticulo-omasal orifice, (4) cranial sac of rumen, (5) dorsal sac of rumen, (6) caudodorsal blind sac, (7) ventral sac of rumen, (8) caudoventral blind sac, (9) reticuloruminal fold, (10) cranial pillar, (11) right longitudinal pillar, (12) caudal pillar, (13) dorsal coronary pillar, (14) ventral coronary pillar, (15) omasum, (16) omasal canal, (17) abomasum. See Sisson and Grossman, 1953, and Sellers and Stevens, 1966, for more information.

smaller and the more liquid ingesta are circulated and generally forced upward through the floating mat of more solid ingesta. Although it is part of the fermentative mechanism, the reticulum is frequently the site for the accumulation of foreign objects such as hardware because of its proximity to the cardia and its generally ventral position. The esophagus terminates at the cardia, which is at the juncture between the reticulum and the rumen. The esophagus also serves as the cranial end of the reticular (esophageal) groove, which, in the adult bovine, extends for 17–20 cm ventrally to the reticulo-omasal orifice.

The forestomach compartments (rumen, reticulum, and omasum) all originate from the same embryological tissue. The organs are lined with nonglandular, non-mucus-producing, keratinized stratified squamous epithelial tissue. As such, the forestomach was long considered incapable of absorbing anything, but today it is recognized as a major site of nutrient absorption. The rumen is lined with finger-like projections called papillae which vary in shape and size (up to 1.5 cm in length). They are larger and denser in the ventral regions where nutrient concentration, and therefore absorption, is most pronounced. The surface of the reticulum contains elevations that provide compartments of four to six sides resembling a honeycomb.

15.2.1 Nerve and Blood Supply

The stomach is innervated by the vagus (both sensory and motor pathways; see Figure 15.3) and sympathetic nerves. The rate of reticuloruminal contractions is controlled by distension of the reticulorumen through reflexes, by the sight of food, and by rumination, all mediated via the vagal nucleus in the brain. Under physiological conditions, abomasal distention inhibits only omasal motility (Sellers and Stevens, 1966). Thus the rate of reticulorumen contractions can be increased by reticular distension. Conversely, abomasal distension suppresses reticuloruminal contractions and abomasal secretion of acid. Iggo and Leek (1970) identified tension receptors in the medial wall of both the reticulum (near the reticular groove) and the cranial-dorsal sac. There are also chemical receptors in those sites which respond to pH.

The blood supply to the forestomach originates from the abdominal aorta by way of the celiac-cranial mesenteric trunk (Figure 15.3). This artery enters the rumen between the esophagus and the mid-dorsal sac. Four branches then feed to the various parts of the rumen as follows: (a) the common hepatic artery supplies the cranial surface and also the pancreas, liver, and gall gladder; (b) the right ruminal artery supplies the right rumen surface plus the pancreas and omentum; (c) the left ruminal artery supplies the left rumen surface plus the reticulum and esophagus; and (d) the

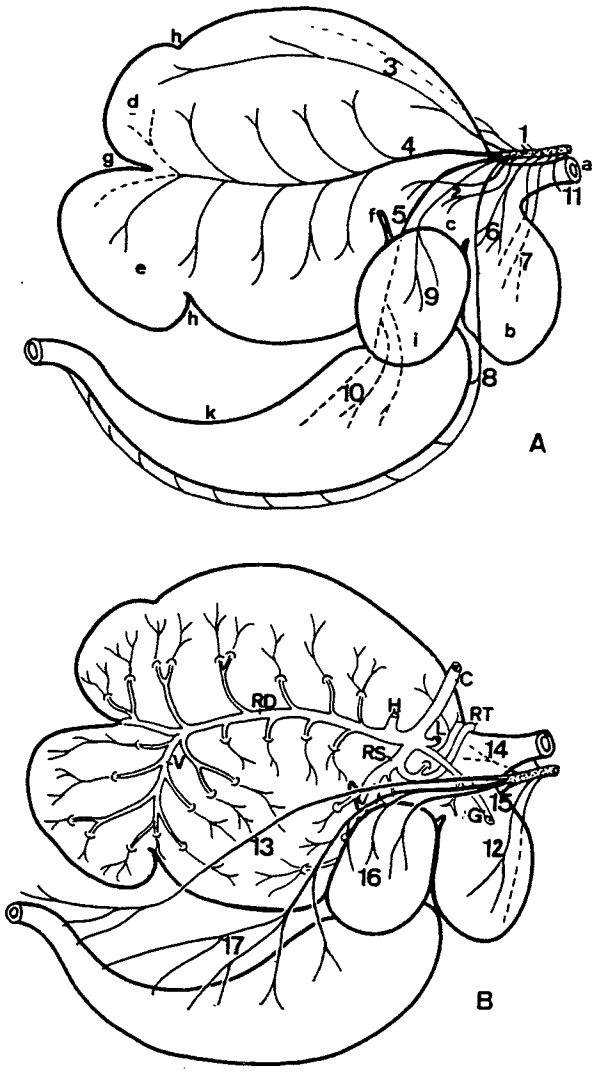

Figure 15.3. Distribution of nerves and blood vessels on the right side of the ruminant stomach (from Hofmann, 1988). (A) Dorsal vagus trunk. (B) Ventral vagus trunk and arteries. Rumen nerves, blood vessels, and lymph nodes are lodged in the grooves; those of the other compartments are in the mesenteries (omenta). Vagal branches: 1–11 in (A), 12–17 in (B). Arteries: C = celiac; G = left gastric; H = hepatic; L = lienal; RD = right ruminal; RS = left ruminal; RT = reticular (supplies atrium also); V = right ventral coronary.

left gastric artery supplies the omasum and abomasum. Venous drainage is by way of four veins: the right ruminal, left ruminal, omaso-abomasal, and reticular veins. All empty into the hepatic portal vein, which feeds directly into the liver.

15.2.2 Rumen Wall Structure and Musculature

The reticuloruminal wall (Figure 15.4) consists of a serous membrane, a muscular tunic, and the epithelium. The epithelium is the site of absorption, active transport of sodium and chloride, and passive transport of VFAs, water, and other substances such as urea.

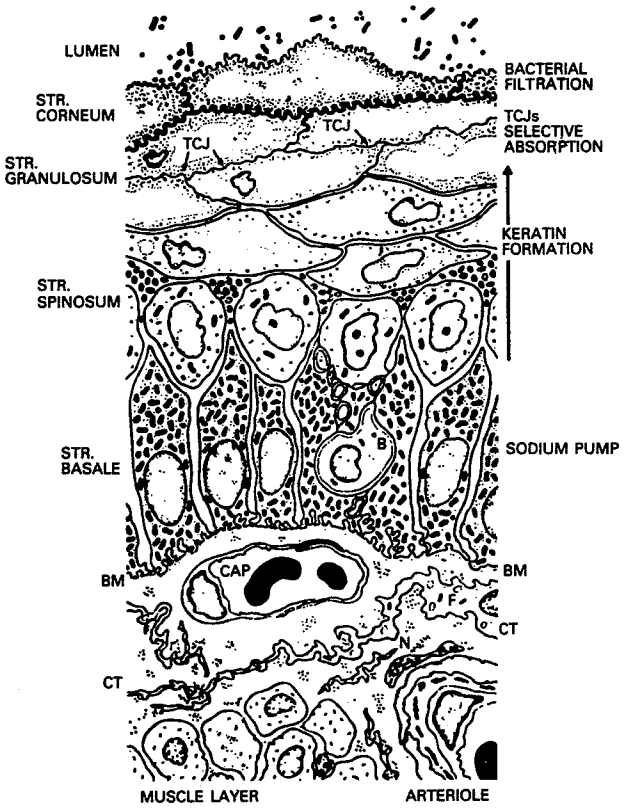

Figure 15.4. Cross section of the fully developed rumen wall depicting the types of cells and layers present (from D. H. Steven and Marshall, 1970). Details of the cell junctions are omitted. B = branching cell; BM = basement membrane; CAP = capillary; CT = connective tissue; F = fibroblast; N = nerve trunk; TCJ = tight cell junction.

The rumen musculature consists of two layers: the ruminal pillars are foldings of the oblique muscle layers, and the reticular groove consists of internal muscle fibers running along the length of the groove and forming a loop around the cardia (Hofmann, 1988).

The cells of the ruminal surface tend to be keratinized and have some of the character of ordinary skin, but the ruminal surface differs from skin in its electrical resistance and its permeability and transport qualities. The keratinization is normally offset by specialized cells that are important in absorption of VFAs. Specialized bacteria also adhere to the rumen wall and are involved in its metabolism.

15.2.3 Surface Structures

The luminal surface includes papillae in the rumen and reticular ridges in the reticulum. The papillae in-

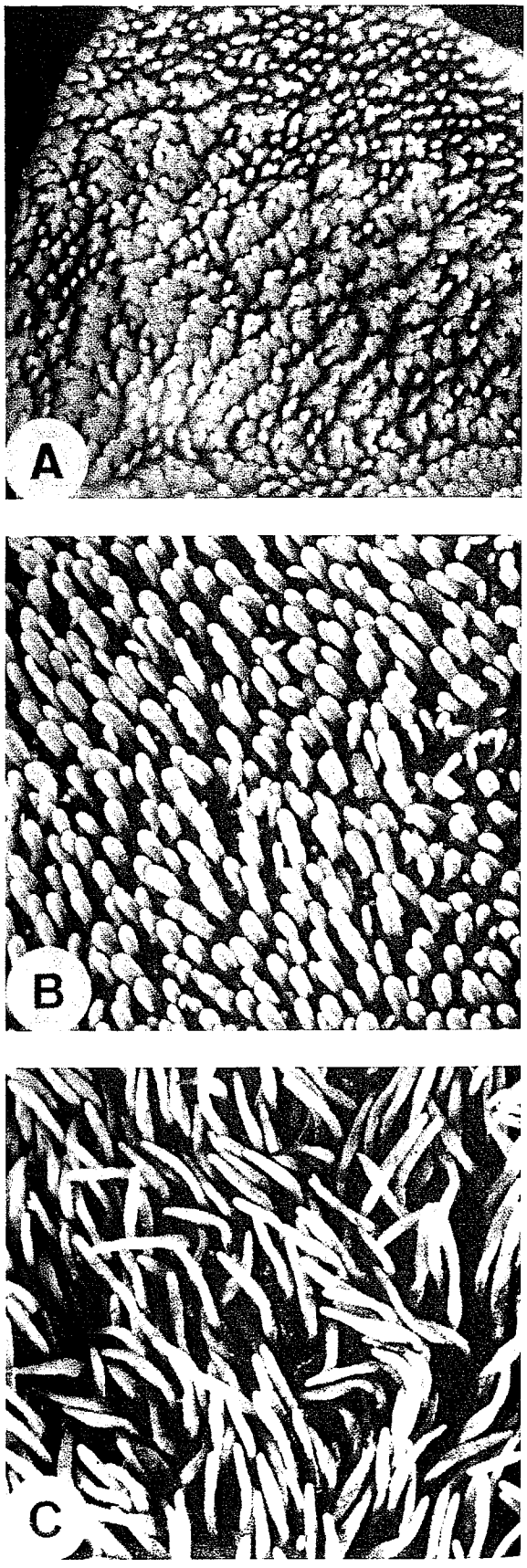

Figure 15.5. Filiform ruminal papillae (oval or circular cross section) are indicative of unstimulated ruminal blood flow and lack of butyric and propionic acids. (A) Atrium papillae of a one-day-old goat kid (intermediate feeder). (B) Dorsal wall papillae of a roe deer (concentrate selector; winter). (C) Atrium papillae of a Bohor reedbuck (grazer; drought); also called "hunger papillae." (From Hofmann, 1988.)

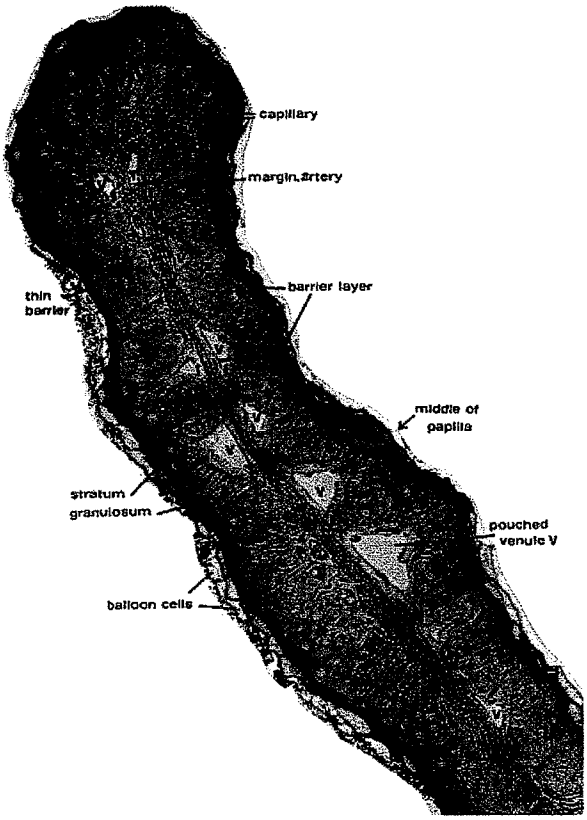

Figure 15.6. Microstructure of an absorptive ruminal papilla (semithin transverse section, ×97 (from Hofmann, 1988). Note the few epithelial cell layers with denser barrier and superficial balloon cells containing ruminal bacteria, and the extensive vascular system (mainly venules with fenestrated endothelium; i.e., absorptive type).

crease the absorptive surface of the rumen. The reticulated surface of the reticulum may be involved in the sorting and handling of particles that pass near the reticulo-omasal orifice.

