The Distribution and Surface Ultrastructure of Airway Epithelial Cells in the Rat Lung: A Scanning Electron Microscopic Study

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Summary. The fine structure and distribution of the epithelial cells of the airway in the rat were studied continuously from the trachea to terminal bronchioles by scanning electron microscopy (SEM). The airway could be divided into three different regions according to cell population: 1) the trachea and extrapulmonary bronchi; 2) intrapulmonary bronchi (larger than 500 μm in caliber); and 3) bronchioles (smaller than 500 μm in caliber). From their surface structures, the epithelial cells could be classified into ciliated and non-ciliated cells, the latter including brush cells, Clara cells and other non-ciliated (secretory) cells.

1. Ciliated cells. The cilia are longer, thicker and more numerous in the trachea; they decrease in length, thickness and number toward the periphery.

2. Brush cells. They possess thin microvilli (0.2 μm in thickness) in the trachea and extrapulmonary bronchi, with a rounded end. In the bronchioles they possess thick microvilli (0.3 μm in thickness) abruptly ending in a right angle edge. The brush cells are distributed sparsely but rather uniformly, and apt to be grouped in two or more cells.

3. Clara cells. Their apical cytoplasm shows a domed or papillary swelling and possesses a few microvilli. The Clara cells are distributed in the bronchioles and can already be found some distance proximal to the bronchial furcations into bronchioles.

4. Other non-ciliated (secretory) cells. Their apical cytoplasm seems to contain secretory granules immediately beneath the cell surface. They often gather in groups in the trachea and extrapulmonary bronchi, tending to form large areas corresponding to sites supported by tracheal or bronchial cartilage.

There were found several orifices in tracheal or bronchial glands whose long axes paralleled the tracheal or bronchial axes.

Dome-shaped elevations sometimes appear near the branching points of the intrapulmonary bronchi. They were regarded as bronchus-associated lymphoid tissue (BALT).

Lung cancer is now the leading cause of death from cancer for males in 35 countries. Since KIMURA (1978) reported that 84% of lung adenocarcinoma resembled non-ciliated bronchiolar cells (Clara cells), the structure and frequency of non-ciliated cells including Clara cells have come to be an important point of attention.

Systematic surveys in mammals of the cell types and their distribution at different levels of the airway by means of light microscopy (LM) and transmission electron microscopy (TEM) have been carried out in the rat (JEFFERY and REID, 1975), hamster (KENNEDY et al., 1978), mouse (PACK et al., 1981), and sheep (MARIASSY and PLOPPER,
1983). In these studies, the frequency of occurrence for the epithelial cells was determined by cell counting in certain sections, and regarded as being identical for each airway level. On the other hand, in studies by means of scanning electron microscopy (SEM) made in the mouse (GREENWOOD and HOLLAND, 1972), rat (ANDREWS, 1979), and man (GREENWOOD and HOLLAND, 1975), the cell types of the epithelial cells were mentioned, but reporting on the distribution was limited.

Several important problems still remain to be elucidated by SEM, and are listed below:

1. Can the non-ciliated cells be classified by their surface structure? ANDREWS (1974, 1979) regarded the extrapulmonary non-ciliated cells (except the brush cells) as goblet cells in his SEM study. On the other hand, JEFFERY and REID (1975) subdivided them into goblet, serous and intermediate cells.

2. Are the cells evenly distributed? JEFFERY and REID (1975) counted the cells on the assumption that their incidence of occurrence at each airway level was even; ANDREWS (1974), however, reported that there were large patches of goblet cells in the extrapulmonary airway.

3. Where is the most proximal site of Clara cell distribution? JEFFERY and REID (1975) indicated that the Clara cells were found proximally as far as the hilus, but were unable to point out the exact limit.

The present study aims to re-examine by the use of SEM the surface characteristics of the rat airway epithelia and to elucidate their fine surface structure and distribution, continuously from trachea to terminal bronchioles.

