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ELECTRON MICROSCOPICAL OBSERVATIONS ON THE TRACHEAL EPITHELIUM OF THE ONE-HUMPED CAMEL (CAMELUS DROMEDARIUS) WITH SPECIAL REFERENCE TO CILIOGENESIS

(With 18 Figures)

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مشاهدات بالمجهر الإلكتروني على طلائية القصبة الهوائية في الجمل وحيد السنام مع إشارة خاصة لعملية التهدب

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أجريت هذه الدراسة علي عشرة جمال بالغة (وحيد السنام) من كلا الجنسين ومختلف الأعمار. تمت دراسة التركيب الدقيق لطلائية القصبة الهوائية بالمجهر الإلكتروني الماسح والنافذ . أظهر المجهر الإلكتروني الماسح وجود خلايا مهدبة وخلايا كأسية بالاضافة الى خلايا غير مهدبة مغطاة بزغيبات . أما الدراسة بالمجهر الإلكتروني النافذ أوضحت أربعة أنواع أساسية من الخلايا : خلايا مهدبة ، خلايا كأسية ، خلايا قاعدية وكذلك خلايا وسطية بالإضافة إلى بعض الخلايا المهاجرة. وقد وجدت أيضا خلايا غير مهدبة ومزودة بزغيبات؛ أظهرت مراحل مختلفة من التهدب والتميز إلى الخلايا المهدبة. أما الخلايا المهدبة فأوضحت الدراسة انها تماثل نظيرتها في الطلائية التنفسية للثدييات الاخرى وتحتوي على جذيرات مهدبة. وبدراسة البنية المستدقة للخلايا الكأسية لوحظ أن بعض الخلايا بها حبيبات إفرازية فاتحة إلكترونيا وتحتوي على لب معتم احيانا والبعض الآخر يحتوى على حبيبات إفرازية معتمة الكترونيا مع وجود هالة حلقية بها. وأظهرت هذه الحبيبات الإفرازية احتوائها على الميوسين الحامضي والمتعادل الذي يتم إخراجه إما بالتسرب أو الإفراز الشبه متفرز. أوضحت الدراسة أيضاً أن التركيب السيتوبلازمى والنووى للخلايا الوسطية يماثل نظيرهما في الخلايا القاعدية غير أن الخلايا القاعدية تكون اكثر عتامة لإحتوائها على عديد من الريباسات والخيوط المؤثرة. هذا وقد شوهدت بعض الخلايا الليمفاوية والخلايا البلازمية في الفراغات البين خلوية للطلائية التنفسية. نوقشت نتائج هذه الدراسة بمثيلاتها في الحيوانات المختلفة.

SUMMARY

This study was carried out on 10 adult, apparently healthy one-humped camels of different ages and of both sexes. The ultrastructure of camel tracheal epithelium was studied by scanning and transmission electron microscopes. Scanning electron microscopy revealed the presence of ciliated cells, goblet cells and occasionally non-ciliated microvilli covered cells. Four main cell types were observed with the transmission electron microscope: Ciliated, goblet, basal and intermediate cells, in addition to the migratory cells as well as the occasionally observed non-ciliated microvilli covered cells. The latter cell type was observed in different stages of differentiation into ciliated cells i.e. undergo ciliogenesis. Ciliated cells were numerous, structurally similar to those of the other mammalian respiratory epithelial cells and contained prominent ciliary rootlets. Goblet cells contained secretory granules variable in number, size and electron density. Some cells contained electron-lucent granules occasionally with electron-dense core, others showed electron dense- granules with a light halo ring. These granules were discharged into the lumen of the trachea either by exocytosis or apocrine-like mode of secretion. Basal and intermediate cells were structurally similar, but the basal ones possessed numerous ribosomes and tonofilaments. Lymphocytes, plasma cells and polymorphonuclear leukocytes were also observed within the intercellular spaces of this epithelium.

Key Words: *Ultrastructure, respiratory epithelium, ciliogenesis, trachea, camel.*

INTRODUCTION

The trachea as a part of the conducting airways of the respiratory system is constantly exposed to inhaled air and its contaminants. The presence of which is especially noticeable nowadays in the atmosphere, as consequence of pollution. In order to study the effects of these contaminants on the tracheal epithelium, it is essential to understand the morphology and ultrastructure of this epithelium. The luminal border of the tracheal epithelium is formed of ciliated and secretory cells, those constitute a primary defense mechanism of the respiratory system. These cells were functioning in a coordinated manner, the goblet cells secrete mucus which entrap inspired foreign particles and cellular debris which

moved by the ciliary beat of the ciliated cells toward the glottis (Sleigh, 1982).

Rhodin and Dalhamn (1956) provided one of the first descriptions of the ultrastructural features of the tracheal epithelium in rat. Later on, this epithelium has been heavily investigated in man and animals. At the light microscopical level, Fath El-Bab (1970) had studied the tracheal epithelium of the camel. By using the electron microscope, Dougbag, Berg, Kassem, Hemmoda and Osman (1984) had investigated this epithelium during the prenatal life. In the available literatures, there is no reports concerning the ultrastructure of the adult camel tracheal epithelium. Therefore, the goal of the current work was to describe in details the respiratory epithelium of the trachea of the adult camel as well as the process of ciliogenesis by using scanning and transmission electron microscopes.

MATERIAL and METHODS

Tracheal specimens from apparently healthy 10 adult camels of both sexes and different ages were obtained from Assiut Slaughter houses. The mucosa was removed rapidly by careful dissection from the underlying tissue.

For light microscopy, the samples were fixed in Bouin's fluid to be prepared for paraffin embedding. 5µm thick paraffin sections were stained with alcian blue, PAS and combination of alcian blue-PAS (Mowry, 1956).

For transmission electron microscopical examination, small samples from the mucosa were fixed in a mixture of 2.5% paraformaldehyde and 2.5% glutaraldehyde in 0.1M Na-cacodylate buffer, pH 7.2 for 2 hours at 4°C. After washing in the same buffer, the samples were post-fixed in 1 % cacodylate buffered osmium tetroxide for further 2 hours. They were dehydrated in ethanol and embedded in a mixture of Epon-araldate. Semithin sections were obtained on LKB ultratome and stained with toluidine blue. The ultrathin sections were stained with uranyl acetate and lead citrate and examined with JEOL 100 CXII transmission electron microscope.

For scanning electron microscopical examination, the fixed samples (5 x 5 mm^2) were washed in the same buffer, dehydrated in ethanol followed by critical point drying. They were then mounted on copper stubs, sputtered with gold and observed and photographed at JEOL 5400 LV scanning electron microscope.

RESULTS

Light microscopical observations:

The trachea of the camel was lined with respiratory epithelium, composed of four main cell types namely: The ciliated cells, goblet cells, intermediate cells and basal cells (Fig. 1a). All these cells were observed resting on the basement membrane, while the basal and intermediate ones did not reach the surface. Histochemically, the goblet cells revealed strong alcianophilia and moderate PAS-reaction (Fig. 1b).

Scanning electron microscopical observations:

The tracheal surface of the camel revealed small longitudinal mucosal folds separated by shallow incomplete grooves. These folds showed somewhat oval indentations (Fig. 2a). At high magnification, the mucosal surface of the camel trachea was formed of numerous ciliated and goblet cells (Fig. 2b). Occasionally few non-ciliated microvilli covered cells among the before-mentioned cell types were also observed (Fig. 3a). Such cells were probably undergo ciliogenesis and conversion into ciliated cells, which indicated by the appearance of short cilia protruding from their apical surfaces in between the microvilli (Fig. 3b).

