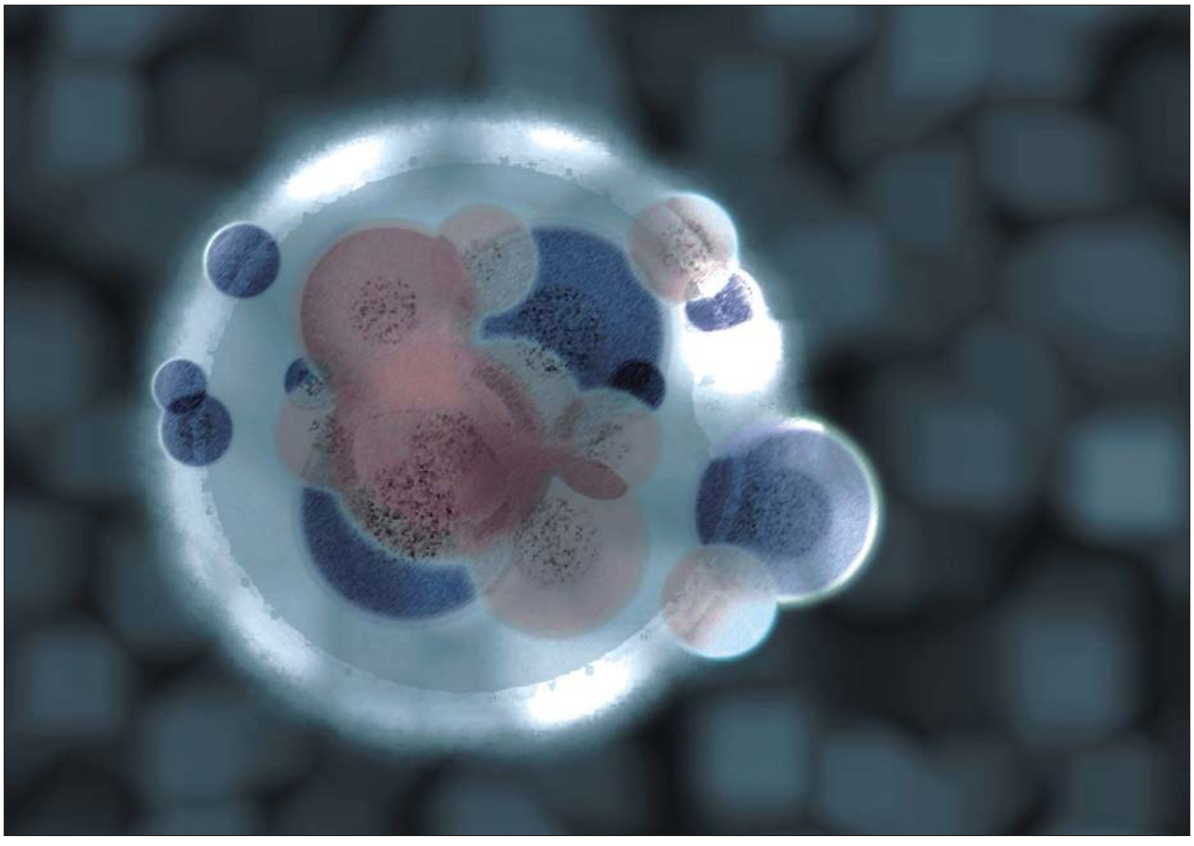

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Macroscopic and Microscopic Anatomy of the Omasum of the Baladi Goat

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Abstract: Scanning and transmission electron microscopy were used to study anatomical and histological features of the omasum in Baladi goats. Omasal laminae were arranged in four or five orders and varied by shape, distribution and direction of papillae. Spaces were present in the interpapillary and papillary surfaces of the omasal laminae as well as at the tips of some conical papillae. The omasal epithelium was keratinized stratified squamous consisting of four strata basalis; spinosum; granulose and cornum. Cells in the stratum basalis contained mitochondria and free ribosomes and had finger-like cytoplasmic processes that connected with neighboring cells via desmosomes. The stratum spinosum was rich in tonofilaments, free ribosomes and cisternae of rough endoplasmic reticulum (rER). The cytoplasm of cells in the stratum granulosum was marked by keratohyalin granules of varying sizes with electron-dense contents. The stratum corneum consisted of several layers of flat, elongated cornified cells with varied cellular constituents.

Key words: Omasal morphology, omasal papillae, Baladi goat, scanning electron microscopy, transmission electron microscopy

INTRODUCTION

The Baladi goat is highly adapted to selectively graze among a wide variety of vegetation. Browse appears to be an important component in the diet of goats, which are regarded as the best users of poor roughage among ruminants (Gihad *et al*., 1980). Comparative morphological studies of the digestive tracts of ruminants indicate that the forestomach and in particular the omasum, structurally adapts to the type of feed the animal ingests (Hofmann, 1982). On this basis, the feeding habits of ruminants have been classified into three groups: grass eaters (bovine), concentrated herbage eaters (deer) and intermediate feeders (sheep and goats) (Hofmann, 1973). The omasum contains many parallel laminae of varying sizes, which are composed of thin muscular layers and covered by non-glandular mucous membrane with numerous papillae on their surface (Yamamoto *et al*., 1994).

