Chapter 1
Anatomy and Physiology of the Rumen

Claudia Maria Bertan Membrive

Introduction

Herbivores can be classified as monogastric or polygastric. Equine, rabbits and elephants represent monogastric herbivores. They have one stomach that does not offer appropriate conditions for fermentative digestion. In these species, the fermentation chambers, which keep a great amount of microorganisms, are represented by the cecum and colon, and both compartments are very developed.

Polygastric herbivores have more than one stomach. In these animals, the true stomach, the abomasum, is preceded by the presence of two to three pre-stomachs. The pre-stomachs consist of an aglandular mucosa and form a compartment where the fermentative digestion occurs exclusively, by the joint action of the microorganisms that live there. The true stomach called abomasum is morphologically and functionally similar to the stomach of monogastric animals, a place of significant enzymatic activity.

Polygastric herbivores can be classified as **Pseudo-ruminants** or **Ruminants**. When they have two pre-stomachs (reticulum and rumen) and a true stomach (abomasum), they are called pseudo ruminants. **Pseudo-ruminants** do not have an omasum and examples are camels, llamas, alpacas and vicunas. **Ruminants** present three pre-stomachs (reticulum, rumen and omasum) and a true stomach (abomasum) and are represented by bovine, sheep, goats, deer, giraffes, reindeer, moose, deer, roe deer and antelopes. After the intake of feed, polygastric herbivores regurgitate it from the ruminoreticular compartment to the oral cavity and chew it again; this mechanism is named rumination. This mechanism, which allows chewing the feed again and reducing it to smaller particles, represents a vital process for the fermentative digestion performed by microorganisms. Figure 1.1 shows the right side view of an adult bovine, illustrating

C.M.B. Membrive (✉)
São Paulo State University (UNESP), Dracena, Brazil
e-mail: cbertan@dracena.unesp.br

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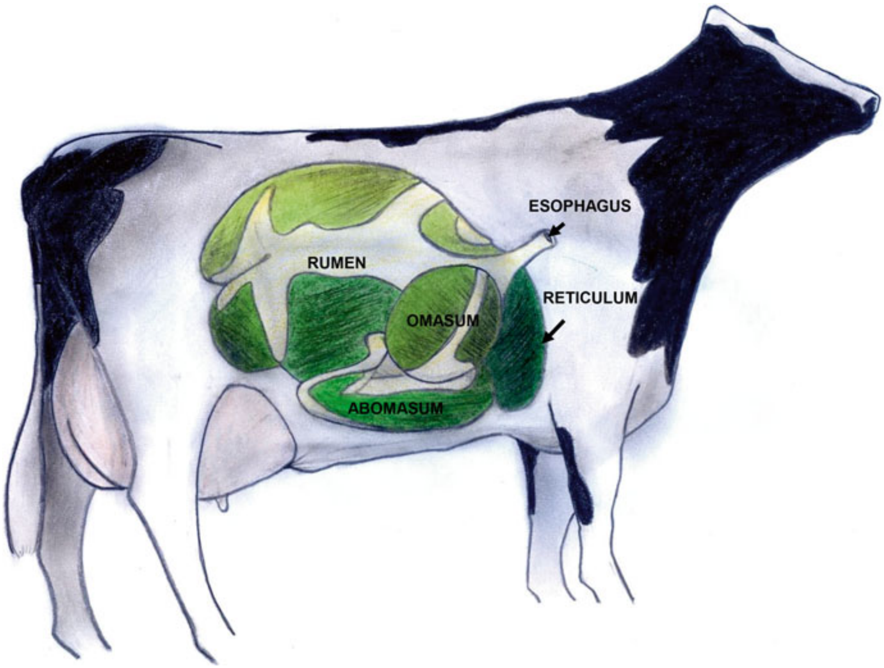

Fig. 1.1 Right side view of an adult bovine illustrating the different anatomic segments that integrate the digestive tube: ESOPHAGUS, RETICULUM, RUMEN, OMASUM and ABOMASUM

the segments that integrate the digestive tube: esophagus, reticulum, omasum and abomasum. Figure 1.2 illustrates the left side view of an adult bovine, showing the esophagus, reticulum, rumen and abomasum. It is not possible to visualize the omasum from the left side.

Making a functional analogy, the digestive system of equines, monogastric herbivores with well-developed cecum and colon, is not as efficient as ruminants' to convert cellulosic matter into energy. Besides having a broad population of microorganisms in the colon where part of fiber digestion occurs, ruminants expose fibers to ruminal digestion anteriorly, a functional condition that provides a more efficient digestion when compared to equines. The ruminants' extraordinary capacity to take advantage of fibers from feed was summarized by Van Soest: "*grazing ruminants have a well-developed and specialized digestion mechanism that allows the best utilization of fibrous feed when compared to other herbivores*".

Ruminants have a voluminous fermentative chamber represented by the rumen and a wide microorganism population, selected throughout billions of years of evolution according to their biochemical functions. This particularity determines these animals' position as the greatest utilizers of vegetal fibers. The fermentative digestion developed by microorganisms reached its greatest evolution in ruminants.

The general objective of this chapter is to describe the main features of the anatomy and physiology of ruminants' digestive system, especially the rumen. In this

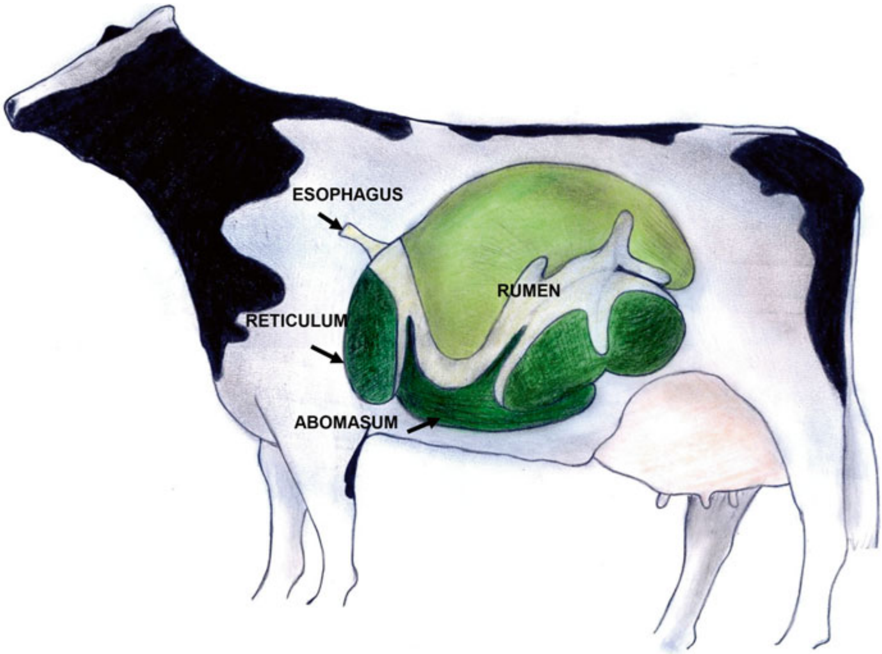

Fig. 1.2 Left side view of an adult bovine illustrating the different anatomic segments that integrate the digestive tube: ESOPHAGUM, RETICULUM, RUMEN, ABOMASUM

chapter, the anatomical and physiological features of the rumen will be approached integratedly with other compartments that come before and after this extraordinary compartment, which characterizes ruminants as the animals that best utilize fibrous feed when compared to other species. This chapter will provide the understanding of anatomical, mechanical and functional features, and the determination of advantages, limitations and disadvantages of these animals because the rumen is one of the main chambers of the digestive tube.

Anatomical and Physiological Properties of Ruminants

In ruminants, the extremely low oxygen concentration in the rumen, allowed throughout three billions years, a selection of microorganisms in the digestive system which represented the maximum biochemical yield under anaerobiosis condition. Moreover, there was the selection of a small percentage of facultative aerobic microorganisms whose function is to remove the small amount of oxygen that reaches the rumen with the feed intake, a fundamental mechanism for the preservation of the anaerobic environment of the rumen. It is interesting to point out that if high oxygen concentrations in the rumen had been kept, there would have been a prioritization of biochemical pathways to form CO_2 and water, compounds that would be unable to be utilized as energy substrates by ruminants. The main products formed in the fermentative digestion are short-chain fatty acids (**SCFA**) that are the greatest energy source for herbivores. Ruminants obtain 50–70 % of their energy from SCFA produced in the rumen.

Considering the broad population of microorganisms kept in the digestive system, their short lifecycle and fast proliferation, part of the microorganisms are daily available as protein source in the digestive tube of ruminants. The rumen is anatomically positioned before the abomasum and duodenum. When moving through them, microorganisms are digested as any protein compound of the diet, becoming an extraordinary protein source for the animal.

A lot of microorganisms need ammonium for growth and multiplication. Ammonium can be provided in the animal feeding using sources like urea, ammonium salts, nitrates and other compounds. Microorganisms convert ammonium into amino acids that are utilized to build up microbial protein. Proteins from the diet that were not digested with the microbial protein generated in the rumen when going through the abomasum and the small intestine are digested by a group of proteolytic enzymes, and the available amino acids are readily absorbed. Therefore, a great advantage of ruminants is their capacity to convert ammonium into amino acids that are used to build up microbial protein, utilized as an essential part of the protein that forms the diet. Thus, besides the energetic contribution through SCFA formation, the microorganisms also represent an important protein source.

In the rumen, microorganisms synthetize all vitamins of B and K complexes in sufficient amounts for the animal's maintenance and growth. Under most conditions, ruminants do not require supplementation of these vitamins. The supplementation of vitamins B and K are necessary for calves and lambs, considering that the synthesis of these vitamins is only started when the ruminal microorganism population becomes active.

Moreover, the longest required time for the digestion of structural carbohydrates determined the need to develop fermentative chambers of great volumetric capacity, represented by the reticulum and rumen in ruminants. Although such compartments are differentiated, both together form a single intern chamber. The reticulum has an average volumetric capacity of approximately 9 l and the rumen from 150 to 200 l (Cunningham and Klein 2008).

In the rumen there is a great group of methanogenic archea that produces great amounts of methane (CH_4) during the fermentative digestion process. The methane production allows the release of exceeding hydrogen ions inside the rumen to the external environment, an essential condition for the maintenance of ruminal pH. Methane cannot be accumulated in the ruminal cavity; therefore, initially it fills out the dorsal part of the rumen and posteriorly is released from the ruminal chamber to the external environment through a mechanism called "eructation". Approximately 500–1000 l of gases are daily eructed by an adult bovine. In general, rumen gases consist of 0.2 % of hydrogen, 0.5 % of oxygen, 7 % of nitrogen, 26.8 % of methane and 65.5 % of carbon dioxide (Cunningham and Klein 2008). Eructation is a vital and essential physiological mechanism for the survival of ruminants.

Main Functions of the Digestive System

In monogastric animals, most of the digestion occurs in the duodenum through the action of enzymes produced in the pancreas and duodenal epithelium. Carbohydrates are reduced to monosaccharides (glucose, fructose and galactose) by amylolitic enzymes. Proteins are reduced to amino acids by the action of a group of proteolytic enzymes. Through the action of lipolytic enzymes, lipids are reduced to fatty acids and glycerol. The bloodstream readily absorbs monosaccharides and amino acids. Fatty acids are transported as chylomicrons through the lymphatic system, reaching the bloodstream afterwards. In monogastric animals, glucose represents the main "energetic currency" of the organism.