Transmission electron microscopical observations:

Four main cell types were observed: Ciliated, goblet, basal and intermediate cells as well as migratory cells and non-ciliated microvilli covered cells.

Ciliated cells:

The ciliated columnar cells (Fig. 4a) were the most numerous cell -type encountered in this epithelium. They were more electron-lucent than other cell-types. The luminal surface of the ciliated cell was provided with cilia, which were attached to the cytoplasm by basal bodies. In addition, frequently branched microvilli of varying lengths were observed protruding from the apical surface in between the cilia (Fig. 4a & b). Ciliary rootlets were seen extending into the apical cytoplasm from the basal corpuscles (Fig. 5a). Apically, the ciliated cells were attached together and with the adjacent goblet cells with tight junction, zonula adherents and desmosomes (Fig. 4b & 5b). Laterally, the plasmalemma was nearly straight and the cells were joined together with few desmosomes and ill-developed interdigitations, which extended into narrow intercellular spaces. Basally, the ciliated cells were attached to the basal lamina with hemidesmosmes.

The ciliated cells contained numerous mitochondria of variable sizes, scattered throughout the cytoplasm and were especially numerous in the apical region of the cell beneath the basal bodies (Fig. 4a& b). Scattered profiles of granular endoplasmic reticulum, supranuclear Golgi-apparatus and tonofilaments were also seen (Fig. 4a&6). The basally located nucleus was ovoid and contained heterochromatin, which concentrated near the nuclear envelope. Small, dense and rounded nucleolei were occasionally visible.

In addition to the before-mentioned ciliated cells, the lining epithelium of the trachea of the camel showed also few ciliated cells, which were characterized by possessing highly electron-dense vacuolated cytoplasm and pyknotic nuclei (Fig. 6&11-16).

Goblet cells:

The goblet cells (Fig. 7a-c) were abundant in the tracheal epithelium of the camel. They possessed large oval basally located nuclei.

The apical portion of the goblet cells (Fig. 7a-c) was frequently filled with secretory granules giving them their characteristic shape. These granules were variable in number, size and electron density. Some cells possessed electron-lucent granules with or without electron-dense core (Fig. 7a&b). Others contained large electron-dense granules with a light halo ring, which located either centrally or peripherally (Fig. 7c). The limiting membranes of the electron-lucent granules fused with each other before their secretion. The secretory granules discharged into the lumen of the trachea either through simple exocytosis (Fig. 7b) or by apocrine-like mode of secretion (Fig. 7c). In addition, the cytoplasm of the goblet cells (Fig. 8) was rich in ribosomes giving them more electron density than the adjacent cells. They contained also abundant cisternae of rough endoplasmic reticulum, well-developed supranuclear Golgi complex, mitochondria, lysosomes and tonofilaments.

The luminal surface of the goblet cells was provided with microvilli, which varied according to the amount of secretory granules (Fig. 7a&b). The cellular junctions of the goblet cells were similar to those mentioned for the ciliated cells.

Basal cells:

The basal cells (Fig. 9a&b) were small columnar or triangular in shape. Their cytoplasm was characterized by the presence of numerous bundles of tonofilaments and mitochondria. They contained also free ribosomes, polysomes and small profiles of rough endoplasmic

reticulum rendering them generally, more electron-dense than the cytoplasm of the adjacent cells.

The nuclei appeared relatively large occupying most of the cell volume. They were irregular in shape with deep infoldings and contained dense clumps of chromatin often in contact with the nuclear membrane. Small dense nucleoli as well as nuclear pores were also observed. The basal cells were attached to the basal lamina with hemidesmosomes (Fig. 9b) and to the adjacent cells with few desmosomes and interdigitations through small cytoplasmic processes, which extended into wide irregular intercellular spaces.

Intermediate cells:

The intermediate cells (Fig. 10) were wedged-shaped and observed above the basal cells. The cytoplasmic and nuclear components of the intermediate cells were similar to those of the basal cells except of fewer tonofilaments and ribosomes.

Non-ciliated microvilli covered cells:

These cells were occasionally seen within the tracheal epithelium of the camel. They were especially present in close relation to the dark ciliated cells (Fig. 11a). Their bulged apexes were provided with numerous microvilli of variable lengths, while the somewhat electron-lucent cytoplasm was characterized by the presence of numerous mitochondria and centerioles in their supranuclear region indicating the existence of ciliogenesis (Fig. 11b & c). These newly formed centerioles (procentrioles) migrated towards the apical plasmalemma (Fig. 12) and aligned themselves in row directely beneath the apical plasmalemma (Fig. 13). With the progress of this process, the centerioles increased in number and became oriented perpendicular to the apical plasmalemma, where the nearest one fused with it and began to mature into basal body (Fig. 14). Lengthening of the microtubules was observed as bud-like and then, the ciliary shaft extended first at the periphery of the luminal surface from the basal body and became enclosed by the plasmalemma forming a cilium (Fig. 15). The process of ciliogenesis continued by appearance of more cilia, replacing gradually the pro-existing microvilli. Some of the latter were also retained (Fig. 16).

Migratory cells:

A variety of migratory cells were also observed at different levels within the intercellular spaces of the respiratory epithelium of the camel trachea. They included lymphocytes (Fig. 9a), polymorphonuclear leukocytes (Fig. 17) and plasma cells (Fig. 18).

DISCUSSION

The present study revealed that, the tracheal epithelium of the camel was a typical example of respiratory epithelium composed of four main cell types: Ciliated, goblet, basal and intermediate cells in addition to some migratory cells. These results simulate in many respects that observed in the trachea of man (Osada, 1963; Rhodin, 1966), rat (Cireli, 1966), rabbit (Konradova, 1966), mouse (HansellL and Moretti, 1969) and guinea pig (Dalen, 1983), bronchi of man (Watson and Brinkman, 1964), dog (Frasca, Auerbach, Parks and Jamieson, 1968) and pig (Baskerville, 1970a) as well as nasal cavity of man (Matulionis and Parks, 1973) and mouse (Busuttil, More and Mcseveney, 1977), larynx (Abd El-Rahman, 1990) and guttural pouch of the donkey (Abd El-Rahman, Salem and, Abou- Elmagd, 1994).

The respiratory epithelium of the trachea of the camel contained neither brush cells, as observed in the trachea of rat (Rhodin and Dalhamn, 1956), man (Rhodin, 1966) and larynx of the goat (Abd El-Rahman, 1990), nor Clara cells as stated by Hansell and Moretti (1969) in the rat trachea, Abd El-Rahman (1990) in the dog larynx and Dellmann (1993) in the trachiobronchial tree of the domestic animals.

Both light and scanning electron microscopical investigations revealed that the ciliated cells were the most numerous cell-type encountered within the tracheal epithelium of the camel. The ultrastructural features of these cells, especially in point of relative abundance of cilia and intracellular components, resemble those described for the trachea of rat (Rhodin and Dalhamn, 1956) and mouse (Greenwood and Holland, 1972), bronchi of dog (Frasca et al., 1968) and pig (Baskerville, 1970a), larynx of donkey, goat and dog (Abdel-Rahman, 1990) and guttural pouch of the donkey (Abd El- Rahman et al., 1994).