**MATERIALS AND METHODS**

Twelve male albino Wistar rats, weighing 200-250 g, were used in this study. They were killed by dislocation of the cervical vertebrae in order to avoid the influence of anesthesia to the airway secretion. The trachea and lungs were then exposed and filled via the trachea with 2% glutaraldehyde in 0.1 M phosphate buffer at pH 7.3 until the lungs were inflated to original size and the larynx was ligated to preserve its dimensions. After several minutes the specimens were quickly removed from the chest area and dissected with fine scissors and razor blades under a binocular microscope in order to expose the luminal surfaces of the airways on cut surfaces. They were then immersed in the same fixative for 6 hrs or more. In accordance with the conductive staining technique by MURAKAMI (1974), the tissues were put in an aqueous solution of 2% glycine, 2% sodium glutamate and 2% sucrose for 5 to 16 hrs, in a 2% aqueous solution of tannic acid for 6 to 24 hrs, and in a 2% aqueous solution of osmium tetroxide for 6 hrs. The specimens were dehydrated in increasing concentrations of ethanol, transferred to isoamyl acetate and critical point-dried using liquid carbon dioxide. The dried specimens were mounted on alminum stubs with silver paste and evaporated with gold-palladium. Observation was carried out with a Hitachi S-450 LB SEM or a Hitachi HFS-2 SEM under an accelerating voltage of 10 kV.

The specimens for TEM were made by conventional techniques using the same fixative. The specimens for LM were fixed with Bouin's solution and the paraffin sections were stained with hematoxylin and eosin, or impregnated according to the Grimelius technique.
RESULTS

In the rat, the right lung is divided into four lobes (the upper, middle, lower and accessory lobes), while the left lung is not divided. Each lung has one major airway (axial or lobar bronchus) with short lateral branches (secondary bronchi). The caliber of the axial bronchus in this study was about 2 mm on the left and 1.5 mm on the right. The generation numbers of the bronchi and bronchioles were not always correlated with their calibers. For our purposes, the rat airway was observed uninterruptedly from the trachea to terminal bronchioles, and was divided into three regions by cell frequency: 1) the trachea and extrapulmonary bronchi; 2) intrapulmonary bronchi (larger than 500 μm in caliber); and 3) bronchioles (smaller than 500 μm in caliber).

1. The trachea and extrapulmonary bronchi

Ciliated cells and non-ciliated cells in this region were clearly visible under the SEM (Fig. 1).

In luminal surface views, the ciliated cells were polygonal in outline and densely covered with cilia (200-250 per cell) and microvilli. The former were approximately 6 μm in length and 0.25 μm in thickness (Fig. 3). At places there were probable immature ciliated cells covered by a small number of short cilia (less than 1 μm in length) and by many microvilli (Fig. 5). The ciliated cells were distributed throughout this extrapulmonary airway; only in a few areas were they at all present (see below).

Fig. 1. Ciliated cells (C) and non-ciliated cells (NC) in the trachea. Non-ciliated cell dominant areas tend to correspond to the sites supported by tracheal cartilages. ×77
Fig. 2. Non-ciliated cells varying in shape and surface structure. ×1,800

Fig. 3. Ciliated cells in the trachea. The cilia here are approximately 6 μm in length and 0.25 μm in thickness. ×1,800

Fig. 4. An orifice of a tracheal gland (arrow). ×820
Brush cells, or one type of the non-ciliated cells, were clearly defined by a dense population of thick microvilli (counting about 130 per cell) on their free surfaces (Fig. 6). Their microvilli were significantly taller (about 2 μm in length), thicker (about 0.2 μm in thickness) and more straight than those of the other non-ciliated or the ciliated cells, terminating in a rounded end. These cells occurred only sparsely (up to 1% of all epithelial cells), and tended to be grouped in two or more cells.

The other non-ciliated cells varied in shape and surface structure (Fig. 2). Most of these non-ciliated cells were polygonal or elliptical in luminal surface outline (about 10 μm in short diameter and 15 μm in long diameter) and projected their cytoplasm into the lumen in various degrees (Fig. 7). They usually had smooth apical surfaces, but were provided with a small number of short microvilli (0.2–0.4 μm in length and 0.2 μm in thickness). Often small elevations were found on their luminal surfaces apparently due to the secretory granules closely beneath the cell surfaces. These elevations were especially developed on the cells with a domed apex. Some of the non-ciliated or secretory cells, which were round in luminal surface outline (4–8 μm in diameter) and protruded a large round cytoplasm into the lumen, possessed somewhat long microvilli (up to 1 μm in length and about 0.2 μm in thickness) on their surfaces (Fig. 8). These secretory cells occurred evenly and occupied 20–30% of the epithelial cells. Sometimes they gathered in groups to comprise more than 80% of the epithelial cells; such secretory cell dominant areas tended to be located in sites corresponding to those supported by the tracheal or bronchial cartilages (Fig. 1). Furthermore, flat non-ciliated cells with fine granular (0.2 μm in thickness) and/or filamentous (0.5–1.5 μm in length) microprojections on their surfaces were found in groups forming what may be