Ruminants are herbivores characterized by the presence of three aglandular pre-stomachs (reticulum, rumen and omasum) and a glandular stomach (abomasum). Thus, in ruminants, substrates that are part of the feed go first into the ruminoreticular compartment to be available for microorganisms. Before the feed goes on to posterior compartments of the digestive system, the microorganisms digest most of the substrates. Thus, the feed is submitted to fermentative digestion first and then submitted to the action of enzymes produced by the digestive tube and attached glands. It should be noted that the pre-stomachs are totally aglandular, which provides an excellent environment for microorganisms. Thus, the fermentative digestion performed by microorganisms exclusively determines every digestion that occurs in the rumen. The ruminal content presents 10^{10}–10^{11} bacteria and 10^{5}–10^{6} protozoas/mL. In the rumen, there is a great number of cellulolytic, amilolytic, proteolytic and lipolytic microorganisms. The fermentative action of microorganisms is not restricted only to structural carbohydrates, but also to non-structural carbohydrates and proteins that are firstly digested in the rumen. The existing microorganisms in the rumen are grouped according to the substrate they predominantly degrade. In general, they are classified as cellulolytic (degrade cellulose), hemicellulolytic (degrade hemicellulose), pectinolytic (degrade pectin), ureolytic (convert urea into NH_3), lipolytic (degrade lipids), amilolytic (degrade starch), methane-producing species and ammonia-producing species (Cunningham and Klein 2008).

Structural carbohydrates (cellulose, hemicellulose and pectin) are degraded by a large group of cellulolytic, hemicellulolytic and pectinolytic enzymes. In the rumen, as one of the intermediate phases of the fermentative digestion, there is the production of a great amount of glucose. In ruminants, differently from monogastric animals, glucose produced in the rumen is not readily available as a source of energy to the animal, but it is rapidly utilized by the microorganisms. Thus, glucose produced by bacteria remains in the ruminal environment to be utilized as substrate by them. Microorganisms perform successive degradations that culminate with the production of a group of short-chain fatty acids (SCFA). The main SCFA produced in the rumen are acetic, propionic and butyric acids. They are rapidly transformed in their ionized forms in the rumen and, therefore, commonly mentioned as acetate, propionate and butyrate, respectively. The most produced SCFA is acetate, followed by propionate and butyrate. The proportion of SCFA is altered in function of the diet composition provided to the animal. The greater the concentrate amount provided to the animal is, the greater the total SCFA production becomes. In addition, the production of propionate is increased when compared to acetate, but it must be pointed out that the acetate production is always the predominant one if rumen pH remains above 5.7 (Cunningham and Klein 2008).

SCFA produced in the rumen are rapidly absorbed by the ruminal wall and get into the bloodstream, where acetate is the main "energy currency" in ruminants. However, some tissues exclusively utilize glucose as energetic substrate, especially the nervous system. This system, which coordinates all the physiological processes of the organism, is not capable of producing or storing glucose. Thus, glucose concentrations in the bloodstream must be constantly kept within a physiological range (35–55 mg/dl in bovines, and 35–60 mg/dl in sheep) to guarantee enough plasmatic glucose concentrations for the nervous system to perform its functions (Cunningham and Klein 2008).

Therefore, considering that glucose produced in the rumen is not available to the animal, and in order to ensure partial maintenance of relatively constant concentrations of glucose in the bloodstream, propionate is converted in glucose and then called glycogenic SCFA. Thus, propionate produced by the rumen is readily absorbed through the ruminal wall, getting into the portal vein, and transformed into glucose when reaching the liver. In ruminants, a second source of glucose is available through carbohydrates that go by the rumen without being digested and reach the duodenum where they are readily digested. The participation of enzymes produced by the pancreas and the duodenal mucosa allows carbohydrate digestion, resulting in a significant amount of glucose. The concentrations of blood glucose in bovines and sheep are naturally lower than those found in monogastric animals, whose glucose is the main "energy currency" of the organism (in humans, the glucose concentrations are kept from 80 to 120 mg/dl).

Butyrate produced in the ruminal environment is mostly utilized as an "energetic currency" inside the rumen itself, where the cells of the ruminal epithelium utilize approximately 95 %. The exceeding butyrate, around 5 %, is absorbed by the ruminal wall, reaches systemic circulation and, in the liver, is converted to acetyl-coA, ketone bodies and long-chain fatty acids that are available in the plasma as lipoproteins. The ketone bodies are also used as "energetic currency" in the organism.

Although ruminants are well equipped to chew fibrous material efficiently, chewing is not efficient in the feed intake phase. Under this circumstance, chewing is enough to mix the feed to saliva, providing a moisture degree that is yet enough to make swallowing possible. Posteriorly, the feed found in the rumen is regurgitated from the ruminoreticular compartment to the mouth through the esophagus, re-chewed, re-salivated and re-swallowed. Together those processes characterize rumination, an essential process for the efficient utilization of fibrous feeds by ruminants. Re-chewing occurs carefully and regularly and is an important stimulus for the production of saliva. Re-chewing during rumination aims to reduce the feed particle size and to form a homogeneous bolus. The reduction of feed into smaller particles is fundamental for bacteria to perform fermentative digestion. According to (Cunningham and Klein 2008), in dairy cows, approximately 20,000–30,000 chewing movements are done daily. It is estimated that ruminants spend 8 h a day ingesting feed and 8 h a day ruminating it. The chemical and physical composition of the feed (fiber, energy and protein content) influences time spent ruminating.

Saliva is the main secretion of the digestive system, and an adult bovine produces 170–180 l of saliva/day. The volume of daily saliva produced depends directly on chewing time. The intake of fibrous feeds provides an abundant production of saliva, which is reduced during the intake of concentrates. The chemical composition of bovine saliva contains 126 mEq/L of sodium, 126 mEq/L of bicarbonate, 26 mEq/L of phosphate, 7 mEq/L of chloride, and 6 mEq/L of potassium. Because it contains a great amount of bicarbonate ions (HCO_3), saliva has a fundamental role in the maintenance of ruminal pH. Phosphate becomes important in the process of microorganism multiplication in the rumen (Cunningham and Klein 2008).

In ruminants, the feed intake capacity is influenced by several factors: animal's age (the intake decreases with age), physiological phase (intake reduction in the final third of pregnancy and in the beginning of lactation), sex (females generally ingest less feed than males), production level (the higher the production is, the greater the nutritional demand and intake are), feed availability (for the maximum intake, feed offering is necessary), feed palatability (taste, smell and texture influence the greater or smaller feed intake), feed presentation (natural, ground, granulated, pelletized or bran) and environmental factors (temperature and relative air humidity, stress, population density, trough structure, trough spacing and hygienic-sanitary conditions).

General Anatomical Aspects of Ruminants' Digestive System

The function of the digestive system is to continuously supply the organism with water, electrolytes, vitamins, proteins, carbohydrates and lipids from feed intake. For the organism to utilize these elements from feed intake, the substrates have to be submitted to a physical (segmentation of feed into smaller particles) and chemical processing (breaking of complex molecules into smaller molecules that can be absorbed). After the chemical processing of the feed, the small molecules generated by the digestion have to be absorbed by the intestinal epithelium to be then available and utilized by the organism.

The ruminants' digestive system consists of a long muscular tube that goes from the mouth to the annus, and of a group of glands attached to this digestive tube. The digestive tube of ruminants comprises the following segments: mouth, pharynx, esophagus, pre-stomachs (reticulum, rumen, omasum), true stomach (abomasum), small intestine (duodenum, jejunum and ileum) and large intestine (cecum, colon and rectum). The rectum is provided with an annal orifice in the caudal portion. The glands attached to the digestive tube are represented by the salivary glands, pancreas, and bile system (which consists of the liver, gallbladder and bile ducts). To understand the ruminal physiology, it is fundamental to understand the general anatomical aspects of ruminants' digestive system. Although this chapter aims to describe the rumen and the pre-stomachs, the anatomical peculiarities of the mouth and component structures, such as pharynx, esophagus, rumen and reticulum, omasum and abomasum, will be described because they are directly involved in the rumination and eructation processes. The anatomical understanding of these structures is fundamental to understand the functional mechanisms of the rumen.

Mouth

The oral cavity contains different attached elements like the teeth, tongue, and salivary glands. The teeth and tongue are responsible for harvesting and physically reducing the feed. The presence of salivary glands, connected to the oral cavity through ducts, is essential to feed moisture, chewing, and swallowing.

Feed intake consists of prehension, chewing and swallowing. Prehension refers to the introduction of the feed into the oral cavity. Prehension varies according to the different species. In species that utilize teeth to prehend the prey or to fight, like dogs, the opening of the oral cavity is quite broad. In herbivores, in general, the mouth opening is quite small. Considering that bovines ingest small portions of the feed, the relatively small opening of the mouth cavity is not a disadvantage for this species. During feed prehension, the lip muscle movement is important not only for the feed capturing process, but also to promote the emptying of mucosal glands located among the lip muscle fibers. In bovine, there is a ventral buccal gland that ends in the buccal vestibule, which presents a great number of ducts connected to the oral cavity. The bovine oral cavity has a great amount of conical papillae formed by horny and cornified projections pointed cranial-caudally towards the back of the mouth. The function of these structures is to avoid the loss of roughage feed when the animal chews with open lips, which allows a greater displacement of the jaw during chewing.

Another characteristic of the oral cavity of bovine is the hard palate that is connected to the basal lamina due to evolutionary loss of upper incisive teeth. The hard palate is formed by a dozen or more transversal ridges whose protrusions progressively decrease until they finally disappear in the posterior part of the mouth, where ridge borders have numerous papillae. The hard palate is large in bovine and narrower in sheep and goats, species whose tongue is not used for feed prehension.

In bovines, the **TONGUE** is big, large, rough and with great mobility. In sheep and goats, the tongue and the hard palate are less rough when compared to bovine. The ventral side of the tongue is thin and medially attached to the floor of the oral cavity by the tongue frenulum. In the cranial-caudal side, the tongue is divided into three distinct regions: apex, body and root of the tongue, respectively. The dorsal side of the tongue is thick and cornified and presents numerous projections called papillae. Papillae favor the movement and grinding of feed inside the mouth, besides directing the feed towards the esophagus. The tongue is a muscle organ utilized to prehend the feed, intake the water and displaces the feed inside the mouth during chewing. In bovines, the tongue moves the feed on the lower jaw of molar teeth and also functions as a pump that moves the feed inward the esophagus during the swallowing process. It is important to point out that because bovines have more than one tasting bud per circumvallate papillae, they first select the feed by tasting while other ruminants select the feed by smelling it.

In bovines, the **LIPS** are thick and have strict mobility. In sheep and goats, the lips are thin and flexible and the upper lip has a medial labial division called "filter". This feature allows them to graze close to the ground, characterizing low grazing, which is not possible for bovine. Regarding the animals' capacity to select the feed that they ingest, bovines, bubalines and sheep are classified as non-selectors. In bovines, the relative lip insensitivity favors the non-selectivity and intake of strange bodies that after being ingested can cause lesions in the lower digestive tract. Thus, due to the low selectivity of this species, the utilization of paddocks without strange elements (for example, plastic bags, pieces of barbed wire, nails and others) is recommended. Sheep are also classified as non-selectors. Among domestic ruminants, goats are the most selective ones regarding feed and are considered intermediate selectors. They have greater mobility of the upper lip and a greater percentage of their tongue length is not attached to the floor of the mouth. As a result, a greater proportion of the tongue is loose and can be exposed when compared to non-selective ruminants.

For some time, it was thought that goats' fiber digestion capacity was superior to sheep's and bovines' due to a more efficient fermentative digestion; however, currently it is believed that this is not true because the greater fermentation capacity is due to the intake of better quality feed since this species is very selective when compared to others.

The **TEETH** have the function to mechanically grind and reduce feed to smaller physical particles through chewing. Grinding allows an increase in the feed surface area, which favors a greater area for enzyme action. This preliminary step is fundamental for the chemical and microbiological degradation of the feed. The teeth are also utilized to cut the feed after prehension. Four kinds of teeth are evident according to their location and function. Incisive teeth are the front most ones and are utilized to cut the feed. The canine teeth come after the incisors and are generally used to cut the feed, but they are absent in ruminants. Pre-molar teeth are caudal to canine. After the pre-molars, there are larger teeth called molars. Pre-molar and molar teeth present appropriate size and shape for grinding.

