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Review Article

Ruminal Development of Small Ruminants: A Review

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Abstract

The development of the rumen in ruminant animals is a complex and dynamic process that involves prenatal and postnatal growth and maturation, as well as ongoing adaptation throughout the animal's life. One of the most significant changes that occur during the development of the ruminant stomach is the enlargement of the rumen. In young ruminants, the rumen is smaller than abomasum and undeveloped, but as the animal begins to consume more solid foods, the rumen expands and becomes more complex. Factors such as diet, nutrition, genetics, age and the microbiome can all influence the development of the rumen. At birth, the rumen organ, rumen epithelium, and rumen microbiota are not fully developed. The most receptive time for rumen development is between the postnatal and weaning periods, during which time the organ and its epithelium grew and the rumen microbiota is established. Overall, the development of the rumen during the postnatal and weaning periods is critical to the health and productivity of the animal.

Keywords: Goat; Development; Prenatal; Postnatal; Rumen

Introduction

The stomach of embryonic ruminant is initially an extension of the primary digestive tube located in the midline of the future cervical region. It is attached to the dorsal and ventral wall of the abdomen by the dorsal and ventral mesogastrium. As the embryo develops, the stomach primordium rapidly grows. Its dorsal margin expands faster than the ventral margin, creating the greater and lesser curvatures. The primordium of the bovine stomach was identified as an enlargement of the foregut near the septum transversarium [1]. The primordia of the different compartments were labelled as cranial and caudal expansions by McGeady., *et al*. [2]. Hejazi and Frick-aghaji [3] observed the stomach of a 38-day-old sheep foetus as a tube. The developing digestive tube had three dilatations in sheep at 24-26 days of gestation [4] and in goat foeti at 34 days of gestation [5,6]. The cranial one on developing greater curvature was rumen, ventro-caudal was reticulum, and the combined omaso-abomasum was located behind them (Figure 1). Hejazi and Frik-aghaji [3] referred these dilatations as bulbs in a 40-day-old sheep stomach. All four compartments of the stomach were clearly demarcated in buffalo foeti at 2 cm CRL [7], in bovine at 40th day of gestation [2], in goat at 38 days of gestation [5,6] and in sheep at 32 days of gestation [8] (Figure 2). Gupta., *et al*. [5,6] additionally reported that at 38 days of intrauterine life, the sacs of the foetal goat stomach were related dorsally with the mesonephros, and by 41 days, the caudal part of the second sac on the left side and a small part of the third sac were in contact with the developing mesonephros and gonads (Figure 3). Second and third dilatations were located on the right side of the median plane and were in contact with the coils of the developing intestine, pancreatic swelling, and covered by the mesentery [5,6]. Farooqui [9] noted that at 30 days of gestation in goats, the stomach was related dorso-laterally with the left gonad.

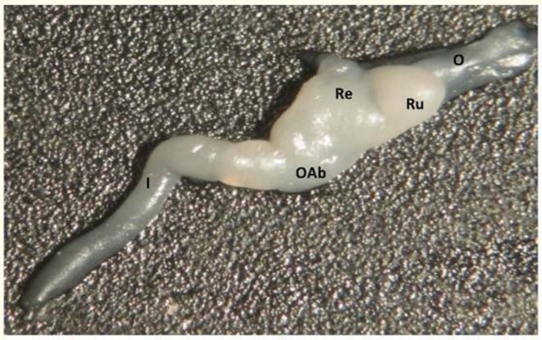

Figure 1: Photograph of 34-day old goat foetal digestive tube showing oesophagus (O), rumen (Ru), reticulum (Re), omasum-abomasum (OAb) and intestine (I).

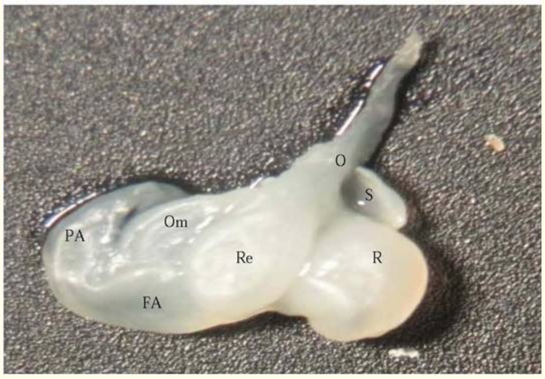

Figure 2: Photograph of 42-day old goat foetus showing oesophagus (O), rumen (Ru), spleen (S) reticulum (Re), omasum (Om), fundic part of abomasum (FA), and pyloric part of abomasum (PA).

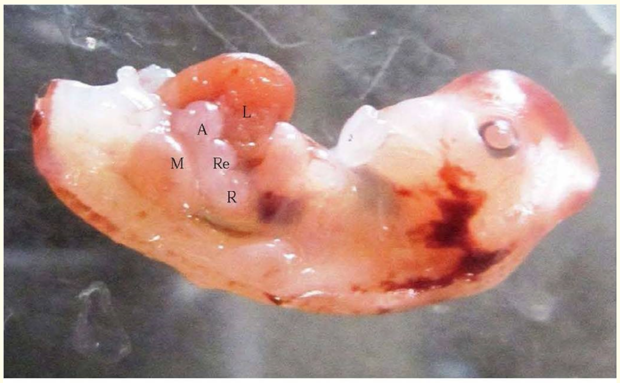

Figure 3: Photograph of 41-day old goat old foetus (left view of abdominal cavity) showing rumen (Ru), reticulum (Re), abomasum (Ab), right lobe of liver (L) and left mesonephros (M).

