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COMPARATIVE ANATOMY OF THE DIGESTIVE TRACT IN CATTLE SHEEP AND GOATS A REVIEW

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A REVIEW

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Summary

Knowledge of comparative anatomy is a necessity for scientists whose research involve food-producing animals. This study attempts to review and compare the available information on the digestive tract anatomy of sheep, goats and cattle. Coordinated motor activites of the forestomach related to rate of passage of digesta are also examined. Although genuine differences exist, data used to describe the anatomy of the digestive tract of domestic ruminants is mainly derived from cattle and to a lesser extent from sheep. Goats have received the least study. In addition, the complex compound stomach of domestic ruminants has long been a source of curiosity and consequently less information concerning the other parts of the digestive tract is available.

(Key Words: sheep, goats, cattle, digestive tract anatomy.)

Introduction

Ruminants occupy a strategic ecological niche through their ability to transform fiber and non-protein resources into useful products of prime importance to man. They have been successful under a wide variety of environmental conditions since they can survive on sparse, dry forage and(or) browse, even in artic or arid environments. Studies have demonstrated physiological differences in various functions of the gastrointestinal tract (GIT) of cattle, sheep and goats. Descriptive and quantitative anatomy of the GIT is an important tool in the understanding of these physiological differences. The present review was written with this objective in mind.

The digestive tract of ruminants includes the mouth, the pharynx, the alimentary canal and several accessory glands. The alimentary canal, a muscular tube lined with a stratified squamous epithelium or a mucous membrane, consists of the following segments: the esophagus, reticulo-rumen, omasum, abomasum, small intestine, large intestine and anal canal. The accessory glands, consisting of the salivary glands, the liver and the pancreas, are connected with the digestive tract by means of their excretory ducts.

The Oral Cavity

Prehension of feed, mastication, the mixing of feed with saliva, and the formation and deglutition of the bolus are physical and digestive processes that involve the oral cavity. In ruminants the lips, the teeth and the tongue are the principal prehensile organs.

The lips

In cattle the lips are thick, firm and comparatively immobile. The middle of the upper lip and the surface between the nostrils is bare, smooth and takes part in the formation of the nasolabial plate (Ellenberger and Baum, 1912; Trautman and Fiebiger, 1952; Frandson, 1974; Habel, 1975; Nickel et al., 1979). The lips of sheep and goats are thin, very mobile and are important for the prehension of food. The outer layer of the skin is covered with hair (May, 1964; Nickel et al., 1979). A deep philtrum divides the upper lip into two parts (Ellenberger and Baum, 1912; Marshall, 1932; May, 1964; Habel, 1975; Nickel et al., 1979), each of which is possessed of independent movement, thus enabling sheep and goats to graze more closely to the ground (Marshall, 1932; Church 1979a) and to be very selective when consuming grass, mixed herbage, browse or forbs (Church, 1979a). The bare nasal plate does not involve the upper lip as in cattle but is restricted to the area

between the nostrils (Ellenberger and Baum, 1912). Habel, 1975; Nickel et al., 1979).

The teeth

By and large the teeth of cattle, sheep and goats are similar. In the small ruminants the eight incisors are long and narrow with a semilunar profile, arranged in a strongly curved arch and meeting the dental pad at a less acute angle than in cattle. The incisors of cattle have a shovel-shaped asymetric crown and form a more flattened arch (Nickel et al., 1979). According to May (1964) the incisors of sheep, although relatively loosely attached, are more firmly implanted and in addition do not have a distinct neck as in cattle. Nickel et al. (1979) reported that the cheek teeth of the small ruminants are simpler in form. In addition, owing to the more pronounced width between the upper and lower jaws, the occlusal surfaces of the cheek teeth slope more steeply, so that the lingual border of the lower occlusal surface and the vestibular border of the upper occlusal surface are quite sharp.

The tongue

The tongue is divisible into the free rostral portion or apex, the bulk of the tongue or body, and the root which slopes ventrally toward the epiglottis. The surface of the tongue opposite the palate is called the dorsum linguae. The tongue is the chief prehensile structure in cattle. It is a

long mobile organ, being first protubed and curled round the forage, then withdrawn into the mouth while the forage is either clipped off between the incisor teeth and the dental pad (Marshall, 1932; Church, 1979a; Nickel et al., 1979) or partially pulled by the tongue and partially bitten off (Church, 1979a). Ellenberger and Baum (1912), May (1964), Habel (1964 and 1975) and Nickel et al. (1979) reported that in cattle the tongue is firm, rather plump and relatively broader than in sheep, especially in the middle of the body. A part of the dorsum is raised and forms an elliptical prominence, the torus linguae, rostral to which in cattle is the transverse and funnel-shaped fossa linguae. Grain husks and barbed awns occasionally lodge in the fossa linguae of cattle and cause infections of the tongue. These features are less pronounced in the small ruminants. In cattle the filiform papillae are thread-like, heavily cornified and pointed, especially at the apex, and impart the roughness which makes the bovine tongue an efficient organ of prehension in grazing. In the small ruminants the papillae are soft, in goats they are described as horny threads giving the mucosa a velvety appearance, and the tongue is comparatively smooth. According to some authors it does not act as a prehensile organ. However, Church (1979a) stated that the tongue and the incisor teeth are considered the principal prehensile structures in sheep and numerous other species.

The tongue possesses taste buds, found in the fungiform papillae located along the edges of the apex and in smaller numbers on the dorsum. These buds are very sparse in cattle and taste bud-free papillae are occasionally encountered. Taste buds are more numerous in sheep and especially so in goats. Additional buds are situated in the vallate papillae that form irregular rows on each side of the caudal part of the torus. They number 8 to 17 on each side in cattle, 14 to 24 in sheep and 8 to 18 in goats (Ellenberger and Baum, 1912; May, 1964; Habel, 1964 and 1975; Nickel et al., 1979). Church (1979b) reported marked differences among ruminant species in both their sensitivity and rejection of the four basic taste sensations: sweet, salty, bitter and sour (acid). His data also pointed out that normal and pigmy goats were more sensitive to and tolerant of bitter substances than the other animals tested.

The salivary glands

Ruminants secrete large volumes of saliva estimated to supply more than 70% of the fluid and most of the Na and Cl entering the reticulo-rumen. Saliva moistens and lubricates feed and assists in mastication and swallowing. It plays a role in stabilizing the pH of the fermenting digesta and provides a source of nitrogenous and mineral nutrients to the micro-organisms of the reticulo-rumen. In addition saliva influences feed and water intake and rate of nutrient removal from the rumen (Bartley, 1976). The relative

composition of ruminant saliva is summarized in table 1. The salivary glands may be classified as serous (thin, watery saliva containing protein but no mucin), mucous (thick, slimy saliva which contains the glycoprotein mucin) and sero-mucous (mixed) , as shown in table 2. The daily production of ruminant saliva has been well documented by Kay (1960), Bartley (1976), Church (1979a) and Van Soest (1981). According to various authors daily saliva production by cattle ranges from 33.5 to 190 l and sheep are estimated to secrete 6 to 16 l. Saliva is secreted at different rates during eating, rest or rumination. Wilson (1963) reported total parotid secretion of sheep on a hay diet to be 27% when eating, 36% when resting and 37% when ruminating. Bailey (1961) observed that in cattle fed hay, silage or grass 40 to 45% of the total mixed saliva was secreted when cattle were resting. Bailey and Balch (1961) estimated the flow of parotid saliva during rumination to be 2.5 times the flow during rest. In addition the quantity and kind of feed eaten (lush vs mature pasture, green vs dry forage, roughage vs concentrate), processing of feed, and rate of eating influence salivation. Feeds that do not induce large quantities of saliva to be secreted are those with either low dry matter content or those eaten rapidly such as ground or pelleted hay or grain concentrate (Bailey, 1959). The parotid, mandibular (submaxiliary) and sublingual glands are considered to be the chief salivary glands, in terms of

relative size and volume of secretion, by several authors (Frandson, 1974; Habel, 1975; Phillipson, 1977; Nickel et al., 1979). Kay (1960) however, reported that the sublingual glands of sheep are much less important than the labial, pharyngeal, palatine, buccal (middle plus dorsal) and inferior molar (ventral buccal) glands (table 3). In addition the combined weight of the labial, palatine, pharyngeal and buccal (ventral, middle, dorsal) glands was 90% of the combined weight of the parotid and mandibular glands. Furthermore the same author estimated that the palatine, pharyngeal and buccal glands plus the inferior molar glands were secreting a greater volume of saliva than the sublingual glands (table 3.).

The parotid gland of cattle lies in an area between the base of the ear and the caudal border of the masseter (Ellenberger and Baum, 1912; Frandson, 1974; Bartley, 1976; Nickel et al., 1979). Habel (1975) reported an average weight of both parotid glands of 230 g. The same authors, along with Bock and Trautman (1914) and Nickel et al. (1979) stated that in sheep the parotid gland is 3.5 to 4 cm wide and 5.5 to 6 cm long. According to Kay (1960) it is the largest salivary gland in sheep and both parotids have an average weight of 15 to 31 g. The same author reported an average of 29 g in 40 kg goats.

In cattle the mandibular (submaxiliary) gland lies in a curve along the medial side of the angle of the mandible.

The large, rounded pendulous end of the gland, easily palpable in the live animal, lies near the midline, almost touching the ventral end of the gland on the other side. According to Ellenberger and Baum (1912), Habel (1975) and Nickel et al. (1979) the gland is 18 to 20 cm long, 8 to 10 cm wide and 2 to 4 cm thick, which is larger than the parotid. Both mandibular glands weigh about 280 g. May (1964) and Habel (1975) reported that in sheep and goats the mandibular gland lacks the pendant rostroventral portion. Kay (1960) estimated the weight of both glands at about 18.2 g in sheep.

The sublingual gland of the ruminants consists of two parts on each side: the ventral monostomatic gland (gl. subl. grandicanalaris) and the dorsal polystomatic gland (gl. subl. parvicanalaris). Ellenberger and Baum (1912), Habel (1964 and 1975) and Nickel et al. (1979) reported that in cattle the monostomatic sublingual gland is 10 to 12 cm long, 2 to 3 cm wide, 1 to 2 cm thick and extends from the incisive part of the mandible to the rostral half of the polystomatic sublingual gland which lies along its dorsal border. According to May (1964) and Habel (1975) the polystomatic sublingual gland of cattle consists of a chain of lobules, about 15 to 18 cm long, 2 to 2.5 cm wide and 0.3 to 0.5 cm thick that extends from the incisive part of the mandible to the palatoglossal arch. The sublingual glands of the small ruminants are similar to those of cattle.