Bovine, sheep and goats present permanent teething consisting of 32 teeth. In the upper jaw, the incisive and canine are absent, and there are 6 pre-molar and 6 molar teeth; therefore, there are a total of 12 teeth. In the place of the upper incisors, bovines present semicircular cuneiform elevations on the surface, which are called dental pads. The dental pads tear the forage when pressed against the lower incisor. The lower jaw has 8 incisors, no canines, 6 pre-molars and 6 molars, totalizing 20 teeth. In bovines, the lower incisors have the shape of a shovel and are located separately from each other, and also have a quite loose implantation, which reduces the lesion risk of the dental pads. During grazing, bovines initially take the grass to the mouth with the help of the tongue and then cut it by pressing the incisors against the dental pad. In ruminants, the upper and lower dental jaws have uneven width, characterizing unilateral horizontal chewing. Although both sides of the dental arch are utilized, most animals tend to favor one of the sides for chewing.

SALIVARY GLANDS release their secretions in the oral cavity through ducts that connect these glands to the oral cavity. Salivary glands are formed by a set of ducts that are internally covered by mucosa and serosa cells. The mucosal cells synthetize a mucous secretion, which is characterized by a group of glycoproteins, called mucin. Salivary mucin consists of albumin, alpha 1-globulin and glycoproteins, and becomes viscous in the presence of water. Mucin gives saliva the viscosity, which is important to reduce the friction between the feed particles and the oral cavity. The serosal cells secrete an aqueous fluid with ions of Na, Cl, and specially HCO_3 in great amounts. In the saliva of ruminant animals, the alpha-amylase enzyme is not present; therefore, the saliva is not important for digestion. It should be pointed out that calves and lambs produce lipase in the oral cavity and it reaches the abomasum with the ingested milk. Such enzyme decomposes around 20 % of ester bonds of fats present in the milk, during milking. The amount of secreted saliva by the calf depends on the milk flow that goes by the mouth. When the calf suckles the milk slowly, in milk feeding using bottles, there is a greater saliva production. Milk feeding in buckets makes the milk pass by the mouth faster, reducing saliva production.

Ruminants have a pair of parotid glands, a pair of submandibular glands and a pair of sublingual glands, besides numerous smaller salivary glands in the lips, cheeks, tongue, gums and floor of the oral cavity. The pair of larger salivary glands that produce predominantly serosal secretion does a greater production of saliva. The mandibular gland is located near the jaw angles and produces serosal and mucosal secretion. In ruminants, this gland is larger than the parotid ones and is located deeply. The parotid gland is a pair of serosal gland that is found ventrally to the ear, is particularly developed in herbivores, and secrets a great amount of an alkaline solution. The parotid glands are responsible for over 50 % of the total saliva production. During chewing, due to the pressure of the muscular movement, the salivary glands that are found among the muscular fibers, through the pressure of the muscular movement secret a lot of saliva. The saliva secretion in ruminants is continuous, but the secretion amount increases greatly in the presence of stimuli associated to feeding, rumination and presence of rough feed in the gastric compartments.

During chewing, saliva is mixed to the feed to provide the necessary moisture for the feed to be swallowed. Drier feed requires a greater amount of saliva to be moist, and therefore the saliva amount is changed in function of the feed composition. Saliva consists of a colorless, odorless, and tasteless solution with alkaline pH. According to, bovines produce 110–180 l of saliva daily and it has a pH ranging from 8.2 to 8.2. Sheep produce from 6 to 16 l of saliva a day, and its pH varies from 8.0 to 8.4. Saliva consists of 99–99.5 % of water and 0.5–1 % of dry mass, represented by inorganic and organic compounds, leukocytes, microorganisms and desquamated epithelial cells (Cunningham and Klein 2008).

Ruminants' saliva also presents a great amount of PO_4, which is not found in non-ruminant species. Through the swallowing of saliva produced in the oral cavity, PO_4 produced in the saliva goes to the rumen where it contributes importantly to the multiplication of microorganisms that live in the rumen because it is directly involved in the process of ruminal buffering. The high concentration of nitrogen in the saliva of ruminants is particularly important, and it ranges from 9 to 30 mg per each 100 mL. Around 65–70 % of total nitrogen corresponds to urea, which reaches the rumen in significant amounts with saliva. Also, in ruminants, saliva represents a possibility to recycle urea. The exceeding urea in the organism can be directed to the saliva, which is excreted by salivary glands, and be re-directed to the ruminoreticular cavity, increasing nitrogen availability to ruminal microorganisms.

The salivary glands receive parasympathic and sympathic fibers originated in the autonomous peripheral nervous system. The parasympathic stimulation by acetylcholine increases the salivary secretion. The sympathic stimulation through noradrenalin reduces the salivary flow in general.

During feed prehension, ruminants have little elaborated chewing, when the feed is moistened just enough to be swallowed. However, these animals ruminate by regurgitating the feed from the ruminoreticular cavity into the mouth and then through the esophagus. After the feed is regurgitated, the water excess of this material is swallowed and then the animal starts the chewing, which becomes more elaborated. Ruminants spend approximately an average of 8 h ruminating daily. A dairy cow makes around 40,000–50,000 chewing movements/day. Rumination follows the circadian cycle: during the day the animal normally ingests a great amount of feed and ruminates intensively at night, a characteristic that ruminants acquired when they needed to feed themselves during the day to protect themselves from predators during the night, which was a period dedicated to rumination (Cunningham and Klein 2008).

Rumination is an important process to stimulate saliva production. During chewing, the moving muscles compress the salivary glands to help their emptying through a system of ducts that end up in the oral cavity. The abundantly produced saliva is swallowed and sent to the ruminoreticular cavity. The bicarbonate ions have the important function of continuously buffering the ruminal pH. The fermentative digestion in the rumen causes the constant formation of SCFA that reduce ruminal pH. The bovine saliva contributes to the daily infusion of 250 g of Na_2HPO_4 and 1–2 kg of $NaHCO_3$. Therefore, the continuous bicarbonate infusion in the rumen through saliva has a buffering function in the ruminal environment so that the pH becomes appropriate for the survival and multiplication of microorganisms, since they in general appreciate ruminal environment with pH ranging from 5.7 to 6.8 (Cunningham and Klein 2008).

Pharynx

The pharynx represents a segment of the passage of feed and air. The pharynx, located between the oral cavity and the esophagus and the choanae and the larynx, is a common region for both the respiratory and digestive organs. During the passage of feed to the pharynx, mechanical factors and reflexes related to the swallowing prevent that feed gets in the glottis and nasal choanae. The passage of feed into the respiratory tube is avoided by the soft palate that becomes horizontally positioned, and by the larynx elevation, while the epiglottis is positioned against the glottis causing it to close. The muscles of the hyoid bone have a close functional relation with the muscles of the tongue and pharynx, and have an important role in the chewing and swallowing of feed. The pharynx is formed by muscles that cause its narrowing and shortening during swallowing. The pharynx is a segment that has voluntary control in both directions, oral-caudal during swallowing and caudal-oral in regurgitation and eructation, depending on the physiological needs of the ruminants. The pharynx receives and directs the regurgitated bolus to the mouth. It also receives the gas that is expelled in great amounts from the ruminal cavity to the external environment. After the end of swallowing, the passage of air is re-established by the pharynx.

Swallowing is a process that is divided into three phases, the first is a voluntary one and the other two have reflexive nature. In the first phase, called voluntary, the feed, after chewed and transformed into the bolus through the action of tongue muscles, is positioned in the posterior upper part of the tongue. Next, the mouth is shut, chewing is interrupted, breathing is stopped, the tip of the tongue touches the hard palate and the bolus is pressed between the tongue and the pharynx that opens through a contraction of the hyoid bone. In that moment, the feed gets into the pharynx, ending the first phase of swallowing. The second phase of swallowing, called pharyngeal or reflexive, is very short and corresponds to the passage of the bolus through the pharynx. The feed presence in the pharynx stimulates local receptors that send signals through afferent nerve fibers to the swallowing center located in the encephalic trunk. Then, through efferents nerve fibers, the trunk sends stimuli to the muscles that form the pharynx. Under this stimulus, the pharynx muscles contract themselves in the cranial-caudal direction, pushing the passage of the feed from the pharynx to the esophagus, ending the second phase of swallowing. The third phase, called esopharingeal phase, comprises the passage of the feed through the esophagus. This passage occurs through the peristaltic movements that start in the anterior portion of the feed in the esophagus and, when propagating through the esophagus, they push the feed towards the ruminoreticular compartment.

Esophagus

It comprises a muscular tube that extends from the pharynx to the ruminoreticulum. In bovines, the esophagus is 90–105 cm long, from the pharynx to the cardia. The length of the cervical part is 42–49 cm long, and the thoracic part is 48–56 cm long. In sheep, the esophagus is approximately 45 cm long. In this route, the esophagus gets into the thorax, goes through the medianistinical space and finally reaches the abdominal cavity where it connects to the ruminoreticulum. The lumen of the esophagus normally remains closed, making the folds evident on its internal surface. In the passage of the feed, the folds are stretched.

In ruminants' esophagus, there is the formation of functional sphincters such as the cranial esophageal sphincter located in the entrance of the esophagus and the caudal esophageal sphincter. The cranial and caudal sphincters function alternately, that is, the contraction of the former causes the relaxing of the latter, and the contraction of the latter results in the relaxing of the former. This reciprocal dependence is especially important in eructation. The esophagus is connected to the dorsal part of the common region to both compartments, the rumen and the reticulum.

Stomach

The stomach consists of four chambers through which the feed passes and that are successively called: rumen, reticulum, omasum and abomasum (Figs. 1.1 and 1.2). The first three chambers are known as anterior stomach and were developed to favor the digestion of structural carbohydrates that are part of ruminants' diet. Only the last chamber, the abomasum, is comparable in structure and function to the simple stomach of most animals of other species.

The stomach of an adult bovine is a huge compartment that practically fills up the whole left side of the abdominal cavity, still occupying most of the right abdominal cavity. In an adult bovine, the stomach occupies nearly 75 % of the abdominal cavity, where the rumen corresponds to approximately 6 % of the animal's live weight. The stomach capacity varies greatly with age and animal size. The volumetric capacity of the rumen is 100–150 l in small-sized bovines, 130–160 l in medium-sized bovines, and 120–300 l in large-sized bovines. It is believed that the bovine rumen has an average volumetric capacity ranging from 150 to 200 l (Cunningham and Klein 2008). In sheep, the volumetric capacity of the rumen is approximately 15 l. Considering that the rumen represents the fermentative chamber where most of the digestion happens, it can be assumed that the volumetric capacity of the rumen determines the capacity of feed intake and, consequently, favors a greater productive capacity of the animal. According to DYCE (2004), it is estimated that in bovines the proportion of the different compartments is represented by 80 % of rumen, 5 % of reticulum, 8 % of omasum, and 7 % of abomasum. In small ruminants, represented by sheep and goats, these proportions are different, 75 % of rumen, 8 % of reticulum, 4 % of omasum and 13 % of abomasum.

The celiac artery that branches out irrigating different cavities does the irrigation of the multicavitary stomach of ruminants. The venous vascular system that carries the products of ruminal fermentation absorbed through rumen epithelium, lead to the portal-hepatic vein.

In order to be able to perform their functions, an adequate motor activity of the pre-stomachs becomes fundamental. The movements in the different pre-stomachs aim to fragment particles mechanically, mix existing components inside the compartment, stimulate absorption of short-chain fatty acids, regurgitate feed from the ruminoreticulum to the mouth for rumination takes place, and release gases from the rumen to the external environment through eructation. The ruminants' stomach innervention is autonomous. The sympathic fibers that originate in the celiac plexus form the gastric plexus, right ruminal plexus and left ruminal plexus. The pattern of the parasympathic innervation is represented by the vagus nerve that is split into dorsal vagus nerve and ventral vagus nerve. The dorsal vagus trunk is especially important for rumen innervation, whereas the ventral vagus trunk is essential for innervation of the reticulum, omasum and abomasum. The sectioning of both trunks eliminates all the motor activity of anterior chambers. The musculature, under parasympathic innervation, assumes a relevant role in the rumen mobility. The development of the muscular layer is associated with the kind of feed ingested by the animal, because the greater the amount of fibrous feed ingested is, the greater the necessity of ruminal motility becomes and, therefore, the greater the development of the muscular layer gets.