The present investigation revealed the presence of few ciliated cells with highly electron-dense vacuolated cytoplasm and pyknotic nuclei. They were considered as dark ciliated cells. The ultrastructural features of these cells indicating that these cells may undergo degeneration, which agree with that observed in the gall bladder of the rabbit (Hayward, 1966; Yamada, 1968). Dark ciliated cells were also observed in the trachea of mouse (Hansell and Moretti, 1969) and camel during development (Dougbag et al., 1984) as well as in the larynx of donkey and dog (Abd El-Rahman, 1990) and guttural pouch of the donkey (Abd El-Rahman et al., 1994). Osada (1963) suggested that the

dark ciliated cells in the human trachea represent an intermediate stage in the transformation of ciliated cells to goblet ones.

The present study revealed that the apical plasmalemma of the ciliated cells was provided also with branched microvilli. These results simulate that observed in the ciliated cells of the dog (Okano and Sugawa, 1965) and human nasal epithelium (Busuttil et al., 1977) as well as guttural pouch of the donkey (Abd El-Rahman, 1994). Busuttil et al. (1977) suggested that the presence of such microvilli might be pathological. These microvilli could be considered as remnant of those of non-ciliated microvilli covered cells during ciliogenesis. Recently, thin film of airway surface liquid (ASL) was observed surrounding and covering the cilia and microvilli (Geiser, Im-Hof, Siegenthaler, Grunder and Gher, 1997; Wu, Lee, Uyekubo, Choi, Bastacky and Widdicombe, 1998). From this point of view, it was suggested that the microvilli might participate in particle retention and clearance where they trap the foreign particles in between them. The latter were expelled out by the beating cilia.

The apical portion of the ciliated cells contained numerous basal bodies, ciliary rootlets and mitochondria. These striated rootlets were clearly seen immediately below the basal bodies simulating those observed by Purcell (1971) in the trachea of the fowl. The rootlets were less prominent in the ciliated cells of the trachea of rat (Rhodin and Dalhamn, 1956) and man (Rhodin, 1966) as well as in the bronchi of dog (Frasca et al., 1968). Konradova (1966) could not found any ciliary rootlets either in rat or rabbit trachea. On the other hand, the accumulation of mitochondria in this region is related to the high metabolic activity and a great need of energy in this cellular region, especially during ciliary beat (Rhodin, 1959; Konradova, 1966).

Numerous goblet cells were observed within the tracheal epithelium of the camel similar to that mentioned by Rhodin and Dalhamn (1956) in the rat trachea, Frasca et al. (1968) and Baskerville (1970a) in bronchi of the dog and pig respectively, as well as Abd El-Rahman (1990) in the larynx of donkey and goat. However, Karrer (1956) and Hansell and Moretti (1969) observed that the respiratory epithelium of the bronchi and trachea of mouse, respectively, are virtually devoid of goblet cells.

The ultrastructural features of the goblet cells in the camel trachea resembled those in the respiratory epithelia of other species in a number of respects. The electron density of the ground cytoplasm was

similar to those of dog (Frasca et al., 1968) and pig bronchi (Baskerville, 1970a) as well as donkey and goat larynx (Abd El-Rahman, 1990).

The density of the secretory granules was varied from cell to cell. Some cells possessed electron-lucent granules with or without an electron-dense core. Others contained large electron-dense granules with a halo ring. These results simulate those described in the mouse nasal respiratory epithelium (Matulionis and Parks, 1973) and guinea pig trachea (Newman, Robichaud and Rogers, 1996). Variations in the electron density of the granules were observed also in the same cell by Pack, Al-Ugaily, Morris and Widdicombe (1980) and Monteiro-Riviere and Popp (1984). However, in the rat trachea (Rhodin and Dalhamn, 1956), as well as in human (Watson and Brinkman, 1964), dog (Frasca et al., 1968) and pig bronchi (Baskerville, 1970a) the content of the mucous granules is fibrillar, homogenous and low density. In airway epithelium of the rat, the electron-dense core was demonstrated in the mucous granules (Jeffery and Reid, 1975). Histochemically, the goblet cells of the present investigation contained both acidic and neutral mucins. Pack et al. (1980) and Newman et al. (1996) suggested that the electron-dense granules and the electron-lucent ones were serous and mucous granules, respectively.

In agree with Newman et al. (1996) in the guinea pig trachea, the secretory granules of the goblet cells of the present study was discharged either by simple exocytosis or apocrine-like mode of secretion. However, Watson and Brinkman (1964) in the human bronchi, Purcell (1971) and Pack et al. (1980) in the fowl and mouse trachea respectively, stated that the discharge of the goblet cell occurred only by simple exocytosis. While, apocrine-like mode of secretion was observed in the goblet cells of the intestine (Palay, 1958; Freeman, 1962) as well as in the human trachea (Rhodin, 1966).

The ultrastructure of the basal cell of the camel trachea was similar to that described by Rhodin (1966) in the rat trachea, Abd El-Rahman (1990) in the larynx and Abd El- Rahman et al. (1994) in the guttural pouch of the donkey. The former author suggested that, the basal cells represented the layer from which the other cells differentiate. Holliday (1971) stated that, certain of the basal cells contained immature mucous granules, which indicate their future development into goblet cells. Recently, Erjefalt, Sundler and Persson (1997) mentioned that the basal cells play an important role in airway defense against sever insults as a barrier structure, where they promptly flattened out to cover the basement membrane at loss of neighbour columnar cells.

In agree with Rhodin and Dalhamn (1956), Rhodin (1966) and Konradova (1966) in the rat, man and rabbit trachea respectively, the intermediate cells were also observed in the tracheal epithelium of the camel. In human trachea, Rhodin (1966) stated that the intermediate cell is an undifferentiated cell transformed into either ciliated or goblet cell. In the rat trachea, the accumulation of fibrogranular material within the cell cytoplasm, suggesting ciliogenesis (Jeffery and Rreid, 1975). Rhodin's opinion is acceptable, where the non-ciliated microvilli covered cells may be considered as an advanced form of differentiation of intermediate cells into ciliated ones. This occurred during ciliogenesis, but their differentiation into goblet cells could not be observed in the present study.

Furthermore, the present investigation revealed the presence of non-ciliated microvilli covered cells, which were occasionally seen in the respiratory epithelium of the camel trachea at different stages of differentiation into ciliated cells, indicating the existence of ciliogenic process within this epithelium. Similar ciliogenic processes were demonstrated also in the trachea of rat (Rhodin and Dalhman, 1956), rabbit (Lesson, 1961) and man (Rhodin, 1966), in mammalian lungs (Sorokin, 1968), in the nasal and tracheal epithelium of the man (Carson, Collier, Knowles and Baucher, 1985), larynx of the donkey (Abd El-Rahman, 1990) and bronchi of the camel (Sayed, 1994). The observed ciliogenic process within the tracheal epithelium of the camel was centriolar pathway simulating that seen in the mammalian retina (Greiner, Bodley, Weidman and Peace, 1983). However, a centriolar pathway of ciliogenesis was observed in the nasal cavity of rabbit (Loots and Nel, 1989). Both a centriolar and centriolar pathways of ciliogenesis occurred in the nasal respiratory epithelium of rat (Menco and Farbman, 1987) as well as in human oviduct (Hagiwara, Shibasaki and Ohwada, 1992). Lemullois, Boisvieux-Ulrich, Laine, Chaulley and Sandoz (1988) and Tamm and Tamm (1988) suggested that migration of centrioles influenced by the actin-myosin system. Recently, Comer, Shires Goode, Leese, Treidosiewicz and Southgate (1999) stated that the process of ciliogenesis may probably regulated by specific protein, which associated with the body system of the cilium specifically with 9+0 microtubule arrays. Ciliogenesis may occur as a function of cellular maintenance to add or replace cilia on the luminal border, in addition to their more obvious occurrence during differentiation of new ciliated cells (Carson et al., 1985). This agrees with the obtained results, where during ciliogenesis new ciliated cells were appeared replacing the actually

degenerated ciliated cells. This was supported by the presence of the ciliogenic cells in close relation with the so-called dark or degenerated ciliated cells.

