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# The Ultrastructural Characteristics of the Apical Cell in the Neuroepithelial Bodies of the Toad Lung (*Bufo marinus*)

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**Summary.** The cytological features and membrane specialisations of neuroepithelial cells (apical cells) in direct contact with the lumen of the lung were studied with transmission and scanning electron microscopy. The luminal surface of the apical cell is characterised by microvilli, a cilium with an 8 + 1 microtubular pattern and numerous coated vesicles. The cytoplasmic region immediately beneath the luminal plasma membrane contains numerous smooth-walled vesicles, tubules and microtubules, a few microfilaments and dense granules (15–20 nm in diameter). The luminal pole of the cell is marked off from the basal or vascular pole by a well-defined terminal web associated with junctional complexes. Protrusion of the luminal pole occurs as a transient phenomenon and is accompanied by a pinching in of the cell at the terminal web. It is proposed that the distinctive features of the luminal pole of the apical cell are comparable to those of recognised chemoreceptor cells. It is also proposed that in view of the common features of apical and basal cells the apical cell functions as a receptor/transducer and the basal cells serve as an accessory source of peptides/5-hydroxytryptamine to be released on stimulation of the apical cell. Furthermore, we have drawn attention to the structural heterogeneity of the neuroepithelial bodies in various vertebrate classes.

**Key words:** Lung, *Bufo marinus* – Neuroepithelial bodies – Apical cell.

The epithelium lining the vertebrate respiratory tract contains groups of cells (neuroepithelial bodies or NEBs) with specific cytological chracteristics (Cook and King 1969; Lauweryns et al. 1972; Hung et al. 1973). These cell groups have been described under a variety of names by different authors, the names suggesting functional properties or embryological origin. We have chosen to use the term

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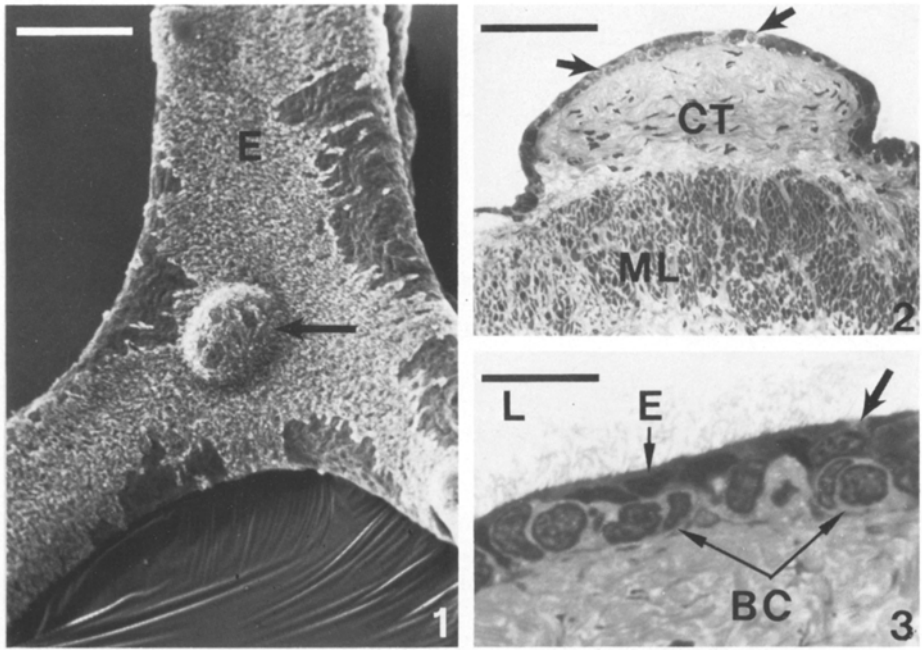



**Fig. 1.** Scanning electron micrograph of the surface features of the junction of three primary septa. Note the ciliated epithelial cells (*E*) and mound (*arrow*) elevated from the surface. Bar = 200 μm

**Fig. 2.** Low magnification light micrograph of a similar mound in cross-section. The neuroepithelial bodies appear as lightly stained groups within the epithelium at the surface of the mound (*arrows*). The connective tissue core (*CT*) of the mound is separated from the muscle layer (*ML*) of the septum by a lightly stained layer of connective tissue. Toluidine Blue stained. Bar = 75 μm

**Fig. 3.** High magnification light micrograph of a lightly stained neuroepithelial body separated from the lung lumen (*L*) by darkly stained ciliated epithelial cells (*E*). Only one apical cell (*arrow*) penetrates into the lung lumen, while the basal cells (*BC*) rest on the basement membrane. Toluidine Blue stained. Bar = 15 μm

neuroepithelial body for the cell groups (Lauweryns et al. 1972), and in conformity with this usage we will refer to the cells with specific cytological characteristics as neuroepithelial cells even though it implies a neuroectodermal origin, a matter that requires confirmation (Andrew 1976).

The NEBs in mice (Hung et al. 1973) and rats (Cutz et al. 1978) form small mounds of tissue elevated above the level of the general epithelium. These mounds are composed of neuroepithelial cells, ciliated epithelial cells and the cells of Clara.

The arrangement of the neuroepithelial cells in birds and mammals with respect to blood capillaries, nerve fibres and the surface of the epithelium has led to speculation that the NEBs have an endocrine/receptor function (Lauweryns et al. 1972; Hage 1976; Lauweryns et al. 1977; Lauweryns and Liebens 1977). This view is based at least in part on the fact that some of the neuroepithelial cells are in direct contact with the lumen of the respiratory tract (the apical cells), while others are not (the basal cells).

Description of the cytological features of NEBs has recently been extended to anuran amphibians (Rogers and Haller 1978; Wasano and Yamamoto 1978).