Organogenesis of rumen

The primordia of the rumen and reticulum were distinguished from the original rumino-reticular primordium at 1.5 cm CR in buffalo foetus [7] and at 38 days of gestation in goat [5,6]. Patra., *et al*. [10] observed that the developing rumen of sheep appeared with a left and a right ruminal bud together assumed the quadrilateral shape at the age between 32 and 44 days of gestation. The whole rumen appeared as a sac like structure with a slight caudo-ventral projection at 63 days of gestation. Whereas, Soni., *et al*. [10] reviewed the morphogenesis of fore stomach of the small ruminant and concluded that the rumen in 38 day old sheep foetus occurred in the form of a tube. The rumen was situated anteriorly infront of reticulum in the 38-day-old sheep [12] and 34 days in goat foeti [5]. In 52 days old foetus, rumen pushed reticulum toward anterior side by a caudal movement with appearance of rumen clefts. The future rumen was placed against the 11th -13th rib in goat and sheep up to 50 days of gestation [5,12]. From 50 to 100 days and 101 to 150 days of gestation, the extent of the rumen increased, and was located between the 9th rib and second lumbar vertebra and 8th rib and first lumbar vertebra, respectively [5] (Figure 4). In sheep the developing rumen was noted to extend from 8th rib to 1st lumbar at 150 days of gestation [8]. Hejazi and Farhoudi [12] reported that the sheep rumen was quadrilateral in shape during the early stages of pregnancy, becoming rectangular in the later stages. Similarly, Gupta., *et al*. [5] observed roughly quadrilateral shaped foetal goat rumen until 100 days of gestation, after which it became caudo-laterally pointed. On the other hand, Bello., *et al.* [13] found that in red Sokoto goats the rumen was like a flattened sac, resembling an incomplete U-shaped structure. Noden and de Lahunta [1] discovered that in bovine foeti, the rumen was in contact dorsally with septum tranversarium. Similarly Patra., *et al*. [10] also reported that in sheep between 63 and 94 days of gestation, the rumen was seen to be attached with septum transversarium dorsally. Gupta., *et al*. [5] in goat at 43 days and Patra., *et al*. [10] in sheep at 44 days of foetal age the cranio-dorsal part of the forming rumen was connected to the developing spleen while the caudo-dorsal part was related to the developing gonads. At 46-47 days in goat and 48 days in sheep, the dorsal part of the rumen was related with the cranial end of the mesonephros and mesonephric duct, while the ventral part was associated with the developing gonads [5,8]. Gupta., *et al*. [5] in goat further reported that the caudo-ventral blind sac of rumen was in contact with the cranial end of the mesonephros at 46 days and with the coils of the intestine and adrenal at 53 days of age. During the period of 50 to 100 days of gestation, the rumen was in contact dorsally with the septum tranversarium. The left or parietal surface was related with the developing kidney, especially mesonephros, left lobe of the pancreas, and adrenal, whereas, the visceral surface was related to the developing coils of the small intestine, colon, and omentum. At around 106 days of foetal age, the caudo-ventral blind sac was related anteriorly with 2/3rd part of the abomasum and caudally with the coils of small intestine. With the progression of age, the caudo-dorsal blind sac became free. At full term, the right or visceral surface of the dorsal sac was in contact with the developing abomasum. Patra., *et al*. [10] in sheep noticed that between 63 and 94 days of gestation, the parietal surface of rumen was related to the developing pancreas and left adrenal gland and the visceral surface was related to the coils of the intestine.

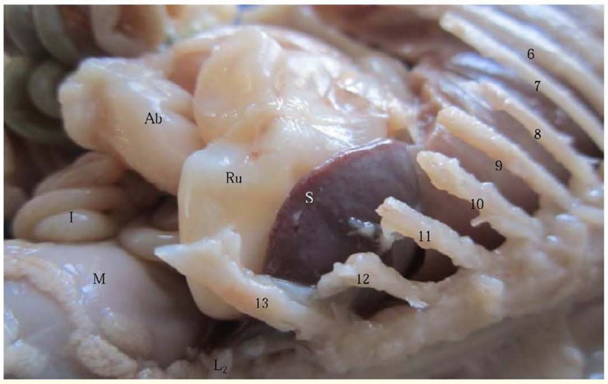

Figure 4: Photograph of 134-day old goat foetus showing location of rumen (R), spleen (S), abomasum (Ab), intestine (I) metapephros (M), 6 to 13 respective rib and second lumbar vertebra (L2).

Exterior of rumen

Externally two longitudinal grooves (left and right) and two transverse grooves (cranial and caudal) and corresponding to the groove internally left and right longitudinal and cranial and caudal pillars are present in rumen which divide it into dorsal and ventral sacs. In buffalo foeti external transverse groove reported at 3.2 cm CRL and left and right longitudinal grooves, coronary grooves and blind sacs appeared at 5 cm CRL [14]. Roy [4] described the left and right longitudinal grooves of the foetal sheep rumen at 34 days and the blind sacs at 43 days of gestation. Hejazi and Frik-aghaji [3] noted the longitudinal cleft by 50 days and the blind sacs at 66 days of development. In goat foeti, Gupta., *et al*. [5] observed the cranial transverse groove first at 38 days, followed by the other grooves at 46 days of gestation (Figure 5,6). Whereas, Patra., *et al*. [10] in sheep reported the cranial and caudal transverse grooves appeared at 32 and 48 days of gestation respectively and right and left longitudinal grooves appeared at 48 and 94 days of gestation respectively (Figure 7). The dorsal sac was larger and grew faster than the ventral sac in caprine and bovine [5,7]. The cranio-dorsal coronary grooves were not observed at any stage of goat foetal life. At full term, all the grooves except the craiodorsal coronary groove were prominent [5]. Panchamukhi [7] in buffalo foeti and Hejazi and Farhoudi [12] in prenatal sheep reported that the length and width of the rumen were equal in early stages (0.2 cm in bovine and 0.05 cm CRL in sheep), however, the length was higher than width in later stages (15.1 cm in bovine and 5 cm in sheep). Gupta., *et al*. [5] observed that, in goats, the length of the rumen was to some extent greater (0.18 ± 0.018 cm to 4.56 ± 0.39 cms) than its width (0.17 ± 0.017 cm to 4.27 ± 0.25 cms) throughout the gestation period.

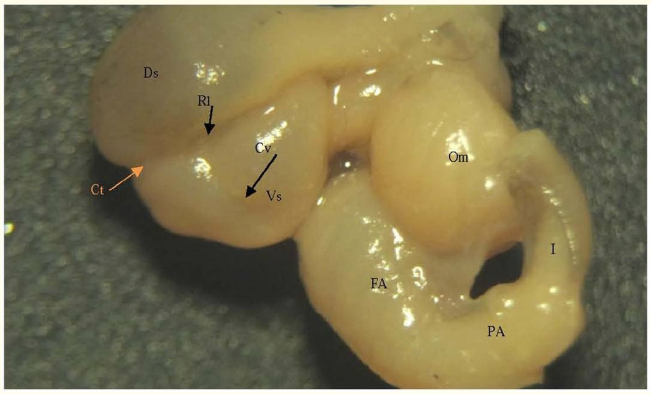

Figure 5: Photograph of 53-day old goat foetus (right view) showing dorsal (Ds) and ventral sacs (Vs) of rumen, caudal transverse groove (Ct), right longitudinal groove (Rl), caudo- ventral coronary groove (Cv), omasum (Om), abomasum (Ab) and intestine (I).

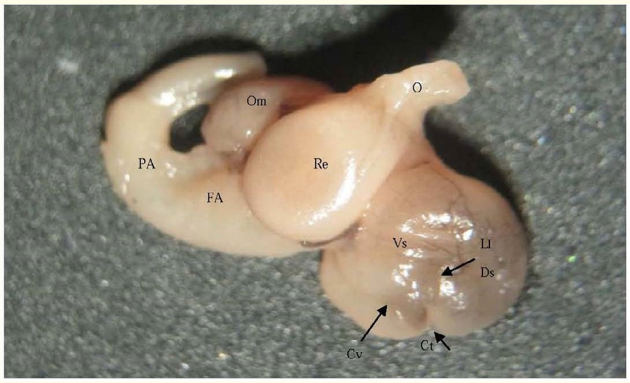

Figure 6: Photograph of 53-day old goat foetus (left view) showing dorsal (Ds) and ventral sacs (Vs) of rumen, caudal transverse groove (Ct), left longitudinal groove (Ll), caudo- ventral coronary groove (Cv), omasum (Om), abomasum (Ab), reticulum (Re) and oesophagus (O).