The current investigation revealed that the tracheal epithelium of the camel contained also inter-epithelial migratory cells as lymphocytes, plasma cells and polymorphonuclear leukocytes. In addition to these cells, macrophages were observed within the respiratory epithelium of the human nose (Busuttil et al., 1977). On the other hand, only lymphocytes were also seen in the respiratory epithelium of the larynx of donkey, goat and dog (Abd El-Rahman, 1990) and that of the guttural pouch of the donkey (Abd El-Rahman et al., 1994). Busuttil et al. (1977) stated that these cells may play an essential role in the formation of local IGA, IGE and in cell mediated immunological response, where the respiratory mucosa is of such importance in allergic and hypersensitive states, these may be the cells which tigger such immunological reactions.

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LEGENDS

Fig. 1a: Toluidine blue stained semithin section of the mucosa of the camel trachea showing pesudostratified ciliated columnar epithelium with goblet cells (arrow). Lumen (Lu), lamina propria (Lp). X 250.

Fig. 1b: Paraffin section of the tracheal epithelium of the camel showing strong alcianophilia and moderate PAS-reaction in the goblet cells. Alcian blue-PAS. X 250.

Fig. 2a: Low magnification scanning electron micrograph of the tracheal surface of camel showing longitudinal folds (arrow) with indentations (*) separated by grooves (arrowhead).

Fig. 2b: High magnification scanning electron micrograph of the tracheal surface of camel showing ciliated cells (C) and goblet cells (G).

Fig. 3a: Scanning electron micrograph of the tracheal surface of camel showing ciliated cells (C) and non-ciliated microvilli covered cell (Nc).

Fig. 3b: Scanning electron micrograph of the tracheal surface of camel showing a cell with short cilia intermingled with microvilli, ciliogenic cell, (arrow).

Fig. 4 a: Electron micrograph of the trachea of the camel showing ciliated cell (C) and goblet cells (G). Lumen (Lu), microvilli (Mv), Cilia (Ci), basal bodies (Bb), mitochondria (M), Golgi- apparatus (Ga). X 7207.

Fig. 4b: High magnification electron micrograph of the ciliated cells showing lumen (Lu), microvilli (Mv), Cilia (Ci), basal bodies (Bb), mitochondria (M), tight junction (Tj), intercellular space (arrow). X 13714.

Fig. 5a: Electron micrograph of the apical portion of the ciliated cell showing cilia (Ci), basal bodies (Bb), ciliary rootlets (Cr) and mitochondria (M). X 23333.

Fig. 5b: High magnification electron micrograph of the ciliated cells showing lumen (Lu), tight junction (Tj) and desmosomes (D). X 35000.

Fig. 6: Electron micrograph of the supranuclear region of ciliated cells demonstrating mitochondria (M) and tonofilaments (arrow). Goblet cell (G), nucleus of ciliated cell (N1), pyknotic nucleus of degenerated ciliated cell (N2). X 17143.

Fig. 7a-c: Electron micrographs of the goblet cells showing:
a) Electron-lucent granules (arrow). X 16667.
b) Electron-lucent granules with dense core (arrowhead). X 28000.
c) Electron-dense granules with halo ring (double arrow). X 4860.
Inset) High magnification of fig. 7c. X 42750. Lumen (Lu), ciliated cells (C), microvilli (Mv).

Fig. 8: Electron micrograph of the supranuclear region of a goblet cell showing Golgi-apparatus (Ga), secretory granules (Sg), mitochondria (M), RER (arrow) and nucleus (N). X 20000.

Fig. 9a: Low magnification electron micrograph showing basal cells (B) and lymphocyte (Ly). Intercellular spaces (arrow), basal lamina (Bl). X 2750.

Fig. 9b: High magnification electron micrograph of the basal portion of basal cells showing tonofilaments (arrow), mitochondria (M), nucleus (N), basal lamina (Bl) and hemidesmosomes (HD). X 19600.

Fig. 10: Electron micrograph of the intermediate cells showing mitochondria (M), nucleus (N) and intercellular space (arrow). X 7000.

Fig. 11-16: Electron micrographs of the non-ciliated microvilli covered cells in different stages of differentiation into ciliated cells (ciliogenesis).
11a) Non- ciliated microvilli covered cell between two dark ciliated cells (*). X 10000.
11b) Low magnification of the upper portion of the respiratory epithelium of the camel demonstrating ciliogenic cells (**) and dark ciliated cells with vacuolated cytoplasm (arrowhead) and pyknotic nucleus (N). X 4500.
11c) High magnification of figure (11b) of ciliogenic cells showing centrioles (arrow). X 13500.
12) Ciliogenic cell demonstrating migration of centerioles towards the apical plasmalemma (arrow). X 20000.
13) Ciliogenic cell demonstrating arrangement of centerioles in row (arrow). X 11486.

14) Ciliogenic cell showing the perpendicular orientation of centeriole to the apical plasmalemma and the nearest one forming basal body (arrowhead). X 12800

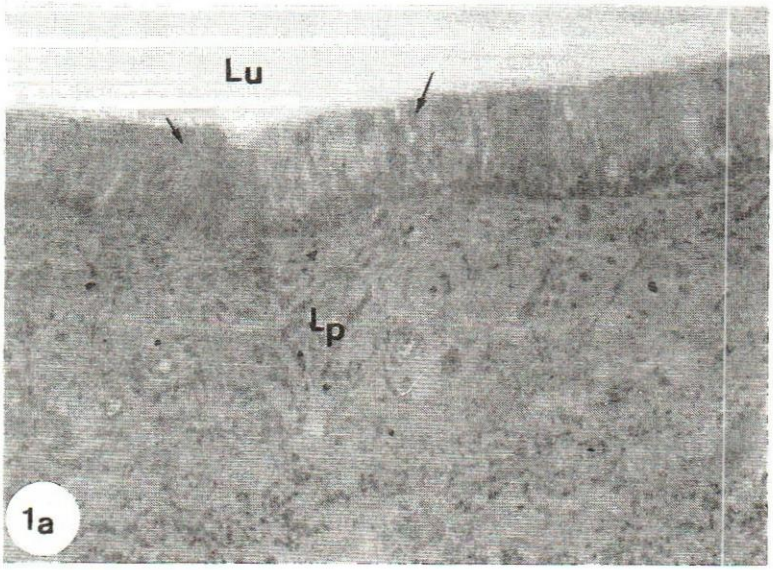
15) Ciliogenic cell demonstrating extended ciliary shaft (double arrow). X 18333.

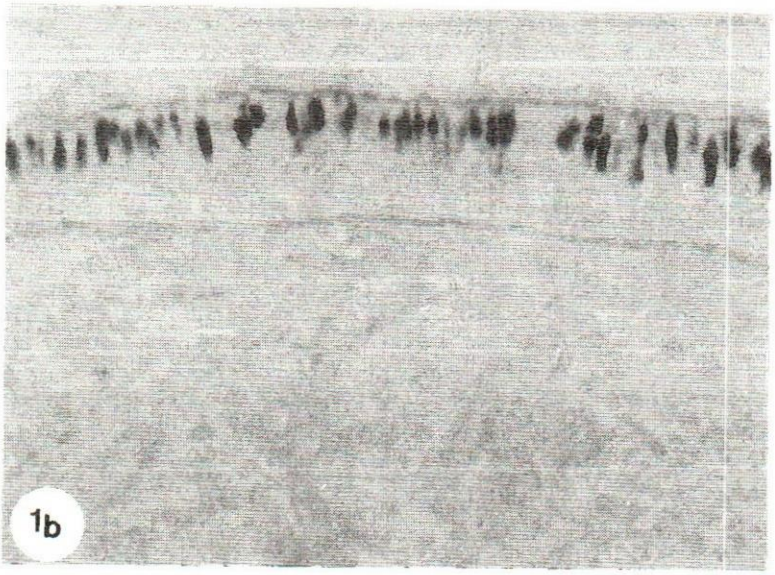
16) Ciliogenic cell showing appearance of more cilia (arrow). X 14867.