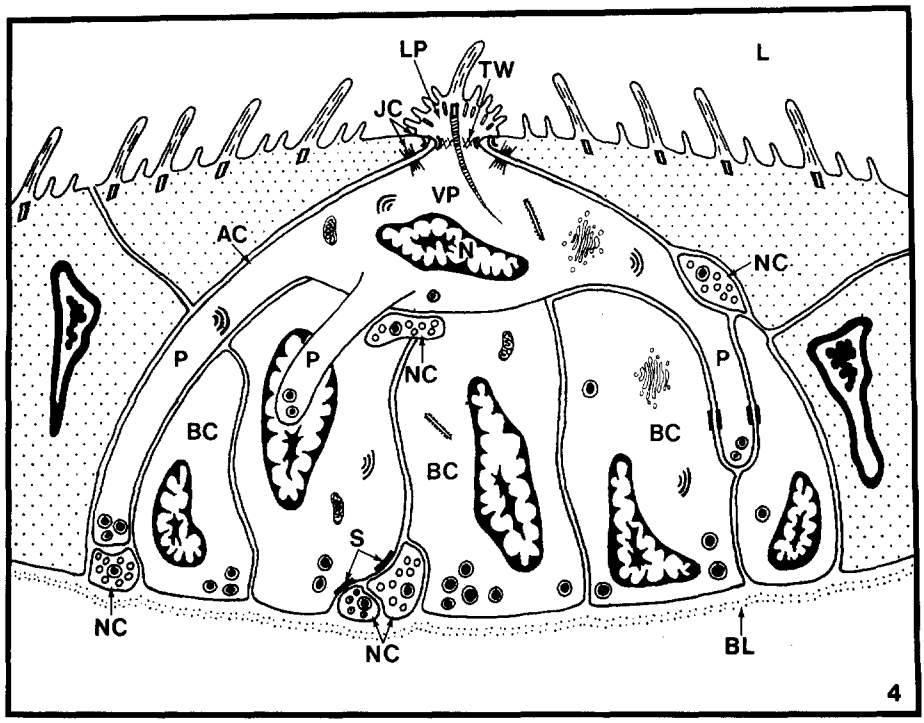



**Fig. 4.** Three-dimensional, diagrammatic representation of a section through a neuroepithelial body. A single apical cell (*AC*) is shown with its luminal pole (*LP*) projecting into the lumen of the lung (*L*) and its vascular pole (VP) containing the nucleus (*N*) resting on the upper surfaces of the basal cells (*BC*). Junctional complexes (*JC*) with an associated terminal web (*TW*) separate the two poles from each other. Three cytoplasmic processes (*P*) of the apical cell are shown radiating out from the vascular pole and passing over the adjacent basal cells. One of these processes reaches the basal lamina (*BL*). Nerve profiles (*NC*) are found in close contact with the cell processes and the vascular pole of the apical cell. Other neural profiles display synaptic specialisations (*S*) at the base of the basal cells. Epithelial cells (*shaded*)

While Wasano and Yamamoto failed to find apical cells in *Rana nigromaculata* leading them to speculate on a mechanoreceptor role for the NEB, Rogers and Haller observed both apical and basal types in *Bufo marinus*.

The present study provides a detailed description of the cytological characteristics of those neuroepithelial cells in an amphibian lung that are exposed to the luminal surface.

## Materials and Methods

Sixteen specimens of the toad *Bufo marinus* were anaesthetised and lung tissue dissected and prepared for transmission electron microscopy (TEM) as previously described (Rogers and Haller 1978). This material was processed either according to the method of Tranzer and Richards (1976) for the identification of biogenic amines, or the control fixative 2.5% glutaraldehyde maintained at pH 7.3 with 0.1 M Sorensen's buffer. Post-fixation was carried out in 1% $OsO_4$ with the same buffer.

Lung tissue from two more animals was prepared with glutaraldehyde fixatives and cacodylate buffer solutions containing ruthenium red according to the method described by Wright and Ross (1975).