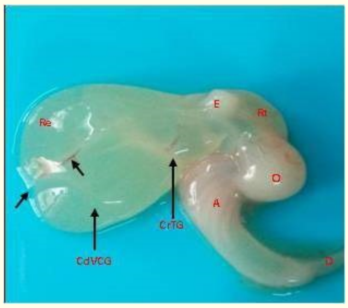

Figure 7: Photomicrograph showing the growing compartments of the stomach i.e. rumen (Re), reticulum (Rt), omasum (O), abomasum (A), esophagus (E) and duodenum (D) of sheep foetus aged 63 days. Note the cranial and caudal transverse grooves (CrTG, CdTG) with blood vessels (arrow), caudo-ventral coronary groove (CdVCG) of rumen.

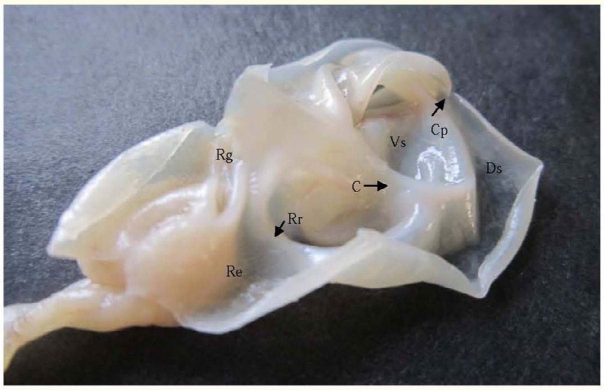

Figure 8: Photograph of 86-day old goat foetal stomach (interior view) showing cranial pillar (C), caudal pillar (Cp), rumino-reticular fold (Rr), dorsal (Ds) and ventral sacs (Vs) of rumen, reticulum (Re) and reticular groove (Rg).

Interior of rumen

In buffalo foeti internal transverse pillars were noticed at 2.2 cm CRL [14]. In the rumen of a goat foetus, both cranial and caudal pillars were identified internally as shelf-like projections at the anterior and posterior ends of the ruminal cavity at 46 days of gestation. The cranial pillar was directed obliquely dorsally and caudally from the ventral wall, and its free edge was concave. The caudal pillar was nearly directed horizontally [5,6] (Figure 8). The internal surface of developing sheep rumen revealed cranial and caudal pillars at 32 and 63 days of gestation respectively [10]. Longitudinal folds started from the cranial pillar and faded out towards the caudal pillar. The right longitudinal fold became apparent first and was completed by 55 days in goat [5,6] and at 44 days in sheep [10]. The left longitudinal fold was completed at approximately 100 days in goat [5,6] and at 94 days in sheep [10]. A well-developed ventral coronary fold was visible at 55 days of gestation, encircling the ventral blind sac. The right ventral coronary fold was more advanced, reaching the ventral margin of the ventral sac, whereas the left one reached the middle [5,6]. The mucosal surface of West African Dwarf goat rumen at 87 days of gestation was smooth and pale to greyish yellow [15]. At 75 days, the internal surface was soft, whitish and smooth, while conical papillae became evident at 113 days in goat [5,6] and 116 days in sheep [10]. Gupta., *et al*. [5] observed fine roughness at 90 days, which sharpened at 145 days.

Post natal development of rumen

The development of the rumen after birth is a complex and dynamic process that involves the growth and maturation of the rumen epithelium, the establishment of a stable microbial community, and the development of muscular and nervous systems that regulate rumen function. At birth, the rumen is undeveloped and non-functional, and the newborn animal relies on milk for nutrition. As the animal begins to consume solid feed, the rumen undergoes a series of structural and functional changes that allow it to process plant material more efficiently. During the first few weeks of life, the rumen epithelium begins to grow and develop complex folds and papillae, which increase the surface area available for nutrient absorption. At the same time, microbial populations begin to colonize the rumen, with bacteria and protozoa playing key roles in breaking down plant material into smaller, more digestible compounds.

The left and right longitudinal grooves along with cranial and caudal transverse grooves clearly demarcated the rumen into dorsal and ventral sacs. In postnatal life, the cavity of the rumen was divided into dorsal and ventral sacs by the pillars. The anterior pillar - which projected obliquely backward and upward from the ventral wall - was connected to the relatively narrow longitudinal right and left pillars, which in turn were connected to the more horizontal posterior pillar. Further, three accessory pillars on either side detached from the posterior pillar, two of which passed around the blind sacs to meet the corresponding pillars of the opposite side. These marked off the posterior blind sacs from the general cavity and were termed the coronary pillars. The distance between the anterior and posterior pillars was about 16-18 inches. Nickel., *et al*. [16] Sisson and Grossman, [17] and Dyce., *et al*. [18] in adult ruminants, described that the dorsal sac of rumen is longer than the ventral and curves ventrally at the round, rear end. The ventral sac of rumen appeared much caudally placed than the overlying dorsal sac. The ventral sac of rumen was significantly larger than the dorsal sac in sheep and goat [19] and in Indian Spotted Chevrotain [20]. The dorsal sac of rumen was connected to the reticulum via the rumino-reticular groove externally and rumino-reticulr fold internally, which mark the demarcation between the rumen and reticulum. The groove is deep ventrally and runs along the lateral surface, but there is no definite separation between the rumen and reticulum dorsally. Together, they form a dome-shaped vestibule known as the Atrium ventriculi, where the oesophagus terminates [16-18]. The rumino-reticular fold lies opposite the seventh or eighth rib. The pelvic extremity of the rumen is divided into dorsal and ventral blind sacs by a deep transverse posterior groove that meets the longitudinal grooves. In small ruminants, the left longitudinal groove runs for a short distance in an upward and backward direction, but does not connect to the posterior transverse groove [16]. The dorsal and ventral coronary grooves mark off the blind sacs from the remaining rumen. However, in small ruminants, the dorsal coronary groove is absent and the distinct ventral coronary groove is present on the right surface. Both the left and right ventral coronary grooves were complete and extended to the ventral curvature of rumen in ox [19] and Indian Spotted Chevrotain [20]. At the cranial end of the rumen, there is a dorsal projection called the Atrium ruminis and a ventral projection known as the Recessus ruminis. The Atrium ruminis continues caudally to the dorsal sac, while in small ruminants, the caudo-ventral blind sac projects further caudally than the caudo-dorsal blind sac, whereas in oxen the two blind sacs are of about equal length [16-18].

The adult rumen mucous membrane was brown in colour except at the rumen pillars whose margins were pale [17]. Ruminal papillae covered the whole mucosa, except the pillars and part of the middle of the dorsal sac [16,21]. However, Agungpriyono., *et al*. [22] documented even distribution of the ruminal papillae and the presence of papillae on the ruminal pillars were characteristic of browsers. The rumen of red Sokoto goat was characterized by a brown or black mucosa covered with dense papillae, a pale-colored edge of the adductor muscle (i.e., ruminal pillar) and a gray caudal sac in animals over three years of age [13]. The size of the papillae decreased toward the pillars and were absent on the pillars themselves. Hofmann [23] described differences between the papillae of grazers and browsers, with the latter are being more extensive and dense. Lesmeister and coworkers [24] considered the papillae length of the rumen as the most important factor for the evaluation of rumen development, followed by the papillae width and rumen wall thickness. However, papillae per square centimeter are not used as an indicator of rumen development. Overall, papillae serve as absorptive structures and their size and shape can vary significantly depending on the type of forage and the amount and quality of food consumed. Reece [25] noted that the prominence of the papillae was dictated by the animal's diet - roughage reduced the size whereas energy food increased it. Radostits., *et al*. [26] stated that animals fed grains have short, narrow and dark ruminal papillae.