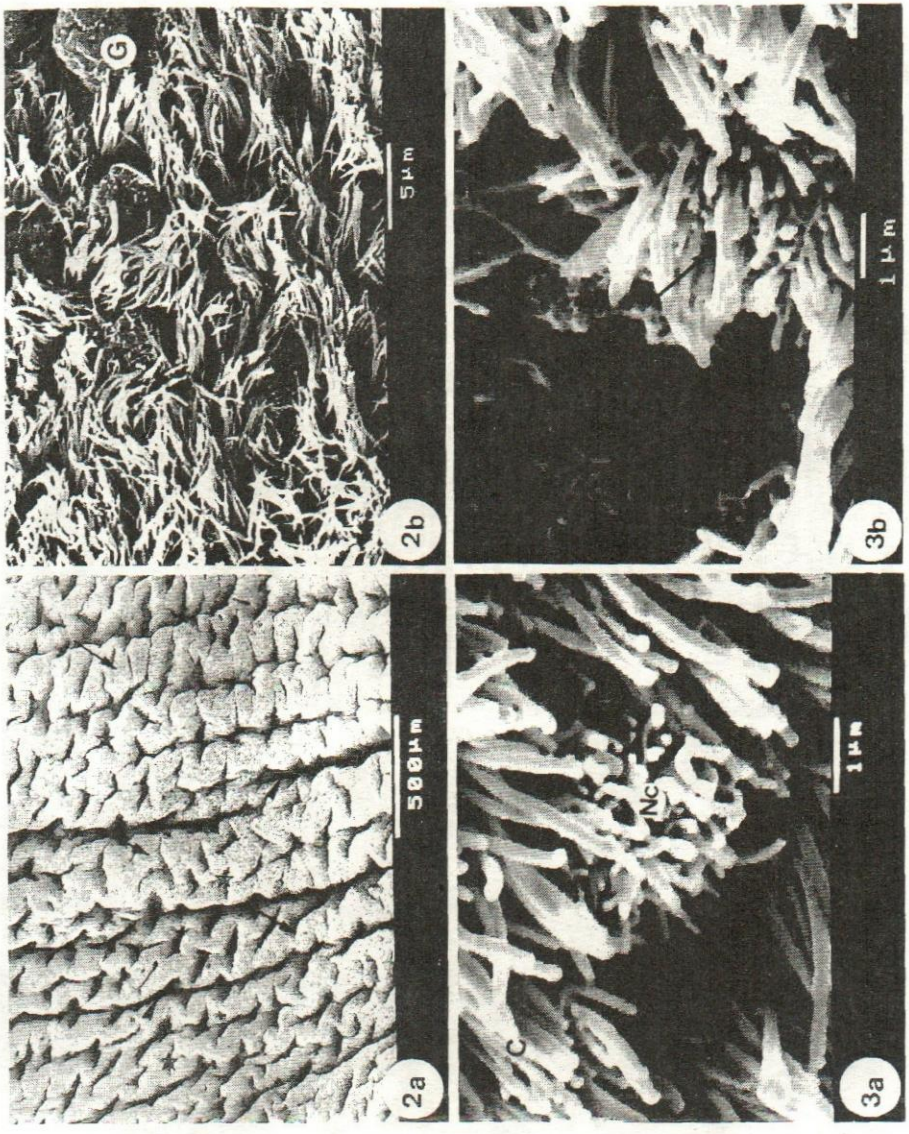
Lumen (Lu), cilia (Ci), microvilli (Mv), centrioles (arrow), mitochondria (M), goblet cell (G), dark ciliated cell (*).

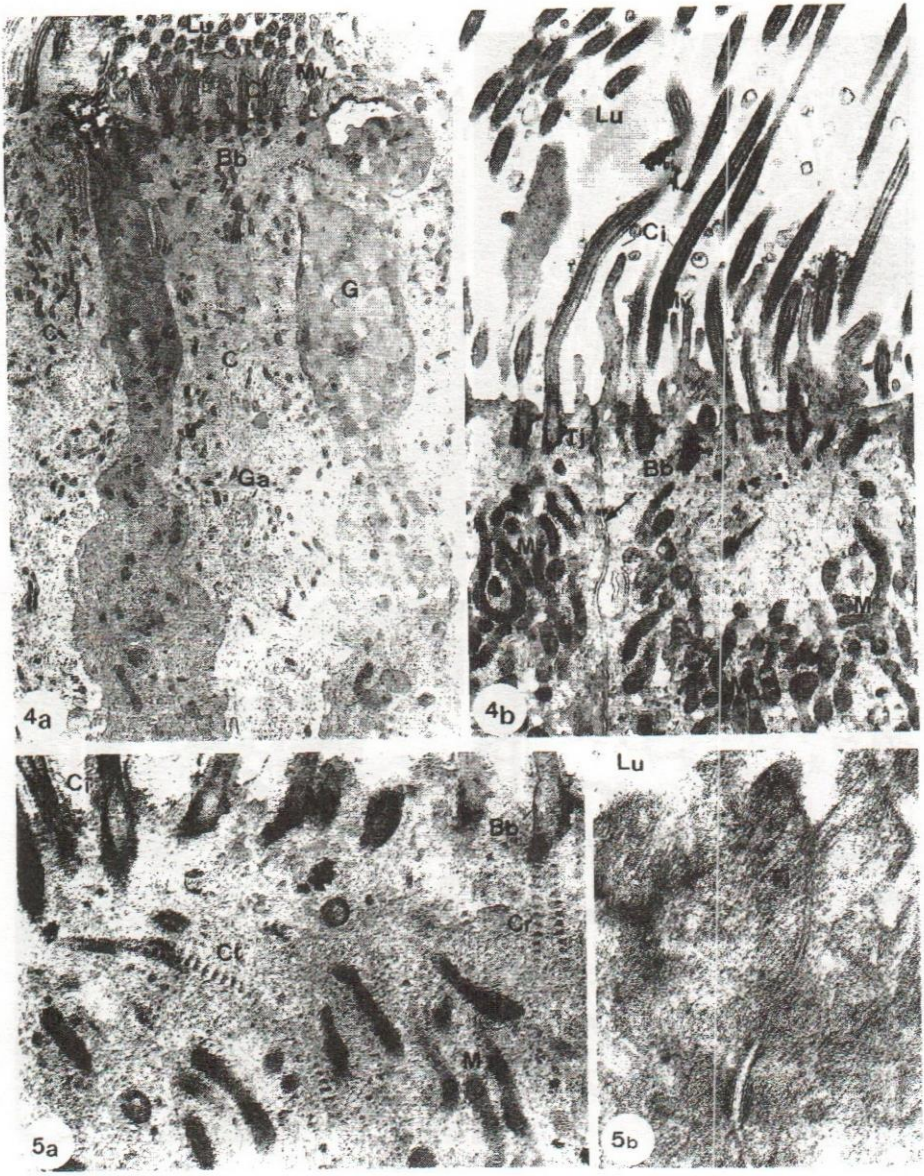
Fig. 17: Electron micrograph showing polymorphonuclear leukocyte (arrow) within the intercellular space (arrowhead). Goblet cell (G), ciliated cell (C). X 8000.