![Fig. 5. A probable immature ciliated cell with short cilia (I) and a brush cell (B). ×3,700](image)

![Fig. 6. A proximal brush cell (B) with thin microvilli (0.2 μm in thickness) and secretory cells (S). ×4,800](image)
designated as the flat cell dominant areas where few ciliated cells could be seen (Fig. 10, 11). These flat cells initially appeared at the extrapulmonary bronchi, occurring generally in the intrapulmonary bronchi. The sizes of these areas varied from a small circle (20 μm in diameter) to a large ellipsoid (about 500 μm in short diameter and 2 mm in long diameter). They were topographically independent of the sites of the tracheal or bronchial cartilages.

There were also found several orifices of tracheal or bronchial glands (Fig. 4). They were cleft-like in shape, measuring 5–30 μm in width and 50–100 μm in length. Their long axes tended to parallel the tracheal or bronchial axes. The epithelial cells around the orifices were chiefly non-ciliated cells.

2. Intrapulmonary bronchi (larger than 500 μm in caliber)

The ciliated cells were diffusely distributed in this region, occupying 70–80% of the epithelial cells (Fig. 9).

Among the ciliated cells could be seen the brush and the secretory cells. The former did not exceed 1%, whereas the latter occupied 20–30% of the epithelial cells. The secretory cells in this region were essentially the same in shape as those in the trachea and extrapulmonary bronchi, although the cells projecting a large cytoplasm decreased in number and ultimately disappeared in this region. The shape of the brush cells in this region was the same as in the trachea and extrapulmonary bronchi. The flat non-ciliated cells were also found in this region and formed the flat cell dominant areas, which became smaller (less than 20 μm in diameter) in the more distal portions.
Fig. 9. Ciliated cells (C) and non-ciliated cells (NC) in the intrapulmonary bronchi. ×160

Fig. 10. A flat cell dominant area. The cells are not ciliated. ×1,100

Fig. 11. High power view of a flat non-ciliated cell. ×4,500
Fig. 12. Clara cells (Cl) first appearing in the vicinity of the branching point to the bronchioles and non-ciliated cells or secretory cells (S). ×2,100

Fig. 13. Clara cells protruding the entire cytoplasm into the lumen. ×3,000

Fig. 14. Clara cells protruding a papillary cytoplasm. ×3,000
(Fig. 10, 11). Furthermore, there were occasional large dome-shaped elevations of the epithelium covered with a few ciliated cells and many flat non-ciliated cells (Fig. 19). These elevations varied from 250-500 μm in diameter at their base and were often found near the branching points to the smaller bronchi or bronchioles. The overlying flat cells were frequently covered with many granular microprocesses on their surface (Fig. 20). Some lymphocytes could be seen at the portion where the epithelium had accidentally peeled off (Fig. 21).

In the distal regions of the axial bronchi or in the vicinity of the branching points to the smaller bronchi or bronchioles appeared a different type of non-ciliated cell (Fig. 12). This had a protruding cytoplasm taller than the cilia of the ciliated cells and possessed granular or knobbed microprojections of various length and density on its luminal, uneven surfaces. Such cells were identified as Clara cells, because they were the same in surface structure as the so-named cells at the terminal bronchioles and, in TEM (Fig. 15), possessed abundant agranular endoplasmic reticulum and numerous membrane-bound ovoid granules in the apical cytoplasm. Furthermore, the apical cytoplasm occasionally contained a membrane-bounded crystalline structure which has been reported in Clara cells of the rat and some other mammals (KUHN et al., 1974; SMITH et al., 1979) (Fig. 15). At furcations of the bronchi and/or bronchioles, aggregations of 30-50 cells similar in surface structure to Clara cells were occasionally found forming irregular elevations. The possible nature of these cell groups will be discussed later.