Nickel., *et al*. [16] described that the ruminal papillae ranged from foliate, narrow filiform, conical and club shaped. Reece [25] noted that the rumen surface was densely covered with club shaped papillae in bovines. Poonia., *et al*. [27] reported conical or tongue-shaped ruminal papillae in sheep. The shapes of the papillae included leaf-like, needle-like, end expansion, top branching and lateral branching, with the maximum length being 2.75 cm. Laxmishree., *et al*. [28] reported that the goat rumen mucosal surface was uneven due to the presence of varying sized spatula shaped papillae, although smaller papillae were also present. These authors noted that the cow rumen mucosa possessed three types of papillae - elongated filiform, short conical and short fungiform - whilst the buffalo had two types - long foliaceous and blunt conical. Large conical, tongue shaped papillae were recorded by Rajani., *et al*. [20] in Indian Spotted Chevrotain which were large in the dorsal sac, in the ventral sac and in the caudo-ventral blind sac. Bello., *et al*. [13] found that, in Red Sokoto goats, the length of the greater curvature increased from 29.01 ± 1.41 cm at 0-6 months to 58.0 ± 1.65 cm at over 3 years of age, while the length of the lesser curvature increased from 23.5 ± 3.53 cm at 0-6 months to 52.1 ± 5.65 cm at over 3 years of age. Also, the width of the rumen was 15.4 ± 1.69 cm at 0-6 months, increasing to 29 ± 6.15 cm at over 3 years of age.

Histogenesis of digestive tube

Franco., *et al*. [29] in sheep at 23-29 days, Gracia., *et al*. [30] in goat at 35 of gestation noticed that the wall of the digestive tube was made of internal epithelium and external pluripotential blastemic tissue. Mc Geady., *et al*. [2] described that the primitive gastric tube was composed of epithelium derived from endoderm and the pleuripotent blastemic tissue derived from mesoderm. Molinari and Jarquera [31] and Gupta., *et al*. [32] in goat at 28 and 38 days, respectively; *Vivo*., *et al*. [33] in cattle at 30 days and Singh., *et al*. (34 2012a) in buffalo at 53 days described three layers, namely, epithelium, pleuripotent blastemic tissue and serosa (Figure 9, 10). Franco., *et al*. [29] and Gracia., *et al*. [30] also observed these three layers of wall of digestive tube at 34 and 38 days of gestation in sheep and goat, respectively. The epithelium was mostly columnar in shape along with some cuboidal cells, with elongated or spherical nuclei that were located towards the apex. The nuclear chromatin was evenly scattered and condensed, and the cell boundaries were indistinct. The infranuclear zone was either lightly eosinophilic or pale. The nuclei of the cells from the upper layer were elongated and situated towards the base [29,30,35]. At 32 days of gestation in sheep pleuripotent blastemic tissue contained diversely shaped mesenchymal cells, ground substance, blood vessels, and immature red blood cells [29]. The stomach wall of the goat was encompassed by a single layer of squamous cells, the mesothelium, which presented as flat cells with rounded nuclei [32,35]

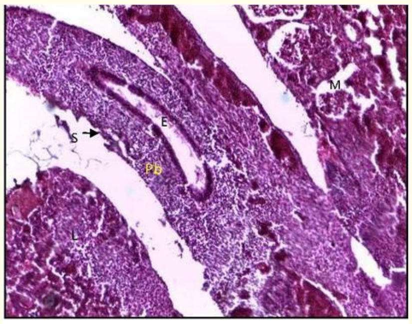

Figure 9: Photograph of 32-day old goat foetal stomach showing undifferentiated stratified epithelium (E), pleuripotent blastemic tissue (Pb) and serosa (S) of stomach, liver (L) and mesonephros (M). H and E X 100.

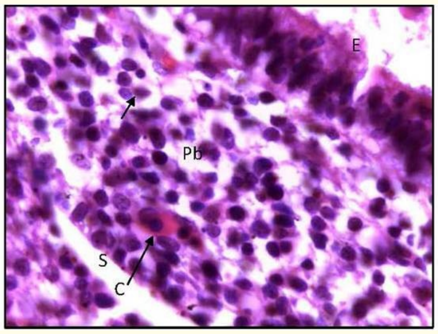

Figure 10: Photograph of 32-day old goat foetal stomach showing epithelium (E), pleuripotent blastemic tissue (Pb), serosa (S), capillary (C) and differentiating mesenchymal cell (arrow). H and E X 1000.

Histogenesis of Rumen

Histo-differentiation of rumen took place at 33 days in sheep [29], 35 and 38 days in goat [30,35] Gupta., *et al.* [36] described that the wall of foetal rumen was made up of three strata i.e., epithelium, pleuripotent blastemic tissue and serosa up to 49 days of foetal age and definite four layers of the wall viz., epithelium, propria-submucosa, tunica muscularis and serosa were observed first at 51 days of gestation. Whereas, Patra [8] described that the four distinct layers were present from 32 days of foetal life in sheep.

Tunica mucosa

Franco., *et al.* [29] in sheep at 32 days of gestation, Singh., *et al.* [34] in 53 days old buffalo and Gracia., *et al.* [30] and Gupta., *et al.* [35] in 38 day goat foeti reported two distinct basal and the superficial zones within the rumen epithelium (Figure 11). The cells in the basal zone were anucleated and had lightly stained cytoplasm [29]. Singh., *et al.* [34] in buffalo and Gupta., *et al.* [35] in goat observed that the basal zone was darkly stained while the superficial zone was lightly stained. The cells of the deepest layer were cuboidal to columnar in outline with vesicular spherical or elongated shaped nuclei placed centrally or apically. The cells of the other layers of the basal zone were either low columnar or polyhedral in shaped and had vesicular spherical or round shaped nuclei Singh., *et al.* [34] in buffalo, Gupta., *et al.* [32,35] in goat and Patra [8] in sheep reported a reduction in the number of layers of the basal zone with increasing age. Gupta., *et al.* [32,35] also noted a reduction in the height of the cells, which varied from 7.53 ±0 .01 μm to 5.96 ± 0.65 μm between 0-50 days and 101 to 150 days of gestation respectively. This is likely due to the accommodation of the different layers of the rumen.

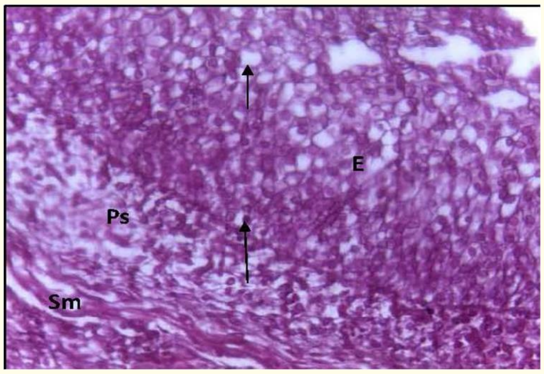

Figure 11: Photograph of 38-day old goat foetal rumen showing ruminal epithelium (E), propria-sub mucosa (Ps), differentiating smooth muscle cells (Sm) and arrow showing vacuolation in epithelial cells. H and E X 400.