For a better anatomical and physiological understanding of the different compartments, they will be described individually.

Reticulum

As shown in Figs. 1.3 and 1.4, the reticulum comprises a relatively spherical compartment, located cranially to the rumen that presents a volumetric capacity of approximately 9 l in adult bovines. Both compartments are partially separated in the ventral portion through the ruminoreticular fold that forms a big orifice of passage between the rumen and the reticulum when contracted. The rumen and the reticulum

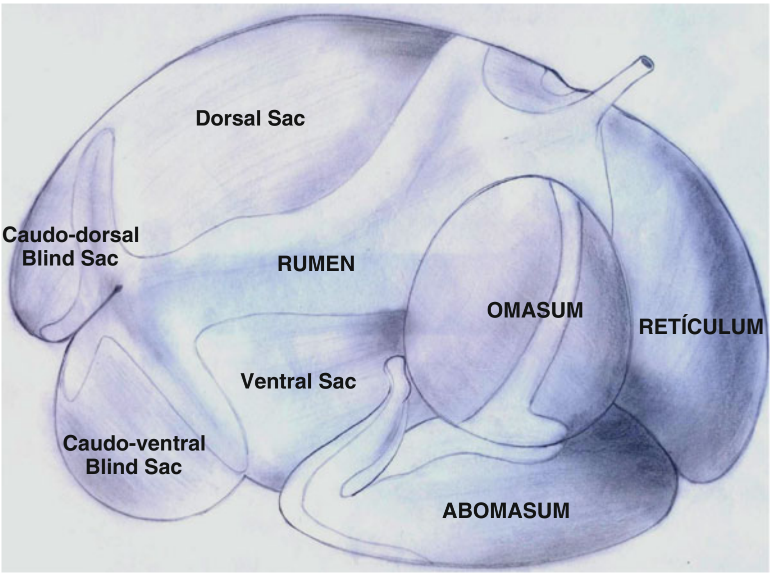

Fig. 1.3 Right side view illustrating the different anatomic segments that integrate the digestive tube of an adult bovine: the aglandular pre-stomachs (RETICULUM, RUMEN and OMASUM), the glandular stomach (ABOMASUM), as well as Dorsal Sac, Caudo-dorsal Blind Sac, Ventral Sac, Caudo-ventral Blind Sac

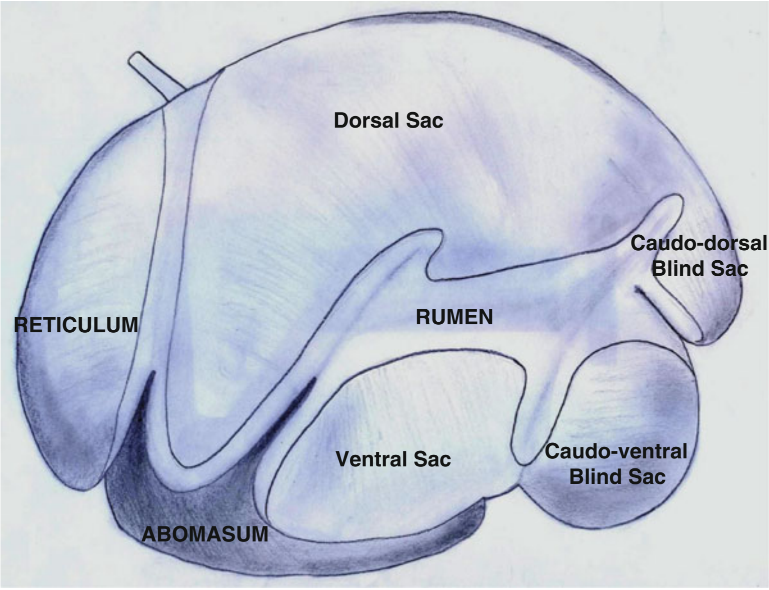

Fig. 1.4 Left side view illustrating the different anatomic segments that integrate the digestive tube of an adult bovine: the aglandular pre-stomachs (RETICULUM and RUMEN), the glandular stomach (ABOMASUM), as well as Dorsal Sac, Caudo-dorsal Blind Sac, Ventral Sac, Caudo-ventral Blind Sac

freely connect to each other internally. The reticulum is considered a conjugated compartment to the rumen. The reticulum is located extremely close to the diaphragm, distant 2–4 cm from the pericardic bag that constitutes the heart of bovines. The reticulum is located cranially to the rumen, under the sixth and eighth rib and mainly to the left of the median plane.

The esophagus ends in the beginning of the stomach in the limit between the rumen and reticulum, internally presenting a continuation through the esophageal canal, also called esophageal or reticular groove. The cardia is the origin point of the esophageal or reticular groove, which goes ventrally 17–20 cm up to the reticular-omasal orifice. This structure is represented by a groove consisting of spiral fleshy labia where the upper opening is connected to the cardia and the lower opening to the omasum. The cardia is located in the junction of the rumen with the reticulum, and, then, ending in both chambers. In unweaned calves, during the intake of milk, the reticular groove becomes a closed tube that directs the milk from the esophagus to the omasum canal, where the milk goes down to the abomasum. After weaning, the diet changes lead to the decreasing utilization of this via. The mechanisms that act on the closing of the reticular groove will be described later.

The ruminoreticular mucosa is totally deprived of aglandular epithelium and is covered with a rough stratified cutaneous epithelium. The reticulum mucosa has numerous primary folds, approximately 1 cm high, called crests (Fig. 1.5). These

Fig. 1.5 Reticulum inside view of an adult bovine. The reticulum presents crests with about 1 cm height that design geometric structures of four to six sides and characterize a quite reticulated structure similar to "honeycombs"

structures limit the tetra, penta or hexagonal spaces that are named "reticular cells" and characterize a quite reticulated structure similar to "honeycombs". These structures present short papillae in their interior. This reticulated pattern becomes less regular in the region of the junction with the rumen, gradually mixing itself to the papillated surface of the rumen. The epithelium of the reticular mucosa is stratified and squamous. The keratinized layer becomes important to reduce the abrasion resulted from the rough diet ingested by ruminants.

The reticulum of small ruminants is relatively bigger than the one of bovines. In the covering of the reticulum there are clear differences among the species. In sheep and goats, the crests that limit the four- to six-sided structures are much shorter and present more prominent cut borders. In these species, the papillated ruminal mucosa also invades most part of the reticular wall. In the smaller curvature of the reticulum, there is a reticular-omasal orifice whose function is to promote the passage of particles that are smaller than 1.18 mm to the posterior tract.

Rumen

According to Figs. 1.3 and 1.4, the rumen consists of a very broad sac-like chamber with an average volumetric capacity of 150–200 l. The microbial digestive capacity of the rumen depends on its volume, among other things. The rumen presents structures represented by thick muscular bands, called pillars, which divide the ruminal space into dorsal sac, ventral sac, blind dorsal sac and blind ventral sac. The main ruminal pillars surround the organ dividing the main sacs into ventral and dorsal. The coronary pillars, which are smaller, limit the blind caudal sacs. The relative proportions of the sacs that constitute the rumen vary among domestic ruminants. The smaller size of the dorsal sac and the extensive caudal projection of the blind ventral sac give the rumen of sheep and goats an asymmetric aspect when compared to bovine rumen, which has a more symmetric aspect. The interior of the ruminoreticular compartment connects to the esophagus and omasum, through an opening located in the extremities of the reticular groove. The esophagus opens itself dorsally to a region that is common to compartments, rumen and reticulum. Posteriorly, the reticular-omasal orifice links the reticulum to the omasum.

The rumen stretches from the cardia up to the pelvic entrance, from the abdominal roof to the floor. This compartment fills up most of the total left antimerus of the abdominal cavity, and through the caudal-ventral segment it goes through the median plane and reaches the abdominal cavity right half (Figs. 1.6 and 1.7).

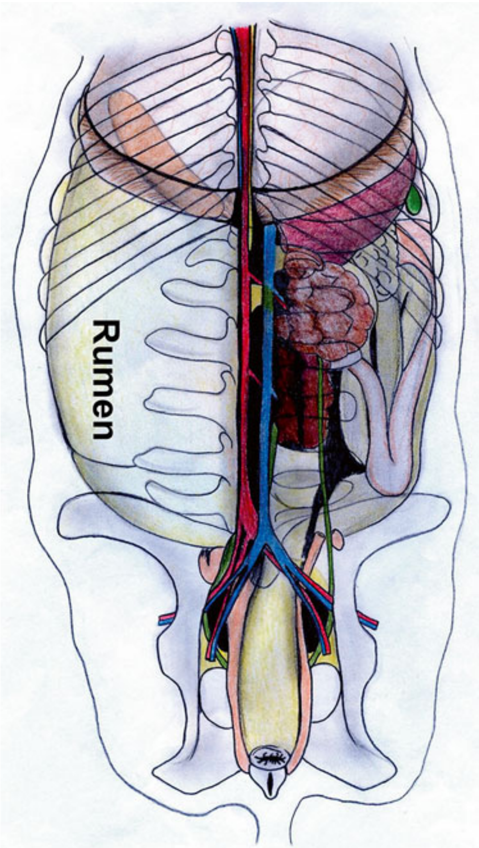

Fig. 1.6 Dorsal view of the abdominal cavity inside of an adult bovine, illustrating the ruminal compartment that fills up the total left antimerus of the abdominal cavity and reaches the abdominal cavity right half

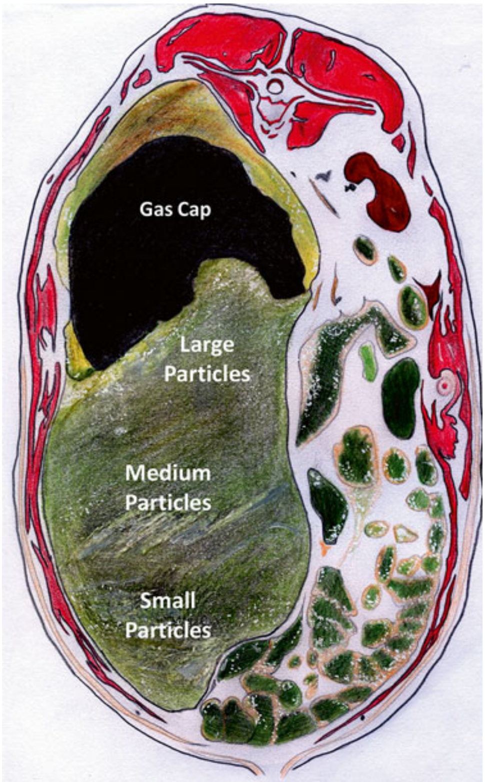

Fig. 1.7 Caudal view of the cross section of the abdominal cavity of an adult ruminant, illustrating the rumen filling up the left antimerus of abdominal cavity, as well as the stratified organization of the feed particles in the rumen according to the different particle size. Smaller particles are located in the ventral part of the rumen, medium-sized particles stay over the smaller particles, and the larger particles float on the surface of the ruminal content. A gas cap fills up the dorsal part of the rumen

The rumen and the reticulum represent compartments that have lost their gastric glands after undergoing deep phylogenetic changes, in size and shape, caused by the rough and voluminous characteristic of the feed. The relative size of the rumen varies according to the age of the animals, and mainly by the type of diet ingested. The rumen is covered by a stratified keratinized epithelium without glands, and therefore all digestive processes carried out in the rumen are exclusively resulted from fermentative digestion.

The ruminal compartment is covered by papillae (Fig. 1.8), especially developed in the ventral sac. Normally, papillae are bigger and denser inside blind sacs, less numerous and prominent in the ventral sac, and much less developed in the center of the rumen roof and the free borders of the pillars. Individual papillae vary from rounded short elevations, going through conical and linguiform ones, to flattened leaves. These papillae can be up to 1.5 cm long and contain a highly vascularized conjunctive tissue axis consisting of thin collagen fibers and elastic fibers. The ruminants' feeding habits determines the number, distribution and length of papillae. It should be considered that the development of papillae is caused by the trophic action of the feed on the mucosa.