The buccal glands are well developed and may be classified as dorsal, middle and ventral (Ellenberger and Baum, 1912); May, 1964; Habel, 1975; Nickel et al., 1979). Kay (1960) referred to the wedged-shaped ventral buccal glands of cattle and sheep, lying in the cheeks opposite the inferior molar teeth, as inferior molar glands. Ellenberger and Baum (1912) reported that the ventral buccal glands of cattle are 3 to 4 cm wide, 20 cm long and weigh about 24 g.

The labial glands are concentrated near the angles of the mouth and are often imbedded between bundles of labial muscles. They decrease in number in the following sequence: cattle, goat, sheep. Ellenberger and Baum (1912) found that in sheep and goats the labial glands of the upper lip are quite numerous and are more developed than those of the lower lip. The nasolabial plate of cattle is kept moist and cool by the serous secretions of the nasolabial glands that form a subcutaneous layer about 1 to 2 cm thick (Ellenberger and Baum, 1912; Habel, 1975). Several other workers pointed out that similar glands also occur in the nasal plate of sheep and goats.

The Esophagus

The esophagus is a musculomembranous tube connecting the pharyngeal cavity with the forestomach. The caudal end, or cardia, is usually slit-like and in cattle measures about 2 to 3 cm in height (Habel, 1975; Church, 1979a). The

esophagus is relatively distensible and thin-walled, and unlike the stomach both muscle layers have a spiral arrangement (Comline et al. 1968). Trautman and Fiebiger (1952), Frandson (1965) and Nickel et al. (1979) reported however that the two layers of the tunica muscularis cross obliquely, then spiral and finally form an inner circular and an outer longitudinal layer. The entire esophageal tunica muscularis of ruminants is composed of striated muscle. However, Boone (1979) in cattle and Comline et al. (1968) in sheep stated that some smooth muscle is present at the distal end, 2.5 cm or so anterior to the junction of the esophagus with the forestomach. According to Habel (1975) the stratified squamous epithelium of the esophagus differs morphologically and histochemically from that of the forestomach. The length of the bovine esophagus is 90 to 105 cm, the cervical part being 42 to 49 cm and the thoracic part 48 to 56 cm. Measurements of the diameter of the esophagus are unreliable because of its dilatability in the living animal. After formalin fixation the diameter of the bovine esophagus measures about 3 cm in the caudal third of the neck and gradually increases, measuring 4 to 5 cm from side to side and 7 to 8 cm dorsoventrally in the caudal part of the thorax. The same author and Nickel et al. (1979) reported that in sheep the esophagus is 45 cm long,

increasing in diameter from 1.8 cm at the pharynx to 2.5 cm at the cardia. No information concerning the esophagus in goats was available.

The Ruminant Stomach

Ruminants have a complex stomach consisting of four compartments occupying nearly 75% of the abdominal cavity. The oral three - the reticulum, the rumen and the omasum - comprise the forestomach. They are lined with a non-glandular stratified squamous epithelium. The most aboral compartment - the abomasum - is lined with a glandular mucosa.

The central axis from which the four compartments of the ruminant stomach develop is called the gastric groove. It extends from the cardia through the reticulum, omasum and abomasum almost to the pylorus. It is divided into three parts, the reticular groove, the omasal groove and the abomasal groove, by the reticulo-omasal and the omaso-abomasal orifices (Habel, 1975; Nickel et al., 1979).

The rumen

The rumen is a large, laterally compressed sac which comprises most of the left portion of the abdominal cavity. Its caudoventral part extends considerably over the median plane into the right part of the abdominal cavity. The major portion of microbial fermentative activity and absorption of nutrients occur in the reticulo-rumen. As fermentation

proceeds, digestion and rumination reduce particle size, and fiber particles become saturated with water and tend to sink. Particles which have an optimum density are circulated back to the reticulum and selectively passed on to the omasum.

The visceral surface of the rumen is divided into several parts by a number of grooves of varying depths. Shallow left and right longitudinal grooves on the left and right surfaces are connected by two deep transverse cranial and caudal grooves. These four grooves divide the rumen into dorsal and ventral sacs (Ellenberger and Baum, 1912; May, 1964; Habel, 1975; Nickel et al., 1979). The cranial end of the rumen is divided ventrally by the transverse cranial groove into the cranial and ventral sacs. Habel (1975) reported that, compared to cattle, the ventral sac of the small ruminants is relatively larger and extends more to the right of the median plane. The cranial sac curves ventrally around the cranial end of the ventral sac and is continuous caudally with the dorsal sac. Cranially the cranial sac communicates with the reticulum, the external demarcation between them being the reticulo-ruminal groove. It is deep ventrally and is distinct on part of the parietal surface but dorsally no natural separation exists, the rumen and the reticulum forming the cardia, a dome-like vestibule at which the esophagus terminates (Habel, 1975; Nickel et al., 1979).

The ventral and dorsal coronary grooves extend in opposite directions from the caudal groove and mark off the caudoventral and caudodorsal blind sacs. According to Nickel et al. (1979) the two caudal blind sacs are of about equal length in cattle. In the small ruminants however, the caudoventral blind sac extends farther caudally than the caudodorsal blind sac (Habel, 1964 and 1975; Nickel et al., 1979). May (1964) stated that in sheep the caudoventral blind sac is larger than the caudodorsal blind sac and occupies most of the left flank. Gueltekin (1953), comparing sheep with goats, reported that in the latter the caudo-ventral blind sac is longer and narrower. The grooves that divide the rumen externally are represented on the inside by corresponding pillars. May (1964) and Nickel et al. (1979) pointed out that some of these pillars are very prominent and are formed by folds of the internal muscle layer of the stomach wall; others are small and mere thickenings of the wall. The thick caudal pillar projects cranially between the two caudal blind sacs. In cattle the right longitudinal pillar connects the cranial and caudal pillars and is split into two limbs which meet caudally, enclosing the insula ruminis (Habel, 1964 and 1975; Nickel et al., 1979). In sheep, according to May (1964), the dorsal limb only extends to the caudal pillar, the ventral limb fading out. The same author pointed out that although the dorsal limb of the right longitudinal groove is more prominent, the internal

pillar corresponds to the ventral limb. The left longitudinal pillar does not reach the caudal pillar in cattle (Habel, 1964 and 1975; Nickel et al., 1979), and leads off to a dorsal branch, the accessory pillar. In the small ruminants the left longitudinal pillar is short and in sheep May (1964) reported that it fades out approximately 7 cm from its origin. The cranial, caudal and longitudinal pillars surround the intraruminal opening through which the dorsal and ventral sacs communicate freely. Habel (1975) in cattle of median size, and May (1964) in sheep, stated that the distance between the cranial and caudal pillars is from 40 to 45 cm and 20 to 25 cm, respectively. The ventral and dorsal coronary pillars are branches of the caudal pillar and separate the caudoventral blind sac from the ventral sac and the caudodorsal blind sac from the the dorsal sac. In sheep however, Habel (1975) stated that the coronary pillars are absent. In the same species May (1964) pointed out that the dorsal coronary pillars are very short and fade out after approximately 2.5 cm, whereas the ventral coronary pillars almost meet at the ventral curvature. During contractions of the pillars the ruminal sacs become smaller and the ingesta, particularly the more liquid part, are circulated, the combined effect of rumen mixing and rumination being to promote the passage of indigestible particles. The differences mentioned here could have implications on mixing or residence time of feed material in the

rumen since epithelial receptors that respond to volatile fatty acids (VFA) have been detected around the cranial and the longitudinal ruminal pillars, and occasionally in other parts of the rumen (Leck and Harding, 1975).

The cranial sac of the rumen communicates with the reticulum through the reticulo-ruminal opening which is almost completely surrounded by the reticulo-ruminal fold. Sellers and Stevens (1966) pointed out that in cattle the cranial pillar is very large compared to the reticulo-ruminal fold whereas in sheep the reticulo-ruminal fold is the more prominent of the two structures.

Numerous authors have reported that the internal surface of the forestomach is lined with a non-glandular, nonmucous-producing keratinized and stratified squamous epithelium. In addition it is expanded into a large area by numerous papillae which vary considerably in size and shape in the various sacs and compartments. The surface is further expanded in the reticulum and the omasum by the presence of permanent thick-walled crests and laminae respectively, which themselves are furnished with papillae (Scott and Gardner, 1973). Stevens and Stettler (1966) calculated that in calves the omasal leaves provide a surface equivalent to about one third of the total epithelial lining of the forestomach. As such the forestomach was long considered incapable of absorbing anything, but today it is recognized as a major site of nutrient absorption. The production of

VFA as products of anaerobic microbial metabolism provides ruminants with a major source of metabolizable energy. Weston and Hogan (1968) estimated that ca. 76% of ruminal VFA was absorbed from the rumen. Na, Cl, ammonia and water are also absorbed by the forestomach. Engelhardt (1970) and Warner and Stacy (1972), however, stated that the rumen wall is not responsible for the net absorption of large amounts of water, although the rumen epithelium is freely permeable to water. In the omasum, on the other hand, the degree of water and VFA absorption are still a matter of controversy. As reviewed by Bost (1970) absorption undoubtedly occurs but quantitative data are very scattered. The principal effect of these processes is to reduce the volume of ingesta entering the abomasum. Van Soest (1981), however, speculated that the absorptive role of the omasum may be of lesser importance in the small ruminants where, in proportion to body size, this organ is relatively smaller than in cattle.

The rumen epithelium of cattle is dark brown to blackish except on the margins of the pillars and the upper part of the dorsal sac where the color gradually turns to a pale brown (Ellenberger and Baum, 1912; Habel, 1975; Church, 1979a). The papillae vary from simple conical thick tongue-like forms to large flattened leaf-shaped structures which often reach 1 cm in length. The cranial, the ventral and the blind sacs of cattle, where presumably most absorption occurs, are the most densely papillated regions and also

contain the largest papillae. On the other hand the papillae decrease in size towards the pillars, on which they are absent. The central part of the dorsal sac also lacks papillae (Comline et al., 1968; Habel, 1975; Church, 1979a; Nickel et al., 1979). According to May (1964) the rumen epithelium of sheep is brown and becomes paler towards and on the pillars. Comline et al. (1968) reported that the entire internal surface is papillated, including the ruminal pillars, where the papillae are reduced and closely packed, giving the pillars a distinctly ridged appearance. The papillae vary in form from short tongue-like forms to large flattened foliate structures, as reported by Scott and Gardner (1973). Ellenberger and Baum (1912), May, (1964) and Comline et al. (1968) stated that in sheep most papillae are shorter and thicker than in cattle and may reach 0.5 cm in length. Comparing the rumen papillae of the cranial sac in sheep and goats, Gueltekin (1953) reported that the free ends are broader and rounder like leaves in goats, but narrower like tongues in sheep. He also remarked that the color of the rumen epithelium is deep honey-colored in sheep, dark brown to blackish in goats.