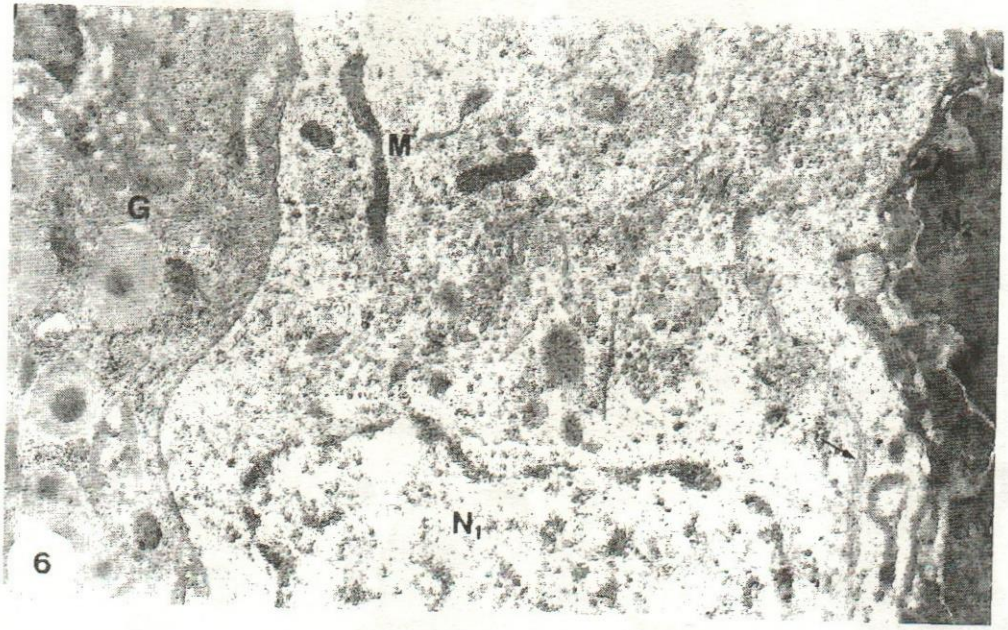
Fig. 18: Electron micrograph showing plasma cell (thick arrow) within the intercellular space (thin arrow). Basal cell (B). X 9380.


Lu
Lp
1a


1b


G
5µm
2b
500µm
2a
1µm
Nc
C
3a
1µm
3b


Lu
MV
Bb
G
C
Ga
4a
Lu
Ci
Bb
M
4b
Ci
Bb
Cr
Ct