Fig. 1.8 Rumen inside view of an adult bovine, illustrating the ruminal papillae

Ruminants that intake more concentrates have a more uniform distribution of ruminal papillae in the ruminal mucosa. The adaptive process of the ruminal mucosa (number, size and distribution of the papillae) due to the animal nutrition requires a period of 3–8 weeks. The adaptive mechanism depends on the production of SCFA, butyric and propionic acids, produced during fermentation. The need of a greater amount of blood to absorb these SCFA provides a greater offer of trophic, hormonal and mitogenic agents that reach the papillae for a greater irrigation of the tissue, and determine their greater development. On the other hand, when ruminants' feeding is based on fibers and fermentation induces the production of large amounts of acetate, there is a reduction in the size of the papillae. Thus, in ruminants with great intake great of forage, the ruminal papillae do not present uniform distribution. In the dorsal ruminal wall, the papillae are absent; therefore, in this region absorption of products derived from microbial action does not occur. The SCFA that go through the papillae by simple diffusion reach the vascular system, through the portal-hepatic system reaches the liver, and by the hepatic vein reaches the caudal cava vein.

The ruminal epithelium is deprived of the muscular layer of the mucosa. The characteristics of the papillary covering initially were related to the rough structure of feeds ingested by ruminants. Posteriorly, it was assumed that the presence of ruminal papillae referred to a structure developed to increase the epithelial surface, once the SCFA produced by microbial fermentation are absorbed in the rumen and reticulum. SCFA, water and vitamins of complex B and K are absorbed through the ruminal papillae. Height, thickness and shape of papillae depend on the feed energy composition. Papillae reduce their size when there is an increase in the availability of rough feed or during a drought period. When animals consume high-concentrate diets, the papillae may become longer and larger.

The rumen has the function of providing a compartment with the adequate conditions to allow chemical reduction of feed by microorganisms. In the rumen, the feeds are stratified according to the particle size (Fig. 1.7). The smaller particles, previously submitted to physical reduction of the feed into smaller particles in the mouth, are positioned in the ventral part of the rumen, favoring the passage of these particles to the omasum through the reticular-omasal orifice. The medium-sized particles stay over the smaller particles, and, finally, the larger particles float on the surface of the ruminal content, positioning them on the dorsal part of the rumen. This stratification by particle size allows that larger particles, which are not sufficiently physically degraded and located on the dorsal portion of the ruminal content, to be sent again to the oral cavity. Therefore, the rumen presents ruminal movements that allow regurgitation of bigger particles from the rumen to the mouth, where they can be re-chewed and physically reduced to smaller particles through rumination since only particles smaller than 1.18 mm pass to the posterior digestive tract through the reticular-omasal orifice. After the feed is re-chewed, it returns to the rumen, which has a highly adequate environment for the feed to suffer the bacterial action and be chemically reduced. The ruminal movements also guarantee the eructation process where the gases positioned in the dorsal portion of the rumen are eliminated to the external environment through their passage by the esophagus and oral cavity.

Omasum

As shown in Fig. 1.9, the omasum has a round shape in bovine and oval shape in sheep similar to the shape of a bean, and is found dorsally right to the reticulum, between the rumen and the liver. The omasum is located to the left between the rumen and the reticulum. The largest part of the omasum is located between the eighth and eleventh ribs. The omasum is relatively smaller in sheep and goats. The volumetric capacity of the bovine omasum is approximately 14–15 l. The omasum interior presents hundreds of semilunar laminas that originate in both sides and from the largest curvature projecting to the smallest one, where there is a more open passage that forms the omasal canal. This characteristic gives the omasum a leafy aspect. In the omasum, there are approximately 12 larger folds and a great number of smaller folds. Besides those larger folds, there are other groups of smaller folds that can be visualized when these laminas are separated or transversely sectioned. The laminas are covered by short keratinized papillae (Cunningham and Klein 2008).

The function of the omasum is not clearly defined. The omasal folds determine a surface area 10 % larger than the rumen, giving the omasal mucosa a great absorptive capacity, especially for water. The absorption capacity of the omasal epithelium is similar to the ruminal papilla capacity. It makes the intake that recently left the ruminoreticular compartment less fluid before reaching the abomasum.

A small orifice, the reticular-omasal sphincter, connects the reticulum to the omasum. A large orifice connects the omasum to the abomasum, called omasal-abomasal sphincter.

Fig. 1.9 Inside view of the omasum of an adult bovine, illustrating the semilunar laminas that give the omasum a leafy aspect

Abomasum

As seen in Figs. 1.3 and 1.4, the abomasum is a pear-shaped sac that is bent on the abdominal floor, involving the inferior portion of the omasum behind. In bovines it has an average volumetric capacity of 18 l. In young calves, the abomasum covers a large ventral part of the abdomen, from the coastal arch to just before the pelvis. In adult bovines, the abomasum extends only up to the transversal plane by the first and second lumbar vertebrae. The back part is found in the xiphoidal region, where most part of the organ is located to the left of the median line. The abomasum is a glandular compartment that is similar to the simple stomach of monogastric species. Similarly to the simple stomach, the abomasum is divided into fundus, body and pylorus, even though the border between these parts is not precise. The abomasum of sheep and goats is relatively large when compared to bovine one. Age and pregnancy are factors that influence the size and topographic location of the abomasum.

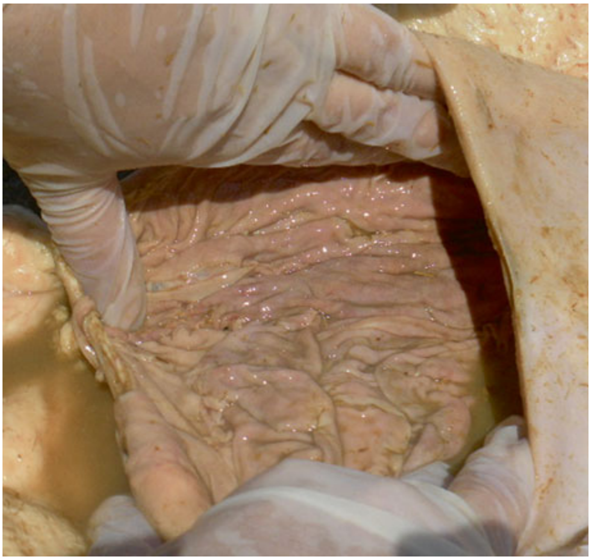

Fig. 1.10 Inside view of the abomasum of an adult bovine, illustrating the glandular gastric mucosa full of rugae

The abomasum has a mucosa full of rugae like the stomach of other mammals (Fig. 1.10), consisting of glandular gastric mucosa. A very viscous mucous layer coats the pinkish mucosa of the abomasum. The physiological mechanisms that occur in the abomasum are like the mechanisms that happen in the stomach of monogastric animals, a place for intense enzymatic digestion. The presence of rugae increases sixfold the surface area of the abomasum. Ruminants that intake protein-rich feed (concentrate) present a larger glandular portion with a great number of HCl-releasing parietal cells in the abomasum.

The digestive system of ruminant species presents several particularities in the first weeks of life. The understanding of these characteristics, discussed here next, is fundamental to adequate diets in the first weeks of life for these species.

Characteristics of the Digestive System of a Newborn Ruminant Animal

Functioning Mechanism of Esophageal Groove

In lactating animals it is important that the ingested milk bypasses from the rumen so that it can be properly developed. The presence of milk in the rumen determines inadequate fermentation that can predispose the animal to disorders of the digestive system. Milk bypass from the rumen is possible due to the specifically developed anatomical structure in the digestive system called esophageal groove or reticular groove. This structure consists of muscular pillars that organize themselves on the

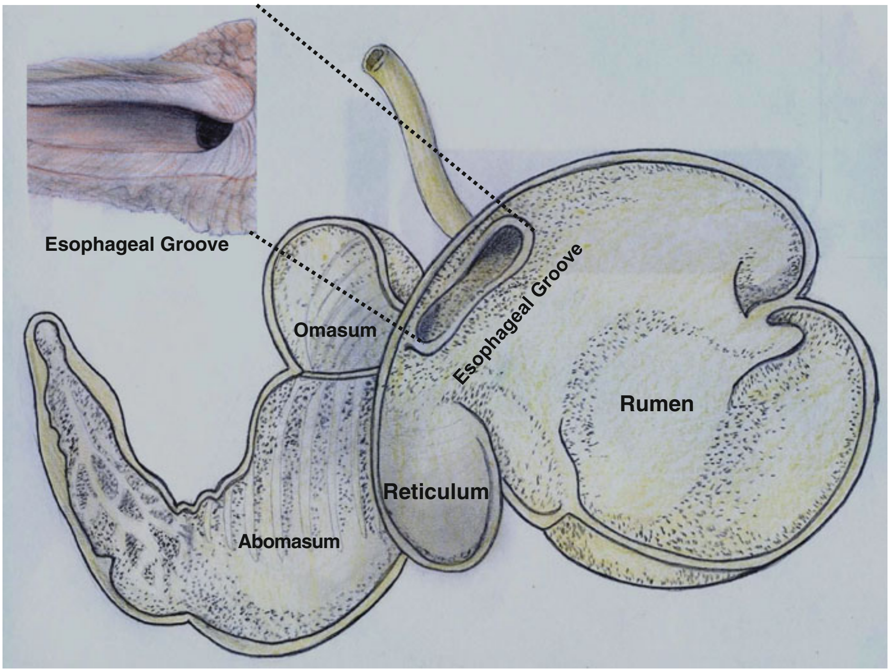

Fig. 1.11 Inside view of the anatomic segments that integrate the digestive system of a calf in the first weeks of life (reticulum, rumen, omasum and abomasum) illustrating in details the ESOPHAEAL GROOVE, also called RETICULAR GROOVE. This structure consists of muscular pillars that organize themselves on the dorsal wall of the reticulum forming a gutter that runs along this wall from the cardia to the reticular-omasal orifice

dorsal wall of the reticulum forming a gutter that runs along this wall from the cardia to the reticular-omasal orifice. Under specific stimuli, the muscles that form this groove are contracted, so that the muscles arrange themselves in a way that the gutter becomes an almost complete tube. This muscular tube connects the cardia to the omasal canal (Fig. 1.11), making the milk bypass from the rumen and reticulum. Thus, when the groove is contracted, approximately 90 % of the milk that reaches the cardia is directed to the omasum whereas 10 % reaches the rumen (Cunningham and Klein 2008).

The act of milk suckling performed by the calf causes the contraction of the esophageal groove. The closing of this groove is a reflexive action, originated by the calf's "suckling desire" and determined by efferent impulses originated in the brain trunk that reach the esophageal groove through the vagus nerve. When milk goes through the pharynx, it stimulates chemoreceptors that, through afferent fibers represented by the glossopharyngeal nerve, direct this sensorial information to the medulla oblongata. The medulla oblongata sends impulses through efferent fibers, represented by the vagus nerve, causing the closing of the esophageal groove and the relaxation of the reticulo-omasal orifice and omasal canal. The contraction of the groove forms a temporary tube that connects the cardia orifice to the reticular-omasal orifice, known as esophageal groove. This temporary structure bypasses the milk from the rumen and the reticulum, goes through the omasum to be directly poured into the abomasum, where the milk will be submitted to enzymatic digestion.

The calf or lamb's head position during milk suckling does not seem to affect the efficiency of the esophageal groove closing. However, when compared to bottle, offering milk in a bucket decreases the efficiency of the groove closing, directing a greater amount of milk to the rumen. Therefore, the use of bottles to feed calves is more recommended than the utilization of buckets.

The reflex for the contraction of the esophageal groove is first triggered by the calf's "suckling desire", and after ingestion, milk salts and proteins may increase the stimulus to form the esophageal groove when going through the pharynx. Up to 2 months of age, milk and water go directly from the esophagus to the abomasum; later, when the calf ingests water or milk, this groove starts working less efficiently. This reflex decreases, as the animal gets older.