The reticulum

The reticulum represents the most cranial compartment of the ruminant stomach. Foreign bodies such as nails and wire that may be swallowed commonly lodge in the reticulum and sometimes perforate the reticulum wall and diaphragm.

The reticular or esophageal groove is formed by two muscular lips extending ventrally from the cardia to the reticulo-omasal orifice. It is 15 to 20 cm long in cattle and 7 to 12 cm in the small ruminants. The groove has a spiral form, the right lip twisting around the left lip. At the ventral end of the groove the relative position of the lips is reversed, the right lip passing around the ventral aspect of the reticulo-omasal orifice from left to right. Under psychic, suckling or chemical stimulus in the young, the esophageal groove closes into a tube and shunts milk from the cardia to the reticulo-omasal orifice, from which point milk rapidly reaches the abomasum (Shalk and Amadon, 1928; Van Soest, 1981). Stevens et al. (1960) reported that in adult cattle the esophageal lips appear to effectively block the entrance to the omasum during reticular contractions, during which the reticulo-omasal orifice remains dilated. At the height of the secondary reticular contractions, however, the esophageal lips are pulled apart at the ventral commisure to form an orifice approximately 2 cm in diameter, through which fluid digesta flows from the floor of the reticulum towards the omasal canal. According to the same authors reticulo-omasal orifice closure occurs during relaxation of the reticulum at the same time that the esophageal groove returns to its resting position and the ventral lips spread about 2 to 3 cm apart. Closure of the orifice occurs during primary and secondary contractions of

the omasal canal. In between omasal canal contractions and during the remainder of the reticulo-ruminal cycle the reticulo-omasal orifice relaxes and forms an oval opening approximately 4 by 6 cm. Reticulo-omasal flow of digesta also occurs during those periods.

The epithelium of the reticulum is raised into permanent crests 0.8 to 1.2 cm high in cattle and 0.2 to 0.3 cm high in sheep. These crests intersect to form honeycomb-like cells having four to six sides. Each cell is subdivided by lower secondary and tertiary crests and both the crests and the floor of the cells are studded with small papillae (Ellenberger and Baum, 1912; May, 1964; Habel, 1975; Comline et al., 1968; Nickel et al., 1979). Gueltekin (1953) pointed out that the secondary crests are fewer and less prominent in goats than in sheep. According to Scott and Gardner (1973) in sheep, and Comline et al. (1968), the change from the honeycomb pattern of the thick-walled crests of the reticulum to the typical tongue-shaped papillae of the rumen takes place fairly sharply at the cranial entrance to the atrium. According to Gueltekin (1953) the area between the lower half of the reticular groove and the right third of the reticulo-ruminal fold is full with papillae in goats but with reticular cells in sheep.

The omasum

The omasum of cattle is a spherical organ, somewhat compressed laterally. In the small ruminants the omasum is

oval, compressed laterally, but has no contact with the abdominal wall, being completely covered by the liver on the right (Ellenberger and Baum, 1912; May 1964; Habel, 1975; Nickel et al., 1979). Comparing sheep and goats Gueltekin (1953) noted that the omasum is longer and more oval in goats.

The most distinctive feature of the omasum interior is the large number of laminae or septa which are thin leaves of tissue that project from the greater curvature and walls of the organ. Their concave edges lie parallel to the omasal canal and they are classified according to size, from those with free borders that almost reach the omasal sulcus (1st order) to others which are mere ridges (5th order) (Becker et al., 1963; Sellers and Stevens, 1966; Comline et al., 1968; Gardner and Scott, 1971). Ellenberger and Baum (1912) and Gueltekin (1953) stated that four orders of laminae (one to four) are present in sheep vs three orders only in goats (one to three). Studying the omasum in 86 calves and yearling cattle Becker et al. (1953) encountered five different sizes of laminae. Habel (1975) considered the smallest laminae as very low folds or lines. On the other hand Ellenberger and Baum (1912) and Nickel et al. (1979) reported the presence of only four orders of laminae in cattle. The same authors pointed out that the omasum of cattle has 16 primary laminae for a total of 90 to 130. In sheep and goats the primary laminae amount to 9 to 10 and 10

to 11, respectively, their total number reaching 72 to 80 in sheep vs 80 to 88 in goats. Becker et al. (1963), counting the laminae in 86 bovine omasa that were cut horizontally into upper and lower portions, observed no regularity in numbers or arrangement of laminae in omasa from different animals or in their distribution in the upper and lower portions. There were more fifth-order laminae and fewer of the first order in the upper portion, but the total number of laminae were usually higher in the upper part. Differences among individual animals were significant ($P<.01$).

The omasum communicates with the reticulum through the reticulo-omasal orifice and with the abomasum through the omaso-abomasal orifice. Connecting both openings is the omasal groove, flanked by two ridges which are covered by thick, long, sharp papillae. Gueltekin (1953) reported that the connection between the omasal groove and the ventral end of the reticular groove is end to end in sheep but notched in goats. According to Ellenberger and Baum (1912), Habel (1964 and 1975), Sellers and Stevens (1966) and other authors in cattle and May (1964) in sheep, the omasal groove length is 10 to 15 cm and 3 to 5 cm, respectively. The main body of the omasum extends caudally from the omasal groove. The omasal canal runs along the omasal groove from the reticulo-omasal orifice to the muscular omasal pillar which transverses the groove and separates the omasal canal from

the omaso-abomasal orifice. The other boundaries of the canal are formed by the free edges of the omasal laminae that run parallel to the omasal canal and groove (Sellers and Stevens, 1966; Habel, 1975; Phillipson, 1977; Nickel et al., 1979). The omaso-abomasal orifice is flanked on either side of its long axis by two folds, the vela abomasica, which may act as "flap" valves in the closure of the orifice. Sellers and Stevens (1966) stated that in the living animal the free edges of the larger laminae contact the omasal pillar and pass across the omaso-abomasal orifice, which is 10 cm long in cattle. There is no anatomical evidence of a true sphincter. Studying the function of the bovine omasum Stevens et al. (1960) reported that the omaso-abomasal orifice remains dilated for extended periods of time and that closure is associated with contractions of the omasal pillar. In cattle the omasal side of the vela is covered with stratified squamous epithelium while the abomasal side has a glandular mucosa. In sheep and goats the glandular abomasal mucosa extends onto the omasal surface of the vela (Trautman and Fiebiger, 1952; May, 1964; Habel, 1964 and 1975; Frandson, 1965; Phillipson, 1977; Nickel et al., 1979).

The epithelium of the omasum and its leaves is relatively non-papillated compared to many areas of the rumen. As in other parts of the forestomach the existing papillae vary in size, form and density within the organ. In sheep

Gardner and Scott (1971) found evidence of three forms of papillae on the lateral surfaces of the larger laminae, the most common being conical in shape with sharply pointed, heavily keratinized tips. The free borders of the larger laminae bear long, horny and heavily keratinized papillae; those and the unguliform papillae found on the omasal groove near the reticulo-omasal orifice and on the reticular groove are among the largest present in the omasum. Habel (1964 and 1975) made a similar statement regarding cattle. The papillae associated with the laminae of the smallest order are much less horny and are completely covered with polygonally-arranged cells. Cheetham and Stevens (1966) speculated that these papillae are actively involved in absorption, with well developed papillary processes at their tips. Rounded conical papillae similar to those described above have been observed in cattle by Becker et al. (1963). These same authors as well as Becker and Arnold (1952) stated that in cattle unguliform horny papillae arise mainly from the free margins of the primary laminae. In addition a few are present on the margins of the reticular groove. Becker et al. (1963) also reported that the primary laminae tend to be pedunculated at the top insertion and partially occlude the passage of ingesta through the reticulo-omasal orifice during reticular contractions. This arrangement with the presence of unguliform papillae tends to allow mainly small feed particles to enter and to divert them between the

laminae. Several authors have reported that in the sheep omasum the ingesta is relatively dry compared to that of the reticulum and rumen. This is attributed to water absorption and other functions. Postmortem examinations have shown this organ to be tightly packed with ingesta. Stevens et al. (1960) suggested that the omasal leaves serve as a grid, preventing passage of large ingesta particles, and that the omasal canal contents in living cows and at necropsy frequently contain a predominance of large particles. The same authors recorded backflow of omasal contents to the reticulum and speculated that such a mechanism could serve to flush the omasal canal of the larger particles of ingesta often found there.

Studying the laminae in the omasum of 576 head of cattle Brownlee and Elliot (1963) found that 48% of the animals showed some degree of depapillation involving areas from about 1 to 20 cm2, depending on the location. In addition 36% showed two or more laminae stuck together by patches or a diffuse layer of dry food and 15% some degree of fenestration. The importance of such extensive damage on animal performance is not known.

The abomasum

Different aspects of the anatomy of the abomasum have been reviewed by Ellenberger and Baum (1912), Trautman and Fiebiger (1952), May (1964), Habel (1964 and 1975), Frandson (1965), Church (1979a), and Nickel et al. (1979). The

abomasum is the most aboral compartment of the ruminant stomach as well as the first glandular portion of the ruminant digestive system. In this organ the ingesta is subjected to the peptic secretion required for digestion. It is an elongated sac, lined with a cardiac proper gastric and pyloric mucosa. In cattle the abomasum lies chiefly on the abdominal floor, with a right angle between the body and the pyloric parts. Sheep and goats have a relatively smaller and higher omasum, hence the body of the abomasum runs obliquely and the pyloric part turns to the right, caudally to the omasum. Comparing goats with sheep, Gueltekin (1953) found that the abomasum is shorter (30.4 vs 33.5 cm) and broader (21.0 vs 18.2 cm) in goats.