The papillae differ among animals of the same species on different diets as well as among species with different feeding strategies. In cattle, the papillar structure is apt to degrade under conditions of high-concentrate feeding, leading to parakeratosis (Section 15.7.3). Starvation also reduces the papillae (Figure 15.5). The internal structure of a papilla is shown in Figure 15.6. Generally, concentrate selectors, which harbor higher VFA concentrations than grazers (Chapter 4), have more papillar surface (in a smaller rumen) that is more generally distributed. The state of the papillae and their surfaces are described by the surface enlargement factor, which is calculated as twice the papillary surface area divided by the basal surface area (Hofmann, 1988).

15.2.4 The Omasum

The omasum, the third compartment, is characterized by the presence of a large number of leaves

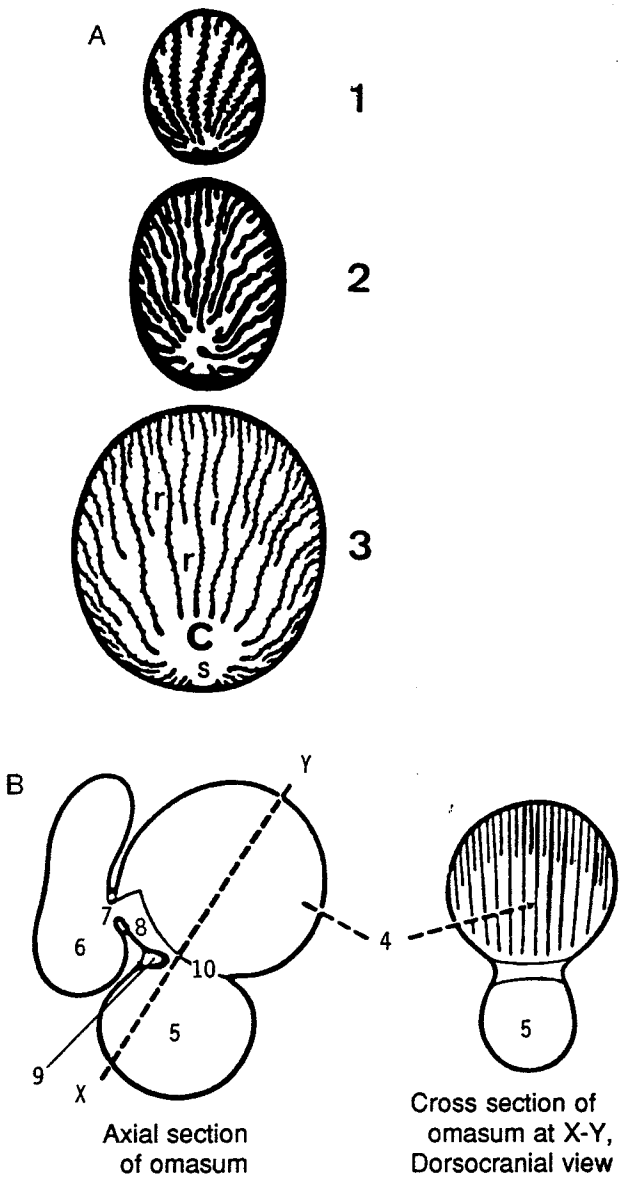

Figure 15.7. (A) Cross sectional of the omasum from a concentrate selector (1), an intermediate feeder (2), and a grazer (3). Note interlaminar recesses (r), omasal canal (C), and omasal groove (s). (From Hofmann, 1988.) (B) Axial and cross section of the omasum; X–Y indicates plane of reference. Structures visible include omasal body and lamina (4), abomasum (5), reticulum (6), reticulo-omasal orifice (7), omasal canal (8), omasal pillar (9), and omaso-abomasal orifice (10). (Modified from Sellers and Stevens, 1966.)

(Figure 15.7), which may absorb some water and nutrients and prevent passage of large particles of digesta. Much fluid can bypass the omasum via the omasal canal if the esophageal groove is closed. One of the omasum's major functions is to pump digesta from the reticulum into the abomasum (C. E. Stevens et al., 1960).

The omasum, which is peculiar to the true ruminants, is a small, compact, oval organ connecting the

Table 15.2. Omasum contents (dry weight as percentage of body weight) for five ruminant species in the wet and dry seasons

	Wet season		Dry season	
	Mean	SE	Mean	SE
Thomson's gazelle	0.007	0.008	0.028*	0.008
Grant's gazelle	0.006	0.008	0.032*	0.007
Kongoni	0.069	0.011	0.132*	0.011
Wildebeest	0.122	0.010	0.274*	0.011
Steer	0.203	0.011	0.535*	0.011

Source: Reed, 1983.
*$P < .05$.

reticulorumen to the abomasum. In true ruminants the arrangement of the organs is such that ingesta flow from the reticulo-omasal orifice through the omasal canal to the omasal-abomasal orifice and into the abomasum. The reticulo-omasal orifice is adjacent to the posterior end of the esophageal groove, so that when the groove is closed, ingesta can pass directly to the omasum and bypass the reticulorumen (Figure 15.2). The interior structure of the omasum consists of leaves attached to the distal wall relative to the neck of the organ. The omaso-abomasal orifice has no sphincter to limit backflow, although contraction may allow the folds of the omasum to act in this way.

The omasum has received much less attention than the reticulorumen, and as a result, its role is not entirely clear. It may serve as a filter pump to sort out the liquid and fine digesta for passage on to the abomasum. The filtration is conducted by leaves attached to the distal wall, which do not allow coarse fiber to enter the distal portion of the organ.

The relative size of the omasum varies among ruminant species. It is generally smaller and perhaps less functional in concentrate selectors (Hofmann, 1989) and also in smaller ruminants. The logarithmic association with body weight is considerably greater than 1 (Reed, 1983). Thus the sheep's omasum is both actually and relatively smaller than that of bovines (Table 15.1). The difference is also apparent in African antelope, which show seasonal changes in omasum size that depend on diet quality (Table 15.2).

In cattle, the omasum is probably an absorptive organ. As much as 30–60% of the water entering the organ is absorbed, along with a considerable amount of VFAs (40–69%), sodium, potassium, and other ions. The principal effect of this action is to reduce the net volume entering the abomasum and remove VFAs (lowering their concentration). The absorptive role may be less important in sheep, goats, deer, and antelope, in which the organ is relatively smaller (in proportion to body size). Perhaps omasal function is more important in grazing species that require this anatomical development to process the large quantities of fiber they consume.

Small concentrate selector ruminants are intolerant of high-fiber diets, which, if imposed, lead to impaction of the omasum (Hofmann, 1973). Impaction of the omasum has also been observed in cattle fed high levels of coarse rice hulls.

15.3 Eating and Ruminating

Ruminants tend to ingest feed rapidly and to ruminate it later. Feed is ingested, chewed, mixed with saliva, and rolled as needed to form a bolus, which is swallowed and ejected with some force into the anterior rumen. The time spent eating is affected by the nature of the feed or forage and the time required to prehend it and reduce it to a swallowable bolus. Concentrates or pellets, being denser and already in a relative fine state, are eaten more rapidly than coarse forage, which requires more chewing. The morphology of the forage also affects the prehension and selection of food for ingestion. Forage or browse that must be picked leaf by leaf limits the eating rate. Browsers are

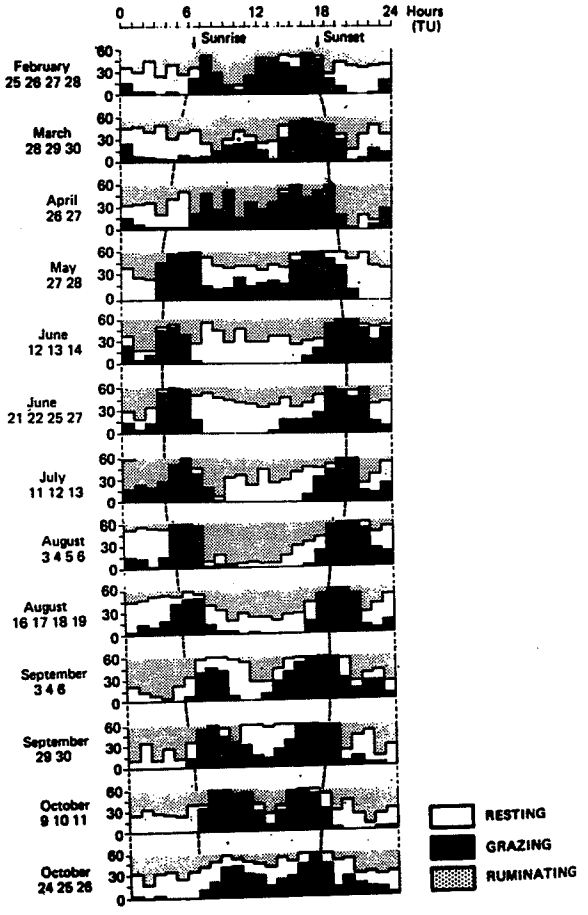

Figure 15.8. Circadian pattern of activities in grazing sheep (from Arnold and Dudzinski, 1978). White areas indicate resting; black areas, grazing; and stippled areas, ruminating.

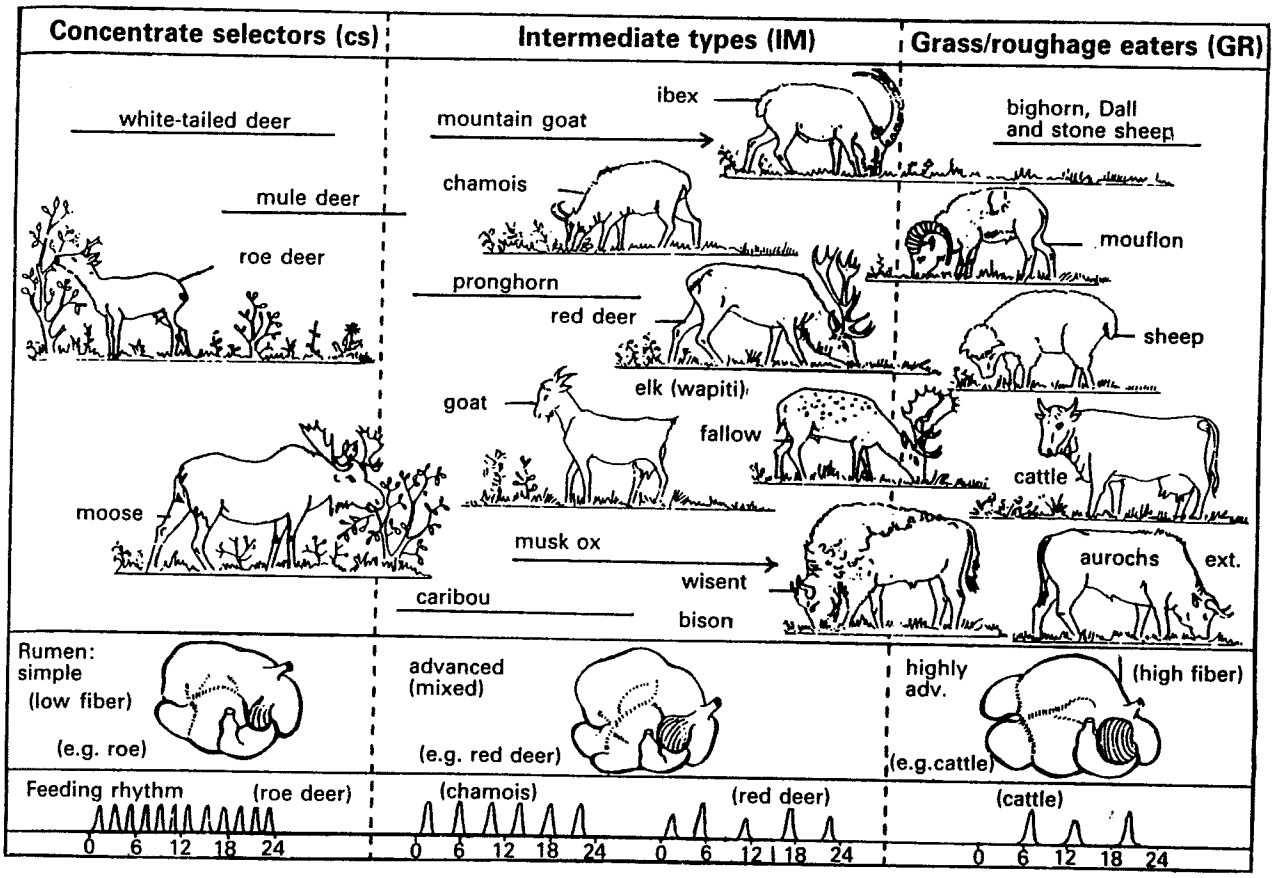

Figure 15.9. The position of European and North American ruminant species along the continuum of morphophysiological feeding types (from Hofmann, 1988). The farther the baseline of a species extends to the right, the greater its ability to digest fiber in the rumen. Feeding on plant cell contents implies shorter intervals between meals since the simple rumen of concentrate selectors (CS) has fewer food passage delay structures than that of grazers (GR).

much more efficient at picking their food than are grazers.