3. Bronchioles (smaller than 500 μm in caliber)

Ciliated cells were found uniformly in this region, occupying 50% of the epithelium; they, however, gradually decreased in population toward distal airways. In the terminal bronchioles, the ciliated cells occupied only 20-30% of the epithelium (Fig. 12). The cilia in the distal region were 3 μm in length, 0.2 μm in thickness and numbered less than 50 per cell. These cilia were characterized by tapered ends, in contrast to the long columnar cilia in the proximal airways.

Brush cells were also observed, albeit sparsely, in this region. There were, however, some differences in surface structure between the proximal and distal brush cells (Fig. 8, 17). The microvilli of the brush cells in this region were thicker and more numerous than those of the proximal brush cells: the microvilli measured 0.3 μm in thickness and counted 90 in number per cell. Furthermore, the microvilli ended in a sharp and abrupt cut, displaying ends with right angle edges.

Secretory cells, as were observed in the upper airways, could not be found in this area, while there did appear a number of the Clara cells with protruding cytoplasm into the lumen, taller than the cilia of the ciliated cells (Fig. 16). The Clara cells were rough surfaced with granular or knobbed microprocesses of different numbers (0.2-1.0 μm in diameter) on them. Some of the Clara cells extended their whole apical cytoplasm into the lumen (Fig. 13), while others projected their cytoplasm papillarily (Fig. 14). Both of the protrusions occurred independently. The Clara cells first appeared near the furcations into bronchioles (smaller than 500 μm in caliber). Their population was 50% of the epithelium in the bronchioles and 70-80% in the terminal bronchioles.

There could also be seen Clara-like cell aggregations at the furcations of the bronchioles—except for the terminal bronchioles—as well as at the bifurcations of intrapulmonary bronchi (Fig. 18).
Fig. 15. TEM view of a Clara cell possessing abundant agranular endoplasmic reticulum (A), numerous membrane-bound ovoid granules (G), a crystalline structure (C) and nucleus (N). ×12,000
DISCUSSION

The present SEM study demonstrated the fine structure and distribution of the ciliated and non-ciliated cells in three different regions of the rat airway.

Ciliated cells

The present study revealed that the cilia in the trachea are longer ($6 \mu\text{m}$ in length) and thicker ($0.25 \mu\text{m}$ in thickness) than those in the terminal bronchioles ($3 \mu\text{m}$ in length and $0.2 \mu\text{m}$ in thickness). The decrease in length and thickness of the cilia depends on the caliber of the airway.

Jeffery and Reid (1975) reported in their LM study of the rat that ciliated cells constituted 17% of epithelial cells in the upper trachea, 33% in the lower trachea, and 35% in the main bronchi. The present study, however, revealed that the percentage of
the ciliated cells to the whole epithelial cells varied from place to place (from less than 10% to 80%) in the trachea and extrapulmonary bronchi, though it was constant in the intrapulmonary bronchi (70-80%) and in the bronchioles (50%). This finding on the heterogenous distribution of ciliated and non-ciliated cells in the rat airway seems to correspond to the report by ANDREWS (1974) who mentioned that areas populated with few ciliated cells are occupied by 'goblet cells'. The reason is obscure as to why these areas tend to be located corresponding to the sites supported by tracheal or bronchial cartilage.

**Brush cells**

The present study is first to reveal structural differences between the proximal and distal brush cells: the proximal ones possess thinner microvilli, about 0.2 \( \mu m \) in thickness, while the distal ones possess thicker microvilli, about 0.3 \( \mu m \) in thickness. This difference has not been noticed in any of the numerous TEM studies in the literature. The detailed nature and the significance of the microvillous heterogeneity deserve further investigations.

LING-YI CHANG et al. (1986) described how brush cells had a distinct topographic location supporting a population of less than 0.5-3% of the epithelial cells. In the present study, however, the brush cells were distributed almost uniformly over the airway, occupying about 1% of all epithelial cells. The reason for this discrepancy remains to be clarified.