The mucosa of the abomasum is divided into a small, light-colored region of cardiac glands adjacent to the omaso-abomasal orifice, a much larger cranial proper gastric gland region, and a pyloric gland region which approximately coincides with the pyloric part of the abomasum. The thin mucosa of the extensive proper gastric glandular area has a reddish-grey color and is thrown into high permanant folds that greatly increase the surface area. According to Ellenberger and Baum (1912) the folds number 13 to 14 in cattle, 13 to 15 in sheep and 16 to 17 in goats. They begin at the omasal end, at first increasing in height and then decreasing towards the pyloric part, running craniocaudally in an oblique fashion. A band-like area along the lesser

curvature is devoid of folds and is considered to be the abomasal groove. The pyloric part is lined with a lighter, more yellowish wrinkled mucous membrane and has no permanent folds. It is more muscular and contains densely crowded pyloric glands. The gastric glands contain parietal cells which secrete hydrochloric acid, necessary for the activation of the zymogen pepsinogen to pepsin and also a bactericidal agent. These same cells also secrete the intrisic factor (IF) important for the absorption of vitamin B12, although its involvement has not been demonstrated in ruminants (Elliot, 1980). Both the cardiac and pyloric glands have mucous-secreting neck cells but in addition the latter glands contain G cells which secrete the hormone gastrin. Gueltekin (1953) reported several differences between the small ruminants. In goats the cardiac gland area is relatively smaller, the cardiac glands are more mucin-producing and the delemorph cells of the gland ducts are prevalent and denser, compared to sheep. In addition the corpus glandulae is wider and the spiral ducts of the pyloric glands are less numerous in goats than in sheep. According to Ash (1961) and Phillipson (1977) the pH of abomasal juice in sheep may vary from 1.0 to 2.5, although fasting often produces a decrease in acidity. Due to dilution the pH of the digesta leaving the abomasum is somewhat lower, ranging between 2.5 and 2.9 (Storry, 1961). Calculations of the volume of gastric juice produced during

normal ad libitum feeding have revealed the large quantity of stomach secretions produced by ruminants. The output of gastric juice from the fundic area of the abomasum has been estimated at 4 to 6 l per 24 hr in sheep (Masson and Phillipson, 1952; Hill, 1960; Storry, 1961a) and up to 30 l per 24 hr in cattle (Kuznetsova, 1950, cited by Hill, 1961). Harrop (1974) reported the output of juice from the pyloric region of the abomasum in sheep to be about 200 to 400 ml per 24 hr. The composition of the gastric juice of sheep is reported in table 4.

Motor functions of the ruminant forestomach

The motor functions of the ruminant forestomach have been reviewed by Sellers and Stevens (1966) and numerous other workers. Reticulo-ruminal motility must accomplish a mixing and maceration process to aid microbial digestion. It must also allow retention of slowly digested feed material, the removal of gases by eructation and the passage of more completely digested contents on through the digestive tract. The movement simultaneously aids the absorption that occurs in these compartments. The above authors indicated that the reticulum is also involved with the regurgitation process, a "regurgitation contraction" of the reticulum flooding the cardia with ingesta prior to inspiration against a closed glottis, which is considered to be the driving force in this process. Stevens et al. (1960), studying the role of the omasum in ingesta transfer, suggested that it serves as a

two-stage pump by aspirating reticular contents into the omasal canal, pumping the more fluid digesta from the canal into the omasal body and finally expressing the omasal body contents into the abomasum.

Investigating reticulo-ruminal motility patterns in cattle, sheep and goats on a hay diet under resting conditions (not eating, not ruminating), Dziuk and McCauley (1965) reported that primary and secondary contractions of the ventral sac are always observed in goats but that primary contractions of the ventral sac are occasionally absent in sheep and usually absent in cattle. A more regular participation of the primary contractions of the ventral sac was recorded in cattle during periods of increased reticulo-ruminal motility, such as eating and ruminating. Phillipson and Ash (1965) pointed out that in cattle and sheep the greatest activity of the ventral sac occurs during feeding. Accordingly the flow of material from the rumen appears to be greatest at that time. They also reported that the activity of the ventral sac is much increased during rumination, although confined to alternate cycles of contractions. Dziuk and McCauley (1965) observed that during standing and rest mean reticulo-ruminal frequencies ranged from .6 to 1.2 cycles/min in cattle, sheep and goats. These values increased during rumination to .9 to 1.5 cycles/min. A slight further increase was recorded during eating in cattle and sheep, the effect of eating having not been

studied in goats. Similar findings have been reported by Ruckebusch and Bost (1963) when comparing the feeding behavior and the motility of the reticulum (table 5) in ewes and does, and Balch (1952) in dairy cows. However, contrary to the observations of Dziuk and McCauley (1965), the slowest rate of reticular contractions was found during rumination. Shalk and Amadon (1928), Balch (1951) and Freer et al. (1962) reported similar results in cattle. Greater differences have been recorded in recumbent animals by Dziuk and McCauley (1965), the interval between reticulo-ruminal contractions being as long as 8 min. in sheep compared to only 3 min. in goats.

Vascular supply

The entire vascular supply to the stomach and fore-stomach is derived from the celiac artery which sometimes arises from the abdominal aorta by a common trunk with the cranial mesenteric artery. Using 10 adult sheep Anderson and Weber (1969) showed that in all dissections both arteries originate from a common trunk. More recently Perreira et al. (1978) described the origin of the celiac and cranial mesenteric arteries from a single stem in 27 of 87 Corriedale sheep (31%). Of the other 68% in which these two arteries arose separately from the aorta they were contiguous in 55% and separated by up to 2 cm in 14% of the animals. In a study involving five Toggenburg goats Horowitz (1966) showed that the two arteries had separate origins. In cattle the

more common situation is for the two vessels to arise individually from the aorta, as demonstrated by Peduti Neto et al. (1970) in 45 of 46 zebu foetuses studied. The celiac artery enters the rumen between the esophagus and the mid-dorsal sac. Four branches then feed to various parts of the stomach. The common hepatic artery originates from the celiac artery in sheep and from either the celiac or the left gastric artery in cattle (Habel 1964 and 1975; Anderson and Weber 1969). However, Yoshikawa et al. (1956) and Horowitz (1966) found that in most goats hepatic and left gastric vessels are briefly united (.5 cm) by a common trunk. The common hepatic artery supplies the cranial surface of the rumen and then gives off the pancreatic branches, the right and left hepatic arteries, the cystic artery that passes to the gall-bladder and the gastro-duodenal artery. Gordon (1967) described the arterial pattern of the gall-bladder as palmate in cattle, pinnate in sheep and bipinnate in goats. The gastroduodenal artery is the terminal branch of the common hepatic. It divides into the cranial pancreatiduodenal artery and the right gastro-epiploic. It contributes blood to the descending duodenum, its sigmoid flexure, and then follows the greater curvature of the abomasum where it anastomoses with the left gastro-epiploic branch of the left gastric artery.

The right gastric artery arises from either the hepatic, its left branch or the gastroduodenal artery in cattle,

according to Habel (1964 and 1975). In sheep (May, 1964) and goats (Horowitz, 1966) the right gastric artery originates from the left branch of the hepatic artery, then runs along the duodenum to the lesser curvature of the abomasum where it anastomoses with the left gastric artery.

The right ruminal artery is the main artery of the rumen and arises in common with the splenic as the splenoruminal trunk. It curves caudoventrally to the right longitudinal groove which it follows, giving off branches to both sacs of the rumen. In addition the right ruminal artery gives off right dorsal and ventral coronary arteries, then passes through the caudal groove to the left side where it supplies left dorsal and ventral coronary arteries. In cattle it finally anastomoses with the left ruminal artery in the left longitudinal groove. In the small ruminants the dorsal coronary pillar arteries are small, and right and left ruminal arteries do not meet (Habel, 1964). However May (1964) reported that in sheep the right ruminal artery reaches the caudal transverse groove around which it passes to anastomose with branches of the left ruminal artery.

The left ruminal artery arises from the left gastric, the splenic or the right ruminal in cattle (Habel, 1964 and 1975), and from the left gastric distal to the origin of the splenoruminal trunk or in a few cases from the right ruminal artery in sheep (May, 1964; Anderson and Weber, 1969). In goats it arises from the left gastric or the splenic,

sometimes briefly in common with the reticular artery (Horowitz, 1966). The left ruminal artery runs ventrally on the right surface of the rumen to the cranial groove, then passes through the groove to the left longitudinal groove, giving off dorsal and ventral branches.

The reticular artery is usually given off either from the left ruminal, the left gastric or the splenic artery in cattle (Habel, 1964 and 1975). According to May (1964) and Anderson and Weber (1969) the reticular artery arises a short interval from the origin of the left ruminal artery in sheep. However its origin may vary; in some cases it arises from the right ruminal and in other cases directly from the left gastric. It passes over the dorsal surface of the rumen, turning down on the left side in the reticulo-ruminal groove and passing the greater curvature of the reticulum to the right. Comline et al. (1968) reported that a separate supply to the right wall of the reticulum is derived in sheep from the omaso-reticular branch of the left gastric artery. In addition a second branch from the left gastric artery sometimes supplies the caudal wall of the reticulum.

The left gastric or omaso-abomasal artery may be considered the continuation of the celiac beyond the origin of the left ruminal artery. The left gastric and its large left gastroepiploic branch are the major vessels to the abomasal fundus and body. The left gastroepiploic artery sends branches to the reticulum, the omasal groove and the

cranial wall of the omasum in sheep (Comline et al., 1968; Anderson and Weber, 1969). It continues ventrally and runs along the greater curvature of the abomasum where it anastomoses with the right gastroepiploic artery. The left gastric artery follows and supplies the greater curvature of the omasum, then runs along the lesser curvature of the abomasum to anastomose with the right gastric artery in the pyloric region. On the surface of the omasum it gives off branches that penetrate the wall to enter the base of each omasal leaf.

Veinous drainage is by way of four veins: the right ruminal, left ruminal, omaso-abomasal and reticular veins. All empty into the hepatic portal vein which goes directly to the liver.

Size of the Ruminant Stomach Compartments

Postnatal development

The amount of tissue weight comprising the various compartments is probably the most precise and objective criterion presently available to describe the process of development, according to Warner and Flatt (1965) who reviewed the subject. In the newborn the weight of the abomasum is about twice that of the reticulo-rumen, development of which is dependent upon access to a fibrous diet and inoculation by rumen bacteria. More specifically reticulo-rumen development is dependent upon stimulation by VFA, the production of which requires the necessary bacteria

and substrate. Immediately after birth the stomach develops rapidly and its various parts enlarge at widely different rates. The rumen has the fastest growth rate, followed by the reticulum, omasum and abomasum. Initially, however, the abomasum has the fastest growth rate of all the parts of the alimentary tract and doubles its weight at birth in about a week; but from that time onward its growth rate slows down and falls below those of the other organs. In fact an inverse relationship is clearly shown between the proportionate development of the abomasum and the reticulo-rumen when expressing the weight of each compartment as a percentage of their combined weights (Godfrey, 1961). At about eight weeks of age the four compartments reach their approximate adult relative proportions, although they are still expanding. For further information the reader is referred to the extensive review of growth and development of the ruminant stomach by Church (1979a).

Size of the various compartments in adult ruminants

One of the main characteristics of the ruminants is the large storage capacity of their stomach, related to the bulky nature of their diet and to the need for retaining the ingesta for the relatively slow process of fermentation. Research workers have used several criteria to quantitatively describe this organ. In the live animal estimates have been made by filling the reticulo-rumen with a measured

volume of water. Other methods for volume measurements involve the use of various markers that can be added to the stomach contents, eventually giving an estimate of the volume of liquid ingesta. Measurements on stomachs of slaughtered animals include the water-holding capacity, the ingesta weight and the tissue weight of the different compartments.