The eating rate and the total time spent eating affect the way time is distributed among eating or grazing, subsequent rumination, and other activities in the day of a ruminant (Figure 15.8). An increase in time spent on eating and rumination necessarily decreases time spent on other activities. The diurnal pattern is also affected by day length and season.

If the ingestion rate is slow, fermentation is continuous and there are no peaks in acid production. Rapid eating allows more material to be fermented simultaneously. Rapid ingestion thus results in a more synchronized peaking of fermentation and an acid production that must be balanced by buffering mechanisms, the most important of which is ensalivation.

Eating and rumination frequency patterns vary among ruminant species according to feeding habit (Hofmann, 1989). Concentrate selectors tend to have simpler rumens and eat and ruminate frequently (Figure 15.9). In very small antelope such as the suni and dik-dik, eating and ruminating are distributed almost evenly over the entire daylight period (Hoppe, 1977). The longer-spaced diurnal patterns of rumination are more characteristic of the larger grazers, while intermediate feeders fall between concentrate selectors and grazers in behavior (Figure 15.9).

A reason for this variation in behavior is that concentrate selectors eat a high-quality diet leading to much higher VFA production rates. Eating constantly allows the animal to avoid peaks of acid production that could be pathological. It may be that the function and purpose of rumination in small concentrate selectors is primarily to regulate the rate of release of nutrients for fermentation. These animals tend to consume whole seeds, fruits, and small plants, and the lack of chewing, which means that cell surfaces are not punctured, both limits and regulates the fermentation rate and VFA production.

15.3.1 Rumination

Rumination is the postprandial regurgitation of ingesta followed by mastication, reforming the bolus, and reswallowing. The process is cyclic and is closely integrated with reticuloruminal motility (or cycles; see

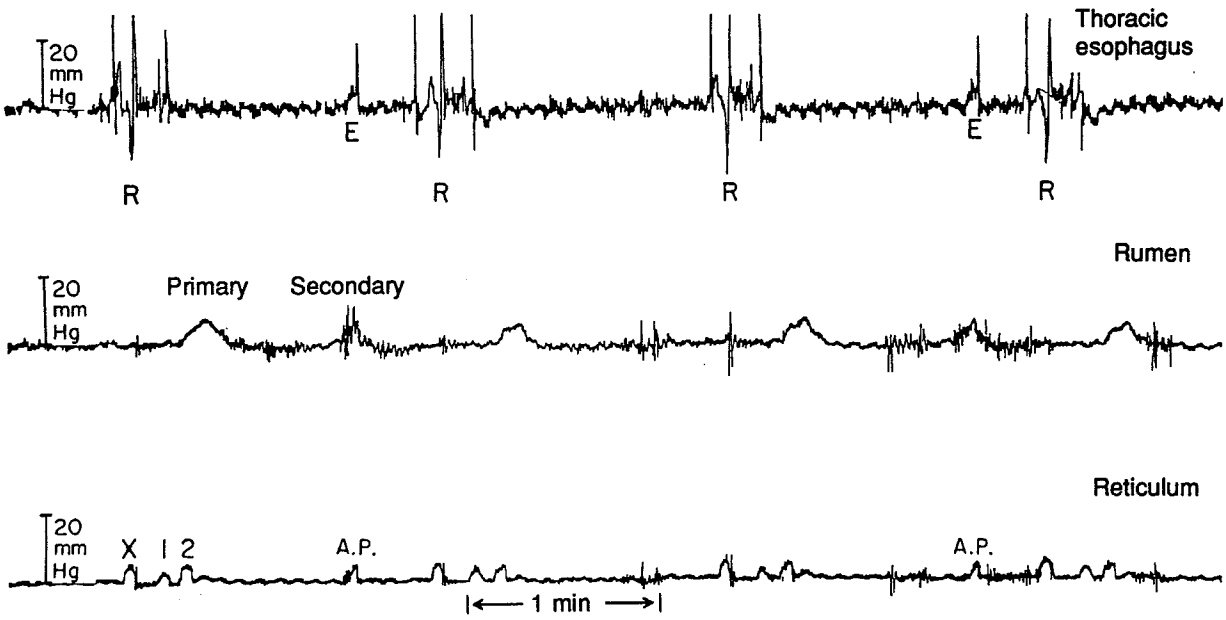

Figure 15.10. Pressure recordings of three complete cycles of reticuloruminal contractions during rumination (from C. E. Stevens and Sellers, 1968). The double reticular contraction (1 and 2) and primary and secondary rumen contractions are evident in the first cycle, as is the extrareticular contraction associated with regurgitation (X). The esophageal pressure changes during regurgitation (R) consist of a small positive pressure wave followed by a negative deflection due to inspiration against a closed glottis, and then, immediately, a large positive deflection due to antiperistaltic esophageal contraction. Regurgitation is usually soon followed by deglutition (not labeled) of the fluid expressed from the bolus at the beginning of mastication. A wave of deglutition, carrying the bolus to the rumen, is also visible on the esophageal trace at the end of each cycle of rumination and just before the next regurgitation. Note the close integration of the rumination and reticuloruminal cycles. Eructation (E) and the associated increase in pressure due to abdominal press can be seen on the reticular trace (A.P.) and also superimposed on the secondary wave of rumen contraction.

Figure 15.10). Rumination commences with an extrareticular contraction, which concentrates digesta and fluid near the cardia. At the same time an increased inspiration of air against a closed glottis reduces the pressure in the thoracic esophagus (Sellers and Stevens, 1966). Ingesta are thus sucked into the esophagus and then moved by rapid antiperistaltic esophageal contractions to the mouth, where excess liquids are swallowed and mastication commences. Mastication reduces particle size, extracts soluble contents with saliva, and enriches the fiber content of the bolus. The chewed mass is remixed with saliva, reformed into a bolus, and swallowed (Schalk and Amadon, 1928; Church, 1975). The cycle is repeated but may be interrupted by other activities.

More time is normally spent chewing during rumination than during eating. Also, the rate of chewing is generally slower and more deliberate during rumination, with more time spent per unit of ingesta. Chewing patterns as related to eating, drinking, and rumination are shown in Figures 15.11 and 15.12. Chewing activity is more intense initially and diminishes as the bolus is masticated. The amount of time spent ruminating is influenced by the nature of the diet and appears to be proportional to the cell wall content in coarse forages. Feeding concentrates or finely ground or pelleted hay may greatly reduce rumination time (Figure 15.13), and feeding forages with high cell wall content tends to increase the rumination time. Increasing the intake tends to reduce the time spent ruminating per gram of

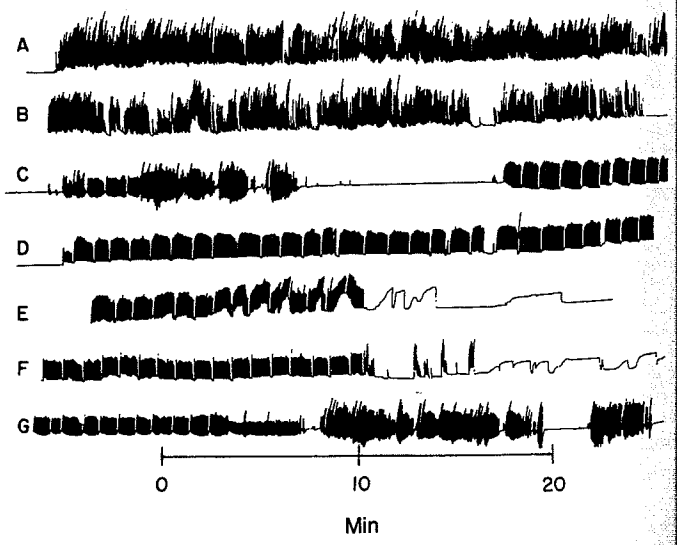

Figure 15.11. Patterns of eating and rumination in cattle (courtesy of J. G. Welch, University of Vermont). (A and B) Eating sequence; each oscillation represents a jaw movement. Eventually the animal begins to tire (B and C). (C) Mixed rumination and feeding is followed by a lapse and more rumination. (D) The onset of rumination in a different animal. (E and F) Termination of rumination followed by drinking. (G) Termination of rumination followed by a return to feeding. The average for each bolus is 62 chews in 56 sec. Individual rumination periods are highly variable and may last up to 2 h.

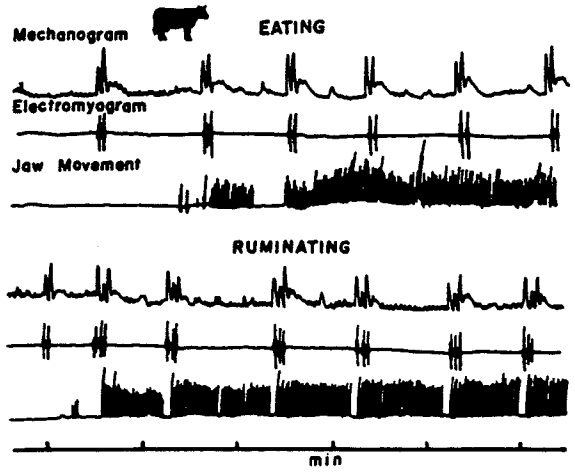

Figure 15.12. Pressure recordings, electrical activity, and jaw movements detected by pressure changes in a balloon fixed on the halter of a cow starting to eat hay (above) and ruminating (below) (from Ruckebush, 1988).

feed, a factor probably responsible for the increase in mean size of fecal particles at higher intakes. The total amount of time sheep and cattle ruminate seems to have an upper limit of about 10–11 h per day (Bae et al., 1979; Welch, 1982). This limit along with time spent eating are probably factors limiting consumption of coarse forages.

Rumination appears to be induced by sensors in the rumen wall, which is innervated principally by the dorsal trunk of the vagus nerve. Sectioning the nerve abolishes the response. Rumination can be stimulated by tactile means or by the pressure of coarse material; hence, the popular term *scratch factor* to describe the dietary characteristic probably responsible for inducing normal rumination. Lack of stimulation may be responsible for the low level of rumination in animals on concentrate and pelleted diets. The scratch factor is related to both particle size and cell wall content of the diet. Plastic or other devices added to concentrate feed or placed in the rumen have had variable success as rumination stimulators. The sites of maximal sensitivity are in the cranial sac of the rumen and regions of the reticulum.

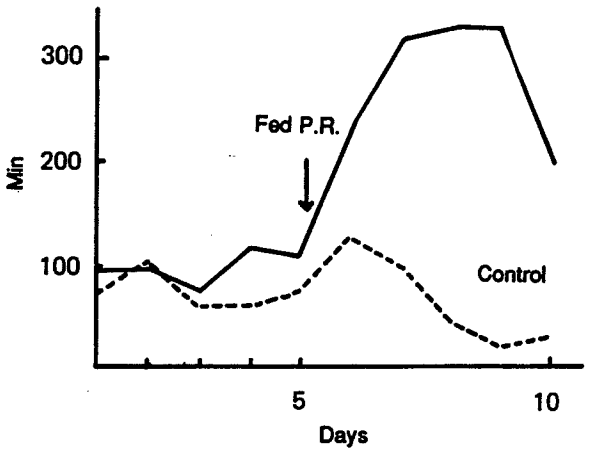

Figure 15.13. Rumination time in minutes of sheep fed 50 g/day of 5-cm-long polypropylene ribbon for 3 days compared with controls fed no polypropylene (from Welch and Smith, 1971). All animals received 400 g/day each of both alfalfa meal pellets and pelleted concentrate during the treatment period. Four rams were used in a single reversal design with 60 days between periods 1 and 2.

15.3.2 Rumen Motility

Contraction and relaxation of the reticulorumen wall and pillars move and mix the ingesta. The motion can be divided into primary contractions, which affect the whole reticulorumen, and secondary movements, which affect only a part of the organ (see Figures 15.14, 15.15, 15.16, and 15.17). The motions require up to 50 sec to complete and occur in total cycles whose length depends on the activity of the animal: whether eating, ruminating, resting, and so on. Church (1975) described representative patterns for bison, cattle, deer, sheep, and goats.

Primary contractions associated with ruminal mixing begin with an initial sharp contraction of the reticulum and reticuloruminal fold followed by a second, more powerful contraction of the reticulum, with the wave of contractions passing over the rumen. This raises the cranial sac and causes the cranial pillars and the caudal and dorsal coronary pillars to contract, and also compresses the dorsal sac of the rumen (partly by contraction of the longitudinal pillars).

Rumen mixing and rumination together promote the turnover of indigestible residues, which, if allowed to accumulate, would clog the rumen. Material requiring further rumination is selectively regurgitated; finer material and liquid are allowed to flow from the rumen through the reticulo-omasal orifice. It has been commonly supposed that the size of the omasal orifice sets the limit on passage, but the selection of finer material probably occurs through other sorting mechanisms such as occlusion of coarse matter in the floating mat of fiber. A finely ground diet increases the rate of passage and results, paradoxically, in an increase in mean size of particles in the feces. The positive effect of adding a small amount of coarse fiber to a concentrate diet may be related to reestablishment of the mat and its consequent stimulation of the rumen wall and sorting of rumen particulate matter.