After weaning, changes in the diet cause a decreasing utilization of this route; however, a part of the soluble nutrients released into saliva during chewing are bypassed by the esophageal groove. In adult animals, when released by the neurohypophysis, the anti-diuretic hormone stimulates the thirst center and affects the esophageal groove bypassing part of the ingested water. It is believed that by action of anti-diuretic hormone most of the water that adult animals intake can be bypassed to the rumen through the esophageal groove. Likewise, the closing of the esophageal groove can be stimulated by copper sulfate, a characteristic that becomes a useful strategy when the introduction of medication in the abomasum is intended without previous dilution in the pre-compartments.

The ingested milk is initially submitted to the action of salivary lipase enzyme, produced by salivary glands, which hydrolyze the butyric and caproic acids. This hydrolysis rapidly occurs before milk reaches the abomasum. The salivary lipase secretion, by salivary glands, is very high in unweaned calves and reduces as forage intake increases. This enzyme progressively decreases the secretion as the animal grows, and practically disappears in the fifth month of the calf's life. When calves suckle the cow's nipples, it stimulates salivary lipase secretion in calves. It was observed that in bucket-fed calves, a smaller amount of salivary lipase is secreted when compared to animals that are fed with nipple bottles.

When the milk reaches the abomasum, renin acts on it causing the coagulation of milk proteins. Milk coagulation in the abomasum by renin is necessary in order to keep milk proteins in the abomasum longer so that they can be initially digested in this compartment. Five minutes after milk intake, milk whey reaches the duodenum.

The only carbohydrates that can be utilized efficiently by a young calf are lactose, galactose and glucose. In the first weeks of life, a calf is not able to utilize sucrose, maltose and starch efficiently. The utilization of starch by a calf results from the fermentation that occurs in the large intestine, where SCFA are produced and utilized as energy source by the calf. However, excessive amounts of starch in calves' diets may cause diarrhea. As these animals grow older, the lactase concentrations gradually decrease due to their smaller dependence on milk, and completely cease when weaning occurs. Nevertheless, if the animals kept on receiving lactose, the lactase activity would not be lost.

Table 1.1 Approximate percentages of the stomach and pre-stomachs at different ages of a bovine

	Age in weeks				
	0	4	8	20–26	34–38
Reticulum—Rumen (%)	38	52	60	64	64
Omasum (%)	13	12	13	22	25
Abomasum (%)	49	36	27	14	11

Source: Dárce (1977)

Development of Pre-stomachs in the First Weeks of Ruminant's Life

The development of pre-stomachs in the first weeks of a ruminant's life has three distinct phases: *non-ruminant phase*, which refers to the birth until the first 3 weeks of life; *transition phase*, which comprises 3–8 weeks of life; and finally, *ruminant phase*, established from the 8th week of life. During the transition phase, there are great modifications in the development of pre-stomachs, which are fundamental to make the animal a ruminant.

As seen in Table 1.1, the size of the pre-stomachs in newborn calves is almost the size of the abomasum, with completely different proportions from the ones found in adult ruminants, where the pre-stomachs represent more than 90 % of the total gastric volume. The increase of the pre-stomachs occurs rapidly after the birth.

During the first 3 weeks of life, the calves' diet basically consists of milk. They start the intake of grains and forages in the second week of life, and rumination in the third week. The interruption of feeding solid feedstuffs greatly reduces the rumen development. In calves that are exclusively fed with milk, the pre-stomachs develop later and remain rudimentary for a longer period of time. The composition of the diet provided during this period dictates how fast the pre-stomach development will be.

At birth, the pre-stomachs do not present microorganisms. Immediately after the birth, bacteria existing in the environment quickly colonize them. Some studies have shown that, at 10 days of life, all microorganisms that are necessary to colonize the rumen are already found in the ruminal cavity. As bacterial fermentation starts, bacteria establish a reductive environment in the rumen, creating favorable conditions for the settling of typical microorganisms that developed in the rumen. These organisms have access to the rumen through the intake of forage contaminated with the dam's or other animals' saliva or feces. At the end of the first month of life, calves are already able to digest 75 % of dry matter and 84 % of cellulose when fed with good quality grasses.

After some weeks, with intake of solid feeds like forage and concentrates, the relationship between the different gastric compartments is changed, as shown in Table 1.1. In modern calves' production systems, the early development of the rumen should be stimulated from the first month of life with the utilization of procedures, such as the use of creep feeding, that make calves intake forage and grains, and become less dependent on milk. However, a single diet containing only grains provided in a large amount or even inadequately can cause rumenitis, that is, lesions or abnormalities in the ruminal epithelium.

These anatomical alterations directly depend on the type of diet fed to the animal, mainly during the transition period, between the first 3 and 8 weeks of life. In calves that receive some kind of coarsely ground concentrate and hay, the volumetric capacity of the ruminoreticulum is four times greater when compared to animals that only consume milk. Moreover, a considerable development of rumen papillae occurs in animals that received solid feedstuffs, whereas the papillae remain rudimentary in animals consuming only milk.

Ruminal papillae reach total development at approximately 2–3 months of age, and their development determines the absorption capacity of the rumen. The development of rumen papillae is stimulated by ammonia, sodium salts and mainly by SCFA, such as propionate and butyrate; and therefore, the earlier the beginning of their production by calves is; the earlier the ruminal epithelium is developed. Also, in order to achieve its maximum functional capacity, the rumen has to develop muscular tissue and this is guaranteed by feeding the calf with good-quality forage.

In calves' intelligent feeding systems, conditions to allow the maximum development of the volumetric capacity of pre-stomachs as well as the development of ruminal papillae should be established. The development of the volumetric capacity depends on feeding of good-quality forages. For the development of ruminal papillae, it is fundamental to provide concentrates, especially those that will be utilized as substrate for propionate production in the rumen. It is important to point out that in first 2 months of a ruminant's life the intake of liquid feed is much easier and preferable when compared to solid feedstuffs. Thus, for calves to become interested in solid feeds in this period, these feeds need to have excellent quality.

Motor Activity of the Rumen

An adequate motor activity is essential for the ruminoreticular compartment to perform its functions completely. In general, two basic types of movements characterize this activity: propulsive peristaltic movements and mixing movements.

The *propulsive peristaltic movements* aim to push the feed along the different segments that form the digestive tube, passing the feed from one segment to the other consecutively. These movements guarantee the feed transit throughout the digestive tube. The ruminoreticular compartment sends the fragmented feed to the omasum so that the digestive processes continue in the next segments. Therefore, the propulsive peristaltic movements occurring craniocaudally determine this action. However, during the eructation and regurgitation processes, part of the content in the ruminoreticular compartment is sent towards the mouth, and caudo-cranial peristaltic movements become necessary.

The *mixing movements* aim to coordinately rotate the feed in a specific segment of the digestive tube without being pushed to the consecutive compartment. The goal of these movements in the ruminoreticular compartment is a set of actions: disperse the feed bolus to be digested within the ruminoreticular compartment, mix saliva with the feed ingested causing an efficient balance of ruminal pH, promote the contact of microorganisms with feed fragments to be digested, and help feed fragmentation. The mixing movements are also important to constantly expose new portions of feed ingested to ruminal papillae, guaranteeing an appropriate nutrient absorption. Part of SCFA produced in the rumen is readily absorbed by ruminal papillae.

The ruminal motility follows a coordinate pattern that starts early in a ruminant's life and, except for temporary periods; it persists throughout the animal's life. Under circumstances where this motility is suppressed for a significant period of time, the ruminal functionality gets extremely compromised.

The motor activity of the ruminoreticular compartment is basically controlled by two systems: (a) by the enteric nervous system represented by a large group of neurons distributed along the whole digestive tube, and (b) by the autonomous nervous system where a group of nervous fibers connects the central nervous system (medulla oblongata) to the ruminoreticular compartment.

The enteric nervous system is displayed alongside the whole extension of the digestive tube wall. This system is formed by a more external network of neurons displayed between the muscular layers of the ruminoreticular compartment called *myenteric plexus*, whose main responsibility is to ensure the adequate motor activity of the digestive tube. A second more internal network of neurons is found in the submucosa of the ruminoreticular compartment and forms the *submucosal plexus*, whose principal responsibility is to control the blood flow, which is important in the absorbing activity of the digestive tube. Although the enteric nervous system in general benefits the autonomy of the digestive system of most compartments, the same does not occurs in the ruminoreticular cavity. Therefore, the neurons that integrate the enteric nervous system are connected to sympathetic and parasympathetic nervous fibers of the autonomous nervous system. Generally, by action of noradrenalin, the sympathetic fibers inhibit the motor activity of the digestive system. On the other hand, by action of acetylcholine, the parasympathetic fibers stimulate the motor activity of the digestive system. The vagus nerve has a great control on the motor activity of the rumen because its section causes the interruption of ruminal motility.

Even though the ruminoreticular compartment is provided with an enteric nervous system, the contractions carried out there follow the motility pattern determined by the central nervous system. In the cerebral trunk, specifically in the medulla oblongata, a motility control center determines the frequency and strength of the contractions in the ruminoreticular compartment. This control is established through efferent fibers represented by the vagus nerve. Moreover, there are afferent fibers, also represented by the vagus nerve, that establish a communication connection between the ruminoreticular compartment and the central nervous system. The ruminoreticular compartment presents stretching receptors, found on the ruminal wall and pillars, aiming to capture information on the rumen volume and distension degree. Diets with large amounts of forage cause a higher frequency of contractions when compared to animals fed high-concentrate diets. The rumen and reticulum wall is also provided with chemoreceptors that monitor ruminal pH, SCFA concentration and ionic force. These receptors capture information from ruminal pH that is sent by afferent via to the motility center in the cerebral trunk, which immediately adjusts the motility in the ruminoreticular compartment. Reductions of ruminal pH cause a decrease in ruminal motility. The normal pH of the rumen ranges from 5.5 to 7.0, depending on the type of diet. When ruminal pH is lower than 5.0, its motility becomes intensely depressed. This response is a protective mechanism considering that fermentation is likely to increase when the feed mixture in the rumen increases. Thus, motility suppression due to pH reduction decreases fermentation allowing SCFA absorption to overcome its production, increasing ruminal pH.

As previously described, the ruminoreticular compartment is divided into compartments or sacs, a division established by the presence of papillary muscles that project themselves from the walls toward the ruminal lumen. These muscles also develop rising and falling movements that occur coordinately with the movements of the ruminoreticular compartment wall.

Two different contraction patterns are evident in the ruminoreticular compartment: the ***primary or mixing contractions*** and the **secondary or eructation contractions**.

The ***primary contractions*** consist of a sequence of very coordinated mechanical events: (a) the reticulum has the first concentric contraction reducing its size approximately 50 % than when relaxed, a determining factor for the liquid reticular content to be pressed toward the center of the rumen during the contraction, mixing itself to the remaining content; (b) the reticulum contracts again (second contraction) reducing almost 100 % of its lumen; this contraction occurs simultaneously to the contraction of the main anterior ruminal fold; (c) after the end of the second reticular contraction, the reticulum opens and the content found in the beginning of the rumen overflows back to the reticular cavity; (d) a peristaltic contraction is started in the cardia region and propagates itself alongside the dorsal ruminal sac craniocaudally, when both longitudinal ruminal folds contract themselves almost simultaneously; these mechanical events push the content of the dorsal sac of the rumen to the ventral sac that is then relaxed; (e) next, there is contraction of the ventral ruminal sac that propagates craniocaudally with consecutive simultaneous contraction of the ventral coronary folds; these mechanical events determine that a great amount of the content in the ventral part of the rumen passes to dorsal part which is relaxed; (f) a contraction starts in the ruminal dorsal sac that propagates caudal-cranially, and (g) finally a contraction begins in the ruminal ventral sac that propagates caudal-cranially. During the contraction of the ruminal ventral sac, the reflux of its content is followed by a long noise within the relaxed dorsal sac; each noise counts for a ruminal contraction.