M
5a
Lu
5b



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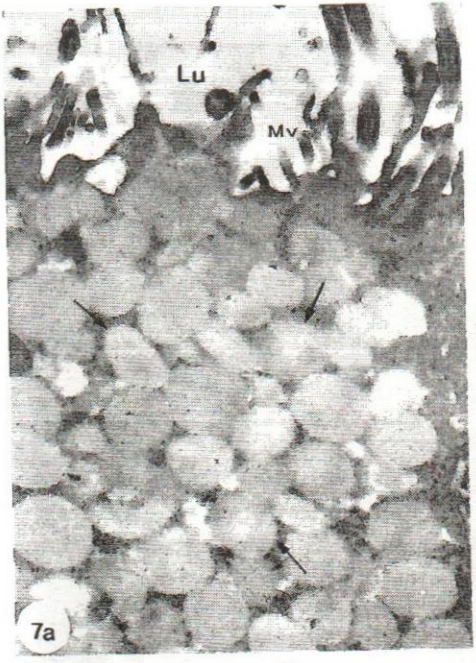
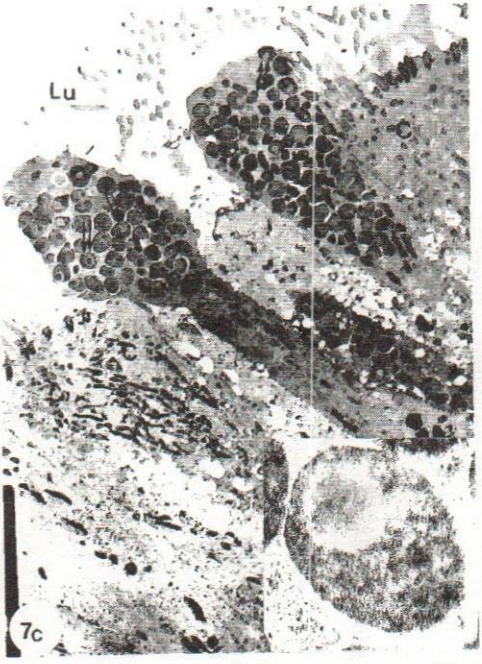
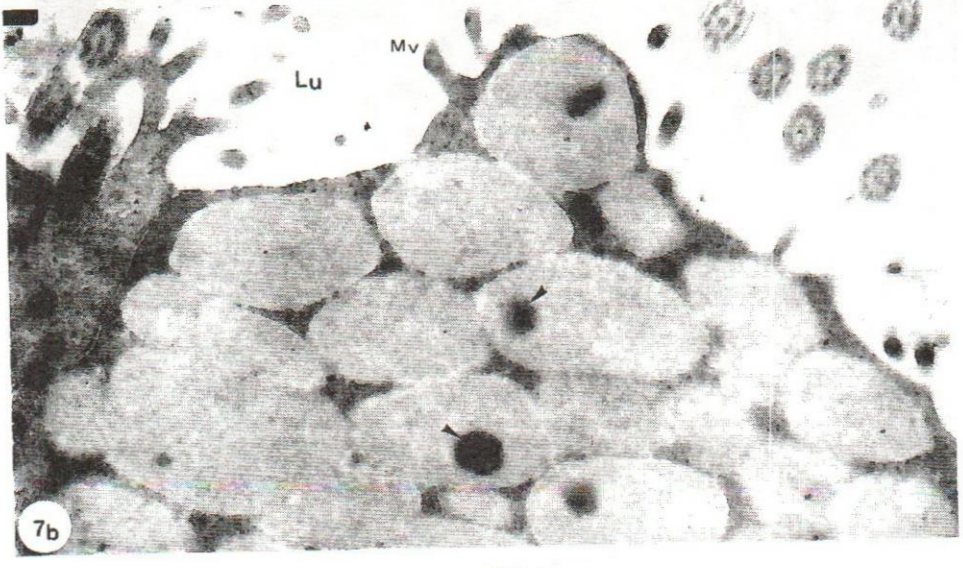
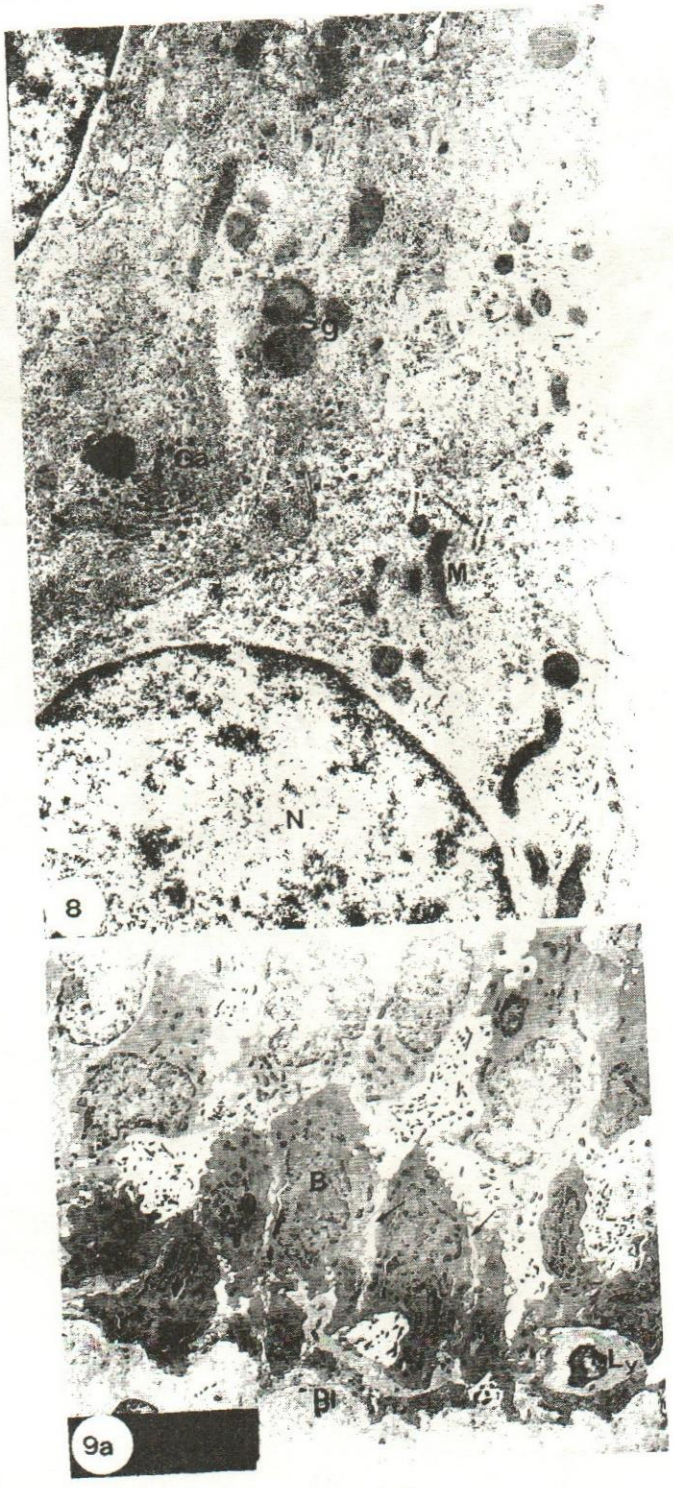
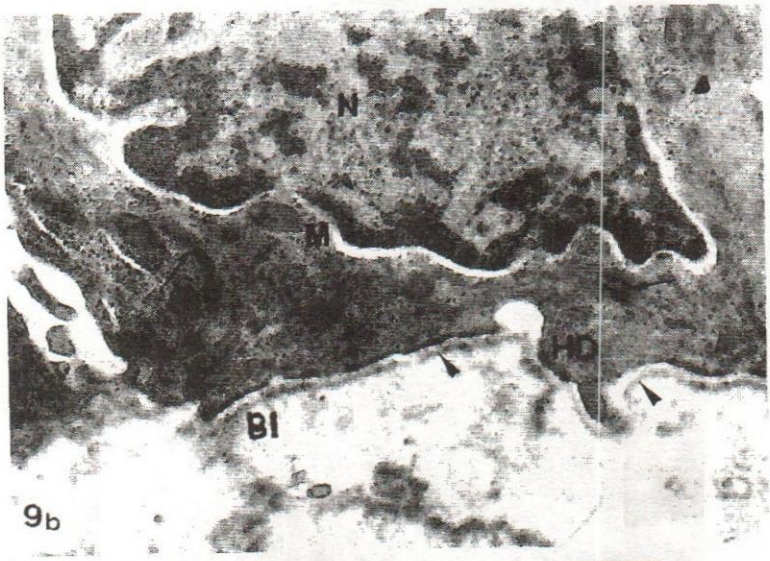