15.3.3 Particle Size Reduction

Most of the published observations regarding the effects of diet on the rate of passage have been determined with the stained particle technique as described by Balch (1950) and others. Although this method

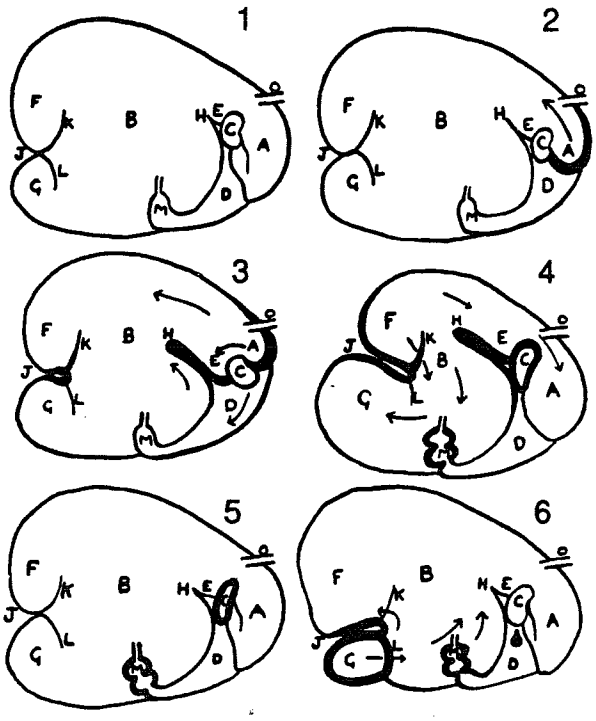

Figure 15.14. The movements of the stomach, shown from the right side (from Phillipson, 1939). (1) The stomach at rest. (2) The reticulum in the first stage of its contraction. (3) The reticulum in the second stage of its contraction. The anterior blind sac of the rumen is relaxed; the anterior and posterior longitudinal pillars are contracting; the omasum is moved downward and forward and the body of the abomasum is lifted up. (4) The reticulum is relaxed. The anterior blind sac of the rumen is contracted; the anterior and posterior longitudinal pillars of the rumen are fully contracted, as are the dorsal and ventral blind sacs of the rumen; the ventral and dorsal blind sacs are relaxed. The omasum is pear-shaped. Strong waves of peristalsis appear in the pyloric antrum of the abomasum. (5) The stomach at rest. The omasum is elongated. (6) The ventral blind sac of the rumen together with the longitudinal and ventral coronary pillars are contracted. A = reticulum; B = rumen; C = omasum; D = abomasum; E = anterior blind sac of the rumen; F = dorsal blind sac of the rumen; G = ventral blind sac of the rumen; H = anterior pillar; J = posterior longitudinal pillar; K = dorsal coronary pillar; L = ventral coronary pillar; M = pyloric antrum of the abomasum; O = esophagus.

yields only relative data and is incapable of quantitative marker recovery, it does provide valuable information.

Ration composition and form have important effects on passage. Generally, grinding forage increases the rate of passage. Concentrates, which usually have smaller particle sizes than forages, are associated with faster passage. Remember that pelleted forage and concentrate diets are often consumed in greater amounts, and the intake factor alone will be responsible for some of the increased passage. Particle size per se does tend to have its own effect on passage (Table 15.3), however, with smaller particles passing faster than larger ones. Larger particles are filtered by the rumen mat and disintegrated through rumination. Finely ground whole diets cause cessation of rumination and the relative elimination of the floating mat of fiber that separates the liquid and gas phases of the rumen.

Table 15.3. Effects of alfalfa hay particle size on retention time and fiber digestibility

Feed	Mean size (μm)	5% transit (h)	Retention 80 − 5 (h)[a]	Fiber digestibility (%)
Long hay	—	22	54	44
Coarse grind	434	16	39	34
Medium grind	393	16	44	31
Finely ground	280	13	27	22

Source: Rodrigue and Allen, 1960.
[a]Retention time is defined in Section 23.4.1.

The floating rumen mat is one of two sorting mechanisms for particles (the other is in the omasum), and its elimination allows the escape of intermediate-size particles that would otherwise be entrapped in the mat.

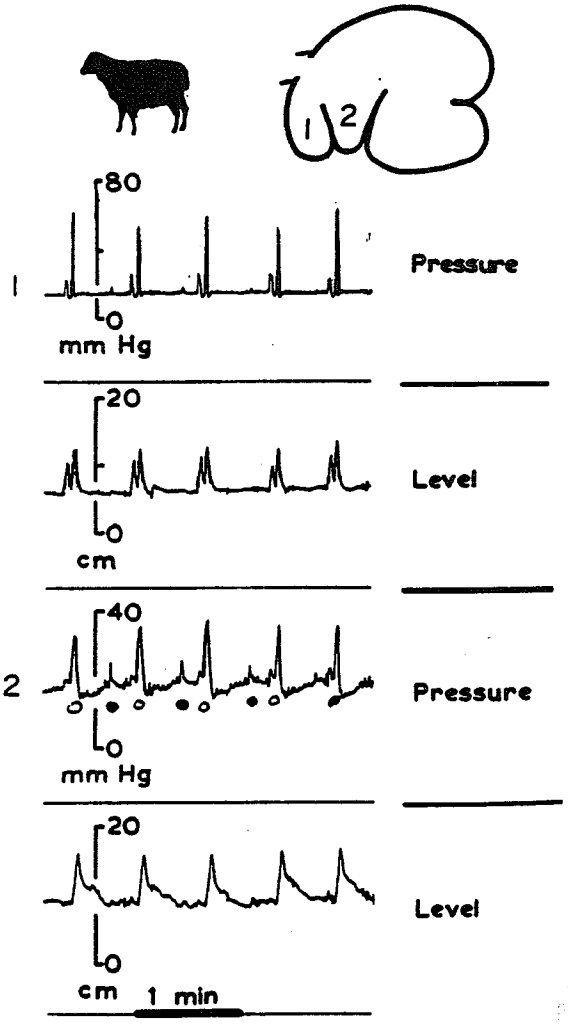

Figure 15.15. Comparison of simultaneous recordings of pressure and vertical displacement of the reticulum and the cranial sac of the sheep rumen during primary (1) and secondary (2) ruminal contractions (from C. S. W. Reid and Cornwall, 1959).

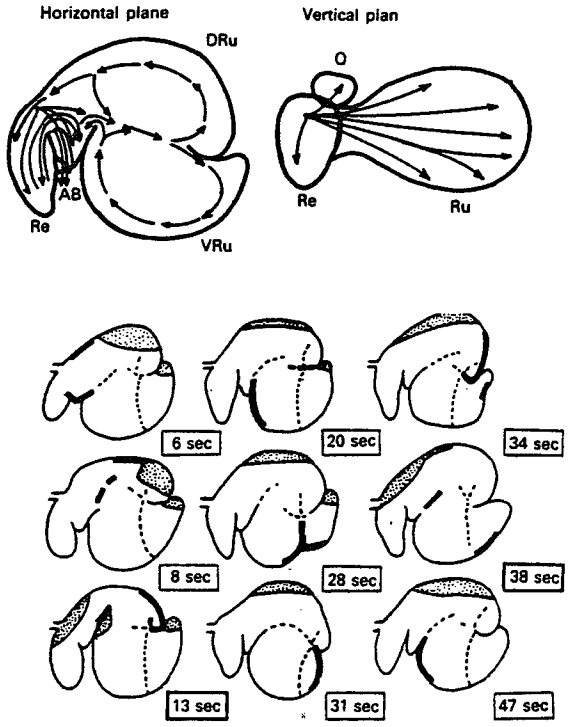

Figure 15.16. Movement of digesta in the reticulorumen as seen radiographically in the horizontal and vertical planes (from Wyburn, 1980). (Top) arrows indicate direction of movement. (Bottom) Main contraction sequences of the sheep's reticulorumen as indicated by X-radiography. Time (sec) indicates the interval after the reticular movement, and the contracting region of the reticulorumen wall is indicated as a heavy line. The gas bubble (stippled area) is brought over the cardiac orifice at 13 sec in the case of a primary contraction and during the secondary ruminal contraction at 38 sec. AB = abomasum; DRu = dorsal rumen; O = omasum; Re = reticulum; Ru = rumen; VRu = ventral rumen.

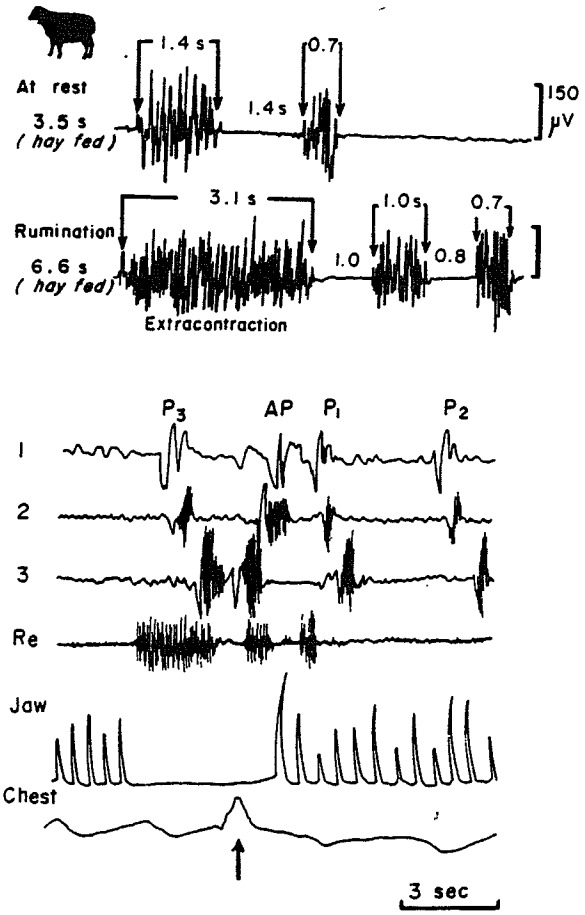

Figure 15.17. (Top) Electromyogram of the sheep reticulum wall showing the biphasic activity in the animal at rest and the superimposed extrareticular contraction during regurgitation. (Bottom) Events in the esophagus, reticulum, jaw, and chest associated with regurgitation (arrow). The esophageal electromyograms were recorded from electrodes placed at an equal distance on the esophagus, near the glottis (1), at the entry of the chest (2), close to the cardia (3), and on the reticulum (Re). The regurgitation of digesta (AP) is followed by swallowing just the excess liquid on two occasions (P_1 and P_2), and later, the bolus (P_3). (From Ruckebush, 1988.)

The operation of the mat differs from the filtration mechanisms of the omasum in that retention is based on occlusion and entrapment. Specific gravity and particle sizes are involved. Particles light enough to float are collected in the mat, which selectively retains them for further rumination (desBordes, 1981).

There is a direct relation between cell wall intake and rumination (Figure 15.18). Increased intake of cell wall promotes more rumination but decreases time spent ruminating per unit of cell wall, a factor that may be associated with the larger mean fecal particle size noted in animals on a pelleted diet and after increased intake of long forage. Heifers fed alfalfa pellets and chopped alfalfa hay showed mean fecal particle sizes of 0.36 and 0.30 mm, respectively (data from L. W. Smith, cited by Van Soest, 1966).

Increased intake increases rumen contents, or fill. The increased intake can be regarded as pressing both gastrointestinal volume and passage, these being the principal means of relief. Rate of digestion is less responsive since it is largely predetermined by ration composition. Balloons or plastic ribbon placed in the rumen also result in increased volume and passage rate (Balch and Campling, 1965; Welch, 1967). The need for food causes some compensatory expansion to allow for the greater ballast. Filling the rumen space tends to produce a smaller reduction in intake than would be expected, although intake and probably rumen volume require some time to adapt to new feeding conditions.