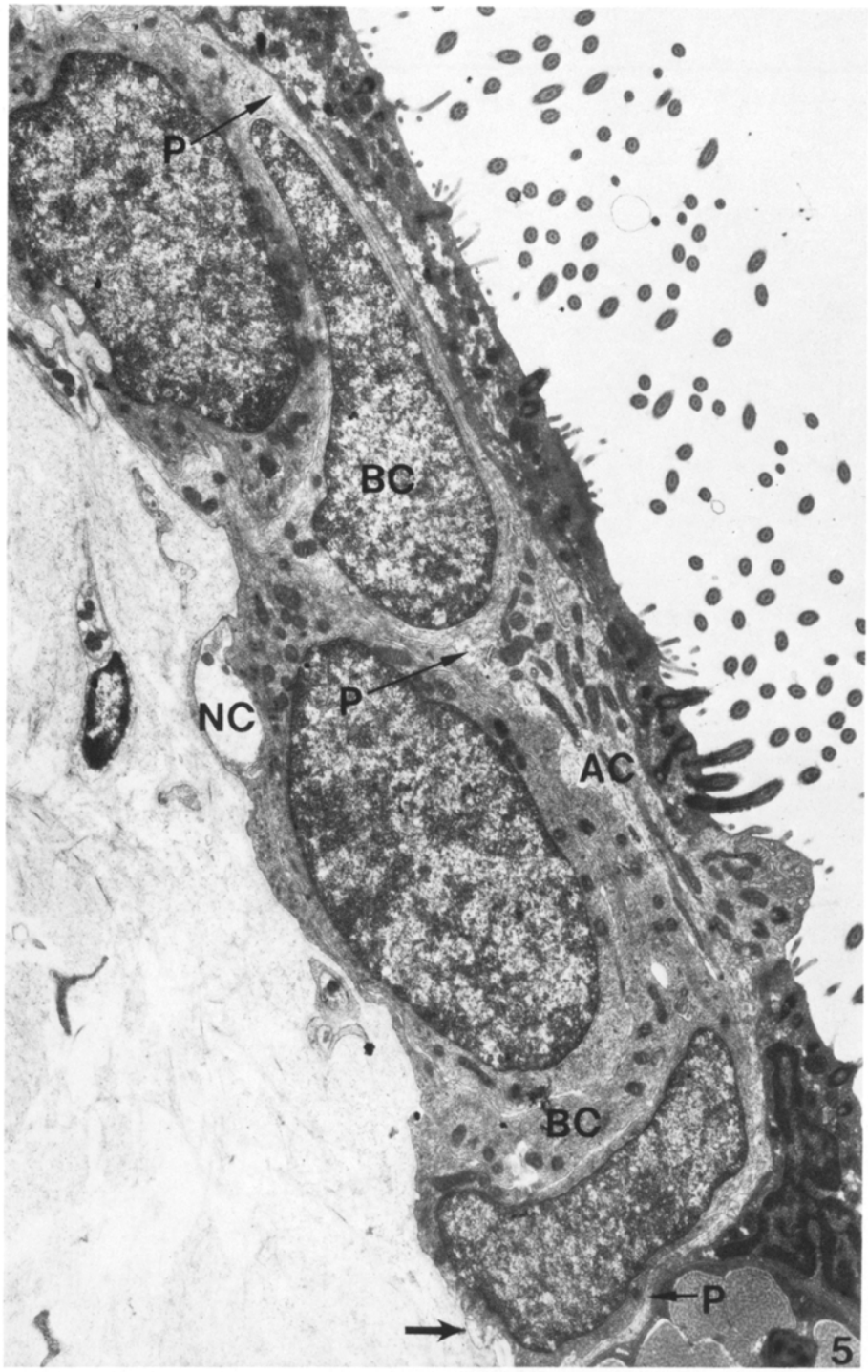



**Fig. 5.** One of a series of electron micrographs showing a neuroepithelial body consisting a five basal cells (*BC*) and one apical cell (*AC*). Three processes (*P*) of the apical cell are visible. One of these processes reaches the basal lamina (*arrow*). A number of nerve fibre profiles (*NC*) are visible below the basal lamina. The nucleus of the apical cell is not included in this section. Tranzer and Richards fixation. × 10,000

All material was dehydrated in a graded series of ethanol and embedded in Durcupan-Araldite. Thin sections were cut on a Huxley ultramicrotome with a diamond knife. Sections were stained with uranyl acetate and lead citrate and examined in a JEOL 100B transmission electron microscope.

*Scanning Electron Microscopy*

Lung tissue was fixed in 2.5 % glutaraldehyde, pH 7.3, (Sorensen's buffer) for 1 h at 20° C. The tissue was subsequently washed in the same buffer, dehydrated in increasing concentrations of ethanol for a total of 1 h before passing to a 1 : 1 solution of ethanol and amyl acetate for 1 h. The preparations were stored in amyl acetate. The tissue was critical point dried, mounted on metal stubs, gold sputter-coated and examined with a Cambridge scanning electron microscope.

*Light Microscopy*

1.0 μm thick serial sections were cut on a Huxley Ultramicrotome with glass knives and were stained with toluidine blue.

## Results

### *Light and Scanning Electron Microscopy*

Neuroepithelial bodies (Figs. 2, 3) invested by cells of Clara, mucous cells, mast cells and ciliated epithelial cells, form discrete, oval mounds (Figs. 1, 2) elevated above the surface of the general ciliated epithelium at the junctions of the primary septa.

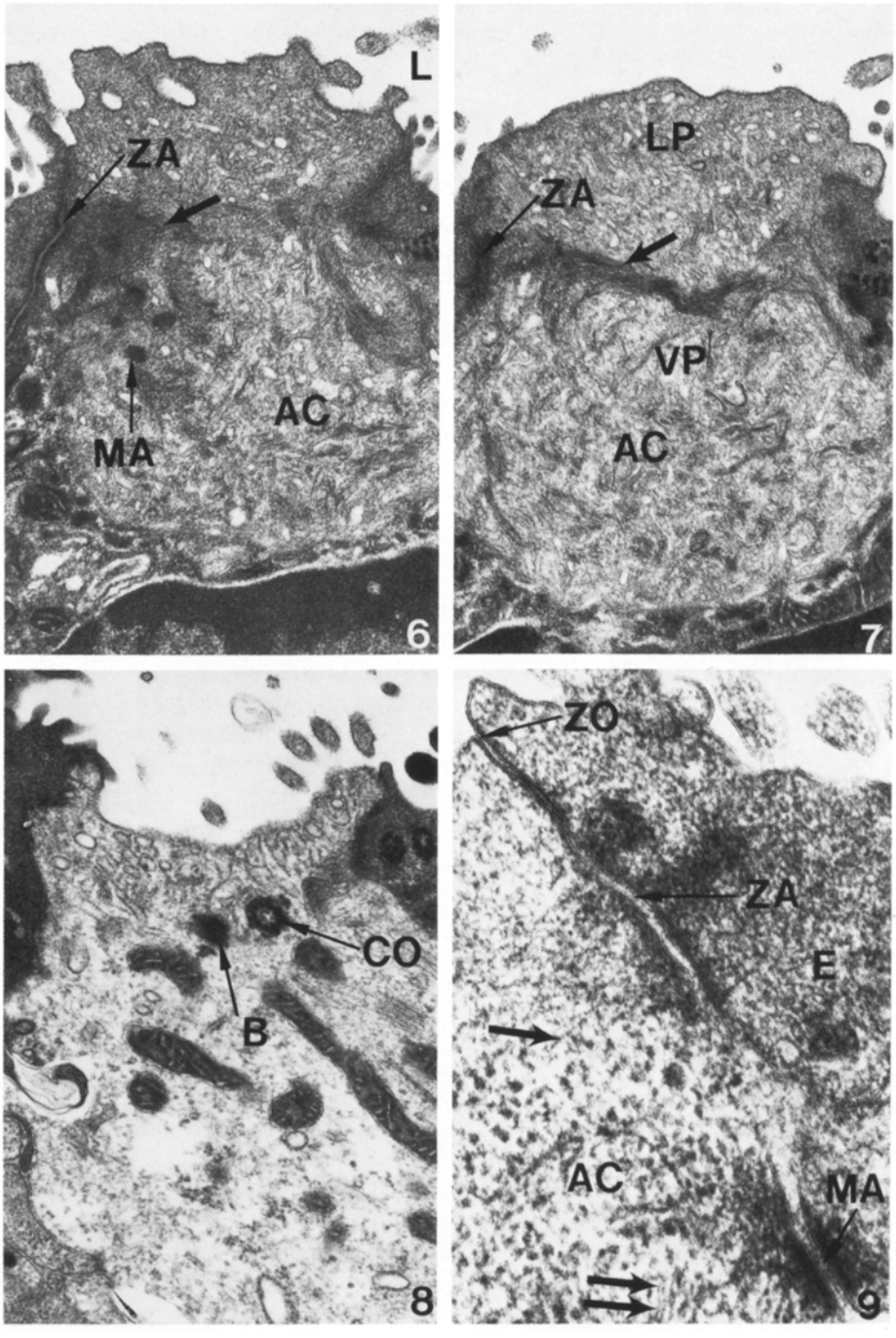
### *Light and Transmission Electron Microscopy*