When they occur, the **secondary contractions** happen immediately after the end of the primary contractions. The secondary contractions usually occur associated with half of the primary contractions, although this relationship may vary in function of the gas formation rate. The triggering stimulus of eructation is the intra-ruminal gas pressure. In the cardia region, there are receptors located in a relatively small area whose stimulation results in deflagration or inhibition of eructation. In secondary contractions, the following mechanical events are evident: (a) the ruminal content is pushed away from the cardia region in function of both reticular contractions that occurred in primary contractions (items a and b); (b) next, there is a contraction of the ruminoreticular fold and the main cranial fold, a mechanical action that prevents the return of ruminal content to the cardia region; (c) a contraction wave starts in the caudodorsal blind sac and propagates alongside the dorsal sac caudocranially, causing the displacement of the dorsal air bubble in the rumen to the cardia region; (d) the cranial sac is relaxed while the cranial pillar rises and allows liquid ingesta in the rumen to move away from the cardia; (e) then, the caudal sphincter of the esophagus opens while its cranial sphincter remains closed, and gases fill up the esophagus; and (f) finally, the caudal sphincter of the esophagus closes and a peristaltic wave propagates itself caudocranially, displacing the gases through the pharynx.

During and immediately after feed intake, the speed of primary and secondary contractions increase from 50 % to 100 %, and that is more evident in sheep than in bovines. The number of ruminal contractions in five minutes is from 7 to 12 in bovine, 7 to 14 in sheep and 6 to 16 in goats (Cunningham and Klein 2008). These contractions can also be observed by placing the hands on the left paralumbar fossa, which is the commonly utilized method to evaluate ruminal motility. The highest frequency of contractions occurs during the feeding periods and the lowest frequency in resting periods.

Rumination Mechanisms

Rumination is an innate behavior of ruminants because in newborns, 5- to 8-day-old bovine and 3- to 5- day-old sheep, even only with milk feeding, irregular chewing movements are observed in the absence of feed in the mouth. In general, bovines, sheep and goats start rumination as soon as they start consuming solid feeds since the first week of life.

Rumination is a process in which a small part of the feed found in the ruminoreticular segments goes back to the mouth, passing through the esophagus and pharynx, and then submitted to additional chewing. Rumination process comprises ingesta regurgitation from the rumen and reticulum to the oral cavity, followed by swallowing of the regurgitated liquid, re-chewing of the solid portion, re-salivation and new swallowing. Thus, this process consists of four distinct phases: regurgitation, re-chewing, re-salivation and re-swallowing, consecutively.

When ingesting feed, ruminants chew it very rudimentarily and this little-chewed feed is transported to the ruminoreticular compartment. In this compartment, the feeds absorb water becoming turgid, increase density, are mixed to the pre-existing ruminal content, are fragmented by movements triggered in the ruminoreticular cavity, and are initially digested by the microorganisms existing there. After a determined period, small portions of the ingested feed are redirected to the oral cavity and chewed a second time. In general, rumination starts 30–70 min after the feed intake in bovines and 20–45 min in sheep.

During rumination there is a mechanical fragmentation of the rough regurgitated ruminal content. This process provides conditions for the feed to be sufficiently reduced in size to go from the reticulum to the omasum through the reticulo-omasal orifice. The increase in the feed density also contributes to this process. Therefore, if the diet is composed by feeds containing high-fiber content, the rumination process becomes fundamental for the ruminant because in its absence, the feed would not be fragmented enough to reach the omasum, interrupting its transit throughout the subsequent compartment of the digestive tube. Rumination allows an acceleration of the feed passage through the pre-stomachs; otherwise, the feed would remain there for much longer until becoming reduced to small feed particles. This acceleration of the passage allows the intake of more feed in a determined period of time and, as a result, a greater amount of digestible substrates or nutrients become available to the animal.

The regurgitated feed for re-chewing comes from the dorsal portion of the reticulum and have characteristic size and gravity of the region located between the doughy course mat and the ventrally fluid area. Thus, the ingesta that will be ruminated do not consist of roughage found in the rumen, but of material that previously occupied the mat and underwent some digestive activity. When regurgitation does not occur, the reticular contraction is characterized as biphasic; however, when there is rumination, this contraction becomes triphasic. The extra reticular contraction occurs simultaneously to cardia relaxation and a deep and long inspiration with closed glottis. This generates a negative pressure within the thoracic cavity, contributing to the opening of the esophagus that generates an increase in the negative pressure, making the content next to the esophagus, between the reticulum and rumen, be aspirated from the cardia region and be taken to the esophagus. Then, the esophageal wall contracts aboral-orally by an anti-peristaltic wave with approximate pressure of 80 mmHg in bovines, enabling the feed to transit at a speed of 107 cm/s under this condition, making the esophageal content be transported up to the mouth. A simultaneous expiration with closed glottis helps esophagus emptying. In rumination, there is no participation of the abdominal muscles, differently from vomit regurgitation because in vomiting there is effective participation of abdominal muscles. During regurgitation the animal keeps the mouth and neck stretched. After the regurgitation and swallowing of the aqueous fraction of the regurgitated material, the content in the mouth undergoes intense chewing followed by abundant saliva secretion, especially from the parotid glands. Finally, this content is swallowed by the same physiological mechanisms of swallowing.

In ruminants, rumination periods are alternated with periods of feed intake and rest. The beginning of rumination occurs between 30 to 60 min after feed intake. The number and duration of contraction cycles vary according to feed fiber content, feed particle size, number of meals, and amount of feed intake. The greater the feed fiber content is, the longer the rumination time lasts. The bigger the feed particle size is, the longer the time spent on rumination is. Numerous meals and amounts of ingested feed increase rumination period. In bovines, there are 4–24 rumination periods that last from 10 to 60 min each; therefore, the animals can spend from 7 to 24 h of their day ruminating. In this species, 360-790 feed boluses, which range from 80 to 120 g/ bolus, are generally ruminated. Feed intake and rumination follow a circadian cycle, because feed intake happens mostly during the day whereas rumination predominantly occurs during the night. Goats ruminate from 7 to 8 h daily, concentrating 75 % of this activity during the night.

Rumination is a reflexive mechanism in which some phases like breathing, chewing and swallowing are subordinate to the animals will. The reflexive nature of rumination is proved by the fact that the mechanical stimulation of specific regions of the pre-stomachs trigger rumination partially. The reticulum undergoes an extra contraction to trigger rumination. The mechanical stimulation of the ruminoreticular fold, the reticulum wall, and the reticulo-omasal orifice results in an increase in ruminal motility. These stimuli are captured by sensitive receptors in the pre-stomachs, continue via afferent nervous pathway (vagus nerve) and reach the rumination center found in the medulla oblongata, which coordinates part of the processes that include rumination.

Eructation Mechanism

Eructation is a physiological process that aims to eliminate gases in the rumen formed by nutrient fermentation. Adult bovines produce 30–50 l of gas/h, whereas sheep and goats produce approximately 5-l/h (Cunningham and Klein 2008). In bovines, CO_2 makes up 60–70 % of ruminal gas whereas methane accounts for 30–40 % of it. Furthermore, a bovine produces 0.5–1 l of gas/min.

Eructation is a physiological process in which the gases produced in the rumen and reticulum are eliminated through the mouth, passing through the esophagus and pharynx. Eructation is a mechanism through which gas accumulation and stretching of the dorsal rumen sac trigger a reflexive chain of events that culminate with its expelling. The triggering stimulus for eructation is the intra-ruminal gas pressure. In the cardia region there are receptors concentrated in a relatively small area whose stimulation and stimulus intensity determine eructation.

The occurrence of eructation requires that the cardia region be ingesta-free which does not occur when it gets in contact with the ruminal liquid. Initially, two reticular contractions, occurring in the primary cycle, allow that the cardia region get rid of the ruminal content. Next, there is a contraction of the ruminoreticular pillar and main cranial pillar preventing the ruminal content reflux back to the cardia. There are simultaneous contractions in the dorsal rumen sac and in the cranial and caudal pillars when the reticulum undergoes relaxation. These mechanical events result in the cranial movement. This gas bubble reaches the cardia region and the lower esophageal sphincter opens whereas the upper esophageal sphincter remains closed, favoring the displacement of air from the ruminoreticular cavity to the esophagus. Next, the lower esophageal sphincter is closed and an anti-peristaltic wave starts aboral-orally up to the mouth. The cycle can be rapidly repeated several times as long as gases remain in contact with the cardia.

The strength of gas release is reduced by the contraction of the nasopharyngeal sphincter located in the pharynx, which contracts itself and directs part of the eructated gas towards the trachea and lungs to be absorbed by the blood. This pulmonary mechanism establishes the most common route by aromatic chemical substances to reach the mammary gland; determining undesirable stains in the milk. Therefore, gases can be either released to the atmosphere or transferred to the trachea and directed to the lungs. It is believed that half of the eructated gas is directed to the lungs instead of being expelled by the nostrils. In a 10-min period, bovines eructate 5–8 times, sheep 6 times and goats 4–7 times.

When the eructation process is interrupted or it occurs less often, gas accumulation in the rumen may cause ruminal bloat, which is more common in bovines than in sheep. When the vagus nerve and its ramifications have some lesion, the ruminal motility is directly altered and may cause disorders in eructation, causing ruminal bloat as well.

Mechanism of Urea Recycling

In ruminants, approximately 60–90 % of nitrogen consumed by the animals is converted into ammonia (NH_3) by ruminal bacteria. It is estimated that 50–to 70 % of nitrogen utilized in the synthesis of new bacteria comes from ammonia. Most of the ammonia found in the rumen is ionized (NH_4). The ammonia concentration within the bacteria is approximately 15 times greater than the one found in the rumen; therefore, ammonia goes through the bacterial membrane by active transportation.

The balance between ammonia production (availability) and utilization by microorganisms in the rumen during their anabolic and catabolic processes is fundamental for ruminants. In the past two decades, it has been profitable to include inexpensive sources of non-protein nitrogen in ruminants' diets as a substitute of more expensive protein sources, such as soybean meal. The primary non-protein nitrogen source used this purpose is urea. Besides exogenous urea provided in animal diet, some endogenous urea is also produced in the organism of the animal and posteriorly directed to the rumen. As shown in Fig. 1.12, ruminal ammonia is absorbed by the ruminal wall, gets into the bloodstream and is carried to the rumen through the portal-hepatic system. The liver extracts most of the ammonia from the blood, keeping only a small amount of ammonia in the bloodstream. Moderate quantities of ammonia in the organism are considered toxic; therefore, this system allows that only a small amount of potentially toxic ammonia reach the systemic circulation. In the liver, ammonia (NH_3) is converted to urea [$(NH_2)_2CO$]. The liver also synthesizes urea from nitrogen originated in the deamination of endogenous amino acids. Most of the urea produced in the liver is excreted in the urine by the kidneys. In monogastric animals, urea is excreted almost exclusively this way. However, in ruminants, urea is also excreted through the rumen. This excretion can occur in two ways: (a) through salivary glands where urea is a compound of saliva and it reaches the rumen when the saliva is swallowed, or (b) by the direct passage of urea from the bloodstream to the ruminal compartment through the ruminal wall.