Plant cell wall represents the structural volume of the feed and as such is a major determinant of rumen volume. Removal of digestible and soluble contents from the interior of plant cells does not diminish their effective volume; the cells simply become filled with gas and water. Reduction in volume occurs only when the cell walls are destroyed by the processes of rumination and digestion. This is termed the *hotel effect* (Van Soest, 1975). Once the cell wall structure is destroyed,

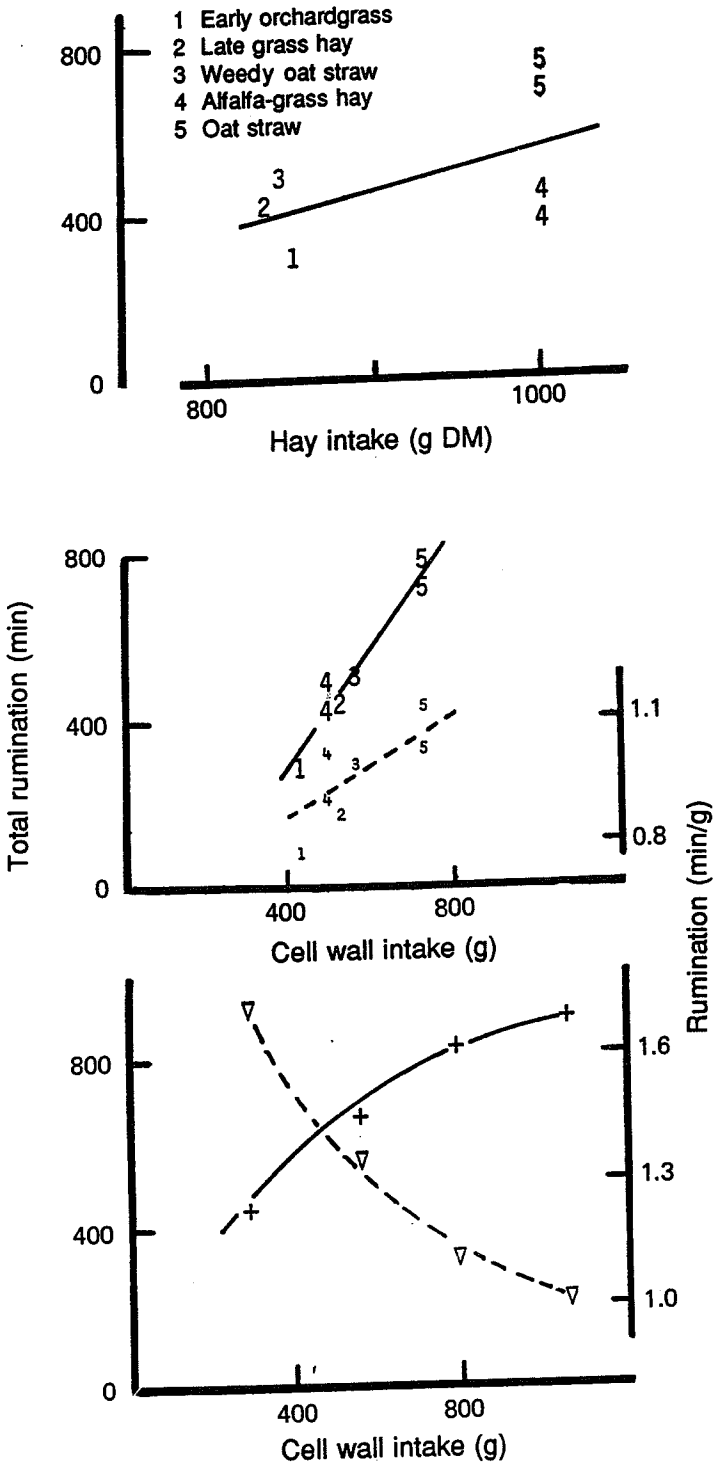

Figure 15.18. The effect of coarse forage on time spent ruminating in sheep. (Top) Rumination response to consumption of five forages at various intake levels (data from Welch and Smith, 1969). (Middle) The relation between rumination time and cell wall intake of the same forages (large numbers and solid line). Note the much closer relation with cell wall intake than with dry matter (upper figure). The time spent ruminating per gram of cell wall consumed (dashed line and small numbers) is greater when more mature forage is consumed (data from Welch and Smith, 1969). (Bottom) Increasing the intake of an individual forage (+) is associated with decreased rumination time per gram of cell wall consumed (▽) (data from Bae et al., 1979).

water held in the sponge of coarser cell wall material becomes available for absorption or passage.

15.3.4 Selective Retention

The selectively retained coarse particles become finer particles after rumination and digestion. These fine particles have a delayed passage, with their retention time being an inverse function of the rate of their production. The fine particles produced by rumination and digestion statistically outnumber those initially in the feed, such that they dominate the fine cell wall fraction of feces and contain an unusually high proportion of lignin (Figure 15.19). Since they have undergone a long period of digestion, fine fecal particles are higher in lignin content and take longer to appear in the feces than coarser material. (See also Figure 23.10.)

Although it is difficult to measure under in vivo conditions, the rate of particle breakdown is of major importance in the alleviation of rumen fill and, consequently, in feed intake. Evidence of its significance includes the very strong association of rumination time with cell wall intake (Figure 15.18), the strong association of feed cell wall content with voluntary intake, and the generally poor relation between rate of digestion and intake. The rate of particle breakdown or ease of rumination is a property of the feed composition, in particular its cell wall content, and the physical proper-

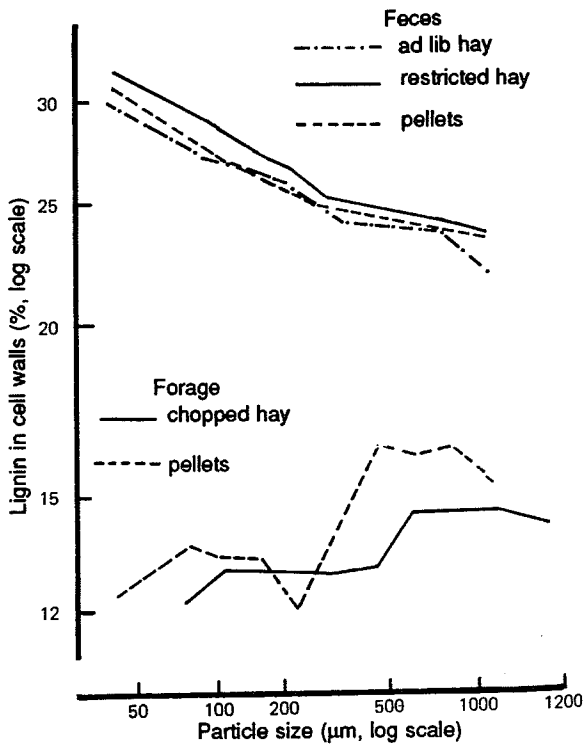

Figure 15.19. Relation between lignin content in the cell walls of alfalfa fed in different forms to heifers and fecal particle size (see Van Soest, 1975). Both axes of the graph use a logarithmic scale.

ties of the fiber that influence the ease or difficulty of comminuting fibrous particles into smaller ones.

When Welch (1967) placed polypropylene ribbons into the rumen, he found that ribbons longer than 9 cm were not ruminated and remained perpetually in the rumen. Longer ribbons that were ruminated passed into the feces as finer material than was the case with shorter ribbons. Since the fine ribbon particles in the feces can only have originated from larger pieces, the difference between appearance rates in feces of larger versus smaller particles is a relative measure of the comminution rate.

15.4 Structure of Ingesta

Rumen contents do not have a uniform composition. They are in the form of stratified layers showing ventral-to-dorsal differences as well as differences between anterior and posterior and between reticulum and rumen. Rumen contractions mix the contents, promoting turnover and accessibility of coarse floating matter for rumination. The mixing is inadequate to randomize distribution of particulate matter, although liquids may be mixed somewhat more efficiently.

The structure and composition of rumen contents are markedly influenced by diet. Coarse hay diets produce contents with a large, dense floating layer beneath the gas dome with relatively liquid contents and suspended fiber beneath (Figure 15.20). The floating mat is composed of the more recently ingested forage. As fermentation proceeds, digestion and rumination reduce particle size; fiber particles become waterlogged and tend to sink. The increase in apparent density is partly due to the loss of cellular gas space. Particles that settle to the floor of the rumen and have an optimum density are most likely to be selectively passed to the omasum. The optimum specific gravity for selective passage obtained with plastic particles appears to be about 1.2 (desBordes, 1981). Very dense objects (e.g., stones or pieces of metal) may be too large or heavy to escape. In animals fed higher-quality diets the floating mat is diminished, and it may be altogether eliminated in animals fed pelleted and concentrate diets. Rumen contents of animals fed concentrate are generally more viscous than those that receive only forage. Viscosity may affect mixing of liquid and the diffusion of VFAs toward the rumen wall.

Rumen fluid has the least amount of dry matter when coarse forage is the diet. Under most conditions of feeding, the fluid is relatively enriched by the cell wall components of the feed, which have a slower turnover rate. The rumen contents of sheep and cattle are similar in composition, while those of deer and other browsers may be somewhat higher in dry matter. Browsing species tend to have a proportionally smaller rumen content relative to body weight, which may be compensated for by a higher concentration of dry matter. The higher concentrations of solids and VFAs in rumens of concentrate-fed animals are often offset by a smaller rumen volume, so total content of dry matter or VFAs is not necessarily greater, and indeed may be less in these animals than in animals fed coarse forage (Balch et al., 1955).

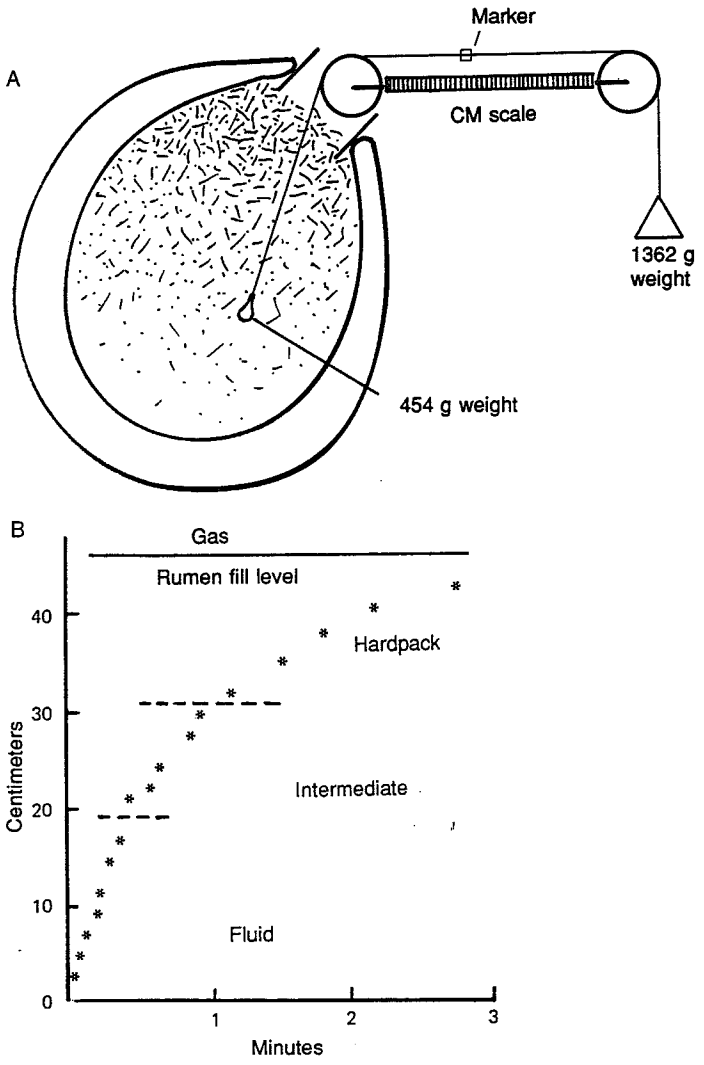

Figure 15.20. Measuring the consistency of rumen ingesta (from Welch, 1982). Figure A shows the device used to obtain the data shown in figure B. (A) Cross section of an open fistulated rumen with the measuring device in place. Support for the 3-lb weight is removed, and the 1-lb weight ascends through the rumen contents. The thicker and tighter the rumen ingesta pack, the longer the ascension time. (B) The ascension time curve obtained from the rumen of a cow fed corn silage. Rumen contents of animals fed coarse forages are stratified into a top layer (hardpack), an intermediate layer, and a fluid layer beneath. The thickness of the hardpack varies with the amount of coarse cell wall in the diet. Rumens of animals fed concentrate or pelleted forage are much more homogeneous, and the time for weight ascent is much shorter with these rations than with hay. Ranges of ascent times: grass hay 300–900 sec; corn silage, 90–200 sec; alfalfa pellets, 4–21 sec; and high concentrate, 60–130 sec. Higher feed intake also promotes a longer ascent time for any given ration. Ascent time decreases after feeding, rumination, and some rumen emptying.

15.4.1 Gases

The dome of gas in the upper part of the rumen is composed mainly of CO_2 and methane, the proportions of which depend on rumen ecology and fermentation balance. Ordinarily, the proportion of CO_2 is twice or three times that of methane. Small amounts of other gases may occur, including hydrogen and hydrogen sulfide. Nitrogen and oxygen are swallowed (as air) during feeding. Nitrogen may constitute as much as 10% of total gases during and after feeding. Most of the nitrogen is eructated with the fermentation gases (some is inhaled in the process). Some of the oxygen is absorbed or used by facultative organisms.

Although oxygen is toxic to obligate anaerobic bacteria, introduction of oxygen into the rumen through a fistula has little effect on fermentation. Accessibility of oxygen is limited to the surface and a few centimeters below it, and the hardpack layer of floating ingesta probably acts as a barrier and a metabolic sink for oxygen. Facultative organisms in this outer layer use oxygen rapidly and help maintain a low redox potential. Another possible source of oxygen is through diffusion from the blood across the rumen wall. The extent to which this occurs in not known. Oxygen in the rumen serves as a hydrogen acceptor and thus could be important in the fermentation balance.

Gases produced in the rumen are eliminated by eructation (a kind of silent belching) and, to a significant extent, also by absorption across the rumen wall and exhalation via the lungs. In the case of methane, the latter may account for 30% of the amount produced (Hoernicke et al., 1965). The fate of CO_2 is more complicated because of the pooling and recycling of animal metabolic carbon as urea and bicarbonates in saliva with that produced by the rumen organisms. Eructation is necessary to maintain rumen balance. Failure to eructate results in bloat, which can be fatal (Section 15.7.1). Eructation occurs through a slight variation of the normal reticular contractions whereby the area near the cardia is cleared of ingesta, the reticuloruminal fold and cranial pillar acting as a dam to hold back liquid. Relaxation of the cardiac sphincter, abdominal pressure, and contraction of the dorsal sac of the rumen combine to force gas into the esophagus, to be transferred to the mouth by antiperistaltic contractions (Sellers and Stevens, 1966). When the pharyngoesophageal sphincter is opened, the gas passes into the nasopharynx. Some gas passes into the respiratory passages. Gas pressure in the rumen stimulates eructation, and ingesta in the area of the cardia inhibit it.