The epithelial linings of the different forestomach compartments (rumen, reticulum and omasum) have similar ultrastructures (Hyden and Sperber, 1965). The forestomach epithelial mucosa of grey, white and black karakul lambs consists of a stratum basalis, stratum spinosum and stratum corneum. Furthermore, in grey and white lambs, the luminal cells of the stratum corneum are electron-dense, non-nucleated and vacuolated (Groenewald, 1993). The cytoplasm of cells in the stratum granulosum of the ovine rumen is electron-dense and contains, in addition to the nucleus, tonofibrils, keratohyalin granules, membrane-coated vesicles and mitochondria (Lavker *et al*., 1969; Henrikson, 1970). In the bovine rumen, Graham and Simmons (2005) reported that cells of the stratum granulosum contain developing cytoplasmic keratohyalin granules. The spiny cells of the stratum spinosum in both goats and cattle are arranged in two layers, called the parabasal and superficial cells. The parabasal cells border the basal layer and are nearly polygonal, with large rounded nuclei and wide intercellular spaces. The superficial cells are small and more flattened, with very wide intercellular spaces (Schnorr and Vollmerhaus, 1967).

The cells of the stratum basalis are attached to the basal lamina by hemidesmosomes. In the rumen, their cytoplasm contains many ribosomes, mitochondria and tonofilaments (Lavker *et al*., 1969). Differences between domesticated ruminant species in voluntary feed intake per unit body weight may be influenced by the structure of the omasum (Kay *et al*., 1980). The present study was designed to determine the anatomical and histological specializations of the omasal surface of Baladi goat.

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MATERIALS AND METHODS

Macroscopic anatomy: The omasa of eight adult Baladi goats of both sexes were collected from the local abattoirs. Animals ranged in age from 1 to 1.5 years old, but were all non-pregnant and of roughly the same body size. The organs were collected immediately after slaughter. The wet tissue weight was determined with and without content and the volume was measured with water fill. Number, arrangement, distribution, size and shape of the various orders of laminae were assessed. The greater and lesser curvatures were also measured. Two organs were frozen until ready for cross-sectioning, at which time, the ingesta was removed.

Scanning electron microscopy: Small specimens were cut from the following regions of the omasal lamina: reticulo-omasal, middle, omaso-abomasal and omasal groove. Sections were immediately immersed in a fixative (2% formaldehyde, 1.25% glutaraldehyde in 0.1 M sodium cacodylate buffer, pH 7.2) at 4°C. Once fixed, the samples were washed in 0.1 M sodium cacodylate containing 5% sucrose, processed through tannic acid and finally dehydrated in increasing concentrations of ethanol (15 min each in 50, 70, 80, 90, 95 and 100% ethanol). The samples were then critical-point dried in carbon dioxide, attached to stubs with colloidal carbon and coated with gold- palladium in a sputtering device. Specimens were examined and photographed with a Jeol scanning electron microscope operating at 15 Kv. Faculty of science, Alexandria University.

Transmission electron microscopy: Samples of 1 mm^3 were cut from omasal laminae in the following regions: reticulo-omasal, middle, omaso-abomasal and omasal groove. Samples were immediately fixed in a 6% solution of phosphate-buffered glutaraldehyde, pH 7.4, at 4°C for 6 h (McDowell and Trump, 1976). After initial fixation, tissues were washed in several changes of cold (4°C) 0.1 M phosphate buffer every 15 min for 2 h. Samples were then rapidly dehydrated through increasing concentrations of ethanol, transferred to propylene oxide and placed overnight in a 1:1 mixture of propylene oxide and epoxy araldite (Hayat, 1986). Semi-thin sections (1 mm) were first cut and stained with toluidine blue and viewed with light microscopy to specify areas suitable for transmission electron microscopy. Ultrathin sections (60-100 nm) were then cut by a glass knife with an L.K.B. microtome and stained with uranyl acetate followed by lead citrate (Hayat, 1986). The ultrathin sections were examined with a Jeol transmission electron microscope operating at 100 Kv. Faculty of Science, Alexandria University.

RESULTS

Macroscopic anatomy: The omasum is a muscular bean-shaped tube with two curvatures and two extremities. On average, the convex greater curvature measured 17.52 cm in this study, while the concave lesser curvature measured 4.36 cm (1, A, 3 and 4). The reticular extremity of the omasum, which constricts to form the neck and communicates with the reticulum, measured 1.5 cm in length. The abomasal extremity is continuous with the abomasum. The dorsoventral diameter at the middle of the omasum measured an average of 10 cm in length and 5 cm in width. The wet weight of the omasum with and without contents averaged 150.31 and 70.82 g, respectively. The omasal volume, as determined by water fill, was 85 mL on average.