Franco., *et al.* [29] in sheep noticed distinct stratum corneum, stratum granulosum, and indistinct lucidum spinosum layers between 53-79 days of gestation. Gracia., *et al.* [30] reported the presence of stratum basale, stratum granulosum, stratum spinosum, and stratum corneum between 76-112 days of gestation in goat foetal rumen. Singh., *et al.* [34] observed centrally placed nuclei in the cells of middle layer of the superficial zone in buffalo, and eccentrically placed nuclei in the basal layer. At 120 days, keratohyline granules were noticed and at 160 days of gestation, the uppermost layer was comprised of flat cells. The eccentric location of nuclei was correlated with absorption [37]. Gupta., *et al*. [35] noted that from 38 days of gestation in goat, the cells of the superficial zone were polygonal in shape, with distinct and highly eosinophilic cell boundaries (Figure 11). The cells of central zone became columnar in shape with a cytoplasmic process at their apical end from 87 days onwards. Eventually, condensation of cytoplasm took place, and the formation of future stratum spinosum was observed. Flattening and desquamation of the upper layer cells were noticed from 101 days of gestation and few cells of the topmost layer had lost their nuclei and had highly eosinophilic cytoplasm. Stratum corneum was reported at 145 days of gestation, in which only the 1-2 upper layers of the superficial zone were involved (Figure 12). The commencement of cornification implies that the ruminal epithelium acts as a protective layer against the potential sharp fibers consumed by adult animals [38]. The presence of clear vacuolated cells in the epithelium enables the transfer of electrolytes, water, and short chain fatty acids [39]. The number of cell layers of superficial zone increased with progression of age [35].

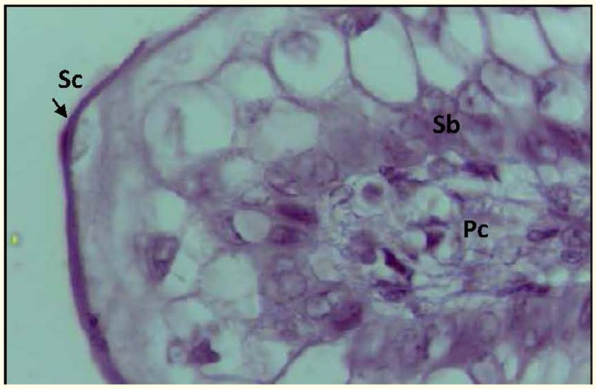

Figure 12: Photomicrograph of section of 145 days of ruminal papilla 'R" showing stratum basale (Sb), stratum corneum (Sc) and core of the papilla (Pc). H and E X 1000.

Ruminal papillae

The formation of ruminal papillae was noticed as evagination of cells of stratum basale towards the lumen at 61 and 48 days of gestation in sheep [8,29], 4 months of gestation and 22.4 cm CRL in foetal buffalo [2,34] and 76 and 51 days of gestation in goat [30,32,35] (Figure 13 and 14). Ramakrishna and Tiwari [40] in goat discovered ruminal papillae late at 126 days of gestation. Vivo., *et al*. [33] identified these papillae shortly before the term in bovine. Gracia., *et al*. [30] observed that in goats, the ruminal papillae had grown to half the height of the epithelium after 76 days. Panchamukhi and Srivastava [41] and Singh., *et al*. (34) also reported similar views regarding papillae in buffalo, though the foetuses were of different ages. Crecenteric, cylindrical, and tongue-shaped ruminal papillae were observed in sheep at 61 and 103 days of gestation, respectively [29,42] and in goat at 76, 112, and 145 days of gestation, respectively [32,35] (Figure 15). The number of layers in the basal zone was greater at the origin of the papillae and decreased as it progressed to the sides and tip. As the gestation advanced, the height and number of papillae increased, while the interpapillary distance decreased. At term, the tip of the papillae was close to the luminal surface of the epithelium. The core of the ruminal papillae was comprised of the lamina propria components including maturing fibroblasts, differentiating mesenchymal cells, connective tissue fibers and blood capillaries [35] (Figure 12). As gestation progressed, some mesenchymal cells converted to fibroblasts and vascularization in the papillae core also intensified. The height and width of rumen papillae were -192.1 ± 2.0 and 59.0 ± 5.1μm respectively for full term foetuses of West African Dwarf goat [43].

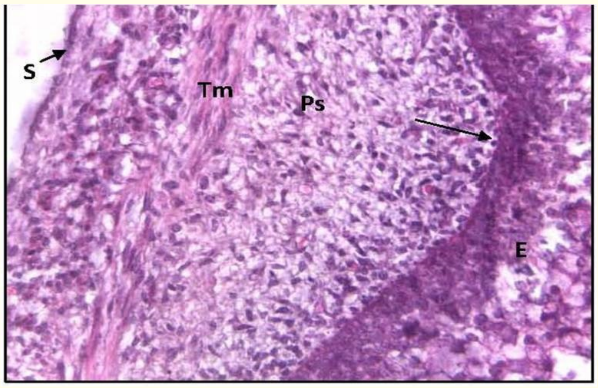

Figure 13: Photomicrograph of section of 76-day old goat foetal ruminal wall showing formation of ruminal papilla (arrow), epithelium (E), propria submucosa (Ps), tunica muscularis (Tm) and serosa (S). H and E X 400.

Lamina propria submucosa

Through out the gestation the lamina propria and submucosa blended with each other without any line of demarcation to form propria- submucosa as lamina muscularis could not be observed (32, 35in foetal goat and 32, 40 in buffalo).

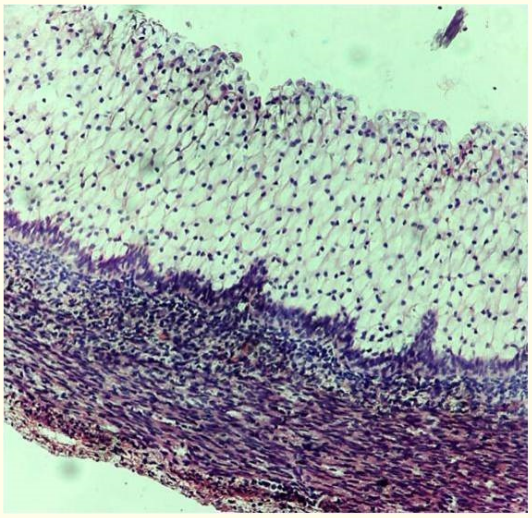

Figure 14: Photomicrograph of rumen of sheep foetus aged 75 days showing formation of ruminal papillae (Rp), inner circular (C) and outer longitudinal (L) layers of smooth muscle and serosa (S). Note the epithelial dome (arrow) at the luminal surface and apical eosinophilia of the superficial zone (SZ). H and E × 100.