15.5 Volatile Fatty Acids

The VFAs produced as end products of anaerobic microbial metabolism provide the ruminant with a major source of metabolizable energy. Removal of these acidic products is vital for the continued growth of cellulolytic organisms in the rumen.

The principal fatty acids, in descending order of usual abundance, are acetic, propionic, butyric, isobutyric, valeric, and isovaleric. The proportions of acetic, propionic, and butyric acids can be markedly influenced by diet and the status of the methanogen population in the rumen. Protozoa may also contribute significantly to the balance. Other organic acids may appear as products of microbial metabolism. Lactic acid is important when starch is a part of the diet, and is itself fermented to acetate, propionate, and butyrate. It appears only as a transient product 1–2 h after fermentation (Figure 15.21). Succinate and formate produced by some rumen species in pure culture do not normally appear as products in mixed cultures.

Rumen concentrations of VFAs are regulated by a balance between production and absorption whereby increased production rate induces higher VFA concentrations (Giesecke, 1970). Since production rates vary diurnally as a consequence of eating patterns, rumen concentrations and pH also vary. The pK's of the VFAs (4.8–4.9) are very much lower than normal rumen pH. The pattern following a meal shows a rise in VFAs and a drop in pH, followed by a slow recovery to the original conditions (Figure 15.22). Fermentation peaks about 4 h after feeding on a hay diet but occurs sooner if the diet contains much concentrate. The peak is largely a function of non–cell wall fermentation. The maximum quantity of cellulose digested from a meal occurs later, between 6 and 18 h after ingestion, depending on the rate of digestion.

15.5.1 Measuring VFA Production

The habit of expressing VFAs as molar proportions rather than normal concentrations has been responsible for much confusion. Molar proportions are valid only if presented along with total acid concentrations. The molar proportions of glucogenic propionate to nonglucogenic acetate or butyrate is of physiological significance to the animal; however, its value as a measurement is offset by the problem that a natural rise or drop in the amount of one acid requires a statistical change of opposite sign in the other acids. It was by this means that the erroneous theory that acetate deficiency caused milk fat depression in lactating ruminants arose (Section 20.7). The drop in molar proportions of acetate is usually caused by the dilutory effect of a large increase in propionate.

Rumen concentrations of VFAs depend on the amount of VFAs absorbed (Giesecke, 1970); however, the quantitative relationship depends on rumen pool size and turnover. Concentrate-containing diets may exhibit higher concentrations of acids relative to the amount absorbed than forage diets due to a smaller

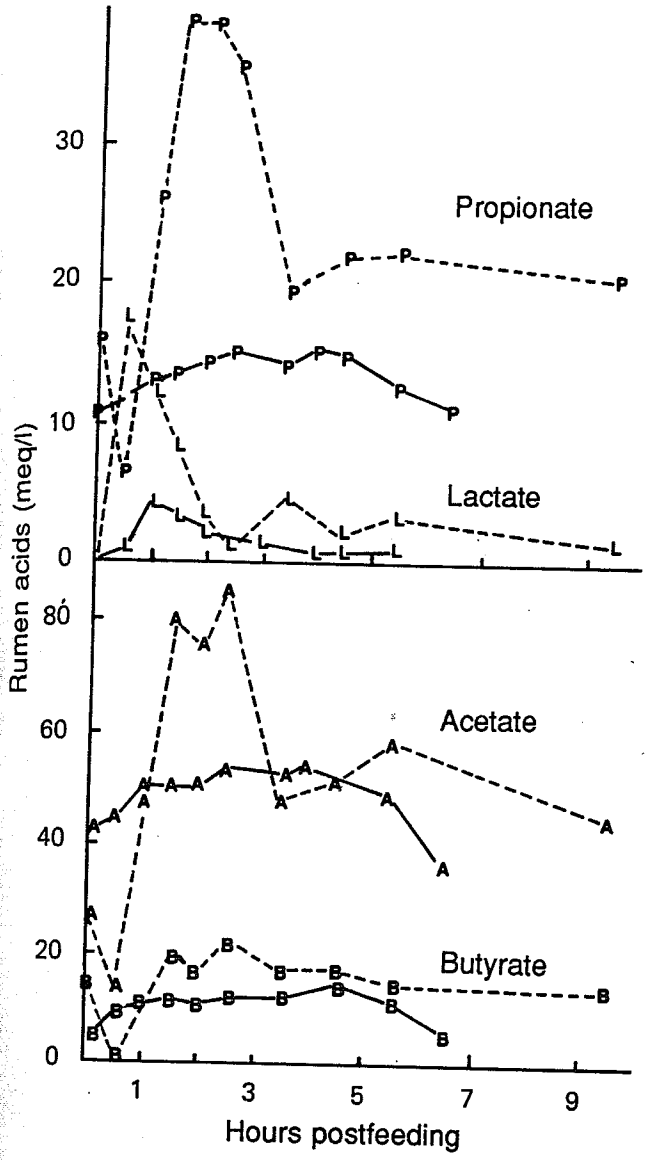

Figure 15.21. Variation in concentrations of rumen acids with the time after feeding. Dashed lines denote high-concentrate rations; solid lines denote all forage. (Compiled from Van Soest, 1955, and Waldo and Schultz, 1956.)

rumen volume and a smaller pool that turns over more rapidly (Bauman et al., 1971). Studies utilizing ^{14}C-labeled VFAs and their rates of disappearance as measures of VFA production and absorption do not provide information on the conversion to other acids or microbial cellular products; this diversion is instead measured as absorption.

Absorption of VFAs

Acids are absorbed across the rumen wall largely in the free form, apparently without active transport. There may be considerable metabolism of the acids (particularly butyrate) in the wall, however, leading to a differential decline in concentration and more rapid

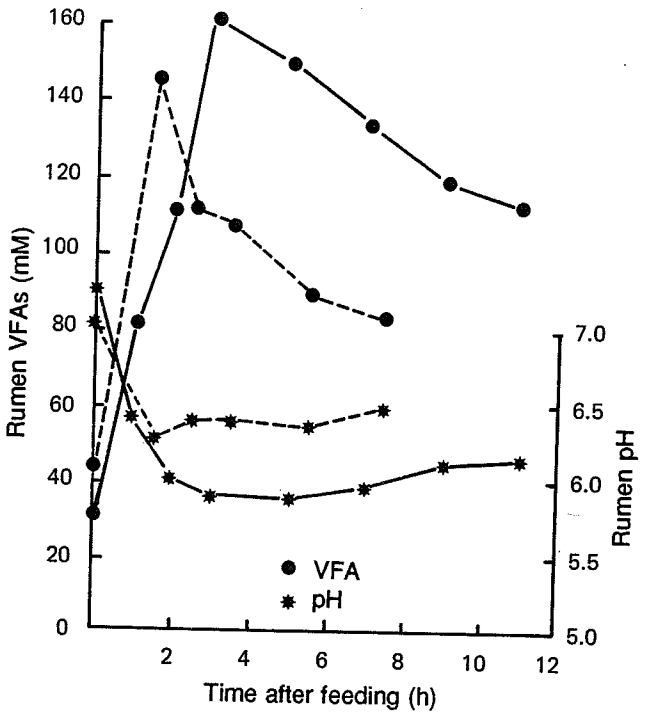

Figure 15.22. Rumen pH and VFA concentrations in two sheep fed chopped alfalfa (from Briggs et al., 1957). Note the different response in the two animals. Rumen pH is a negative mirror of acid production and disappearance.

absorption. At normal rumen pH, only small amounts of VFAs are present in the free acid form. The removal of free acid is balanced by formation of more free acid through the reversal of the ionization equilibrium by mass action. The proportion of free acid is favored by lower pH and higher concentrations of VFA. The pH of the blood is ordinarily more alkaline than that of the rumen, favoring movement of acid toward the blood through the free energy of neutralization. This gradient similarly discourages flow of fatty acid anion. Thus rumen pH influences rates of VFA absorption (Bergman, 1990; Dijkstra et al., 1993). A high rumen pH narrows the rumen to blood gradient and increases anion absorption, which has been observed to be about one-half of the acetate absorbed at pH 7.06 (Ash and Dobson, 1963). Bicarbonate, sodium ions, and some urea flow in the reverse direction, toward the rumen (Figure 15.23). The mechanism of VFA absorption in the lower tracts of ruminants and nonruminants is similar to that in the rumen (Sellers and Stevens, 1966).

Cannulae in the portal vein show low values for butyrate and propionate relative to acetate because of the selective removal and metabolism of the former as they pass through the rumen wall. The flow of acids is not in order of their molecular weights, which suggest that diffusion is not a limiting factor.

The major factor affecting quantities of VFAs absorbed is their concentration (Figure 15.24). Therefore, it follows that the order of absorption will be

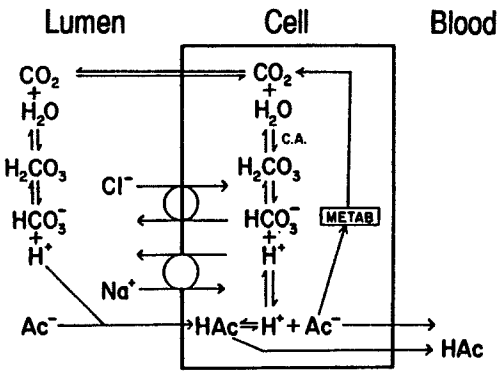

Figure 15.23. Hypothesis for the mechanisms of VFA, Na, Cl, and HCO_3^- transport by rumen epithelium and colon mucosa (from C. E. Stevens, 1988). High levels of CO_2 produced by microbial fermentation in the lumen allow for its rapid hydration in the absence of carbonic anhydrase (C.A.). This provides H^+ for the nonionic diffusion of acetate or other VFAs into the cell and releases HCO_3^- into the lumen. Similar intracellular hydration of CO_2, derived from metabolism of VFAs and other substrates, is catalyzed by carbonic anhydrase, providing HCO_3^- and H^+ that can be exchanged for the Cl^- and Na^+ in the lumen. The relatively low levels of Cl^- normally present in the lumen could result in the more rapid secretion of H^+ than HCO_3^- into the lumen, which would aid in VFA absorption and favor release of cellular HCO_3^- into the blood. Acetate is transported to the blood by diffusion of both the dissociated and undissociated forms of the fatty acid. Transport of Cl^- and Na^+ to the blood (not depicted) is accomplished by diffusion of Cl^- down its electrochemical gradient and Na^+-K^+ ATPase transport of Na^+.

acetate, propionate, butyrate, provided that the absorption rates are calculated as quantities per unit time. If rates are compared in terms of absolute kinetics (i.e., independent of unit concentration), the rates are more equal.

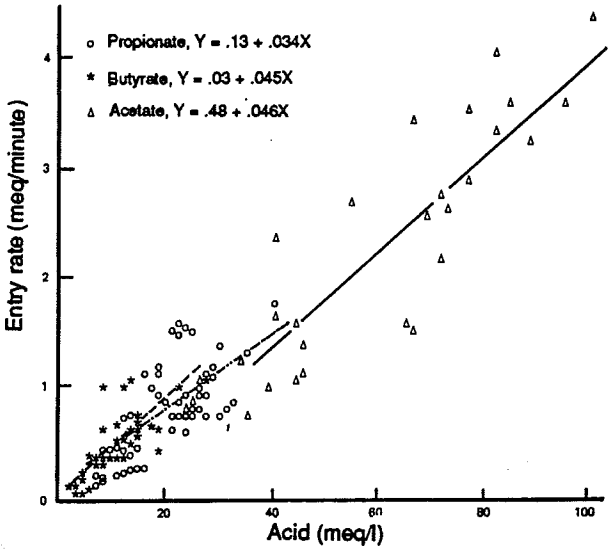

Figure 15.24. Relation between measured entry rate and concentration in ruminal fluid for acetate, propionate, and butyrate. The lines indicate the relation between production and concentration for each VFA. The solid line indicates the relation after results were combined (summarized by Leng, 1970). The individual kinetic rates of absorption (slopes of the lines in the figure) are less important than concentration in determining net amounts absorbed. Entry rate and concentration are better correlated in animals and diets with similar rumen pool sizes and turnovers.

Other factors influencing absorption are rumen pH, surface, and volume (Dijkstra et al., 1993). Lower pH increases the proportion of unionized acid and promotes absorption. Papillar surface is maintained by VFA concentrations and ruminal wall metabolism of butyrate and propionate. High-concentrate diets tend to promote lower rumen volumes leading to less than expected amounts of VFA absorbed relative to ruminal concentrations (see Table 19.3).

15.6 Regulation of the Rumen Environment

Ecological conditions within the rumen must be kept within limits to maintain normal microbial growth and metabolism and thus the well-being of the host ruminant. Cellulolytic organisms grow optimally at pH 6.7, and deviations substantially higher or lower than this are inhibitory. The range for normal activity is about ± 0.5 pH units. In particular, pH below 6.2 inhibits the rate of digestion and increases lag (Richard Grant and Mertens, 1992). The osmolality of rumen contents is maintained within narrow margins by the large volume of isotonic saliva, rapid absorption of water from hypotonic solutions, and iso-osmotic absorption of water along with sodium, chloride, VFAs, and other substances. A low redox potential is maintained by the presence of fermenting digesta and is also required for the continued maintenance of the host.