Size, fatness and breed of individual animals are among the factors which will influence these measurements. Estimating rumen capacity by measuring the rumen lithium sulfate space, Nutt et al. (1980) reported that structurally large Angus cows had greater ($P<.05$) rumen capacities than did structurally small cows. Expressed as a percentage of live weight however, rumen capacity was not related ($P>.10$) to structural size. They also found that fatter, heavier cows had distinctly smaller ($P<.01$) rumen capacities as a percentage of live weight than did thinner, lighter cows. Makela (1956), Crabtree (1967) and Forbes (1969) working with cows, wethers and ewes, respectively, found a negative relationship between volume and fatness.

The absolute and relative volumes of the various compartments as determined by their capacity to hold water up to certain pressures are listed in table 6. Warner and Flatt (1965) and Makela (1956) have discussed the errors involved with this technique but described it as being extremely helpful in evaluating relative capacity as

affected by different dietary treatments. In addition it is well known that in all ruminants the dorsal rumen contains a pocket of gas that is principally the result of cellulose digestion and consists predominantly of CO_2 and methane (Sellers and Stevens, 1966; Van Soest, 1981), indicating that the stated absolute capacities are never fully utilized in the live animal. Furthermore, Stevens (1977) acknowledged that a considerable exchange of water can occur between body fluid spaces and gut contents after death, further altering the values for capacity. Relaxation of muscles and ligaments might also affect the volume of the excised stomach (Church, 1979a). According to Habel (1975) and Nickel et al. (1979) the capacity of the four compartments would rank as follows in cattle: rumen, abomasum, omasum and reticulum. In sheep and goats the only difference would be that the omasum is smaller than the reticulum. The data presented here are consistent with these statements, although in cattle the abomasum and omasum capacities do not differ greatly. Warner and Flatt (1965) pointed out that the omasum is not as expandable as the other compartments and therefore its size is underestimated by this technique. The data also show that, compared to cattle, the omasum of the small ruminants is relatively smaller while the abomasum is relatively larger. Considering the small ruminants, the relative capacity of the rumen is greater in sheep while the reticulum and omasum relative volumes tend to be larger in goats. In

addition, according to the only available comparative study between goats and sheep (Gueltekin 1953), the relative capacity of the abomasum is greater in goats. There is an obvious difference between the Kil and Angora goat breeds in terms of absolute capacity of the stomach. In the Kil the volume of the four compartments is even greater than in the Ak-Karaman sheep, with identical live weights.

The amount of wet ingesta in the several compartments of adult cattle and sheep, summarized in table 7, should represent the best measure of "physiological fill". However, the weight of stomach contents for animals of comparable size is rather variable and influenced by numerous factors, primarily the nature of the diet, the consumption of feed and water, the physiological state of the animal (gestation, lactation, stress, etc) and the time elapsed between the last meal and slaughter. On the other hand there is evidence (Parra, 1979; Van Soest, 1981) indicating that gastrointestinal contents increase isometrically with body weight interspecies comparisons. Studying the changing composition of the digesta along the alimentary tract of sheep, Badawy et al. (1958) reported that the reticulo-rumen, omasum, cecum and colon contents were higher in those animals having the greater dry matter and crude fiber intakes. In the data presented by these authors the weight of the stomach wet ingesta amounts to 9.0 to 17.5 % of live weight in cattle and 9.0 to 15% in sheep. The relative

proportion of the reticulo-rumen contents correspond rather well with the water fill data, and by this method the omasum of cattle is more prominent than suggested by its relative volume, even surpassing the abomasum. The omasum is clearly the smallest compartment in sheep.

The fresh weight of the tissue of the stomach compartments represents another useful criterion. These data are summarized in table 8. In cattle and sheep the proportion occupied by the reticulo-rumen is smaller compared to the water fill and stomach contents methods. On the other hand the omasum is most significant by this technique, the amount of tissue per unit volume being much larger because of its structure (Van Soest, 1981). The abomasum is likewise more prominent, although to a smaller extent. The methods reported for the goat data gave somewhat comparable values. Comparing sheep and goats Gueltekin (1953) reported that the empty stomach weights were greater in goats. Their data indicate that the fresh stomach weights amount to 2.5 to 3.2% of live weight in sheep versus 3.6 to 4.1% in goats.

The Intestines

The intestines extend from the pylorus of the abomasum to the anus and are suspended from the roof of the abdominal cavity by a common mesentery which collects them into a large disc-shaped mass. The proximal part having a relatively small lumen is called the small intestine and is

subdivided into the duodenum, the jejunum and the ileum, the jejunum being by far the longest segment. The large intestine consists of the cecum, the colon and the rectum. The short terminal portion of the digestive tract is called the anal canal.

The cranial mesenteric artery provides arterial supply to the intestines, giving off several branches. One of them, the collateral branch, absent in sheep and goats, is given off the concave surface of the cranial mesenteric artery distal to the ileocolic and passes obliquely across the intestinal mesentery to rejoin the cranial mesenteric artery (Habel, 1964 and 1975).

The small intestine

Beginning at the pylorus the cranial part of the duodenum passes dorsally to the visceral surface of the liver where it forms a S-shaped curve, the cranial flexure, and is continued by the descending duodenum. The ascending duodenum forms the last part and runs from the caudal flexure to the jejunum. The jejunum is indistinctly separated from the duodenum and is continuous with the ileum, which ends at the ileo-cecal junction. Except in cattle where it decreases, the thickness of the muscularis mucosa of the small intestine increases in the ileum (Trautman and Fiebiger, 1952). The small intestine serves as a major site for absorption of required nutrients, and for the synthesis and release of several hormones. In addition the small

intestine adds biliary, pancreatic and its own secretions to the gastric chyme. According to Trautman and Fiebiger (1952), the permanent folds of the mucosal membrane, the intestinal villi and the microvilli serve to increase the intestinal surface area available for absorption. The villi are roughly conical projections measuring on the average 0.5 to 1.0 mm in height and 0.2 mm in width. In the center of each villus, lined by endothelium, occurs a tubular lymph space known as a lacteal. Two or more lacteals are found in the thicker villi of sheep. Studying the movement of digesta in the duodenum of small ruminants, Singleton (1961) expressed retrograde flow as a percentage of total aboral flow. He reported mean retrograde flow from the duodenum back to the abomasum of 40% in goats and 5% in sheep. According to Hill (1968) the passage of digesta through the abomasum is rapid. However, it is obvious that proteolysis does not cease immediately when the digesta leaves the abomasum, the pH of duodenal contents being little different from that of the abomasum, before getting mixed with duodenal, pancreatic and biliary secretions. Also backflow of digesta from the duodenum to the abomasum increases the time during which the digesta is subjected to peptic proteolysis.

Intestinal glands and secretions

Trautman and Fiebiger (1952) indicated that the glands of Lieberkuehn, which are tortuous in goats only, furnish

mucous and several enzymes which attack peptides, fats and carbohydrates. They also produce enterokinase which activates the trypsinogens of the pancreatic juice. However, which of the gland cells produce the enzymes has not been satisfactorily determined. Phillipson (1977) reported that the secretions of surgically isolated fragments of the duodenum in goats exhibit only a weak proteolytic activity. Scott (1965) determined the electrolyte composition of juice from the small intestine of sheep, which is shown in table 9. Harrison and Hill (1962) reported that the duodenal secretions have a pH of 6.7 and flow at the rate of about 13 ml per hr in sheep fed once daily. When fed three times daily the secretion rate rose to 26 ml per hr with a pH of 7.4. On the other hand pH values of 1.6 to 3.4 have been reported for the duodenal chyme, rising up to 7.5 to 7.8 in the ileum (Hogan and Phillipson, 1960). The duodenal glands, also called Brunner's glands, extend a variable distance from the pylorus: 20 to 25 cm in goats, 50 to 70 cm in sheep and 4 to 5 meters in cattle (Ellenberger and Baum, 1912; Trautman and Fiebiger, 1952; Frandson, 1965; Habel, 1975). According to Nickel et al. (1979) solitary lymph nodules are abundant throughout the small intestine. In addition patches of aggregate lymph nodules (Peyer's patches) varying in number from 18 to 40, the most distal patch extending

through the ileal opening a short distance into the cecum, are up to 2 cm wide and reach a length of 25 cm in cattle and 15 cm in the small ruminants.

Bile and pancreatic ducts and secretions

The common hepatic duct proceeds from the junction of the right and left hepatic ducts, unites with the cystic duct from the gall-bladder and forms the bile duct. According to Paiva et al. (1948, 1949 and 1975), Peduti Neto et al. (1971) and various other authors the bile duct enters the duodenum at the second bend of the sigmoid loop, about 40 to 70 cm distal to the pylorus in cattle and 25 to 40 cm in sheep and goats. In a comparative study Mann (1960) reported an average distance of 60 cm in goats. Habel (1975) pointed out that in the small ruminants several small hepatic ducts enter directly into the gall-bladder. The flow of bile from a fistula in sheep was found to vary between 20 and 40 ml per hr by Harrison (1962) when the bile was returned to the intestine. The chemical composition of the bile also varied according to the technique used and the timing of collection (table 10). More recently Caple and Heath (1975) reviewed the regulation and roles of biliary and pancreatic secretions in sheep.

In cattle the entire pancreas is usually drained by the accessory pancreatic duct which arises from the right lobe of the gland and enters the descending duodenum 25 to 40 cm distal to the major duodenal papilla formed by the bile

duct. Occasionally part of the left lobe is drained by another duct, the pancreatic duct, which enters the duodenum in common with the bile duct. Therefore whether or not the entire output of pancreatic juice can be obtained experimentally by cannulating the accessory pancreatic duct is uncertain. In sheep and goats the only pancreatic duct joins the bile duct before it enters the duodenum (Hill, 1960; May, 1964; Habel, 1975; Nickel et al., 1979). The volume of pancreatic juice secreted daily amounts to 2.2 to 4.8 l in cattle (Colin, 1886; Sineschekow, 1963) and to 0.32 to 0.42 l in sheep (Storry, 1961; Taylor, 1962, table 11). Both deoxy- and ribonucleases are present in the pancreatic juice of sheep; however, the ribonuclease activity of duodenal juice is much greater than the activity present in pancreatic juice (Martinez-Arias, 1974, cited by Phillipson, 1977).