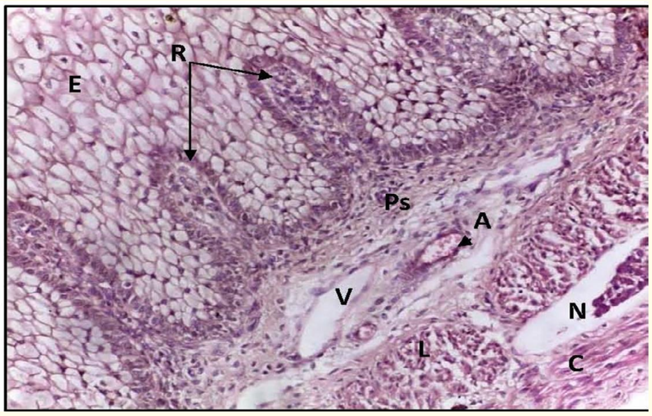

Figure 15: Photomicrograph section of 134-day old goat foetal ruminal wall (dorsal sac) showing ruminal papillae (R), epithelium(E), propria -submucosa (Ps), neuronal element (N), serosa (S), artery (A), vein (V), inner longitudinal (L) and outer circular (C) arrangement of smooth muscle bundles of tunica muscularis. H and E X 200.

At the beginning of prenatal life, three layers of the wall of the gastrointestinal tract-the lamina propria, submucosa, and tunica muscularis were not separate entities and were instead classified as pleuripotent blastemic tissue. This tissue was made up of undifferentiated mesenchymal cells and had a high concentration of ground substance (Figure 10 and 11). The mesenchymal cells were spindle-shaped with vesicular, spherical, or oval-shaped eccentrically or centrally placed nuclei. The cytoplasm of these cells was pale. Panchamukhi and Srivastava [40] observed that the lamina propria was thin and faintly colored while the submucosa was darker and more densely populated with cells. Whereas, Gupta., *et al*. [32], at 38 days of gestation in goats, observed that the area below the epithelium was darker and had more cells while the deeper region was diffusely populated and had more ground substance (Figure 11). Differentiating myocytes were noticed in the pleuripotent blastemic tissue in sheep at 30-32 days of gestation [29] and in goats at 38 days of gestation [30,32]. Gupta., *et al*. [32] reported that between 44-46 days of gestation in goats, the number of differentiating smooth muscle cells increased (Figure 16). The cells had vesicular nuclei that were centrally placed and spindle shaped, with more eosinophilic cytoplasm. After 48 days of gestation, the process of proliferation of smooth muscle cells was enhanced, forming clusters of 3-4 cells that were directed obliquely, longitudinally, or circularly. This differentiating tunica muscularis was well-supported by a capillary network, and isolated reticular fibrils were seen surrounding the clusters of smooth muscle cells from 46 days of gestation. The authors also reported the presence of differentiating plasma cells between 38-49 days of gestation. These plasma cells showed cytological characters that were identical to those of adult plasma cells. In 2012, Singh., *et al*. studied the presence of neuronal elements and blood vessels close to the serosa in 19.6 cm CRL buffalo foeti, while Gracia., *et al*. [30] observed nerve tissue at 113-150 days of gestation in foetal goats. Gupta., *et al*. [35] revealed the existence of neuronal elements at 38 days of gestation in the vicinity of differentiating myocytes. At 46 days of gestation, these neuronal elements had two distinct types of cells. Type I, ganglionic cells, were large, spherical to ovoid in shape, featuring an indistinct contour, evenly distributed nuclear chromatin and lightly stained cytoplasm. Type II, supporting cells, were smaller, having an obscure cell boundary, a spherical nucleus with darkly stained chromatin and pale cytoplasm (Figure 16). At this stage, they were found in a disorganised state. Later on neuronal elements were present either between the tunica muscularis and serosa or in between the muscle bundles (Figure 15). The presence of nerve elements between smooth muscle bundles is essential for controlling the contraction of the muscles and secretion of digestive substances. The myenteric plexuses could not be observed in the ruminal wall of the sheep foeti upto 63 days of gestation. It appeared first at 67 days of gestation as a diffusely aggregated mass of neuroblasts and neuroglia cells between the inner and outer layers of smooth muscles [8].

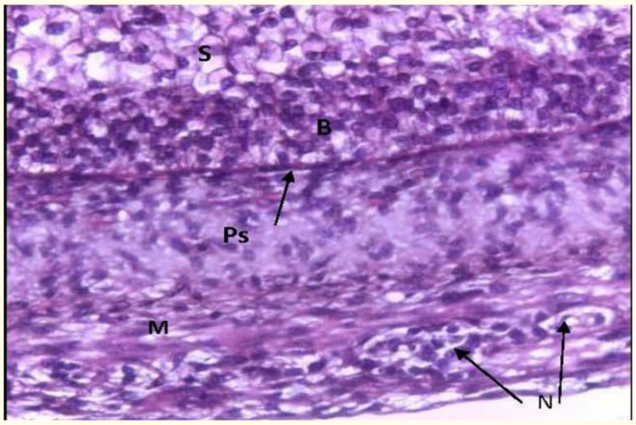

Figure 16: Photomicrograph of section of 44-day old goat foetal ruminal wall showing basal (B) and superficial zones (S) of epithelium, propria-submucosa (Ps), differentiating myocytes (M), nerve elements (N).

Singh., *et al*. [32] first reported the presence of collagen fibers in the 5.5 cm CRL buffalo foetal rumen in the deeper part of propria submucosa, which eventually became fully differentiated at 20.1 cm CRL. Additionally, Franco., *et al*. [29] in sheep, and Gracia., *et al*. [30] and Gupta., *et al*. [32] in goat all reported the presence of loosely arranged elastic and collagen fibers along with blood vessels and submucosa near term and around nerves in the serosa (Figure 18). Moreover, Gupta., *et al*. [32] in goat rumen noted that reticular fibrils became coarser and their concentration increased towards the submucosa from 60-70 days, and isolated thin collagen fibrils and elastic fibers were found around the blood vessels from 112 days of gestation onwards (Figure 19). Furthermore, Gracia., *et al*. [30] and Gupta., *et al*. [32] in goat recorded that the thickness of propria submucosa decreased with age.