Rumen pH is maintained to a major degree through the high buffering capacity of saliva and the removal of VFAs through absorption. There is also evidence that the rumen epithelium can secrete bicarbonate (A. Dobson, 1959; other factors involved in buffering are discussed in Section 15.6.2). Lowering the pH interferes with rumen fermentation and may lead to acidosis in the host. It may also allow facultative lactic acid–producing organisms to proliferate if there is too much starch in the feed. Osmotic pressure works against the flow of water across the rumen wall. If the osmotic pressure in the rumen exceeds that in the blood, water will flow toward the rumen. Ordinarily osmotic pressure is lower in the rumen, and water is lost to the blood. Osmotic pressure promotes the flow of liquid out of the rumen to the omasum; VFA absorption helps to keep osmotic pressure within the necessary limits. Resorption of sodium, chloride, phosphate, and other salivary ions is necessary for the maintenance of electrolyte, water, and acid-base balances in the host; it occurs in the rumen, omasum, and other sites farther down the digestive tract (A. Dobson, 1959). The entrance of these inorganic ions is enhanced by rumination and ensalivation, and they in turn promote liquid turnover and washout of finer particulate material.

Table 15.4. Characteristics of ruminant salivary glands

Gland	Calf Weight (g)	Calf % of total weight of salivary glands	Sheep Weight (g)	Sheep % of total weight of salivary glands	Cell type	Factors governing volume	Approx. rate of flow (l/day)	Saliva type
Both parotid	63.5	32.2	23.5	29.3	Serous	Continuous flow when denervated; respond to stimulation by mouth, esophagus, and rumen	3–8	Fluid and isotonic; strongly buffered with HCO_3^- and HPO_4^{2-}
Both mandibular	64.0	31.6	18.2	22.6	Mixed	No flow when denervated; strongly stimulated by feeding; little or no response to stimulation by esophagus or reticulorumen	0.4–0.8	Variably mucus and hypotonic; buffered
Both sublingual	11.3	5.6	1.3	1.6	Mixed	Continuous flow when not stimulated; little or no response to stimulation by esophagus or reticulorumen; other reflexes not studied	0.1 (?)	Very mucus and hypotonic; weakly buffered
Labial	8.9	4.4	10.9	13.5	Mixed	Little or no flow when not stimulated; little or no response to stimulation by esophagus or reticulorumen; other reflexes not studied	?	Very mucus and hypotonic; weakly buffered
Both ventral buccal	13.5	6.7	5.9	7.3	Serous	Continuous flow when denervated; responds to stimulation by mouth, esophagus, and reticulorumen	0.7–2.0	Fluid and isotonic or nearly so; strongly buffered with HCO_3^- and HPO_4^{2-}
Both medial buccal	13.1	6.5	6.0	7.5	Mucus	Very slow continuous flow when not stimulated; responds to stimulation by mouth, esophagus, and reticulorumen	2–6	Very mucus and isotonic or nearly so; strongly buffered with HCO_3^- and HPO_4^{2-}

Source: Kay, 1960.

The rumen is more or less a continuous fermentation system, although its continuity is perturbed by meals, leading to cyclic patterns. Continuity requires that all substances entering the system via the diet, or saliva, and those produced by fermentation, be either absorbed or passed down the digestive tract. Net exit must balance net entry. Any imbalance leads to abnormal or pathological conditions. Gas production beyond the limits of the eructation capacity leads to bloat. Interference with the rumination process may lead to rumen impaction and an "off-feed" condition. Reduction in intake also can result from a dietary deficiency of the nutrients necessary for microbial growth and the maintenance of a normal rate of fermentative digestion. Generally, digesta are eliminated and kept in balance with intake through disappearance of dry matter via digestion and passage. The passage of indigestible residues is assisted by rumination and comminution to a particle size that will pass.

The cyclic pattern following eating shows a significant but normal diurnal variation. This cyclic variation may be important for some of the more fastidious rumen protozoa. Some tend to accumulate starch and burst after the host eats much concentrate. These populations (and methanogenic organisms as well) probably recover during the slower phases of rumen fermentation that precede the next meal. Survival of slower-growing species such as large protozoa require turnover times that are not in competition with generation time. Liquid ordinarily passes too quickly for these organisms to use it, and their maintenance thus depends on occlusion in the mass of fibrous matter with slower turnover. Pelleting and grinding of food disturbs this balance and often results in reduction or elimination of rumen protozoa.

15.6.1 Saliva

Saliva is produced by the parotid and other glands (Figure 15.25 and Tables 15.4 and 15.5). The parotid is rich in mineral ions—particularly sodium, potassium, phosphate, and bicarbonate—which provide buffering capacity. Ruminant saliva is also rich in mucins, giving it viscosity and, perhaps, resistance to the formation of foam in the rumen. It does not contain any amylolytic activity, although there is some lipase, which is important in newborns. Ruminants produce a large amount of saliva every day (sheep produce 15 l/day or more, and cattle produce 180 l/day or more), and animals depend on recycling the mineral bases it contains, particularly sodium. About 70% of the water entering the rumen comes from salivary secretion (Church, 1988).

Table 15.5. Relative composition of ruminant saliva

Gland	Saliva produced (l/day)	Na^+ (meq/l)	K^+ (meq/l)	HCO_3^- (meq/l)	HPO_4^{2-} (meq/l)	Cl^- (meq/l)
Sheep						
Parotid	3–8	147–185	5–31	91–125	25–71	9–16
Inferior molar	0.7–2	175	7–10	97–110	44–51	7–12
Palatine	2–6	179	4	109	25	25
Submaxillary	0.4–0.8	4–16	10–25	5–14	2–10	7–15
Sublingual	0.1	16–47	6–25	8–18	0.3–2	16–40
Labial	(small)	29–47	3–9	2–4	2–10	34
Calves						
Parotid	—	163–168	6–14	88–94	17–47	16–34
Submaxillary	—	11–24	24–41	5–8	0.4–4	6–15
Inferior molar	—	151–156	6–18	77–95	18–54	12–21

Source: Kay, 1960.

Urea in saliva varies in concentration, and small amounts of sulfate, calcium, and magnesium are usually present in saliva as well. Salivary composition is affected by many factors. The composition of secretions by the various glands that produce saliva varies depending on the rate of secretion. Increasing the rate of secretion by a factor of 5–10 causes a drop in potassium and phosphate and an increase in sodium and bicarbonate up to 10-fold (Kay, 1960). Generally, the sum of cations and anions tend to remain constant and equal to each other. Composition is also affected by sodium depletion and salt intake.

The flow of saliva is stimulated by eating and ruminating, although some flow continues constantly. The rate of eating is important in determining the buffering capacity of the feed-saliva mixture (Table 15.6, Section 15.6.2). The intake rate is faster for concentrate feeds, which also tend to ferment more rapidly. Faster eating rate in combination with maximum flow decreases the amount of saliva per gram of feed. Total salivary flow also is related to time spent eating and ruminating. Thus high-concentrate and pelleted forage diets are characterized by less net flow (Bauman et al., 1971). The combination of these factors with salivary flow leads to lower rumen pH in animals fed concentrates. Changes in rumen flora may follow the reduction in rumen buffering capacity and the slower turnover and washout characteristic of high-concentrate diets.

Saliva composition reflects the ruminant's need for mineral balance and recycling as well as its symbiotic relations with the rumen bacteria and their requirements for optimal growth. Apart from their need for a fairly stable pH and osmotic pressure, bacteria are tolerant of wide ranges in ion concentrations. Ruminant saliva is relatively low in phosphate and high in carbonate, but rumen bacteria can tolerate a wide range in the ratio.

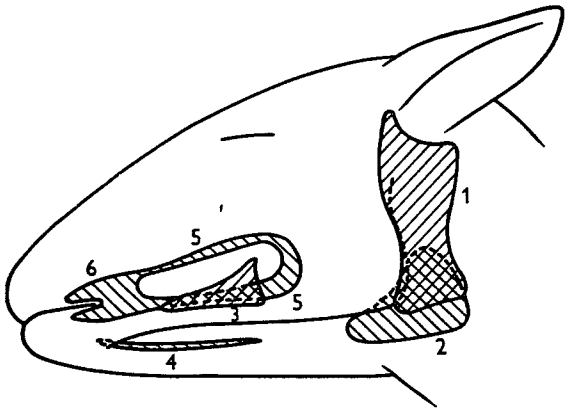

Figure 15.25. The main salivary glands of the sheep (from Kay, 1960). 1 = parotid; 2 = submaxillary; 3 = inferior molar; 4 = sublingual; 5 = buccal; 6 = labial. Glands are paired on both sides of the head and mouth.

15.6.2 Buffering

The total buffering system in the rumen includes not only the saliva but also the feed. The nonprotein nitrogen fractions of forage are rich in glutamate, aspartate, glutamine, and asparagine. Feed proteins may also contribute to buffering capacity (Tables 15.7 and 15.8). Lactate and VFA buffering occurs at a pH too acidic for any practical affect in the rumen. The plant cell wall also has a cation exchange capacity that contributes to rumen buffering (McBurney et al., 1983). The net buffering capacity in the rumen varies with the

Table 15.6. Effect of ration on saliva production and eating rate

Feed	Eating rate (g food/min)	Salivary production (ml/min)	Salivary production (ml/g food)
Pelleted ration	357	243	0.68
Fresh grass	283	266	0.94
Silage	248	280	1.13
Dried grass	83	270	3.25
Hay	70	254	3.63

Source: C. B. Bailey, 1958.

Table 15.7. Factors contributing to rumen buffering

	Promoted by	Buffer source
Washout (passage)	Osmotic pressure Feed intake	Dilution
Absorption	VFA concentration	Removal of free acid
Saliva	Coarse fiber and rumination	Bicarbonate Phosphate
Fiber	Cation exchange	Neutralization
Mineral salts of plant organic acids	Forage composition	Fermenting of plant acids to CO_2
Protein	NH_3 production	Neutralization
Microbial efficiency	Microbial growth	Diversion of carbon to cells instead of acids

feed. Salivary buffering capacity also varies depending on the feed source (Figure 15.26). The pK's of various acids in feed and rumen contents are given in Table 15.8. Urea provides buffering through its conversion to ammonium bicarbonate and allows for nitrogen recycling, which is important in the economy of protein and nitrogen balance in the ruminant.

15.6.3 Rumen Volume and Liquid Flow

Rumen volume can be measured either directly by emptying the contents through a rumen fistula, by measurement at the time of slaughter, or by the dilution technique with a liquid marker. The latter procedure involves the same principles and assumptions as rate of passage measurements. Failure of the rumen to equilibrate and postprandial variation in rumen contents are the most important causes of measurement errors. The lack of equilibration is more serious for particulate matter than it is for liquid components because rumen volume must be assumed to be constant over the period of dilution measurement, and the marker (particularly polyethylene glycol) may not penetrate all the water space, particularly that within living microorganisms. These factors contribute to systematic errors.

Data collected by Colucci (1984) indicate that the systematic error of marker measurement varies depending on the intake. At low intakes the marker method overestimates water space in the rumen, while at high intakes it underestimates. If the marker is unable to enter the cells of living rumen organisms, as much as 20% of the fluid space may not be measured. Loss of marker through absorption could add to the error. Higher osmotic pressure promotes marker absorption, leading to overestimation of kinetic rate and rumen volume (A. Dobson et al., 1976).

Rumen volume tends to increase with ad libitum feeding (Colucci, 1984). This stretch factor counterbalances the increased rate of passage. The net effect is that increases in passage rate with incremental feed intake may be less than anticipated.

Table 15.8. Approximate pH (pKa) of maximum buffering capacity of various metabolites and feed components

Reaction	pH (pKa)
Phosphoric acid, 2d hydrogen	7.1
Carbonic acid, 1st hydrogen	6.4
Acetic acid	4.8
Propionic acid	4.9
Butyric acid	4.8
Formic acid	4.0
Lactic acid	3.9
Feed components	
Glutamate (2d hydrogen)	5.6
Forage (mean pH, H_2O extract)	5.5
Citrate (3d hydrogen)	5.4
Aspartate (2d hydrogen)	5.2
Malate (2d hydrogen)	5.1
Alfalfa protein isoelectric point	4.5

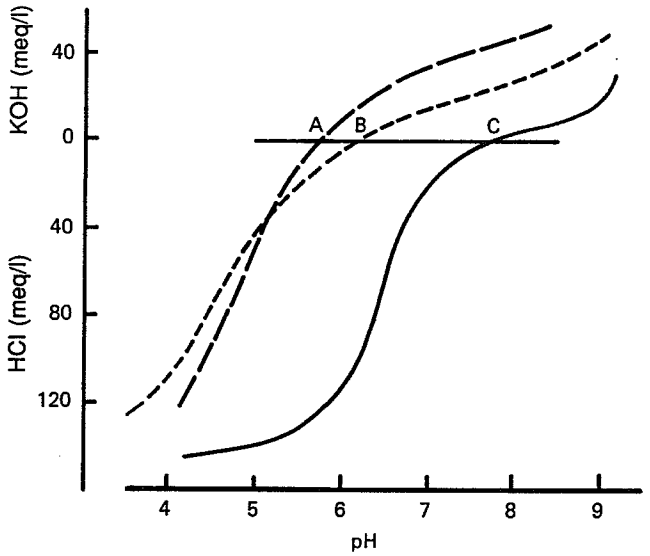

Figure 15.26. The buffering capacity of rumen liquor and ruminant saliva (modified from Turner and Hodgetts, 1955). (A) Rumen liquor from sheep on alfalfa and ryegrass pasture. (B) Rumen liquor from sheep fed wheat and oat chaff. (C) The buffering capacity of parotid saliva. Note that the higher-quality alfalfa-ryegrass diet produces a more acidic rumen compared with the wheat and oat chaff diet; however, the legume-containing diet has greater buffering (steeper curve) in the region of pH 5.