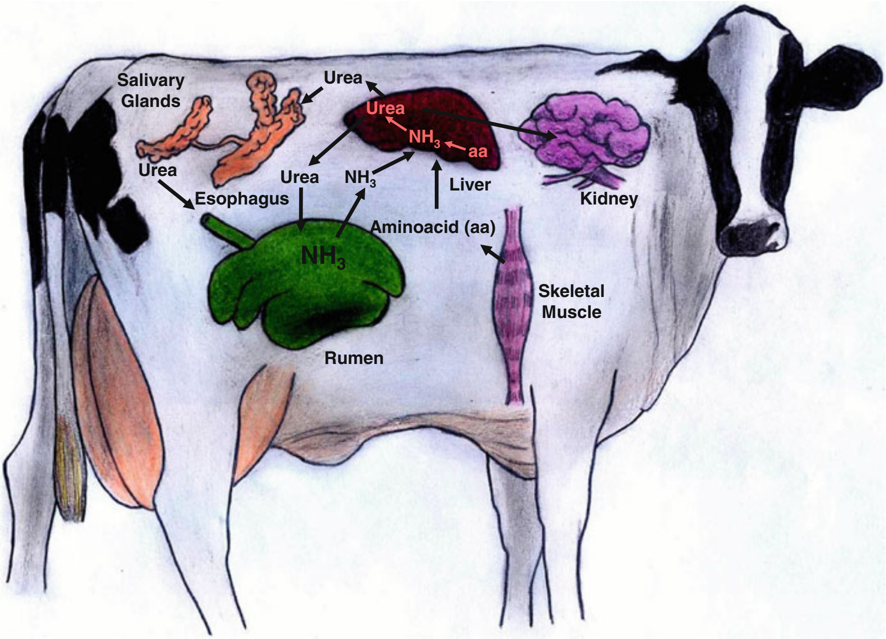

Fig. 1.12 Circulation of nitrogen through different organs of a ruminant animal. When enough amounts of carbohydrates are available in the rumen, microorganisms are capable of synthetizing protein from a non-protein source, such as urea. This urea is rapidly converted to ammonia (NH_3) in the rumen, which is absorbed by the ruminal wall, and carried out by the bloodstream to the liver, where it is converted back into urea. Most of the urea produced in the liver is excreted in the urine by the kidneys. However, in ruminants, urea is also excreted through the rumen. This excretion can occur in two ways: (**a**) through salivary glands where urea is a compound of saliva and it reaches the rumen when the saliva is swallowed, or (**b**) by the direct passage of urea from the bloodstream to the ruminal compartment through the ruminal wall

Thus, significant amounts of urea continuously get into the rumen by three distinct manners: (a) through diet components; (b) through saliva; or (c) by the passage of the molecule present in the bloodstream to the rumen through the ruminal wall. In the rumen, urea is quickly transformed into ammonia and carbon dioxide due to the great amount of urease found in the rumen. The nitrates found in the diet are also rapidly reduced to ammonia. In the rumen, ammonia is immediately available as ruminal nitrogen for the synthesis of microbial proteins. This mechanism is commonly referred to as urea recycling process in ruminants.

Considering that ammonia absorption in the rumen is proportional to its production, and that its production depends on the availability of proteins and carbohydrates in the rumen, the existing relationship between them is essential for the success of diet formulation. The amount of non-protein nitrogen that leaves the rumen and goes into the bloodstream, and the quantity of non-protein nitrogen that reaches the rumen through saliva or by bloodstream depends on the concentrations of ammonia in the rumen. Therefore, when non-protein nitrogen availability in the rumen is relatively high when compared to carbohydrate availability, a great amount of ammonia is produced inside the rumen, and the main nitrogen flow goes from the rumen to the bloodstream, producing a large quantity of ruminal nitrogen. In this case, there will be great concentrations of blood urea and great losses of nitrogen through the urinary route. This is not economically recommended, because besides the energetic use for urea formation, approximately 12 Kcal/g of nitrogen, there is the loss of nitrogen compounds, making ruminants nutritionally inefficient. However, when carbohydrate availability is high compared to nitrogen availability in the rumen, the main nitrogen flow goes from the bloodstream to the rumen, a circumstance in which the ruminal ammonia concentration is low and most of this urea is excreted to the rumen so that it can be utilized in the synthesis of proteins that will contribute to the host's amino acid needs. Thus, ruminants fed low-protein diets are considered efficient nitrogen keepers. Thus, under ideal conditions, in which the animal is supplied with an appropriate combination of carbohydrate and protein amounts, the main nitrogen flow goes from the bloodstream to the rumen.

After extracellular degradation of proteins that get into the rumen, peptides and amino acids resulting from this digestion are readily captured by ruminal bacteria, showing the low concentration of amino acids in the ruminal flow. Peptides are hydrolyzed when they get into the bacterial cell and most of the amino acids are deaminated. The deamination of valine, leucine and isoleucine results in isobutyrate, isovalerate, and 2-methylbutyrate, respectively. These products, called branched-chain fatty acids, are extremely important for the growth of bacteria that degrade structural carbohydrates. In ruminant feeding, generally there are nitrogen bases that are ingested in small amounts, comprising 5–9 % of nitrogen in forages. When this nitrogen reaches the rumen, bacteria rapidly capture it. A part of it is utilized for the synthesis of the bacterial nucleic acid, but most of it is used in fermentation to produce SCFA, CO_2 and ammonia.

Based on its dry weight, the average nitrogen content of ruminal bacteria is 10 %, 75 % of which are amino acids and 25 % nitrogen bases. Ruminal microorganisms require energy to multiply. In general, almost all microorganisms utilize carbohydrates as energetic source, very few species use protein, and no species has the capacity to utilize fat as energetic source. The greater the carbohydrate degradability in the rumen is, the more energy for microbial growth will be available. In the rumen, non-structural carbohydrates determine a greater microbial production when compared to structural carbohydrates. Thus, diets containing highly degradable ruminal starch provide more energy to microorganisms, which will present faster multiplication, increasing its population.

Energetic Metabolism in Ruminants

SCFA production from substrate fermentation in the rumen is the greatest energetic source for ruminants, providing at least 50 % of the total amount of digestible energy. The relative concentrations of main SCFA are essential for energy utilization by ruminants. Ruminants have to perform gluconeogenesis to obtain the most part of their glucose, and propionate is the greatest glucose source for ruminants. On the other hand, acetate, as well as butyrate, is also used as energetic source, but for oxidative metabolism and for lipogenesis. Diets that increase propionate production, and as a result decrease acetate concentration, are related to reduction of milk fat.

As shown in Fig. 1.13, when reaching the rumen, forage and grains, make several substrates available, especially cellulose, hemicellulose and starch. These substrates are utilized by a large group of bacteria that, through fermentative digestion, transform substrates initially into glucose and then into SCFA, mainly acetate, butyrate and propionate. Nutrients that are not digested in the rumen are pushed to the small intestine where they undergo enzymatic digestion by pancreatic, hepatic and enteric enzymes, and their final products are absorbed by the portal circulatory system whereas the non-digestible portion of the feed is excreted through feces. SCFA produced in the rumen are readily absorbed by the ruminal epithelium to reach the systemic circulation. Acetate is the main energetic substrate and is available to the animal as energy. Acetate is converted to triglycerides in the adipocytes where it is stored as fat, as well as transformed into fat in the mammary gland. Propionate is converted into glucose in the liver, and is the main source of glucose for ruminants. Glucose is utilized as an energetic source in the muscular tissues and others. In the mammary gland, glucose is converted into lactose and it is fundamental for increasing milk production. Butyrate is mostly utilized by ruminal epithelial cells (95 %) and the rest of it (5 %) goes to the bloodstream where it is converted into ketone bodies (ketones) and long-chain fatty acids in the liver. Ketones are available as energetic source for ruminants and, like acetate, are also converted to triglycerides in adipocytes and in the mammary gland of these animals.

In summary, acetate is utilized by the liver in a very small amount, and most of it is used for the oxidation to generate ATP and for the synthesis of acetyl-CoA, which is utilized in lipid synthesis. Propionate is almost totally sequestered by the liver where it is utilized as an extremely important substrate for gluconeogenesis, transforming it into glucose. Butyrate is oxidized in several tissues for energy production.

Final Considerations

The digestive system of ruminants is extraordinarily efficient in the utilization of vegetal feed. This characteristic makes ruminants a great promising source of animal protein supply to human population. The worldwide demand for foods has been growing quickly and proportionally to population increase. Under low-efficiency conditions of meat and milk production, the only way to increase productivity is by increasing the number of animals and area destined to livestock farming. However, as this is an undesirable practice due to the obvious negative economic and environmental implications, it is evident how important it is to increase meat or milk production without necessarily increasing the number of animals.

A lot of advances have been achieved aiming the genetic improvement and animal nutrition and many other areas. In order to improve production levels, a greater number

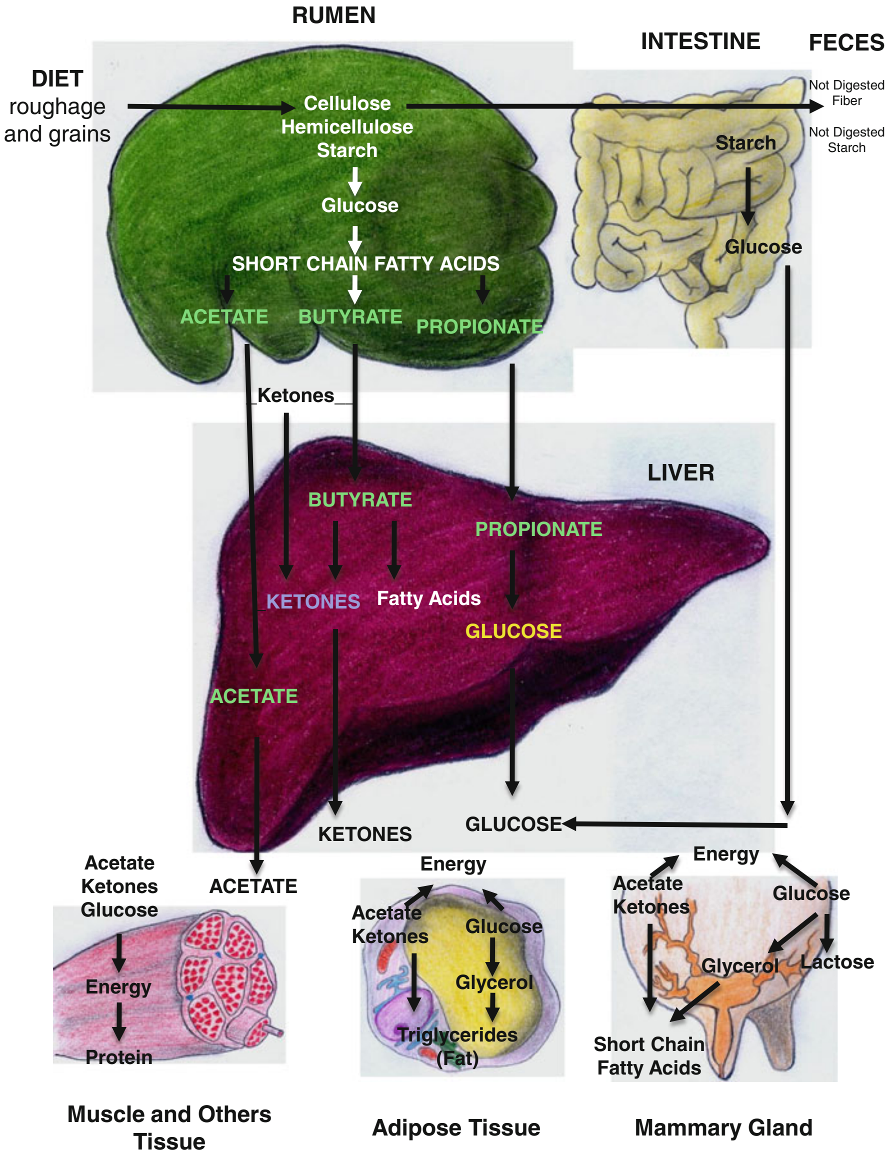

Fig. 1.13 Schematic representation of the feed energy utilization by the ruminant animal (Adapted from Wattiaux and Armentano in http://babcock.cals.wise.edu/downloads/de_html/ch03.en.html). The roughage and the grains, which compose the diet of a ruminant animal, when reach the rumen provide several substrates; specifically CELULLOSE, HEMICELULLOSE AND STARCH. Such substrates are utilized by a large group of bacteria, which beyond the fermentative digestion, transform the substrates first in glucose and after in short chain fatty acids specially ACETATE, BUTIRATE and PROPIONATE

of animals are being fed significant amounts of concentrate while on pasture. Likewise, it is common nowadays the use of feedlot systems to improve performance and produce more meat and milk in shorter periods of time. However, diet formulation for ruminants has to be based on a great knowledge of the physiology of the digestive system. It should be considered that, even though it represents one of the most extraordinary symbiotic mechanisms between microorganisms and host, the ruminal environment is also represented by a fermentative chamber that requires a set of ideal conditions that should be kept relatively stable.

The management of the ruminal environment is a practice established to increase the utilization of this symbiotic relationship, however, the established modifications have to be always very well dimensioned.

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