Tunica muscularis

Observation of the differentiation of lamina propria submucosa and tunica muscularis from pleuripotent blastemic tissue was documented in various studies. At 33 days of gestation in cattle [33] and 33 and 32 days of gestation in sheep [8,29] and at 49 days of gestation in goat [30,32] the separation of these components from the pleuripotent blastemic tissue was first recorded. Panchamukhi and Srivastava [40] and Franco., *et al*. [29] revealed that smooth muscle cells were arranged in bundles and oriented in different directions with capillary networks and connective tissue elements in between them. The pattern of orientation of smooth muscle fibers were not constant during entire gestation [35]. In buffalo foeti, circular smooth muscle fibers were observed at 1.5 cm CRL while longitudinally directed fibers were observed at 3.2 cm CRL. In sheep, at 57 days of gestation, inner circular and oblique and external longitudinally oriented muscle fibers were noted, with the fibers of external bundles being long and thin. The inner circular and outer longitudinal arrangement of tunica muscularis in bovine foetus was noticed by Roy [4] at 53 days of gestation. Gracia., *et al*. [30] and Gupta., *et al*. [32,35] in goat foeti and Singh., *et al*. [32] in buffalo foeti also confirmed this arrangement of smooth muscle fibers. As the foetus develops, the length of the fibers as well as the length of their nuclei increased. The cytoplasm of the muscle cells is more eosinophilic than other mesenchymal cells and the nuclei start off as oval or spherical before becoming elongated or spindle-shaped. In goats, at 94 days of gestation, the smooth muscle fibers of the rumen were arranged in an inner longitudinal and outer circular pattern in the dorsal sac, while the orientation was reversed in the ventral sac [32,35]. By 112-118 days gestation, the smooth muscle fibers of the dorsal sac had become transverse and longitudinal, and the orientation was reversed in the ventral sac. In addition, oblique fibers were seen between these two types of muscle bundles. Singh., *et al*. [32] reported the presence of connective tissue elements and blood vessels between smooth muscle bundles in the terminal stages of gestation in buffaloes. Such connective tissue and blood capillaries are necessary to provide strength and nutrition to the smooth muscle cells [38]. Gupta., *et al*. [35] observed reticular fibers between muscle bundles which branched and became coarser with time. The author noticed thin collagen fibrils between the smooth muscle bundles and around blood vessels between the 69th and 87th days of gestation, which became wavier and denser at 112 days (Figure 18). Moreover, isolated elastic fibers were found between the smooth muscle bundles from 112 days onward. Panchamukhi and Srivastava [40] in buffalo, and Gracia., *et al*. [30] and Gupta., *et al*. [35] in goat, reported that the thickness of the tunica muscularis increased with age. Gupta., *et al*. [35] further found that the thickness of the tunica muscularis was higher in the ventral sac than the dorsal sac, which may be because of the rising pressure from the digestive viscera and ingesta. The tunica muscularis has been associated with the mechanical mixing of ingesta and the expulsion of gas through eructation, contraction, and regurgitation.

Ruminal pillar

Rudimentary ruminal pillars were present in cattle, sheep and goat at 44, 42, 46 and 38 days of gestation, respectively [29,30,33,35]. The ruminal walls were evaginated towards the lumen with all layers participating in the formation of the pillar [35,43] (Figure 17). The pillar was composed of a core of muscle from the tunica muscularis [43]. In foetal goats the core of the ruminal pillar was made up of loosely-arranged mesenchymal cells, unchanging fibroblasts and scattered undeveloped RBCs [35] (Figure 17). Myocytes which had begun to differentiate were oriented outwards from the tip of the ruminal pillar. Additionally, neuronal cells were also present in the core. As the animal grew, the connective tissue became thicker and coarser, accompanied by networks of reticular fibers and bunches of collagen fibers which surrounded the blood vessels. There was a small amount of propria-submucosa in the core and a larger amount of tunica muscularis and serosa (Figure 18-20). Initially, the tunica muscularis was situated in the middle of the core and as gestation advanced, its thickness increased in the middle and sides of the core, arranged in bundles which were held together by collagen, reticular fibers and capillaries. The main component of the ruminal pillar was tunica muscularis. *Vivo*., *et al*. (33) in cattle, Franco., *et al*. [29] in sheep and Gracia., *et al*. [30] and Gupta., *et al*. [32,35] in goat all concluded that the pillars were without ruminal papillae.

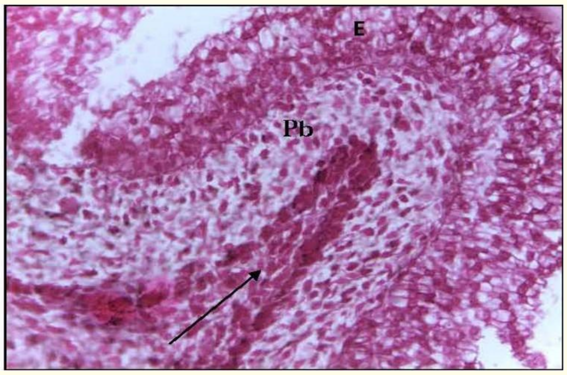

Figure 17: Photomicrograph of section of 38-day old goat foetal ruminal wall showing formation of ruminal pillar (arrow), epithelium (E) and pleuripotent blastemic tissue (Pb). H and E X 400.

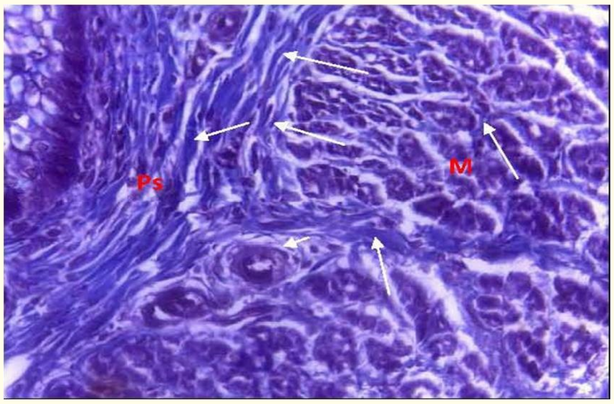

Figure 18: Photomicrograph of section of 145-day old goat foetal ruminal wall showing bundles of collagen fibers (arrow) in propria- submucosa (Ps) and in between muscle bundles (M). Masson's trichrome stain X 400.

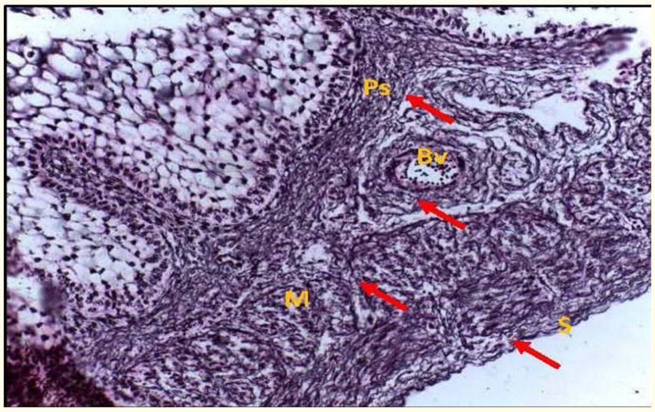

Figure 19: Photomicrograph of section of 134-day old goat foetal ruminal wall showing reticular fibers (arrow) in the form of rete in propria- submucosa (Ps), in between muscle bundles (M), around blood vessel (Bv) and serosa (S). Wilder's reticular stain 200X.

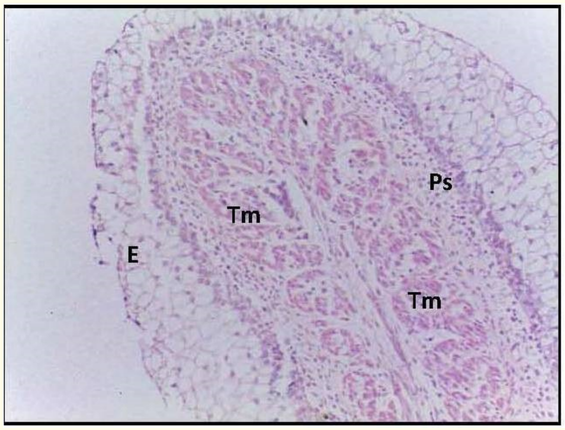

Figure 20: Photomicrograph of section of 134-day old goat foetal ruminal pillar showing epithelium (E), propria -submucosa (Ps) and smooth muscle bundles of tunica muscularis (Tm).H and E X 400.