Both 1.0 μm thick sections and ultrathin serial sections show that only one to three apical cells are present in each NEB. The majority of neuroepithelial cells do not make direct contact with the lumen of the lung and can therefore be referred to as basal cells.

Each apical cell can be divided into topographically distinct regions which are characterised by differences in number of organelles and secretory vesicles. To facilitate description of the specific features of these cells, reference should be made to Figure 4 where the following regions of the apical cell are shown in diagrammatic form:

(a) A luminal pole with a free surface exposed to the lumen of the lung and separated by a terminal web from (b) the vascular pole containing the nucleus and from which (c) cell processes diverge in a radial fashion.

The vascular pole of the apical cell has a semi-spherical appearance and lies embedded between the epithelial and basal cells (Fig. 5). The intercellular space between the apical and basal cells is for the most part fairly uniform and approximately 15 nm in width. Occasionally irregularly shaped expansions of the intercellular space occur.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Three to five cytoplasmic processes of variable length and thickness originate from the vascular pole (Figs. 4, 5). One or more of these processes reach the basal lamina (Fig. 5), the remainder clasp the upper poles of the basal cells that lie adjacent to each apical cell (Figs. 4, 5). These processes contain small dense granules (20 nm diameter), mitochondria, lysosomes and a few dense cored vesicles (Figs. 12, 13). At indefinite intervals accumulations of electron-dense material occur on the cytoplasmic margins of adjacent plasma membranes of apical cell processes and basal cells (Figs. 12, 13). These membrane specialisations take the form of discrete patches approximately 225 nm in diameter. The width of the intercellular space is reduced at these sites but we have not observed any specific structures within this space.

The luminal and vascular poles of the apical cell show marked quantitative and qualitative structural differences from each other. The cytological differences between these regions are particularly evident in those profiles that show the luminal pole bulging out into the lung cavity (Figs. 10, 14, 15). The cytoplasm at the luminal pole contains closely packed, numerous smooth-walled vesicles, tubules, mitochondria, microtubules and a few small dense granules (20 nm in diameter) (Fig. 14). The cytoplasm at the vascular pole contains numerous dense granules (20 nm in diameter), profiles of rough endoplasmic reticulum and mitochondria (Fig. 10). Cisternae of the Golgi complex (Fig. 12), coated vesicles and microtubules are thinly scattered throughout the cell body below the junctional complexes. A conspicuous and characteristic feature of the cell processes and vascular pole are microfilaments 10 nm in diameter grouped into distinct bundles (between 200 to 300 nm in diameter) (Fig. 10). These bundles weave throughout the cytoplasm, and we have not been able to observe if they attain any direct, structural connection with the plasma membrane. Dense-cored vesicles (average diameter 80 nm) occur sporadically throughout the cytoplasm below the junctional complexes (Figs. 11, 12).

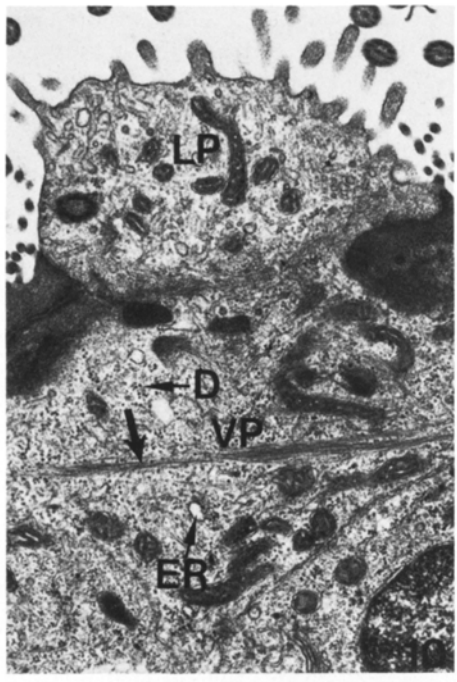
Microvilli (0.5–1.0 μm long, 0.16 μm in diameter) project from the surface of the luminal pole (Figs. 5, 10, 14). Between the bases of the microvilli, coated vesicles are occasionally observed (Fig. 14). The basal body and centriole of a cilium are situated in this region (Fig. 15). The root of a cilium with its typical banded pattern