The interior of the omasum is characterized by numerous crescent-shaped longitudinal laminae with ingesta packed closely between them. The omasal laminae could be classified into four orders in most specimens. In two specimens, rows of small, flattened, dome-shaped papillae were present, which may have been the remnant of 5th-order laminae (Fig. 2, 5). On average, we counted 64 laminae, which were subdivided into groups of 8, 8, 16 and 32 for the 1st, 2nd, 3rd and 4th-order laminae, respectively. The number of 5th order laminae was 50 on average. There was also a defined sequence in the arrangement of the various orders, which followed a pattern of 1, 4, 3, 4, 2, 4, 3, 4, 1, 4, 3, 4, where 1, 2, 3 and 4 represent laminae of decreasing heights (Fig. 2). The 1st-order laminae were the tallest, measuring 4.1 to 5 cm. These laminae were pedunculated at their top insertions and partly occluded the reticulo-omasal orifice. The pedunculated bases measured 2 to 2.5 cm in length and 0.4 cm in height (Fig. 1, 6 and 2, 7). The 2nd-order laminae, which were also pedunculated, were measured to be 2.3 to 2.8 cm in height and inserted about 0.7 to 1 cm below those of the 1st order. The 3rd-order laminae were 0.5 to 0.8 cm in height and inserted 0.9 to 1.3 cm below those of the 2nd order. The 4th-order laminae inserted 1.4 to 2 cm below the 3rd order, but their heights varied from 0.2 to 0.3 cm to a line of conical and dome-shaped papillae that were close to each other (Fig. 2, 4). The omasal groove, which connects the reticulo-omasal and omaso-abomasal orifices along the lesser curvature, measured about 2.5 to 3.4 cm in length and 1.6 to 2 cm in width. The omasal groove was bordered on each side by lateral folds with large conical papillae (Fig. 2, 10 and 3, 7).

Scanning electron microscopy: The omasal surface was characterized by papillae that were regionally distributed in various patterns. There were no significant differences in papillar shape among the 1st, 2nd and 3rd orders of

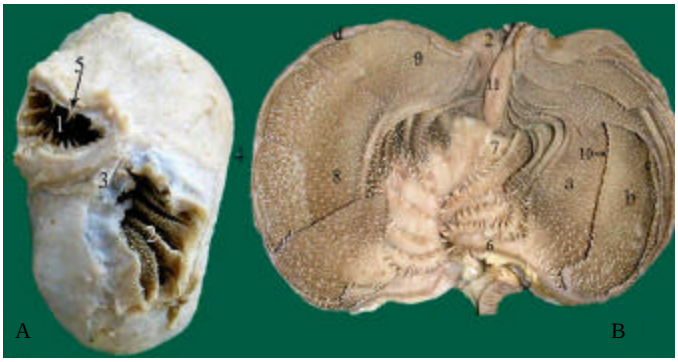

Fig. 1: A light photograph of the omasum of goat (A. closed B. opened by sagittal section).1. Reticulo-omasal orifice, 2. Omaso-abomasal orifice, 3. lesser curvature, 4. greater curvature, 5. large conical papillae, 6. Pedunculated base, 7. Omasal groove, 8. Conical and hooked papillae, 9. dome-shape papillae, 10. Free border of laminae, 11. Vela abomasica and a, b, c, d were 1st, 2nd, 3rd and 4th order laminae

Fig. 2: A light photograph showing the cross sections in omasum at level of. (A) Reticulo-omasal orifice B andC. Lesser curvature D. Omaso-abomasal orifice 1, 2, 3 and 4 were 1st, 2nd, 3rd and 4th order laminae 5. remenant of 5th order laminae 6. Reticulo-omasal orifice, 7. Pedunculated base, 8.Bifid conical papilla, 9. Omasal groove, 10. lateral fold with large conical papillae, 11. Omaso-abomasal orifice, 12. Abomasum, 13. Small conical and hook papillae, 14. Dome shape papillae and 15. Vela abomasica

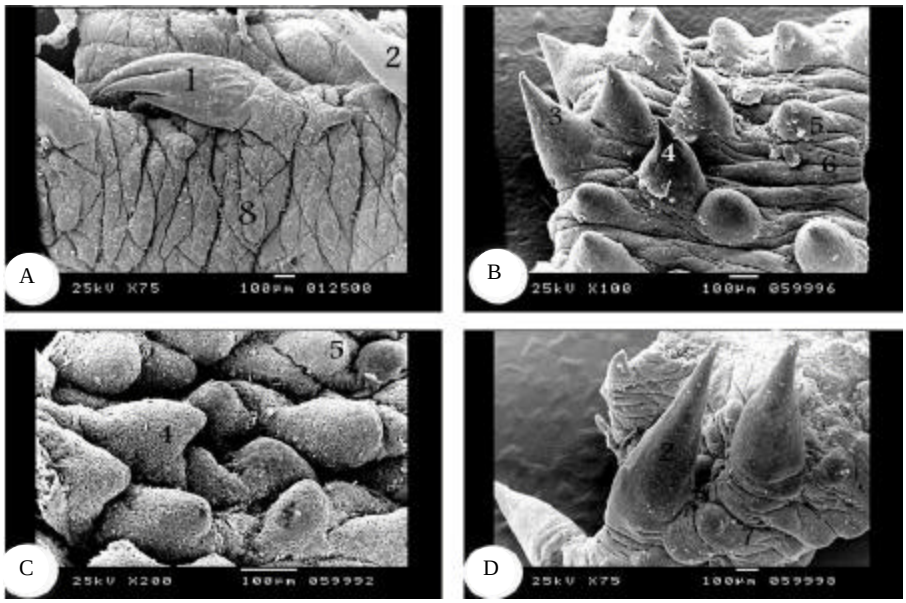

Fig. 3: Scanning electron micrograph of lateral surface of 1st laminae at (A) Reticulo-omasal orifice, (B) in the mid region near the border, (C) Omaso-abomasal orifice and (D) Omasal groove 1. Trifid large conical papillae (unguiculiform papillae), 2. large conical papillae 3. small conical papillae on free border, 4. hook papillae, 5. dome-shaped papillae, 6. Grooves, 7. Lateral fold of omasal groove and 8. Pedunculated base