The large intestine

The large intestine of ruminants, with the exception of the cecum and the proximal part of the colon, is only slightly wider than the small intestine, according to Habel (1975) and Nickel et al. (1979). The cecum is a simple tubular structure with a blind sac that projects caudally. There is no clear demarcation between cecum and colon but the site of the ileo-cecal valve is the acknowledged junction. The ability of the large intestine to absorb water is one of the main physiological functions of the organ. It

is also of great importance in VFA and Na absorption and vital to the water economy of ruminants in arid regions (Ulyatt et al., 1975). May (1964) and Habel (1975) reported that the cecum has an average length of 75 cm and a diameter of 12 cm in cattle, and for the small ruminants they indicated respective values of 30 and 8 cm . The diameter of the colon, at first similar to that of the cecum, decreases in the course of the ansa proximalis to 5 and 2 cm in cattle and the small ruminants, respectively. The colon may be divided for descriptive purposes into ascending, transverse and descending parts. The ascending portion is itself separable into three regions: ansa proximalis, ansa spiralis and ansa distalis. The ansa spiralis of the ascending colon, where pellet formation occurs in the small ruminants, begins by coiling centripetally. At the center of the coils the colon sharply reverses direction and runs centrifugally between the centripetal turns. The arrangement of the ansa spiralis has been investigated by Smith and several other workers, using the former author's method which resulted in a half more centrifugal than centripetal coils. The results are summarized in table 12. The proportion of regular spirals is larger in cattle (97%), followed by goats (90%) and finally sheep (83%). Smith and Meadows (1956) speculated that this may well be connected with the relatively simpler ansa spiralis of cattle (1.0 to 2.5 centripetal coils) compared to sheep (2.0 to 4.0) and goats (2.5 to 4.0). In

addition Smith (1958) reported that in sheep 25% of the irregularities occurred in the last centrifugal coil, compared to none in cattle in which all the coils lie very close to one another. In sheep and goats, however, the last centrifugal gyrus is displaced from the remainder of the spiral, from which it is separated by the cranial mesenteric artery and lymph nodes imbedded in the common mesentery (Ellenberger and Baum, 1912; Smith, 1955 and 1956; Habel, 1964 and 1975). Comparing Merino and Corriedale sheep one can notice a difference in the percentage of regular and irregular patterns.

The large intestine lacks villi, its mucosa is thicker and its glands of Lieberkuehn are longer, straighter (except in goats, in which all the intestinal glands are tortuous) and very rich in goblet cells, compared to the small intestine. Its secretions are mainly composed of mucous and little if any enzyme is secreted (Trautman and Fiebiger, 1952). Information on the secretions entering the large intestine is scarce. Phaneuf (1952) reported that in sheep secretions into pouches of the cecum are in the order of 50 to 75 ml per 12 hr with a pH of 8.0 to 8.2. According to Nickel et al. (1979) solitary lymph nodules are only occasionally found in the cecum and colon of cattle and are absent in the large intestine of the small ruminants. They form a lymphatic ring in the columnar zone of the rectoanal junction in cattle and sheep. A patch of aggregate lymph

nodules is regularly observed at the distal end of the proximal loop of the ascending colon, being 7 to 20 cm long in cattle and 4 to 20 cm long in the small ruminants (Benzie and Phillipson, 1957; Hecker and Grovum, 1971).

Size of intestinal compartments in adult ruminants

The dimensions and capacity of the intestinal tract and of its respective segments are listed in tables 13 to 18. According to Stevens (1977) removal of the gastrointestinal tract from its attachments can increase its length and obliterate many of the features used by anatomists to designate various segments of the intestines. However it allows a more direct comparison of species and breed variations in the relative size, length and compartmentalization. Shmaltz (1894) attributed the high capacity of the GIT compartments reported by Colin (1886) in table 14 to some degree of overpressure. Compared to the small ruminants, in cattle the relative length of the small intestine at autopsy is smaller and the relative length of the cecum and colon are larger. No appreciable difference is seen between Bos Taurus and Bos Indicus. The weight of the wet ingesta, the capacity to hold water and the wet tissue weight measurements clearly indicate that cattle have a relatively larger stomach than sheep and goats. However, in terms of tissue weight the small intestine of cattle is relatively smaller than in the small ruminants.

Anatomy, physiology and rate of passage

Review of the literature failed to reveal major anatomical differences that could explain the considerably faster rate of passage of digesta in goats, compared to sheep, as reported in a comparative study in table 19, in which the differences could not be explained by discrepancies in body weights or intakes. According to Balch and Campling (1965) and Phillipson and Ash (1965) size and specific gravity are important factors determining which particles pass through the reticulo-omasal orifice. In addition size may well be related to specific gravity since small particles are likely to become saturated more rapidly than large particles. The latter authors also reported that the material in the ventral sac of the rumen is more liquid and contains finer particles than in the other rumen compartments, thus being the more probable material to be passed on to the omasum after being forced to the reticulum by the contractions of the ventral sac. In that respect, comparing fiber particle size in several gastrointestinal tract compartments, Uden (1978) found larger particles in the reticulo-rumen of goats, compared to sheep (table 20).

In a comparative study on feeding behavior and rumination in goats and sheep on hay-based diets, Geoffroy (1974) has shown a greater frequency of meals per day (8.1 vs 6.0, $P<.01$) in goats, for similar dry matter (DM) intake per unit of metabolic size. In addition goats spent more

time eating (min/g DM intake per unit of metabolic size) than did sheep ($P<.01$); time spent ruminating (min/g DM intake per unit of metabolic size) on the other hand was similar in both species. Ruckebusch and Bost (1963) also observed that ingestion of hay was more regular, more methodical and more rapid in sheep. These reports failed to investigate however, whether the greater time spent eating by goats is due to diet selection or results in a more effective mastication, or both. Houston (1978) reasoned that in an animal with a smaller rumen, food particles would be expected to pass through the rumen more quickly. Stomach compartment measurements have failed to show a decisive difference in digestive tract size between goats and sheep. The data reported by Uden (1978) and shown in table 20 suggest that goats pass larger size particles through the reticulo-omasal orifice than sheep. Whether such a small difference is an important factor in the overall rate of passage of digesta is not known. However, the smaller particles found in the reticulo-rumen seem to indicate that in sheep more surface per unit volume is subjected to bacterial degradation. From the observations of Wester (1926), Shalk and Amadon (1928), Balch et al. (1951) and Stevens et al. (1960) it appears that the rate of flow of digesta is related to the amount of digesta transferred during each appropriate reticular contraction. Frequency of the reticular contractions, which is highest during feeding

(Shalk and Amadon, 1928; Balch, 1952; Freer et al., 1962; Ruckebusch and Bost, 1963; Dziuk and McCauley, 1965), seems to be another important determinant in the rate of digesta transfer. Available comparative motility data suggest that goats have a greater rate of passage of digesta:

- goats eat more frequently and spend more time eating for similar DM intake (Geoffroy, 1974), thus increasing their total number of reticular contractions per day compared to sheep.
- motility of the ventral sac is more consistent during standing and rest in goats; in addition in recumbent goats and sheep reticulo-ruminal cycles are in a ratio of 2.7:1 (Dziuk and McCauley, 1965).

Both observations imply that in goats more material is moved to the reticulum at a faster rate, prior to its passage to the omasum. Phillipson and Ash (1965) reported that in sheep distension of the duodenum has a controlling effect on outflow from the abomasum; in turn, as the abomasum volume increases, flow from the omasum is inhibited. Rapid emptying of abomasal contents, on the other hand, resulted in extremely strong contractions of the omasal canal. No information is available as to whether a similar feedback mechanism exists in the lower parts of the gastrointestinal tract. Faster emptying of the reticulo-rumen, however, should also increase the passage of digesta further down the alimentary tract. Sellers and Stevens (1966) indicated that

an almost immediate strong contraction of the omasal body followed rapid addition of fluid into the omasal canal, suggesting that the stimulus for contraction of the omasal body may be that of distension or filling. Thus it appears that the passage of digesta through the omasum is affected by the volume of the contents in both the reticulo-rumen and the abomasum. Singleton (1961), recording the flow of digesta through the duodenum of sheep and goats, reported that the mean flow rate per hr is 28% higher (609 vs 475 ml) in goats. However, the nature of the diet and level of intake, as well as the live weights of the experimental animals, confounded the results.

Investigating possible reasons for the shorter retention times with increased levels of hay feeding in dairy cattle, Campling et al. (1961) and Freer et al. (1962) found that decreasing retention times are associated with greater DM intakes and an increase in reticulo-ruminal motility. They recorded a rise in total number of reticular contractions as well as in the number of contractions during eating and ruminating. In addition Freer et al. (1962) found a linear relationship between the amount of food eaten and the mean amount of organic matter transferred per reticular contraction, regardless of the type of feed (hay, straw, straw + urea). The mean daily rate of flow of organic matter was also directly related to the mean frequency of reticular contractions, mainly because more time was spent in eating a

larger quantity of feed and contractions were more frequent during feeding. These results show however, that a change in the mean flow rate per contraction is of much greater importance than a change in the mean frequency of contractions in effecting a change in the rate of flow of organic matter. The mechanisms described above could explain the faster rate of passage of digesta in goats under ad libitum feeding of highly fibrous feeds, since goats have a greater DM intake than sheep when offered low quality roughages (Luginbuhl and Johnson, 1982). This suggests differences in optimal feeding strategies between the two species. Forcefullness of the reticular contractions could play a role in determining the amount of digesta transferred per contraction. In that respect Gueltekin (1953) pointed out that the thickness of the muscular bands of the reticulum is greater in goats than in sheep. In addition greater backflow of digesta from the duodenum to the abomasum in goats, as reported by Singleton (1961), could be an adaptative mechanism to increase abomasal and duodenal breakdown of digesta subjected to a more rapid rate of passage.

Conclusions and Recommendations for Future Research

Numerous anatomical differences in the gastrointestinal tract have been found between cattle, sheep and goats. However, purely descriptive anatomy that disregards the

physiological functions of the organs involved fails to fully account for all differences. Other related factors are the paucity of comparative studies, the lesser importance given to sheep and particularly goats, as well as the use of the sheep as a model for the goat, especially in earlier work.

Data related to the size and capacity of the gastrointestinal tract compartments, the descriptive and quantitative anatomy of certain organs and the various gastrointestinal secretions show the existence of genuine species and breed differences and that between-animal within-breed variations can be quite large. Another notable observation is that compared to the forestomach less information is available concerning the abomasum, the intestinal tract and their respective secretions, including pancreatic and hepatic secretions.

Future research should be designed to determine if there are indeed significant differences in stomach capacity between the small ruminants, and if present to assess the physiological implications of these differences. Furthermore, a more comprehensive understanding of the capacity of the ruminant stomach could be made if the following quantitative observations were available on all animals: nature of the diet, feed and water intake, age, live weight, ingesta-free body weight, and for each compartment weight of contents, tissue weight and water fill volume under

standard procedures. Other observations should include breed, sex, physiological state and condition of the animals, and time between last meal and slaughter. In addition carefully planned experiments are definitely needed in order to determine the implications of gastrointestinal motility on particle size reduction and passage under various feeding regimens.