Various functions such as absorption (RHODIN and DALHAMN, 1956), chemoreception (LUCIANO et al., 1968) or endocrine function (Taira and SHIBASAKI, 1978) have been proposed for the brush cell. In this study, however, no evidence suggesting any of these functions was found.
Clara cells

SMITH et al. (1979) and PLOPPER et al. (1980) demonstrated in their SEM and TEM studies of rat bronchioles that the Clara cells projected their entire apical surface high above the surrounding ciliated cells. On the other hand, ANDREWS (1979), in his SEM study of the rat bronchioles, described Clara cells as knobby-surfaced. The present study, however, showed both surface structures of Clara cells in the rat bronchioles. The various surface structures may possibly reflect differences in active secretory phases or cell maturation.

The present study revealed the Clara cell distribution in the rat airway. In their LM and TEM studies in the rat, JEFFERY and REID (1975) briefly noted that the cells were located proximally as far as the hilus of the lung. The present study, however, demonstrated that the Clara cells occurred distal to the furcations of the bronchi into

Fig. 18. A Clara-like cell aggregation at the furcation of intrapulmonary bronchi. 
×2,000
Fig. 19. A large dome-shaped elevation of the epithelium which presumably corresponds to a bronchus-associated lymphoid tissue (BALT). \( \times 160 \)

Fig. 20. High power view of a flat non-ciliated cell of the elevation shown in Figure 19. \( \times 2,700 \)

Fig. 21. Some lymphocytes \((L)\) appearing at the portion where the epithelium has peeled off. \( \times 1,800 \)
Fig. 22. Schematic representation of the distribution of rat airway epithelial cells. A. Ciliated cells: these number from less than 10% up to 80% of the total population of epithelial cells in the trachea and extrapulmonary bronchi, 70-80% in the intrapulmonary bronchi and 50% in the bronchioles. B. Non-ciliated cells (except for brush cells and Clara cells) or secretory cells: they vary in shape from flat forms to cells projecting a large round cytoplasm into the lumen. Note that areas with a dense population of this cell type (more than 90%) correspond to the zones supported by tracheal or bronchial cartilages. The cells are rather thinly distributed (20-30%) in the intrapulmonary bronchi, to eventually disappear from this region. C. Clara cells: These occupy almost 50% of the population from the vicinity of bronchial furcations into bronchioles to the terminal bronchioles. D. Brush cells: they often appear in two or more cells and occupy about 1% of all the airway.
bronchioles (less than 500\,\mu m in caliber) as well as in the distal regions of the lobar bronchi.

**Other non-ciliated cells**

In their TEM Study in the rat trachea, RHODIN and DALHAMN (1956) identified the non-ciliated cells (except for the brush cells) with the goblet cells. ANDREWS (1974) also gave a similar interpretation of the non-ciliated cells. On the other hand, JEFFERY and REID (1975) wrote in their TEM study of the rat airway epithelium that the non-ciliated cells (except for the brush cells and the Clara cells) could be divided into three types: the goblet, serous and intermediate cells. The present study could not distinguish these three types. Our TEM observations indicated that most non-ciliated cells (except for the brush cells) in the trachea or bronchi can be identified as secretory cells with electron-dense granules of a more or less typical serous nature (unpublished data). If the observed cells correspond to the serous cells, the variety in surface structure of these cells may presumably reflect differences in the secretory phases of the cells.

The flat surface cells appeared in two patterns. The first of these was a formation of the flat cell areas which arbitrarily occurred in the trachea or bronchi. Although they may possibly correspond to secretory cells which do not project their cytoplasm into the lumen, no description for such flat cells has previously been offered by LM or TEM. The identification of these flat cells thus remains a subject for further studies. The second pattern was a cell distribution covering large elevations which tended to occur near the branching points of the intrapulmonary bronchi. In this case, there is the possibility that these flat cells are the covering cells of a lymphoid tissue (see below).

**Other findings**

At the branching points of the intrapulmonary bronchi, or in all bronchioles except the terminal bronchioles, several non-ciliated cell aggregations were recognized. Similar aggregations were observed by FOLIGUET et al. (1982) using SEM in the newborn rat airway, who noted that such aggregations corresponded to the neuroepithelial bodies. In the airways of the adult rats examined in the present study, however, we could not find any cell clusters suggesting neuroepithelial bodies, either by Grimelius silver impregnation or immunocytochemistry for serotonin and gastrin releasing peptide (unpublished data). The possibility that the non-ciliated cell aggregations may correspond to neuroepithelial bodies can not be excluded, but our findings support the view that the neuroepithelial bodies are lacking in the adult rat airway.