**Fig. 6.** One of a series of oblique sections through an apical cell (*AC*) at the level of the terminal web. Note the 7 nm-microfilaments (*arrow*) at the level of the zonula adhaerens (*ZA*) and a number of oblique sections through a group of maculae adhaerentes (*MA*). The luminal pole of the apical cell projects into the lumen of the lung (*L*). Tranzer and Richards fixation. × 24,000

**Fig. 7.** One of a series of oblique sections through an apical cell (*AC*) at the level of the terminal web. Note the 10 nm-microfilaments (*arrow*) at the level of the zonula adhaerens (*ZA*). The cell body of the apical cell is clearly divided into a luminal pole (*LP*) and a vascular pole (*VP*). Tranzer and Richards fixation. × 24,000

**Fig. 8.** A section through an apical cell with an indented luminal pole. Note the basal body (*B*) and centriole (*CO*). Tranzer and Richards fixation. × 22,500

**Fig. 9.** High magnification of the junctional complex between an apical cell (AC) and an epithelial cell (E). Zonula occludens (*ZO*), zonula adhaerens (*ZA*), macula adhaerens (*MA*). Note 7 nm-microfilaments (*arrow*) and 10 nm-microfilaments (*double arrow*). Control fixation. × 75,000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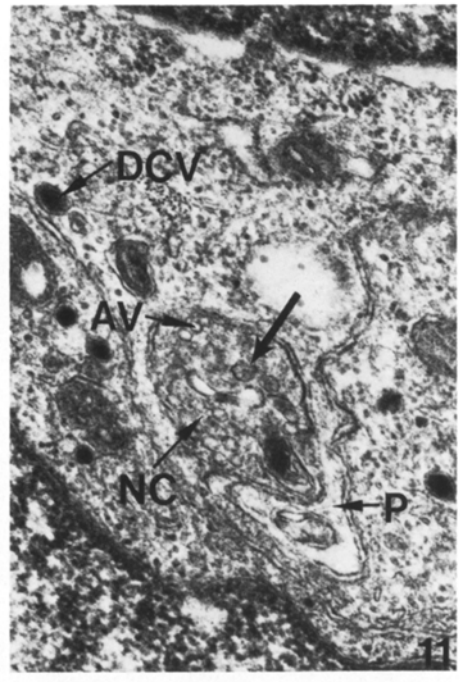
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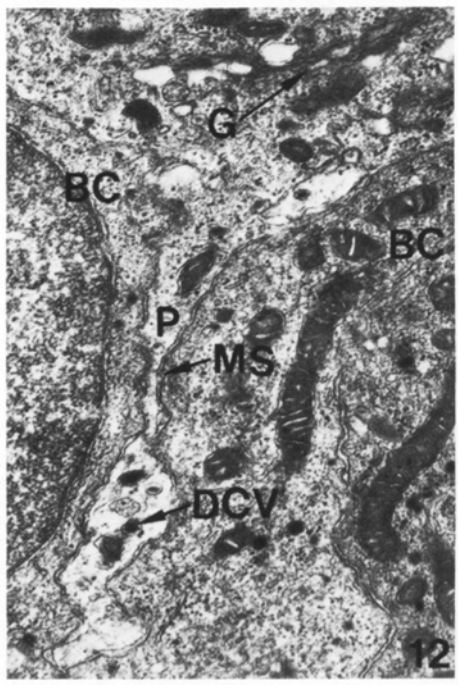
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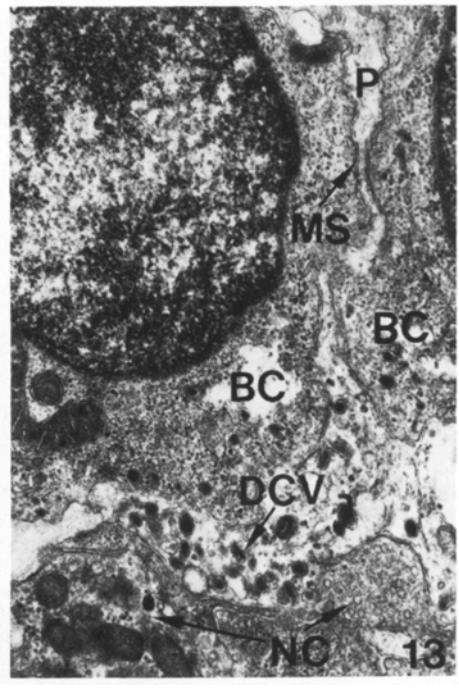
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passes from the luminal pole deep into the cytoplasm of the vascular pole (Fig. 15). The cilium has an 8 + 1 microtubular arrangement and can be clearly distinguished from the cilia of the epithelial cells which have a 9 + 2 pattern (Figs. 14, 15).

The apical cell is attached to the adjacent ciliated epithelial cells by well-defined junctional complexes consisting of a *zonula occludens, zonula adhaerens* and *macula adhaerens* (Fig. 9). These areas of membrane specialisation form a discrete group demarcating the boundary between the luminal and vascular poles. Core filaments of the microvilli intermingle at this boundary with a web of microfilaments associated with the junctional complexes (Figs. 4, 6, 7, 9). The microfilaments form a conspicuous feature, due to their dense packing, in those profiles showing the luminal pole cytoplasm bulging out into the lumen of the lung (Figs. 6, 7). The web of microfilaments is more dispersed and less conspicuous in those profiles showing the luminal pole indented (Fig. 8).