Serosa

Gracia., *et al*. [30] and Gupta., *et al*. [35] reported that, in goats, the serosa was present at 58 and 38 days of gestation, respectively. At this time, the mesothelium was surrounded by a single line of differentiating squamous cells, as well as loose vascular connective tissue, collagen, reticular and elastic fibers (Figure 19). Roy [4] in bovine, and Gracia., *et al*. [30] and Gupta., *et al.* [35] in goats, reported that these structures were well-developed at 53 and 58, and 51 days of gestation, respectively. The presence of these components helped to protect the stomach from friction, as the serosa secreted a thin watery secretion known as fluid. Further, Gupta., *et al*. [35] observed two types of neuronal cells surrounded by connective tissue fibers in goats. The thickness of the tunica serosa varied from 117.7 ± 17.8 to 24 ± 4.4 µm (29 in sheep). However, Gupta., *et al*. [35] reported reverse data, with a thickness ranging from 5.2 µm to 11.39 ± 1.15 µm.

Post natal histology of rumen

The mucosa of the rumen was lined by stratified squamous keratinized epithelium [21,45-47]. This non-glandular mucosa of sheep is characterized by a rich subepithelium vascular plexus [27]. Mahesh., *et al.* [48] noted that in goats, the dorsal and ventral walls of the rumen were lined by stratified squamous keratinized epithelium that possessed varying numbers of rows in the strata basale, spinosum, granulosum, and corneum. Further, the stratum corneum formed a protective shield against the rough and fibrous ingesta, while the deeper layers' cells were responsible for metabolizing short-chain, volatile fatty acids. Laxmishree., *et al*. [28] in goat reported that the epithelium was comprised of 4-6 layers for the stratum basale to stratum granulosum and 3-4 flat layers in the stratum corneum. The stratum corneum of the mucosa of rumen varies in thickness, ranging from one to two cells to as many as ten to twenty cells with stainable nuclei [45-47]. The lamina epithelium is composed of a thin layer of stratified squamous epithelium, and the stratum corneum is usually one to two layers thick and lacks nuclei [49]. Nwaogu and Ezeasor [42] in West African Dwarf goats observed that the ruminal papillae were tiny and covered by thin keratin layer in 4- week-old neonates. They were very tall especially in the ventral ruminal sac and the epithelium covered by thick keratin in adult goats. The height and width of rumen papillae were 358.0 ± 11.4 and 210.5 ± 14.3µm respectively in 4 week old neonate. In adult goat The papillae were very tall especially in the ventral rumen sac and tunica muscularis had increased thickness. The dorsal rumen sac contained short but wider rumen papillae when compared with those of the ventral sac. The height and width of rumen papillae were 1630.0 ± 19.5µm and 283.0 ± 30.0µm respectively. Laxmishree., *et al*. [28] observed in goat rumen that the cells of the stratum corneum had elongated, darkly stained nuclei, and more eosinophilic cytoplasm than the cells of the stratum granulosum. The superficial cells were highly keratinized which provide physical protection from the potentially sharp fibers consumed by animals. The stratum granulosum is usually one to three cells thick and its cells possess distinct flattening and keratohyalin granules in the peripheral cytoplasm [46,49]. Cells near the stratum corneum are often swollen with pyknotic nuclei and contain clear, electro lucent cytoplasm [28]. The stratum spinosum is one to ten cells thick and contains polyhedral cells which are larger than the basal cells [46,49]. In 2017, Laxmishree., *et al*. [28] conducted an examination of goat rumen and determined that the cells of the stratum spinosum and stratum granulosum were so intermixed that they could not be differentiated from each other. The cytoplasm was eosinophilic and granular, while the round to oval nuclei had a fine chromatin material dispersed throughout the nucleoplasm. Nucleoli were located centrally or eccentrically. The stratum basal was lined by a single cuboidal layer and its cellular features were comparable to those of the stratum spinosum. Also, these cells extended multiple processes to the basement membraneas reported previously [45,46,49]. The stratum basale of the intestine was distinct and comprised of simple cuboidal to low columnar epithelial cells with less eosinophilic cytoplasm and basophilic nuclei [28]. Multiple small folds forming papillary bodies or pegs were observed in lambs [27]. These papillary bodies could reduce the distance between the mucosal surface and the absorptive site, and thus increase the absorptive area by expanding the external surface of the epithelium., papillary bodies or pegs were found in the basal layer of the epithelium in calves, adult goats, and lambs; these formations reduce the distance between the mucosal surface and the absorptive site, and also increase the absorptive area by increasing the external surface of the epithelium.

In goats, the lamina propria is composed of dense connective tissue, which forms the core of the ruminal papillae. At the junction between the lamina propria and submucosa, a layer of condensed connective tissue can be found, as lamina muscularis is absent. The submucosa is composed of loose connective tissue and forms the core of the papillae, and contains large blood vessels. The absence of lamina muscularis in ruminants made lamina propria and submucosa blend together to form propria submucosa [21,45,46]. This layer is made up of a dense network of collagen, reticular and elastic fibers, and is loosely arranged near the tunica muscularis. Additionally, the propria submucosa contains a rich network of blood vessels and submucosal nerve plexus. Poonia., *et al*. [27] reported that in sheep, the lamina propria and submucosa have a mixed distribution of collagen, elastic and reticular fibers, with the core of the papillae being composed of loose connective tissue. Lamina muscularis was absent except for at the oesophageal ruminal junction, where it was thin and interrupted. The propria submucosa in goats is made up of loose, irregular connective tissue and comprises collagen, reticular and elastic fibers [49].

The tunica muscularis of the ruminants particularly goats has been reported to comprise of inner circular and outer longitudinal layers of smooth muscle, with the myenteric plexus and ganglia situated in between them [45-48]. However, Ramakrishna and

Gadre [49] in goat rumen noticed that the tunica muscularis was formed by two or three layers of striated muscles arranged as inner circular and outer longitudinal directions, or inner oblique, middle circular and outer longitudinal layers. Poonia., *et al.* [27] in sheep observed thick inner circular and thin outer longitudinal muscle layers, and a third layer of striated oblique muscle at the oesophageal-ruminal junction.

Dellman and Brown [45] and Eurell and Frappier [46] described that the serosa of the rumen was composed of loose connective tissue covered by mesothelium. Additionally, this tissue was observed to have varying amounts of white adipose tissue, as well as blood and lymph vessels, and nerves. The ruminal serosa of goats was especially rich in adipose tissue, located in the ruminal groove [49]. Furthermore, Ghose [47] described that the serosa was covered by mesothelium and comprised of collagen and elastic fibers, blood and lymph vessels, and some amount of fat.

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