15.7 Rumen Dysfunctions

Diseases of the rumen are most often related to diets that deviate from the diet to which the ruminant species is evolutionarily adapted. Problems thus arise from feeding high-concentrate diets to dairy cattle, beef cattle, and sheep, and from abnormal levels of nitrogen fractions (urea, ammonia, and nitrate) from inadequate feed mixing or overfertilization of crops. Pathologies such as bloat result from single-species pastures or too much of one kind of feed, and thus have an ecological basis.

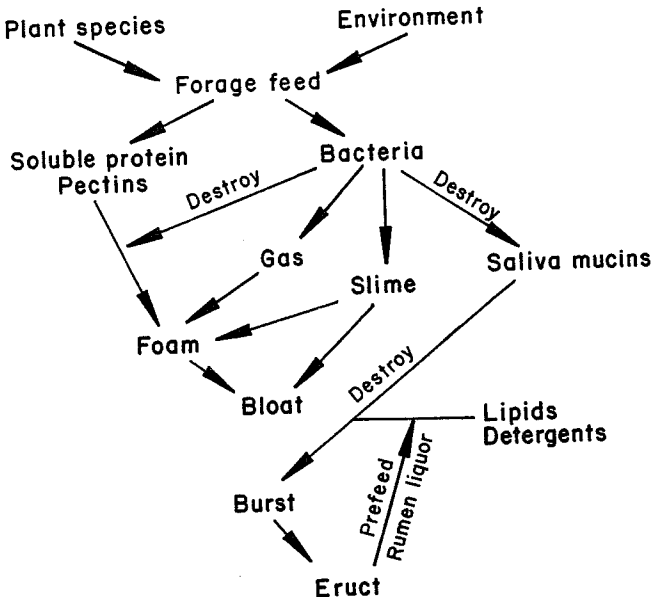

Figure 15.27. Hypotheses explaining bloat. The various models are not mutually exclusive, and their relative importance may vary with the animal's diet.

15.7.1 Bloat

Bloat is the distension resulting from the failure to eliminate gas produced in the rumen. Pressure levels in the normal animal are low, but they may rise to 100 mm mercury in cases of acute bloat.

The main recognized categories of bloat are legume bloat, frothy bloat, and grain bloat, although other forms have been described (Essig, 1988). Bloat may be acute, subacute, or chronic, reflecting the severity of the condition. Acute bloat is often fatal. The nomenclature considers both dietary and animal factors. For example, an animal described as a "chronic bloater" may reflect genetic factors predisposing a tendency toward bloat (C. S. Reid et al., 1975).

Bloat is relatively unknown in wild ruminants and in domestic animals on the range. It is likely to be the result of humans' mismanagement of the normal balance between diet and animal. Like some other nutritional problems, bloat is associated with grazing on certain plant species and with intentional or inadvertent feeding of high-starch diets.

Bloat is generated by a complex interaction among environment, animal/plant species, and rumen microbes. Factors leading to stable foam promote bloat; those that reduce foam by causing bubbles to burst reduce it. Foam stability is a function of surface tension. The more important bloat factors are outlined in Figure 15.27.

Rapid fermentative production of gas is required to make foam. Pectin, abundant in legumes, produces much gas and has been suggested as a cause of foam. It should be pointed out that rapid fermentation could also destroy the foam-promoting factor, and gas production, although required, is insufficient in itself as a principal factor. Foam stabilization probably involves soluble proteins in fresh forages as well as rumen bacteria that can ferment the protein and also ferment protective salivary mucins. Bacteria are seen as a force both promoting and destroying conditions for bloat because they can ferment soluble protein as well as salivary mucus and may produce slime themselves. The slime increases the tendency for foam.

Legume or Frothy Bloat

Legume bloat occurs in animals grazing on legume pastures, usually white clover or alfalfa. Not all legumes produce bloat; it is unknown on pastures of tropical legumes or temperate pastures of trefoil, sanfoin, or vetch. These forages contain tannins that inhibit bloat through protein precipitation (W. T. Jones and Lyttleton, 1971).

The rumen of a bloated animal usually contains much foam, hence the description "frothy bloat." Only limited attention has been paid to the factors promoting formation and stability of the foam, which appears to inhibit eructation and elimination of gas. Substances in legumes that might contribute include proteins and pectins, since both increase viscosity and foam stability.

Foam stability involving protein as the cause of legume bloat has received more support, particularly since detergents and oils are effective foam suppressants and also decrease surface tension and form complexes with proteins (Laby, 1975). Legume hays do not produce severe bloat, perhaps because proteins are denatured to the insoluble form in the hay-curing process.

Legumes contain other components that have been suggested as contributing factors as well, including saponins and the amines produced from protein (e.g., histamine, tyramine, etc.), which might have toxic effects on the animal and on rumen motility (see Church, 1975, for discussion).

Grain Bloat

Feeds containing large amounts of concentrate or pelleted diets often cause bloat, usually of the chronic variety. This type of bloat seems to be different from that seen in animals on legume pasture (Bartley et al., 1975). In grain bloat the rumen contents are characterized by high viscosity and foam resulting from the production of extracellular slime by amylolytic bacteria. The mucin fraction of ruminant saliva, which may ordinarily protect the animal from bloat, might be inactivated by rumen organisms with mucinolytic activity. The smaller amounts of saliva per unit feed and low

rates of rumen turnover characteristic of high-concentrate diets could be responsible. A large production of rumen acids, particularly lactic acid, may also reduce rumen motility.

Acute and Chronic Bloat

In some animals subacute bloat conditions occur continuously, a possible cause of discomfort but not of acute distress. In New Zealand, geneticists have shown the existence of sheep strains more tolerant to legume bloat conditions. Grain bloat is commonly chronic and less often acute compared with legume bloat.

An animal in a state of acute bloat is in distress and may become prostrated and die. High pressures of air or oxygen in the rumen introduced experimentally do not produce the distress of an equivalent pressure of CO_2. The final stages of bloat may involve pressure on the heart and cardiovascular collapse.

Prevention is the most efficient method of handling bloat. This may be accomplished by good feeding management or the administration of oil or detergents that reduce surface tension and foam stability in the rumen. The detergents also form complexes with the proteins involved in producing foam. Periodic drenching of the animals or spraying oil or detergents on legume pastures may prevent bloat. Polyoxaline is an approved detergent for treating bloat. Allowing animals to graze only when they can be observed helps managers detect the onset of bloat. In severe acute bloat, the last resort is to puncture the rumen and allow the gas and foam to escape (Essig, 1988).

15.7.2 Acid Indigestion

Most rumen disorders involve some disruption of the balance and control of the internal rumen environment. Imbalances may develop as a result of the sudden introduction of feed or substances to which the rumen flora are unaccustomed, leading to a rapid change in fermentation that cannot be controlled. Acute (acid) indigestion and urea and nitrate toxicities all result from imbalances.

Starch or cereal concentrates ingested in large amounts provide the substrate for rapid proliferation of facultative organisms that produce lactic acid and low cell yields (Allison et al., 1975). Lactic acid is a considerably stronger acid than volatile fatty acids (pK 3.9 vs. 4.8 for acetic acid) and is produced in both natural (D) and unnatural (L) forms by bacteria. In severe cases lactate may constitute 50–90% of total rumen acids. Succinate and formate may also occur in substantial quantities, although normally they appear only in trace amounts in the rumen. Rumen pH may drop to as low as 4, causing severe rumenitis. If large amounts of lactic acid are absorbed across the rumen wall into the blood, systemic acidosis can result. The hyperosmolality of the rumen contents and uncompensated acidosis cause systemic dehydration; death results from failure of hemoglobin to carry oxygen (Huber, 1976).

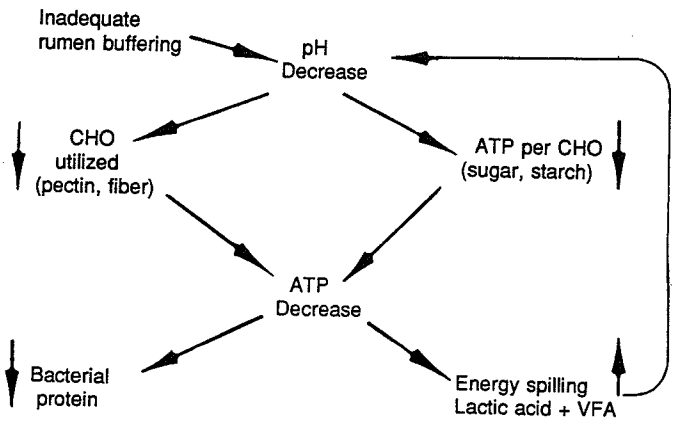

Figure 15.28. Metabolic activities in the rumen that might lead to decreased synthesis of microbial protein and increased acid production (modified from Strobel and Russell, 1986). The system is self-inductive in the face of inadequate rumen buffering.

Similar disorders occur if animals break into a field of corn or if high-quality hay is given to hungry animals. Acute indigestion does not occur if the new diet is introduced gradually so that rumen flora are allowed to adapt. All-concentrate rations may produce a chronic acidosis leading to rumen parakeratosis. Treatments for acidosis include the administration of carbonate salts and evacuation of the rumen.

Lactic acid–producing organisms are typically more tolerant to lowered pH and thus do not reduce their utilization of substrate. The metabolic pathway yielding lactate provides only 2 ATPs per mole of sugar for microbial growth, however, whereas normal VFA production (acetate, propionate, and butyrate) affords 4 ATPs per mole of sugar. Thus fiber-digesting, VFA-producing bacteria theoretically have twice the capacity of lactic acid–producing organisms for production of microbial protein. The behavior of the important lactic acid producer *Streptococcus bovis* in response to pH shift is instructive. At normal rumen pH this organism shifts to VFA production so as to more effectively compete with the more efficient non-lactate producers, but it reverts to lactate production at lowered rumen pH. Since lactic acid is a much stronger (10 times) acid than VFAs, rumen acidity is greatly increased, and the feedback of this acidity on the induction of more acid production is likely a major factor in the development of rumen acidosis (Figure 15.28). This sequence can be prevented by providing adequate-quality fermentable fiber to maintain cellulolytic organisms and buffering capacity. Of the nonfibrous carbohydrates only starch and sucrose produce lactic acid. Pectin, hemi-

Table 15.9. Effect on fermentation of some carbohydrates of lowering rumen pH

Rumen factor	Sucrose or starch	Pectic or xylan (hemicellulose)
Lactic acid	Increase	None
ATP/unit digested	Decrease	Unchanged[a]
Energy spilling	Unchanged	Increase
Digestibility	Unchanged	Decreased

Source: Strobel and Russell, 1986.
[a]There will be a net reduction in ATP from pectin and xylan because of a reduction in digestion.

cellulose, and other more fiber-like polysaccharides produce acetate but no lactate (Table 15.9).

15.7.3 Parakeratosis

The rumen epithelium is responsive to fermentation acids, the production of normal volatile fatty acids being necessary for normal development of papillae. Excess production of lactic acid or a high concentration of acid in the diet, in combination with less saliva and buffering capacity per unit of feed, results in lower rumen pH. These conditions are unfavorable to the rumen lining and lead to a dark, abnormal appearance and atrophy of the papillae. In severe cases of rumenitis the lining may actually be sloughed away. These conditions of chronic acid production are also related to displaced abomasum syndrome.

Treatment or prevention consists of feeding carbonate buffers or enough coarse forage to induce rumination and neutralization of rumen contents. Other treatments have included plastic particles added to feed with the object of stimulating rumination, rumen motility, and mixing. Added plastic is apparently ineffective in alleviating milk fat depression in lactating cows.

15.7.4 Urea Toxicity

Urea toxicity occurs when large amounts of urea are ingested, followed by enzymatic hydrolysis to ammonia and CO_2. Ammonia is toxic to animal cells at quite low levels (Visek, 1978). Some evidence indicates that it is also carcinogenic. Like nitrate, urea itself is not toxic. It is the substance formed when ammonia derived from proteolysis is detoxified or from feeds high in nonprotein nitrogen and ammonia (e.g., high-moisture, high-nitrogen silages). Chronically high blood urea levels limit intake, and therefore an acute stage of toxicity is rarely reached.

The efficient utilization of urea as a nitrogen source depends on an adequate supply of fermentable carbohydrate to increase microbial needs and provide for conversion of urea nitrogen into microbial protein. There is no set level at which urea in the diet will cause toxicity. A more accurate indicator of status is blood ammonia. Toxicity symptoms occur at blood levels higher than 0.5 mg/100 ml, becoming more severe at higher levels. Blood ammonia levels of about 4 mg/100 ml are lethal. Such levels are reached when rates of rumen production and absorption of ammonia overwhelm the liver's capacity to form urea.

Treatment includes the administration of soluble carbohydrate or, in extreme cases, the evacuation of the rumen. Attempts at prevention have included the use of urease inhibitors to slow the rate of release of ammonia. Practical prevention includes admixture of the nitrogenous source with sufficient soluble carbohydrate or starch and ensuring that feed is always well mixed.