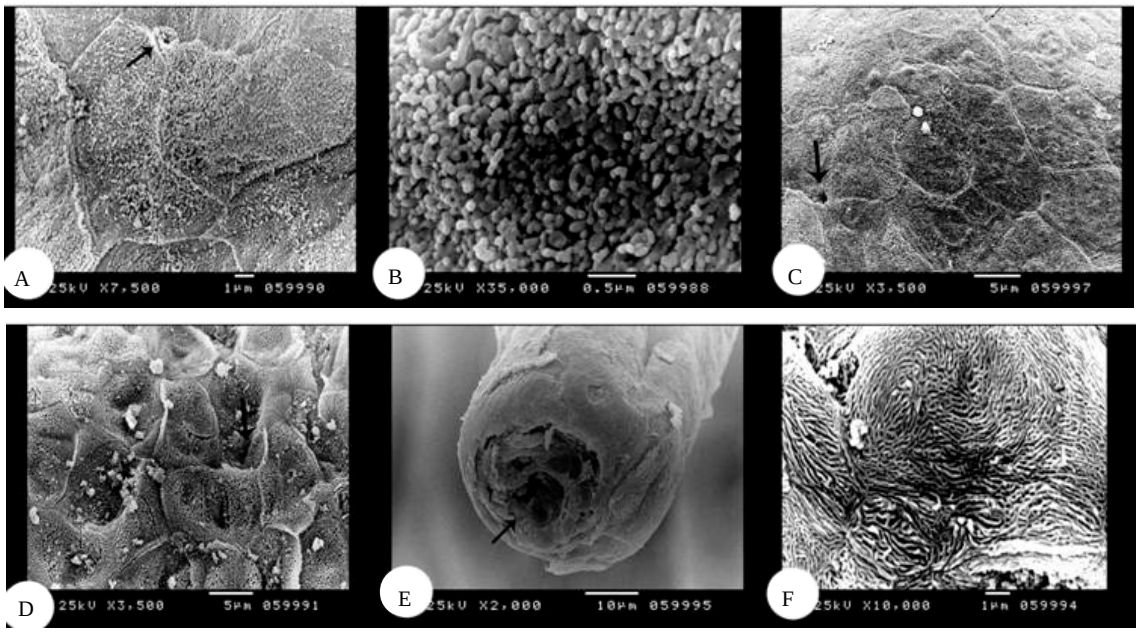

Fig. 4: Scanning electron micrograph showed the epithelium lining of omasum at (A) interpapillary surface mucosa of lamina formed by polygonal shaped cell with microplicae-like cytoplasmic protrusion, (B) and spaces (arrow), (C) Small conical appeared as the polygonal and oval cells with microplicae-like cytoplasmic protrusion and holes (arrow), (D) dome-shape papillae where epithelium appeared as nearly rectangular shaped with microplicae-like cytoplasmic protrusion and holes and (E) Tip of large conical papillae showing the superficial layers of the stratum corneum sloughing off and large hole (arrow) (F) large conical papillae appeared as flap-like in form concentric waves. Arrow refers to the spaces

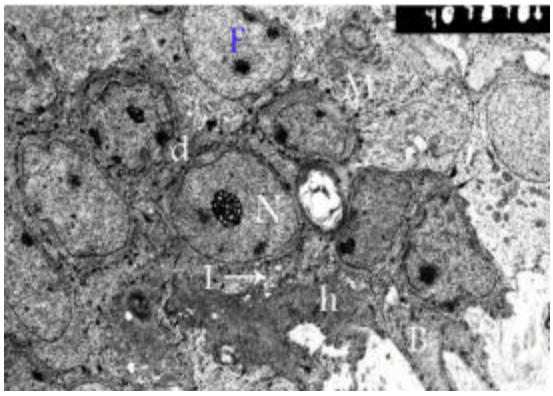

Fig. 5: Transmission electron micrograph of stratum basale cells depicting abundant mitochondria (M), numerous desmosomes d and finger like cytoplasmic processes in inter cellular spaces (I) nuclei (N) contained some mitotic figures (F) Basal lamina (B) hemi desmosomes (h) (x4,0000)

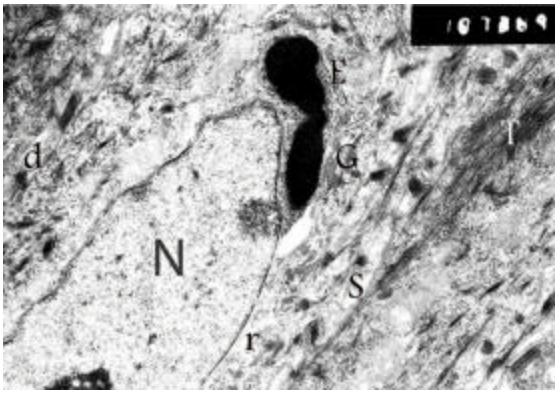

Fig. 6: A higher magnification of the previous photo showed numerous free ribosomes (r), rough endoplasmic reticulum (E) and Golgi complex (G). Tonofilament parallel to cell membrane (T). Note numerous desmosomes d inbetween neighboring cells .Nucleus N (X10.000)