Many questions remain unanswered. This review will hopefully open additional research areas or stimulate interest in reinvestigating certain topics with more scrutiny. Future projects, however, should place more emphasis on a multidisciplinary approach, providing answers to several related fields of scientific research.

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TABLE 1. RELATIVE COMPOSITION OF RUMINANT SALIVA

Gland	Constituents (mEq/l)				
	Na	K	Cl	HCO3	HPO4
CATTLE[a]					
Parotid	137-168	6-14	7-34	88-127	17-47
Mandibular	11- 24	14-41	6-31	5- 16	.4-4
Inferior Molar	151-156	6-18	12-21	77- 95	18-54
Sublingual, Cheek and Buccal	110	17	49	98	20
GOAT[b]					
Parotid	162-195	4- 7	6-18		
SHEEP[c]					
Parotid	147-185	5-31	9-17	91-125	25-71
Mandibular	4- 16	10-25	7-15	5- 14	2-10
Sublingual	16- 47	6-25	16-40	8- 18	.3-2
Labial	29- 47	3- 9	34	2- 4	2-10
Inferior Molar	175	7-10	7-12	97-110	44-51
Palatine	179	4	25	109	25

[a] Phillipson and Mangan, 1959; Bailey, 1961; Bailey and Balch, 1961

[b] Komi and Snyder, 1963

[c] Kay, 1960; Mc Dougall, 1948

TABLE 2. CLASSIFICATION OF SALIVARY GLANDS ACCORDING TO THEIR SECRETIONS

Gland	Cattle	Sheep	Goats	Reference[a]
Parotid		serous		2
	serous	serous	serous	1
		mucous end-pieces in lambs		1
Inferior Molar		serous		2
	serous			1
- ventral part		serous	serous	1
- dorsal part		mucous	mucous	1
Mandibular		mixed		2
	mixed	mixed	mixed	1
Sublingual		mixed		2
	mixed	mixed	mixed	1, 5
Labial		mixed		2
		mucous	mucous	1
Nasolabial	serous	serous	serous	1, 3 4
Buccal		mucous		2
	mucous	mucous	mucous	1
Pharyngeal		mucous		2
Palatine		mucous		2
	mucous			5

TABLE 2. (continued)

Gland	Cattle	Sheep	Goats	Reference[a]
Lingual				
- Paracaruncular			mucous	1
- Apical lingual	mucous	mucous	mucous	5
		mixed	mixed	1
- Ebner's	serous	serous	serous	1
- Root of tongue	mixed			1

[a] Trautman and Fiebiger, 1952 (1); Kay, 1960 (2); Habel, 1964 (3); Frandson, 1974 (4); Nickel et al., 1979 (5).

TABLE 3. MEAN WEIGHTS OF THE SALIVARY GLANDS IN ADULT SHEEP AND ESTIMATED SECRETION OF SALIVA[a]

Salivary glands	Weight g	Weight %	Volume 1/24 hr
Both Parotid	23.5	29.3	3.0-8.0
Both Mandibular	18.2	22.6	0.4-0.8
Both Inferior Molar	5.9	7.3	0.7-2.0
Both Sublingual	1.3	1.6	0.1-(?)
Both Buccal	6.0	7.5	
Palatine	8.8	10.9	2.0-6.0[b]
Pharyngeal	5.9	7.3	
Labial	10.9	13.5	(?)

[a] Adapted from Kay, 1960

[b] Buccal, pharyngeal and labial combined

Table 4. COMPOSITION OF THE GASTRIC JUICE OF SHEEP

Constituent	Concentration (mEq/l)
Hydrogen ions	Up to a maximum of 124
Potassium	2- 19
Sodium	21-167
Calcium	1.0-2.2
Magnesium	0.5-0.9
Chloride	138-172
Bicarbonate (when the abomasum is empty and the juice is neutral)	6-9
Nitrogen	15-33 (mg/100ml)

[a] From Phillipson (1977)

TABLE 5. MEAN RETICULAR CONTRACTIONS PER 10 MIN.

Animals	Dairy Shorthorn[a]		Does[b]	Ewes[b]
Diet	long hay		hay	hay
Eating	14.2		16.0 +/- .76	16.2 +/- 1.1
	standing	lying		
Resting	11.7	10.9	12.0 +/- .28	12.3 +/- .65
Ruminating	11.1	9.4	9.4 +/- .54	10.2 +/- .79

[a] Balch, 1952

[b] Ruckebusch and Bost, 1963

TABLE 6. VOLUME OF STOMACH COMPARTMENTS OF ADULT RUMINANTS AS DETERMINED BY THEIR CAPACITY TO HOLD WATER

	No. of animals	Live weight	Volume of compartments: Reticulum	Rumen	Omasum	Abomasum	Total	Volume as % of total volume: Reticulum	Rumen	Omasum	Abomasum	Reference
		kg	Liters									
CATTLE												
			90-200[a]		9-15	8-15[a]		84		9	7	1
			132-208[d]									1
			250-276[d]		14-18	17-24[d]		88		6	8	1
		272-419	90-199[b]		6-20	6-13[b]		87		7	6	6
		272-419	104-225[c]		6-20	7-15[c]		88		6	6	6
								5	80	7	8	11
								84		7	9	13
SHEEP												
Ak-Karaman	10	38.8	1.6	18.5	0.6	2.0	22.7	7	82	2	9	8
Corriedale	40		0.8	8.8								12
			0.7	8.8	0.4	1.4	11.3	7	78	3	11	9
			1.0	13.0	0.3	1.8	16.1	6	81	2	11	2
							19.0					7
			1.0	9.0								3
			1.0									4
			1.5	12.0								10
			0.9									5

TABLE 6. (continued)

			Volume of compartments					Volume as % of total volume				
	Number of animals	Live weight	Reticulum	Rumen	Omasum	Abomasum	Total	Reticulum	Rumen	Omasum	Abomasum	Reference[e]
		kg	Liters									
GOATS												
Angora	10	36.6	1.6	14.2	0.75	2.15	18.7	9	76	4	11	8
Kil	10	38.1	2.1	21.3	1.0	2.9	27.3	8	78	4	11	8
			2.3	28.0	1.2	4.0	31.5	7	79	3	11	14

[a] stretched and well rounded

[b,c] filled to an overpressure of 5 and 10 cm H_2O, respectively, with compartment excised and resting on a hard sufrace

[d] distended to point of rupture

[e] Schwartz, 1894 (1); Ellenberger and Baum , 1912 (2); Lesbre, 1922 (3); Caradona, 1930 (4); Mazel, 1939 (5); Paloheimo, 1944 (6); McGregor, 1952 (7); Gueltekin, 1953 (8); May, 1964 (9); Schwarze and Schroeder, 1970 (10); Habel, 1975 (11); Pereira et al., 1975 and 1979 (12); Nickel et al., 1979 (13); Devendra, 1980 (14).

TABLE 7. WEIGHT OF WET INGESTA IN STOMACH COMPARTMENTS OF ADULT RUMINANTS

	No animals	Live weight	Weight of ingesta in stomach compartments: Reticulum	Rumen	Omasum	Abomasum	Ingesta % Live weight	Ingesta as % of total stomach ingesta: Reticulum	Rumen	Omasum	Abomasum	Reference[g]
CATTLE		kg	kg	kg	kg	kg						
Cow	6	554	73.4		9.0	2.5	15.3	86		11	3	4
Cow	18					2.3	14.0	87		10	3	4
Steer	6	377	28.0		3.8	1.2	8.8	84		12	3	1
Steer	1	364	54.1		8.4	1.1	17.5	85		13	2	2
SHEEP		kg	g	g	g	g						
	3	82	7217		85	597	9.6	91.4		1.1	7.5	2[a]
	1		8400		30	1099		88.2		0.3	11.5	2[b]
Ewe, Cheviot	21	58	7750		171	910	15.2	88.0		2.0	10.0	3[c]
Wether, Greyface	6		5108		113	273		93.0		2.0	5.0	4[d]
Masai	2		277	3263	247	106		7.0	83.5	6.5	3.0	5[e]
Masai	1		164	1913	24	239		7.0	82.0	1.0	10.0	5[f]

[a] pasture grass; [b] hay + concentrate; [c] 400 g hay, 1150 g concentrate.

[d] hay + concentrate: animals slaughtered 4 hr after last feeding.

[e] Rhode grass hay + concentrate: animals slaughtered 16 hr after last feeding.

[f] 300 g pure kibbled maize: animals slaughtered 16 hr after last feeding.

[g] Ewing and Wright, 1918 (1); Elsden et al., 1946 (2); Boyne et al., 1956 (3); Makela, 1956 (4); Rogerson, 1958 (5);

TABLE 8. WET TISSUE WEIGHT OF STOMACH COMPARTMENTS IN ADULT RUMINANTS

	No. of animals	Live weight	Weight of tissue in stomach compartments: Reticulum	Rumen	Omasum	Abomasum	Tissue weight as % of Live weight	Tissue weight as % of total tissue weight: Reticulum	Rumen	Omasum	Abomasum	Reference[a]
CATTLE		kg	g	g	g	g						
Cow, Jersey	24							10.0	46.5	30.0	13.5	1
	26							60.0		26.0	13.0	8
Cow	24	517	11,000		5,000	2,300	3.54	60.1		27.3	12.6	3
								64.0		25.0	11.0	5
SHEEP												
Ewe, Western Whiteface Cross	4	66.0	1,197		437		2.48	73.3		26.7		7
								11.0	63.0	5.0	21.0	6
Ewe, Cheviot	21	58.0	1,160		187	343	2.91	68.6		11.1	20.3	9
Ewe, Merino Cross			121	625	86	247		11.2	57.9	8.0	22.9	4
Ak-Karaman	10	38.8		1,220			3.14					2
GOATS												
Angora	10	36.6		1,310			3.48					2
Kil	10	38.1		1,570			4.12					2
Barbari	12								88.3	2.1	9.6	10

[a] Becker and Arnold, 1952 (1); Gueltekin, 1953 (2); Makela, 1956 (3); Wardrop and Coombe, 1960 (4); Godfrey, 1961 (5); Church et al., 1962 (6); Boda et al., 1963 (7); Swett, 1964, cited by Warner and Flatt, 1965 (8); Boyne et al., 1956 (9); Rai and Pandey, 1982 (10).