The present study revealed the presence of large dome-shaped elevations near the branching points of the intrapulmonary bronchi. Using LM, similar elevations of the lumen due to lymphoid tissue were observed (unpublished data). The elevations as seen in SEM are thus suggested to be, at least to a majority, bronchus-associated lymphoid tissue (BALT). BIENENSTOCK and JOHNSTON (1976) reported in their SEM and TEM studies of the bronchial epithelium of rabbits that islands of lymphoepithelium consisted of lymphocyte aggregations and flattened non-ciliated cells possessing microvilli. The present study, however, showed that the covering epithelial cells of rat BALT were flat. The difference between the rabbit and rat may be derived from the thickness of the cytoplasm of the non-ciliated cells which cover the lymphoid tissue.
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REFERENCES

Andrews, P. M.: A scanning electron microscopic study of the extrapulmonary respiratory tract. Amer. J. Anat. 139: 399-424 (1974).
Andrews: The respiratory system. In: (ed. by) G. M. Hodges and R. C. Hallowes: Biomedical research applications of scanning electron microscopy. Academic Press, London, 1979 (p. 177-202).
Bienenstock, J. and N. Johnston: A morphologic study of rabbit bronchial lymphoid aggregates and lymphoepithelium. Lab. Invest. 35: 343-348 (1976).
Chang, L.-Y., R. R. Mercer and J. D. Crapo: Differential distribution of brush cells in the rat lung. Anat. Rec. 216: 49-54 (1986).
Foliguet, B., C. Desplechain, G. Grignon, L. Marchal and F. Touati: Etude du poumon en microscopie electronique a balayage. Bull. Assoc. Anat. (Nancy) 66: 297-358 (1982).
Greenwood, M. F. and P. Holland: The mammalian respiratory surface. A scanning electron microscopic study. Lab. Invest. 27: 296-304 (1972).
Jeffery, P. K. and L. Reid: New observations of rat airway epithelium: a quantitative and electron microscopic study. J. Anat. 120: 289-294 (1975).
Kennedy, A. R., A. Desrosiers, M. Terzaghi and J. B. Little: Morphometric and histological analysis of the lungs of Syrian golden hamsters. J. Anat. 125: 527-553 (1978).
Kimura, Y.: A histochemical and ultrastructural study of adenocarcinoma of the lung. Amer. J. Surg. Pathol. 2: 253-264 (1978).
Kuhn, C., L. A. Callaway and F. B. Askin: The formation of granules in the bronchiolar Clara cells of the rat. 1. Electron microscopy. J. Ultrastr. Res. 49: 387-400 (1974).
Luciano, L., E. Reale and H. Ruska: Uber eine "chemorezeptive" Sinneszelle in der Trachea der Ratte. Z. Zellforsh. 85: 350-375 (1968).
Mariassy, A. T. and C. G. Plopper: Tracheobronchial epithelium of the sheep: I. Quantitative light-microscopic study of epithelial cell abundance, and distribution. Anat. Rec. 205: 263-275 (1983).
Murakami, T.: A revised tannin-osmium method for non-coated scanning electron microscope specimens. Arch. histol. jap. 36: 189-193 (1974).
Pack, R. J., L. H. Al-Ugaily and G. Morris: The cells of the tracheobronchial epithelium of the mouse: a quantitative light and electron microscope study. J. Anat. 132: 71-84 (1981).
Plopper, C. G., A. T. Mariassy and L. H. Hill: Ultrastructure of the nonciliated bronchiolar epithelial (Clara) cell of mammalian lung: 1. A comparison of rabbit, guinea pig, rat, hamster and mouse. Exp. Lung Res. 1: 139-154 (1980).
Rhodin, J. and T. Dalhamn: Electron microscopy of the tracheal ciliated mucosa in rat. Z. Zellforsh. 44: 345-412 (1956).
Smith, M. N., S. D. Greenberg and H. J. Spjut: The Clara cell: A comparative ultrastructural study in mammals. Amer. J. Anat. 155: 15-30 (1979).
Taira, K. and S. Shibasaki: A fine structure study of the non-ciliated cells in the mouse tracheal epithelium with special reference to the relation of “brush cells” and “endocrine cells.” Arch. histol. jap. 41: 351-366 (1978).