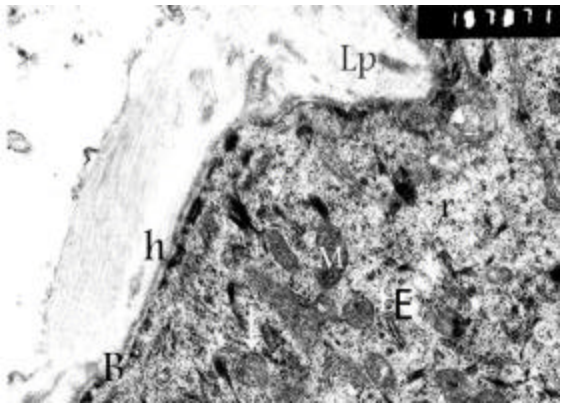

Fig. 7: Tangential section of basal portion of statum basale denoting dark staining mitochondria (M) with prominent cristae (arrow), free ribosomes (r) and rough endoplasmic reticulum (E). Note numerous hemidesmosoms (h) on the basal plasma membrane (B) Lamina propria (LP) (X 15.000)

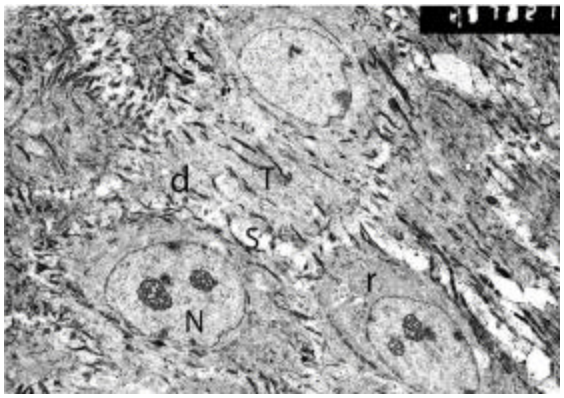

Fig. 8: Transmission electron micrograph of the upper cells of stratum spinosum cells denoting the relation among the tonofilaments (T), desmosomes (d), intercellular space (s) and free ribosomes (r). Nuclei (N) (X 2.500)

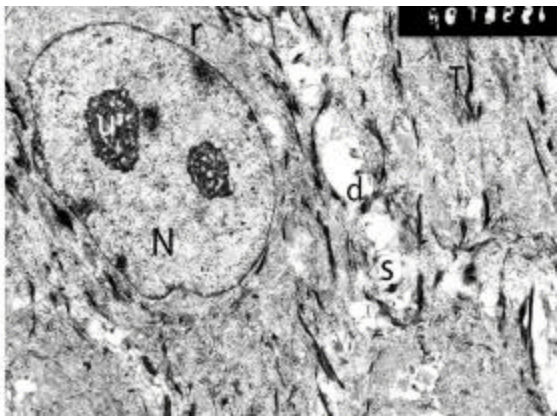

Fig. 9: A higher magnification of previous electron micrograph showing tono filaments (T), desmosomes (d) free ribosomes (r) and inter cellular space (s). Nucleus (N) nucleoli (u) (X4.000)

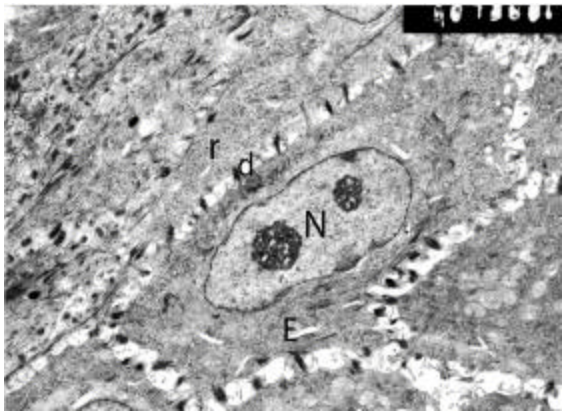

Fig. 10: Transmisson electron micrograph of the superficial spinosum cells illustrating desmosomes (d) in between neighboring cells, free ribosomes (r) and rough endoplasmic reliculum (E). Nucleus N (X 5.000)

omasal laminae. At the reticulo-omasal orifice, large keratinized conical papillae were commonly seen in the pedunculated bases of the 1st laminae. The largest of these papillae were forked into 2 or 3 processes and measured about 0.2-0.3 cm (unguiculiform papillae) (Fig. 3A1). These papillae were directed toward the reticulo-omasal orifice (Fig. 2A, 8) and at the lateral fold of the omasal groove (Fig. 3, 2). The pedunculated base was fissured (Fig. 3A). Small keratinized conical and hook papillae occurred on the free border and lateral surface in the cranial third of the laminae and were directed toward the reticulo-omasal orifice (Fig. 3B). In the middle third of the laminae, the papillae were directed toward the omaso-abomasal orifice. They decreased in size and density toward the omaso-abomasal orifice. Dome-shaped papillae present in the middle third were distributed among the conical and hook papillae and the longitudinal grooves on the interpapillary surface were apparent (Fig. 3B, 6). In the terminal third of the omasum, the dome-shaped papillae became smaller and more numerous, obscuring the interpapillary surface (Fig. 3C) near the omaso-abomasal orifice.