TABLE 9. THE ELECTROLYTE COMPOSITION OF JUICE FROM THE SMALL INTESTINE OF SHEEP[a]

	mEq/l	
Composition	Upper jejunum	Lower ileum
pH	7.1	8.1
Sodium	136	135
Potassium	8.1	9.0
Calcium	1.2	2.1
Magnesium	0.5	0.6
Chloride	134	105
Bicarbonate	11.8	41.5
Phosphate	1.5	

[a] Adapted from Scott, 1965

TABLE 10. COMPOSITION OF THE BILE OF SHEEP TAKEN FROM THE GALL-BLADDER AFTER DEATH OR COLLECTED DURING EXPERIMENTS IN WHICH BILE WAS NOT RETURNED TO THE INTESTINE[a]

Bile	Gall-bladder	First hour of collection	4-24 hours of collection (mean values)
Volume (ml/hr)		60	17
Total solids (g/100ml)	8.7	5.9	2.9
Chloride (mEq/l)	74	83	122
Sodium (mEq/l)	197	179	154
Potassium (mEq/l)	8	7.6	6.7
Nitrogen (mg/100ml)	248	150	76

[a] Adapted from Harrison, 1962

TABLE 11. COMPOSITION OF THE PANCREATIC JUICE OF SHEEP[a]

	mEq/l
Sodium	135 - 165
Potassium	3.9 - 5.4
Chloride	110 - 126
Bicarbonate	15 - 30
Calcium	4.0 - 5.7
Magnesium	0.7 - 1.5
Nitrogen	0.5 - 0.7
pH	7.2 - 7.8

[a] Adapted from Storry, 1961 and Taylor, 1962

TABLE 12. PATTERN OF ANSA SPIRALIS OF THE ASCENDING COLON[a]

	No. Animals	Patterns		Centripetal coils							Reference[b]
		Regular	Irregular	1.0	1.5	2.0	2.5	3.0	3.5	4.0	
		%	%	% of regular patterns							
Bos taurus	735	97	3	<1	25	74	1				2
Bubalus Bubalis	62				27	73					11
Bos indicus	1,261	97	3		9	84	7				5
Mean		97	3								
Sheep Corriedale	100	93	7				7	60	32	1	12
Sheep Merino	400	84	16				6	52	38	4	9, 10
Sheep	1,061	79	21			<1	17	61	21	<1	1
Sheep foetuses	50	76	24			2	16	58	24		3
Mean		83	17								
Goat	50	88	12				9	57	34		4
Goat	946	93	7				4	57	37	2	7, 8
Goat foetuses	77	88	12				6	52	38	4	6
Mean		90	10								

[a] The method used resulted in 0.5 more centrifugal than centripetal coil

[b] Smith, 1955 (1); Smith and Meadows, 1956 (2); Smith, 1957 (3); Smith, 1959 (4); Paiva and Borelli, 1963/1964 (5); Borelli and D'Errico, 1965 (6); Borelli and Fernando Filho, 1965 (7); Paiva and Borelli, 1965 (8); Paiva and Borelli, 1966 (9); Borelli and Santis Prada, 1966/1967 (10); Peduti Neto et al., 1971 (11); Santis Prada et al., 1971 (12).

TABLE 13. CAPACITIES OF PART OF THE GUT AT AUTOPSY[a]

	Average absolute capacity	Relative capacity	
	liters	%	
Cattle			
Stomach	252.5	70.8	
Small intestine	66.0	18.5	63.5
Cecum	9.9	2.8	9.5
Colon and rectum	28.0	7.9	27.0
Total	356.4	100.0	100.0
Sheep and Goat			
Rumen	23.4	52.9	
Reticulum	2.0	4.5	
Omasum	0.9	2.0	
Abomasum	3.3	7.5	
Small intestine	9.0	20.4	61.6
Cecum	1.0	2.3	6.9
Colon and rectum	4.6	10.4	31.5
Total	44.2	100.0	100.0

[a] Adapted from Colin, 1886

TABLE 14. LENGTH OF PART OF THE INTESTINE AT AUTOPSY

	No animals	Average absolute length (m)					Reference[a]
		Duodenum	Jejunum	Ileum	Cecum	Colon	Rectum	
CATTLE								
Bos indicus	40	-----	31.2	-----	.5	6.8	+	8
Bos taurus		-----	46.0	-----	.9	10.0	+	1
Bos taurus		-----	39.5	-----	.8	10.5	+	7, 10
Bos taurus	40	-----	35.9	-----	.6	7.1	+	9
Bos taurus		-----	38.0	-----	---10.0---		+	2
Bos taurus	24	-----	39.7	-----	---10.2---		+	3
Bos taurus		1.1	----37.0--		.7	9.6	+	4, 11
SHEEP								
Corriedale	50	-----	24.2	-----	.35	5.5	+	6
Merino Ewe	6				--- 4.3---		+	5
		.75	----25.8--		.25	4.5	+	4
SHEEP AND GOATS								
		.90	----25.8--		.33	5.5	+	11
		-----	25.3	-----	--- 4.9---		-	2
		-----	26.2	-----	.36	6.2	+	1

[a] Colin, 1886 (1); Ellenberger and Baum, 1912 (2); Makela, 1956 (3); May, 1964 (4); Hecker and Grovum, 1971 (5); Santis Prada et al., 1971 (6).; Habel, 1975 (7); Paiva and Borelli, 1977 (8); Paiva et al., 1977 (9); Boone, 1979 (10); Nickel et al., 1979 (11).

TABLE 15. LENGTH OF PART OF THE INTESTINE AT AUTOPSY

	No animals	Relative length (%)					Reference[a]
		Duodenum	Jejunum	Ileum	Cecum	Colon	Rectum	
CATTLE								
Bos indicus	40	-----	81.0	-----	1.3	17.7	+	7
Bos taurus		-----	80.8	-----	1.6	17.6	+	1
Bos taurus		-----	77.7	-----	1.6	20.7	+	6, 9
Bos taurus	40	-----	82.3	-----	1.4	16.3	+	8
Bos taurus		-----	79.2	-----	---20.8---		+	2
Bos taurus	24	-----	79.6	-----	---20.4---		+	3
Bos taurus		2.3	----76.4--		1.5	19.8	+	4, 10
SHEEP								
Corriedale	50	-----	80.6	-----	1.2	18.2	+	5
		2.4	----82.4--		.8	14.4	+	4
SHEEP AND GOATS								
		2.8	-----79.3--		1.0	16.9	+	10
		-----	83.8	-----	---16.2---		-	2
		-----	80.0	-----	1.1	18.9	+	1

[a] Colin, 1886 (1); Ellenberger and Baum, 1912 (2); Makela, 1956 (3); May, 1964 (4); Santis Prada et al., 1971 (5).; Habel, 1975 (6); Paiva and Borelli, 1977 (7); Paiva et al., 1977 (8); Boone, 1979 (9); Nickel et al., 1979 (10).

TABLE 16. WEIGHT OF WET INGESTA IN THE GUT OF ADULT RUMINANTS

	No. animals	Weight of ingesta: Stomach	Small intestine	Cecum	Colon	Rectum	Ingesta %	Live weight	Reference[a]
CATTLE		kg	kg	kg	kg	kg	%		
Steer	1	54.3	6.3	2.0	1.4	1.3	23.9		1
	24	75.6	6.1	-------	7.4	-----	17.2		3
SHEEP		g	g	g	g	g	%		
Greyface wether	6	5,494	598	401	389				4[e]
Cheviot ewe	21	8,831	932	908	407		19.1		2[d]
Masai	2	3,893	521	336	---533---				5[f]
Masai	1	2,340	554	165	---557---				5[g]
	1	9,529	876	748	351	287			1[c]
	3	7,899	837	749	268	179	12.1		1[b]

[a] Elsden et al., 1946 (1); Boyne et al., 1956 (2); Makela, 1956 (3); Badawy et al., 1958 (4); Rogerson, 1958 (5).

[b] Pasture grass; [c] Hay + concentrate; [d] 400 g hay, 1150 g concentrate

[e] Hay + concentrate: slaughter 4 hr after last feeding

[f] Rhode grass hay and concentrate; [g] 300 g pure kibbled maize

[f,g] slaughter 16 hr after last feeding

TABLE 17. WEIGHT OF WET INGESTA IN THE GUT OF ADULT RUMINANTS

		% of total GUT ingesta					
	No animals	Stomach	Small intestine	Cecum	Colon	Rectum	Reference[a]
CATTLE							
Steer	1	84.3	9.4	3.3	1.5	1.5	1
Cow	4	85.0	6.8	-------	8.3	------	3
		85.5	8.5		6.5		6
SHEEP							
Greyface wether	6	79.8	8.7	5.8	5.7		4[e]
Cheviot ewe	21	79.7	8.4	8.2	3.7		2[d]
Masai	2	73.7	9.9	6.4	---10.0---		5[f]
Masai	1	64.7	15.3	4.6	---15.4---		5[g]
	1	80.8	7.4	6.4	3.0	2.4	1[c]
	3	79.5	8.4	7.6	2.7	1.8	1[b]

[a] Elsden et al., 1946 (1); Boyne et al., 1956 (2); Makela, 1956 (3); Badawy et al., 1958 (4); Rogerson, 1958 (5); Parra, 1978 (6).

[b] Pasture grass; [c] Hay + concentrate; [d] 400 g hay, 1150 g concentrate

[e] Hay + concentrate: slaughter 4 hr after last feeding

[f] Rhode grass hay and concentrate; [g] 300 g pure kibbled maize

[f,g] slaughter 16 hr after last feeding

TABLE 18. WET TISSUE WEIGHT OF THE GUT COMPARTMENTS IN ADULT RUMINANTS

			Weight of tissue					% of total tissue weight				
	No. of animals	Live weight	Stomach	Small Intestine	Cecum	Colon	Tissue Live weight %	Stomach	Small Intestine	Cecum	Colon	Reference[a]
SHEEP		kg	g	g	g	g						
Cheviot Ewe	21	58	1,690	702	230	550	5.5	53.3	22.1	7.3	17.3	1
Merino cross Ewe	7		1,079	-----	1,119	----		49.0	-------	51.0	-------	3
GOAT												
Japonese meat type	1	21	439	280	74	133	4.4	47.4	30.2	8.0	14.4	4
CATTLE			kg	kg	kg	kg						
Cow	24	517	18.3	5.1	---4.9--		5.5	64.7	18.0	---	17.3---	2

[a] Boyne et al., 1956 (1); Makela, 1956 (2); Wardrop and Coombe, 1960 (3); Hamada, 1973 (4).

TABLE 19. RETICULO-RUMINAL MEAN RETENTION TIME OF GRASS HAY DIETS[a,b]

Animal species	Method	Retention time hr
Cattle	Mordanted-Cr	62-79
Sheep	Mordanted-Cr	70
Goat	Mordanted-Cr	52

[a] Adapted from Uden, 1982
[b] chopped to 5 cm

TABLE 20. COMPARISON OF FIBER PARTICLE SIZE INDEX OF GUT CONTENTS IN RUMINANTS[a]

	Reticulo-rumen	Omasum	Abomasum	Cecum	Feces
	microns				
Large heifers	2290				890
Small heifers	1670				640
Goats	1470	530	570	520	460
Sheep	1290	550	530	490	460

[a] Adapted from Uden, 1982