After treatment with ruthenium red the outer surfaces of the microvilli, cilium and apical plasma membrane were densely stained (Fig. 16).

Nerve fibre profiles containing a few large dense-cored vesicles (100 nm in diameter) and numerous clear vesicles (50 nm in diameter) lie in close proximity to the tips of those apical cell processes which reach the basal lamina (Fig. 13). No membrane specialisations or accumulations of vesicles at these sites has been observed. Nerve fibres of similar type have been observed adjacent to the tips of the apical cell processes and vascular pole of the cell body which remain deep within the NEB and do not reach the basal lamina (Fig. 11). No membrane specialisations have been observed at these sites.

## Discussion

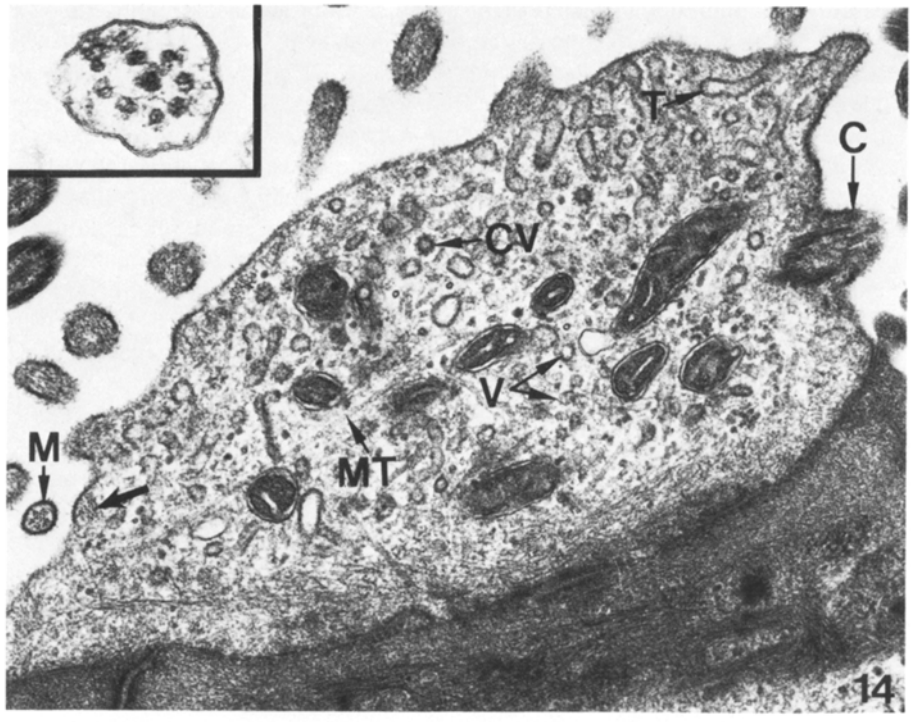
Although there have been numerous publications dealing with neuroepithelial bodies (NEBs) in mammals, birds and amphibians, the unique features of the

**Fig. 10.** Section through the luminal (*L*) and vascular pole (*VP*) of an apical cell. Note in the luminal pole vesicles and tubules, a basal body and the microvilli on the face surface. Note in the vascular pole bundles of 10 nm-microfilaments (*arrow*), small dense granules (*D*) and rough endoplasmic reticulum (*ER*). Tranzer and Richards fixation. × 15,000

**Fig. 11.** One section from a series showing a nerve profile (*NC*) situated at the base of a cytoplasmic process (*P*) arising from the vascular pole of an apical cell. Note the dense cored vesicles in both the apical cell (*DCV*) and nerve profile (*arrow*). Agranular vesicles (*AV*). Tranzer and Richards fixation. × 42,500

**Fig. 12.** Section through the base of the vascular pole of an apical cell. A cell process (*P*) passes down between two basal cells (*BC*). Note the Golgi complex (*G*), dense cored vesicles (*DCV*) and a membrane specialisation (*MS*). Tranzer and Richards fixation. × 20,000

**Fig. 13.** A section through an apical cell process (*P*) which reaches the basal lamina as it passes between two basal cells (*BC*). The tip of the process is in close contact with nerve fibre profiles (*NC*). Note the dense cored vesicles (*DCV*) in the cell process and the membrane specialisation (*MS*). Tranzer and Richards fixation. × 20,000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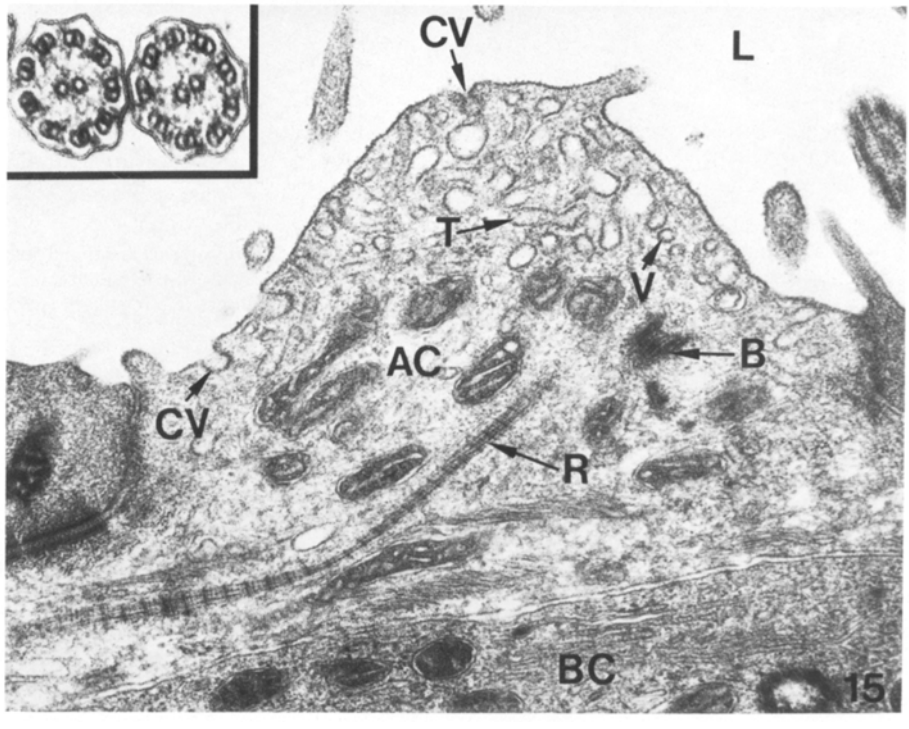
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luminal pole of the apical cell have not previously been given sufficient attention. This region of the apical cell is the only area of the NEB that comes into direct contact with the gases contained in the airways of the respiratory system.