The lining of the omasum is stratified squamous epithelium with varying degrees of keratinization. Heavily keratinized caps completely covered the large conical papillae (Fig. 4A) and accumulated many sloughed keratinized cells (Fig. 4E), while the dome-shaped papillae were covered in only a few cells layers and lightly keratinized. The epithelial lining of the interpapillary and papillary surface also exhibited different shapes. It was formed by polygonal cells with microplicae-like cytoplasmic protrusions and holes that were 1 μm in diameter at the interpapillary surface. Flap-like in the form of concentric waves (Fig. 4F) were present on the large conical papillae, while polygonal and oval cells with spaces were present on the small conical and hook papillae (Fig. 4C). The dome-shaped papillae contained nearly rectangular cells with microplicae-like cytoplasmic protrusions and more spaces (Fig. 4D). Some of the large conical papillae contained a vacuole or space at their tips (Fig. 4E).

Transmission electron microscopy: The only difference found in the ultrastructure of the epithelium lining the different parts of the omasum were the varying degree of keratinization observed in the omasal lining and papillae. The epithelium was typically keratinized stratified squamous consisting of four cell layers: stratum basalis, stratum spinosum, stratum granulosum and stratum corneum.

Most of the cells in the stratum basalis were cuboidal or short columnar, with their long axes perpendicular to the basal laminae. Basal cells were characterized by large ovoid nuclei containing mitotic figures and darkly stained chromatin. These cells constituted of two to three cell layers and contained abundant mitochondria with darkly stained matrices and prominent cristae (Fig. 5). Among the mitochondria were numerous free ribosomes, short cisternae of rough endoplasmic reticulum and cisternae of the Golgi apparatus (Fig. 5, 6). Some keratohyalin granules were also detected. Finger-like cytoplasmic processes were observed extending into the lateral intercellular space, where they were connected to those of the neighboring cells by desmosomes (Fig. 5, 6). Occasionally, the basal cells were connected to each other by tight junctions. Tonofilaments extended from the desmosomes into the cytoplasm, forming bundles parallel to the cell membrane (Fig. 6). Hemidesmosomes were scattered along the basal cell membrane facing the basal lamina. The basal lamina appeared as a moderately electron-dense structure that did not follow the contours of the basal cell membranes but rather was sometimes deeply folded (Fig. 7).

In the stratum spinosum, the lower cells bordering the stratum basalis were nearly spherical with large rounded nuclei and prominent nucleoli (Fig. 8). The intercellular spaces were subdivided by radially arranged cytoplasmic processes, which were attached to adjacent processes of neighboring cells by obliquely placed desmosomes (Fig. 8, 9). The cytoplasm of these cells was rich in tonofilaments and free ribosomes. Cisternae of rough endoplasmic reticulum were found among the tonofilaments (Fig. 9). The superficial cells bordering the stratum granulosum were flattened and the mitochondria in these cells seemed to have undergone some degeneration. These cells also contained some tonofilaments, cisternae of rER and flattened nuclei (Fig. 10).

Cells of the stratum granulosum lay parallel to the luminal surface and contained flattened nuclei (Fig. 11). The cytoplasm of these granular cells was characterized by the presence of keratohyalin granules of varying sizes. Large granules with electron-dense content were the most numerous (Fig. 12). Many cisternae of rough endoplasmic reticulum were scattered among the keratohyalin granules and were dilated and filled with a fine, filamentous material called ER-protein (Fig. 12, 13). Most of the mitochondria were degenerated in this layer, but free ribosomes, lysosomes and some lipid droplets were observed (Fig. 13). Toward the upper limit of this layer, the intercellular spaces were obliterated by numerous desmosomes in close association with cell membranes adjacent to desmosomes (Fig. 12). Occluding junctions were also identified between adjacent granular cells.

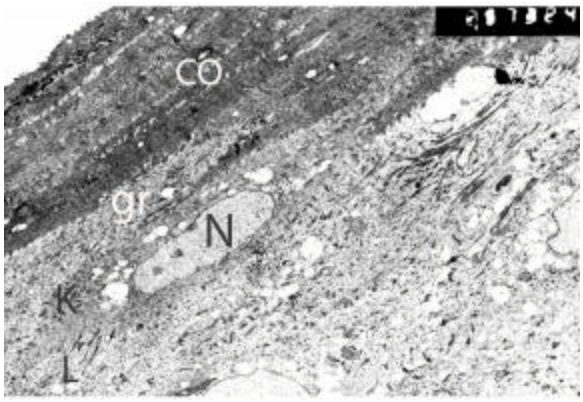

Fig. 11: Transmission electron micrograph of stratum corneum (co) and stratum granulosum (gr) showing keratohyaline granules (k), lipid droplet s (L) and nucleus (N) (X2.500)