Lu
Mv
7a

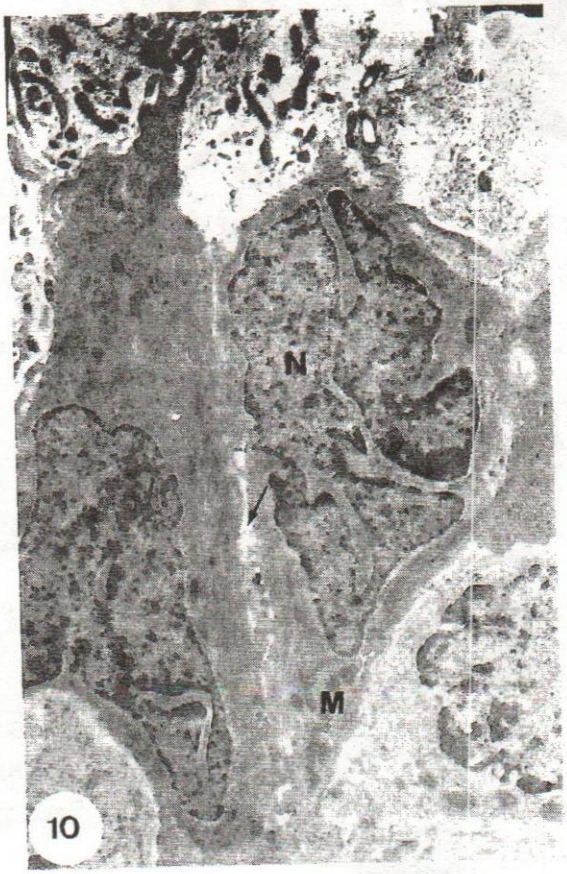

Lu
7c


Mv
Lu
7b


g
Ca
M
N
8
B
Ly
Bl
9a



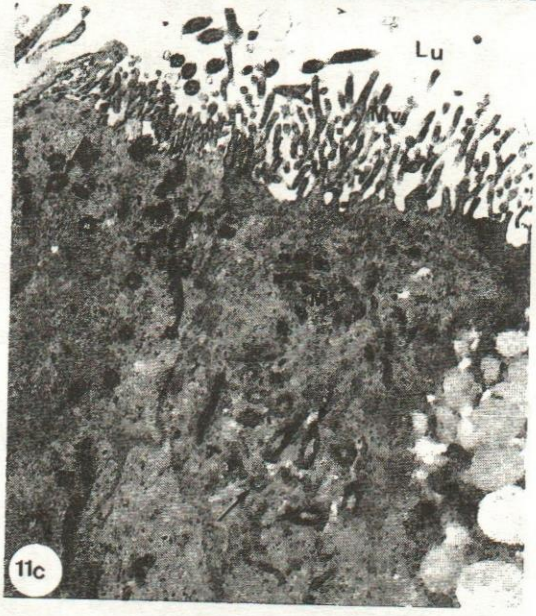
9b



10

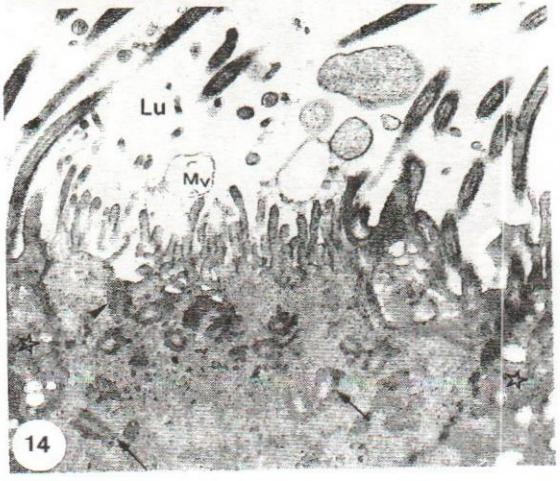

Mv
Lu
M
11a

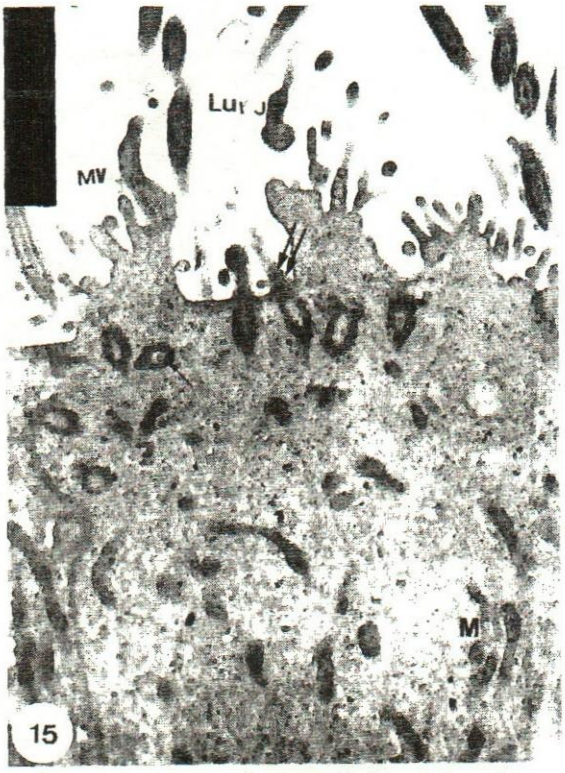

Ci
Lu
Mv
G
11b


Lu
11c


Mv
Lu
M
12


Lu
Mv
M
13


Lu
Mv
14


MV
M
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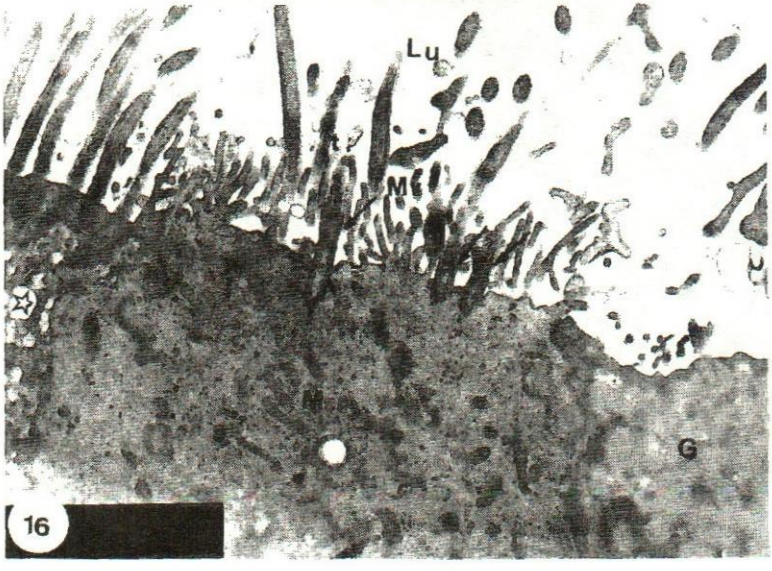
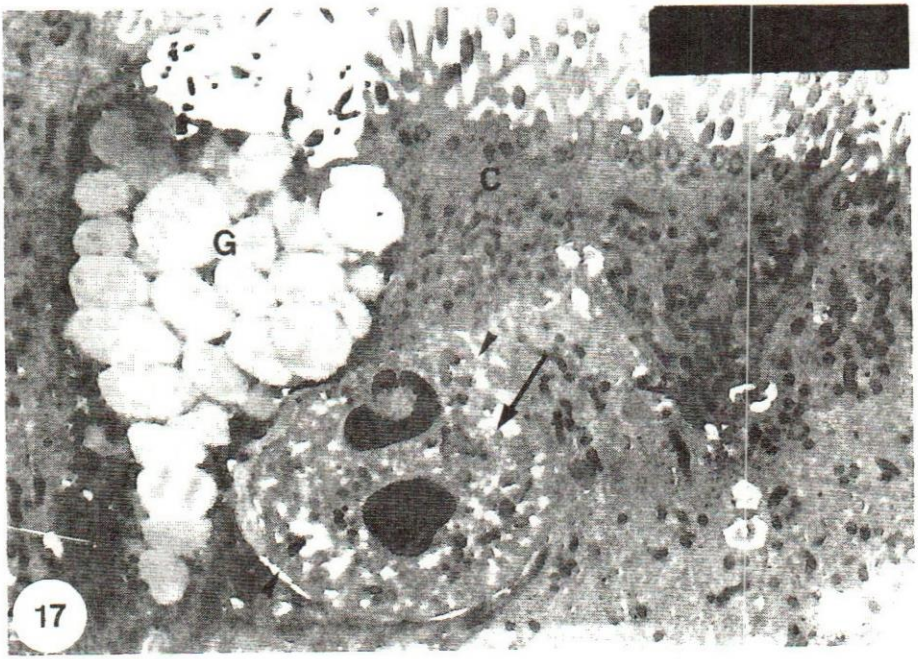

Lu
M
G
16


C
G
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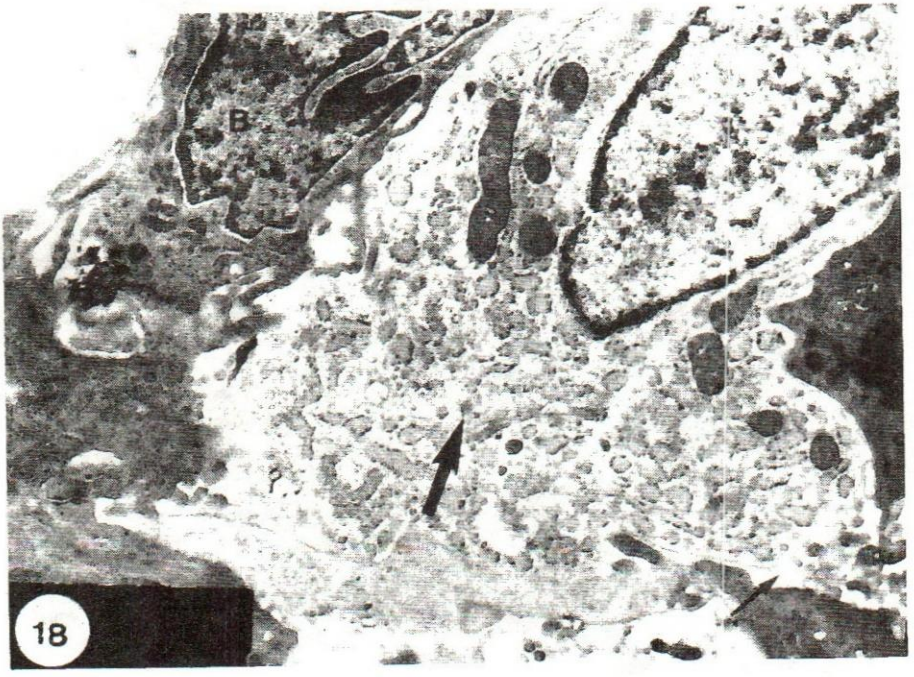
B
18