Various authors (Lauweryns et al. 1972; Hung et al. 1973, 1979; Cutz et al. 1974; Cutz et al. 1978) have observed neuroepithelial cells reaching the luminal surface and some have commented on the presence of microvilli, the slight protrusion or indentation of the cell surface and the presence of a terminal web. These publications, however, fail to emphasise the fact that the luminal pole of the apical cell differs markedly from the basal or vascular pole both with respect to membrane specialisations and relative, quantitative distribution of cytoplasmic organelles and inclusions.

A striking feature of the NEB of *B. marinus* is a cilium located at the luminal surface of the apical cell with an 8 + 1 microtubular arrangement and a root deeply embedded in the cell body. The form of the cilium suggests that it is a sensory, non-motile type (Sorokin 1968). Structurally well-differentiated microvilli of the apical cell in Amphibia stand in some contrast to previous reports of rather poorly differentiated, irregularly arranged surface protrusions of mammalian neuroepithelial cells. The significance of these apparent differences will not become clear until serial section studies have been carried out on further mammalian and amphibian material. Recent scanning electron microscopic studies (Hung et al. 1979) on neonatal mice and near-term rabbit foetuses (Cutz et al. 1978) indicate that in these mammals the microvilli have a form and arrangement comparable to that of *B. marinus*. Although microtubules and filaments are distributed throughout the cytoplasm of the apical cell, microtubules are relatively more abundant in the region between the junctional complexes and luminal cell surface. Whereas a similar pattern of distribution applies to the dense granules (20 nm in diameter), the dense-cored vesicles are confined to those regions of the cell lying below the junctional complexes. The luminal and vascular poles of the cell differ in their liability for deformation. The noticeable bulbous protrusion of the luminal pole above the surface of the general epithelium is probably a transient phenomenon brought about by the "purse-string" effect (Rodewald et al. 1976) produced by forces generated in and transmitted through the microfilament/microtubular terminal web apparatus (Tilney and Cardell 1975; Rodewald et al. 1976). Protrusion of the cell is accompanied by the appearance of an increased number of smooth-surfaced vesicles and tubules in the cytoplasm immediately beneath the cell surface. The ruthenium red-experiments demonstrated that these structures were not open to the surface of the cell.

**Fig. 14.** High magnification of the luminal pole of an apical cell. A cilium (*C*) projects from one margin of the cell. A transverse section through one of the microvilli (*M*) arising from the surface of the apical cell shows a core of filaments. These filaments enter the cytoplasm (*arrow*). Smooth walled vesicles (*V*), tubules (*T*), microtubules (*MT*) and coated vesicles (*CV*) are prominent features of the cytoplasm. Tranzer and Richards fixation. × 37,500. *Inset:* Cross-section of an apical cell cilium. Note the 8 + 1 arrangement of tubules. Control fixation. × 75,000

**Fig. 15.** High magnification of the luminal pole of an apical cell (*AC*) showing the banded pattern of the long cilium root (*R*). Lung lumen (*L*), smooth walled vesicles (*V*) and tubules (*T*), coated vesicles (*CV*), basal body (*B*) and basal cell (*BC*). Tranzer and Richards fixation. × 37,500. *Inset:* Cross-section of two cilia from an epithelial cell. Note the 9 + 2 arrangement of tubules. Control fixation. × 75,000