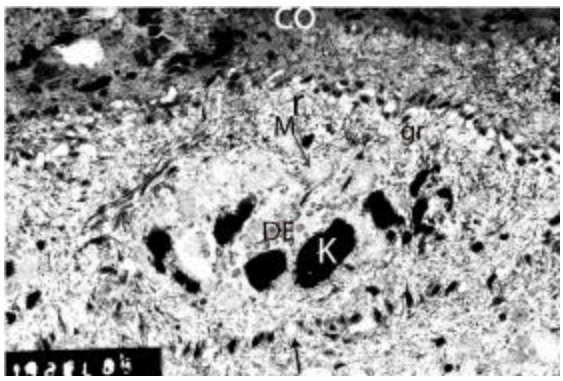

Fig. 12: Another electron micrograh of stratum granulosum (gr) denoting kerato hyaline granules (k). Note desmosmes (d) obliterating intercellular space (arrow), occluding junction (j), dilated rER (DE), free ribosomes (r) and stratum corneum (co). (X 5.000)

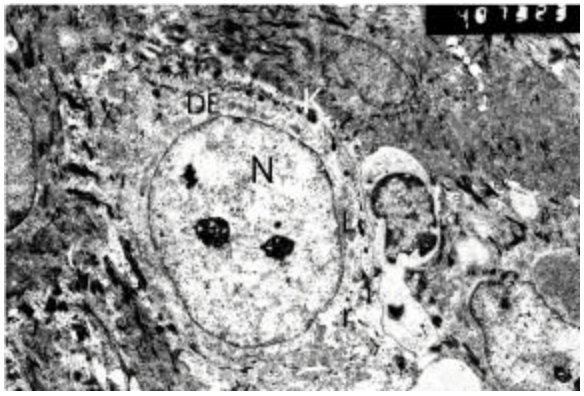

Fig. 13: Electron micrograph of granular cell depicting endoplasmic reticulum (DE) in association with free ribosomes (r), lipid droplets (L) and keratohyaline granules (k). Nucleus (N). (X 4.000)

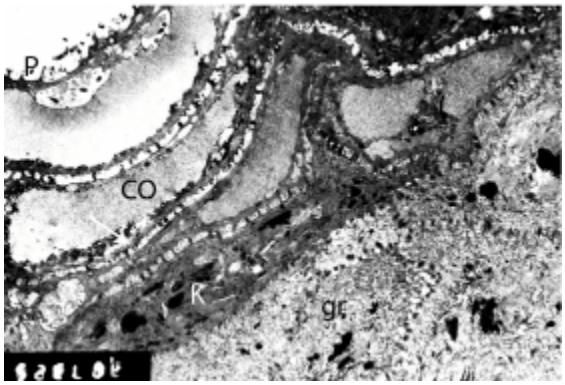

Fig. 14: Transmission electron micrograph of cornfied cells of stratum corneum (co) showing fine particles of keratohyline like granules (k) and desmosomal retention (arrow). Note plasma membrane projection (p). Stratum granulosum cells (gr) (x3.000)

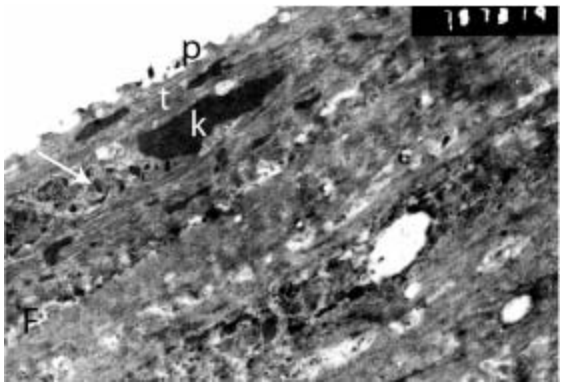

Fig. 15: Another electron micrograph of cornified cells showing bundles of tonofilaments (t) in association with keratohyaline granules (k) and remnants of nucleus (arrow), fuzzy material (F) and plasma membrane projection (p). (X 7.500)

The stratum corneum consisted of several layers of flat, elongated cornified cells that demonstrated considerable variation in their cellular constituents (Fig. 14). Generally, these cells contained heavy aggregates of tonofilaments, especially at the cell peripheries. Keratohyalin granules and free translucent ER-protein were observed in the cytoplasm. The other cytoplasmic structures were not present, although nuclear remnants were observed (Fig. 14, 15). The plasma membrane was thickened with small projections and the retention of desmosomal junctions throughout the entire length of the stratum corneum resulted in a narrowing of intercellular space (Fig. 14).

DISCUSSION

In this study, the number of the omasal laminae was 64 laminae in 4 orders in most specimens, while the previous studies have described a wide range in the number of omasal laminae between the species of domestic ruminants and within a single species. The omasum of African goat have 27-33 laminae in 3 orders (Green and Baker, 1996), the Australian cross-bred have 33-35 in 5 orders (McSweeny, 1988) and the European goat and Indian goats have 80-88 and 56-80 laminae in 4 orders (Schummer and Nickel, 1979; Chandrasekar *et al*., 1993). Wide variation has also been reported in the number of laminae within cattle breeds; one study described 100-152 laminae in 5 orders (Becker *et al*., 1963), while another identified 90-130 laminae in 4 orders (Schummer and Nickel, 1979). The difference in numbers of omasal lamina orders between different breeds could be due to the influence of the different foliage available to goats in each region (Hofmann, 1973).

The shape and distributional density of omasal papillae significantly varied among the different examined regions. A continuous increase in the density of papillae,

along with their considerable shape change from the reticulo-omasal to the omaso-abomasal regions, may reflect a mucosal adaptation to the changing environment in the omasal lumen due to the degree of feed particle coarseness and the chemical nature of the contents (Yamamoto *et al*., 1994).

Previously, the large keratinized conical papillae located on the pedunculated bases of the 1st-order laminae and lateral folds of the omasal grooves were described as almost finger- or wart-like in shape, with blunt or pointed conical tips at the reticulo-omasal orifice in goats (Green and Baker, 1996), sheep (Scott and Gardner, 1973) and cattle (Yamamoto *et al*., 1994). Unguiculiform papillae were reported in both Baladi and African goats (Green and Baker, 1996) but were absent in cross-bred goats and sheep (Yamamoto *et al*., 1994). The heavily keratinized caps observed covering the large papillae here were similar to those reported in sheep (Scott and Gardner, 1973). Small keratinized conical and hook papillae occurred on the free border of laminae; these papillae were directed toward the reticulo-omasal orifice in the cranial third of the laminae. In the middle third of the laminae, they were directed toward the omaso-abomasal orifice, suggesting an involvement of the direction of ingesta between laminae to increase absorption. These papillae have also been observed at the distal edges of laminae in sheep (Gardner and Scott, 1971) and goats (Yamamoto *et al*., 1994). The dome-shaped papillae are the common type in both cattle (Becker *et al*., 1963) and sheep (Yamamoto *et al*., 1994) in caudal part. In the Baladi goat, the dome-shaped papillae were present in the middle third of the laminae, distributed between the conical and hook papillae. The dome-shaped papillae became smaller and more numerous in the terminal third of the laminae, obscuring the interpapillary surface toward the omaso-abomasal orifice.

In this study of Baladi goats, grooves were present in the interpapillary space in the middle third of the laminae and at the pedunculated base. By contrast, grooves were present on the omasal papillae and interpapillary surface of laminae in sheep (Scott and Gardner, 1973) and in the African goat, grooves were only present in the interpapillary surface (Green and Baker, 1996). Empty spaces, present in both the interpapillary and papillary surfaces of the Baladi goat omasa, but they were limited only to the interpapillary surface in the African goat (Green and Baker, 1996). We also observed that some of the large conical papillae contained vacuoles or spaces in the tips that might be involved in absorption.

We observed that the lining from different parts of the Baladi goat omasum was keratinized stratified squamous epithelium that consisted of four layers: stratum basalis, stratum spinosum, stratum granulosum and stratum corneum. This result was consistent with a previous report (Banks, 1986). In the present study, cells of the stratum basalis contained a higher density of mitochondria relative to cells of the stratum spinosum or stratum corneum. These increased numbers of mitochondria are likely to contribute to the metabolic properties of the tissue and ketogenesis (Graham and Simmons, 2005; Baldwin, 1998). In the ruminal epithelium, ketogenesis is performed in mitochondria (Leighton *et al*., 1983). Keratohyalin granules were detected in the basal cells; consistent with previous findings that biosynthesis of keratinous substances in the ruminal epithelium starts in the basal cells, which initiate post-mitotic differentiation or aging (Henrikson, 1970; Steven and Marshall, 1970). Occluding junctions were identified between basal cells and are thought to act as barriers to back-diffusion of metabolites into the lumen (Steven and Marshall, 1970).

We detected numerous desmosomes among neighboring basal cells and hemidesmosomes were scattered along the basal cell membrane. Green and Jones (1996) identified desmosomes and hemidesmosomes as the major cell-surface attachment sites for intermediate filaments at cell-cell and cell-substrate contacts. Hemidesmosomes in the skin, along with other complex epithelial multi-protein complexes, are involved in adhesion of epithelial cells to the underlying basement membrane (Borradori and Sonnenberg, 1999).

In the intercellular space of all epithelial strata and in particular in the stratum basalis and stratum spinosum, extensive proximal projections of the basal cells were accompanied by deeply folded basal lamina. These features provide increased surface area for the proximal basal cells and improve nutrient exchange between epithelial tissue and the circulatory system, as noted in a study of sheep feeding on concentrates (Siddig and Geburtsort, 2007).

The granular cells of the omasa in Baladi goats were characterized by the presence of keratohyalin granules of varying sizes and numerous dilated cisternae of rER. Another study reported the same result in the sheep rumen, further noting that ER cisternae become dilated as keratohyalin granule formation begins and increase as keratohyalin granules grow. This ER protein is not secreted or transferred to Golgi vesicles but is stored and

ultimately released by lysosomal hydrolytic enzymes in the advanced stages of epithelial differentiation, when it assumes its specific function as part of the horny matrix. The cells of the stratum corneum exist in several layers of flat, elongated cornified cells that show considerable variation in their contents. These flattened cells form the barrier layer of the epithelium (Zitnan *et al*., 1999).

Changes in the barrier layer of flattened horny cells are related to diet. This layer becomes thicker in winter or in the dry season, when animals eat food with increased amounts of fiber. One role of the omasum is to act as a flood gate between the reticulum and the abomasum (Bost, 1970). This organ also synthesizes glucose, comprising 5% of total digestible nutrients (Hungate, 1970) and it has been reported to prevent conditions such as ketosis.

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