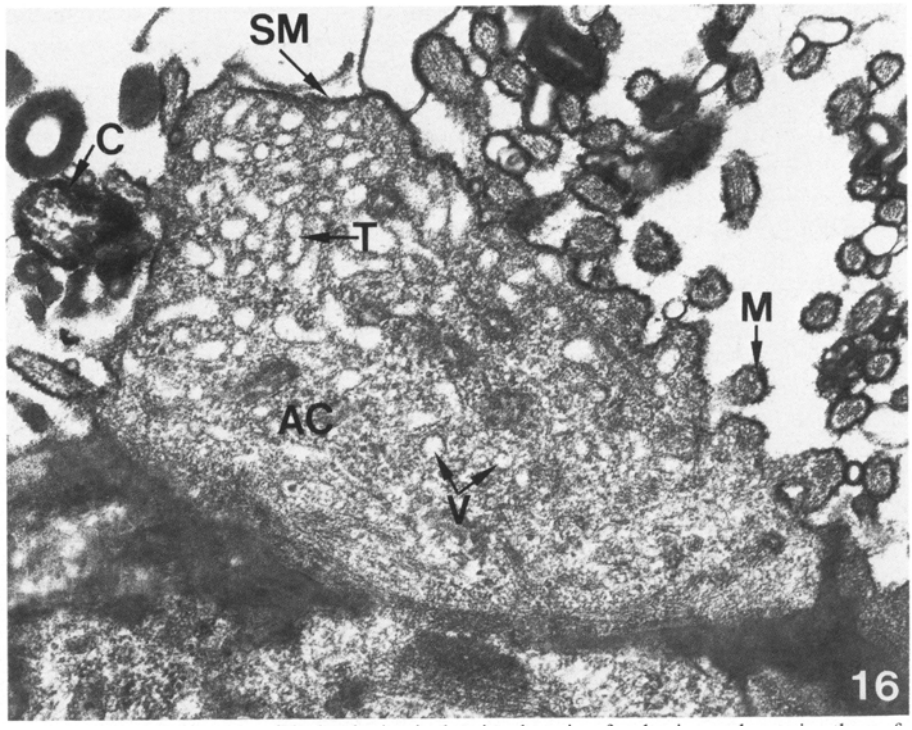


**Fig. 16.** High magnification of the luminal pole showing deposits of ruthenium red covering the surface plasma membrane (*SM*), the cilium (*C*) and the microvilli (*M*) of the apical cell (*AC*). Note that no stain has been taken up by the smooth walled vesicles (*V*) and tubules (*T*). Ruthenium red-fixation. × 37,500

Discussion of the potential role of the apical cell is necessarily limited by the lack of definitive information on the functional properties of the NEB as a whole. The experimental study of Lauweryns et al. (1973) has demonstrated that the neuroepithelial cells show cytological changes in response to hypoxic conditions in the respiratory airways. Further work has shown that various peptides (Lauweryns and Liebens 1977) and 5-hydroxytryptamine (Lauweryns et al. 1973; Lauweryns et al. 1977) are bound in different populations of dense-cored vesicles suggesting that the neuroepithelial cells have an endocrine role as well as a sensory/receptor one.

The proposed sensory role of the NEB has revolved around either reception of mechanical disturbances such as deformation of the epithelium (Fujita and Kobayashi 1973; Wasano and Yamamoto 1978) or alterations in the quantitative level of chemical substances such as pollutants, oxygen or carbon dioxide (Lauweryns et al. 1974). A comparison of the structural features of the luminal pole of recognised chemoreceptor cells, such as those of the olfactory mucosa and gustatory epithelium, with that of the apical cell provides further reasons for assigning a chemoreceptor role to the NEB. Attention should be drawn to the type of cilia, form of microvilli, abundance of smooth and coated vesicles and a terminal web associated with the junctional complexes (Graziadei 1971; Murray 1971).

The individual functional roles of basal and apical cells in the NEBs are not known. There have been speculations that the basal cells are mechanoreceptors (Fujita and Kobayashi 1973). The study of Lauweryns and Cokelaere (1973) on the effects of hypoxia did not distinguish between basal and apical cells as far as their reaction to shifts in the partial pressure of $O_2/CO_2$. The intimate cell-to-cell associations via membrane specialisations, cilia, membrane interdigitations (Hung et al. 1973) and *en passage* innervation (Lauweryns et al. 1972; Rogers and Haller 1978) certainly make it likely that there is considerable interaction between apical and basal cells. This proposition is further enhanced by the "octopus-like" arrangement of the apical cell processes over the basal cells. We suggest that the opportunities for interaction between neuroepithelial cells raises the possibility that in amphibians particularly the basal cells serve as an accessory source of peptides/5-HT, which are released on stimulation of the apical cell. This mode of action would account for the similar aspects of the cytological features of the two cells (Hung et al. 1973; Rogers and Haller 1978), the common *en passage* nature of the innervation and the presence in amphibians of only one or two apical cells in each NEB.

We have previously described the general arrangement and number of neuroepithelial cells in an amphibian NEB (Rogers and Haller 1978). Only a few cells in a population of up to 100 can be described as apical in the NEBs of *B. marinus*. A comparable situation appears to exist in the adult mouse NEB (Hung et al. 1973). This is in contrast to the arrangement in the rabbit where, as far as can be ascertained from published descriptions, a much larger proportion of cells in each NEB reach the luminal surface of the epithelium directly (Lauweryns et al. 1972). The illustrations of Cutz et al. (1978), however, on near-term rabbit foetuses clearly demonstrate that in these mammals there may be up to 80 neuroepithelial cells in each NEB and of these only a few appear to reach the surface of the epithelium. Some NEBs in the rabbit did not possess any apical cells (Cutz et al. 1978). Reference has been made to a re-arrangement of neuroepithelial cells in the rabbit NEB during ontogeny (Lauweryns et al. 1972). It would be interesting to know whether this involved a shift of basal cells into a position where contact with the lumen of the airway was achieved. Preliminary observations of our own on a lizard (*Trachydosaurus*) and tortoise (*Chelodonia longicollis*) suggest that in these particular species very few if any of the NEBs have apical cells.

The observations of Rogers and Haller (1978) and Hung et al. (1979) that the NEBs occur on raised mounds of tissue elevated above the general epithelium is interesting, but its significance is obscure. We have noted that this is a feature of *B. marinus* and *T. rugosus* but not of *C. longicollis*. Cutz et al. (1978) made no mention of this feature in their scanning electron microscopic study of the NEBs of rabbits.

In conclusion, we feel that attention should be drawn to the following features suggesting that the cell groups included under the term NEB are a structurally heterogeneous group: (i) histochemically and morphologically different types of innervation (Rogers and Haller 1978); (ii) presence or absence of apical cells (Rogers and Haller, 1978; Cutz et al. 1978); (iii) presence or absence of cilia on apical cells. Such structural heterogeneity may also reflect differences in functional properties.

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