

The Ontogeny of the Olfactory Epithelium: An Ultrastructural Study in Sheep

I. KOCIÁNOVÁ, M. BUCHTOVÁ, A. GOROŠOVÁ, S. HOLUBCOVÁ, P. ČÍŽEK

Department of Anatomy, Histology and Embryology, Faculty of Veterinary Medicine,
University of Veterinary and Pharmaceutical Sciences, Brno, Czech Republic*Received May 30, 2002**Accepted November 18, 2002***Abstract**Kociánová I., M. Buchtová, I. Gorošová, S. Holubcová, P. Čížek: *The Ontogeny of the Olfactory Epithelium: An Ultrastructural Study in Sheep*. Acta Vet. Brno 2003, 72: 3-10.

Ultrastructure of the olfactory epithelium was studied in ovine foetuses aged 74 and 79 days, in newborn and 30-day-old lambs, and in a 730-day-old sheep. Differentiation of apical parts of supporting cells, cilia on sensory cell dendrite endings, redistribution of centrioles from dendrite into endings and presence of a large amount of glycogen inclusions in supporting cells were apparent at day 74 of the intrauterine development. Supporting cells represented the major portion of the olfactory epithelium at day 79. The epithelial surface was covered by a dense network of cilia, but distal segments were seen only sporadically. The amount of microtubuli increased in dendrite cytoplasm. At birth, the cytoplasm of olfactory endings contained numerous light vesicles, mitochondria and centrioles. The free surface of supportive cells was furrowed into numerous microvilli. Distal segments of olfactory cilia were observed at the age of 30 days only. The segments contained a reduced number of axial microtubuli and contacted microvilli of supporting cells. The pattern and ultrastructure of olfactory cells of an adult sheep did not differ from those of a 30-day-old lamb. Degenerating olfactory cells were observed only sporadically. Supranuclear cytoplasm of supporting cells contained glycogen inclusions and bundles of tonofibrils.

Sense organs, transmission electron microscopy, olfactory epithelium, ontogenesis

The ultrastructure of the olfactory epithelium of a variety of mammalian species (Yamamoto 1976; Menco 1977; 1988; Menco et al. 1978; Míšek et al. 1996; Holubcová et al. 1997; Kociánová et al. 2001 and others), including humans (Moran et al. 1982), has been described and comparative studies have been published (Getchell 1986).

Most of the morphological studies describe receptor and supporting cells of the olfactory epithelium (Moulton and Beidler 1967; Menco 1977; Naguro and Iwashita 1992). The structure of olfactory endings on the surface of the olfactory epithelium was studied by Menco (1977; 1988) and that of olfactory cilia, including their function in the perception of olfactory stimuli in association with the presence of intermembrane receptor loci, were described by Kerjaschki and Hörander (1967), Menco et al. (1978), Morrison and Moran (1994).

Besides supporting cells, cell types, characterised by microvilli on the free surface, were studied by Agasandyan (1990). The function of supporting cells has been compared with that of neuroglia and their secretory function has also been mentioned (Yamamoto 1976).

Numerous studies dealt with the development and regeneration of the olfactory epithelium. Basal cells were regarded as the cell population from which other cell types of the olfactory epithelium differentiate (Moran et al. 1982). However, information on this topic in companion and farm animals is insufficient.

Materials and Methods

Samples of olfactory mucosa lining the caudal part of 3rd endoturbinale were collected from ovine foetuses at days 74 and 79 after fertilisation, from lambs at the day of birth and at the age of 30 days, and from an adult

Address for correspondence:

MVDr. Irena Kociánová
Department of Anatomy, Histology and Embryology, Faculty of Veterinary Medicine
University of Veterinary and Pharmaceutical Sciences
Palackého 1/3, 612 42 Brno, Czech Republic

Phone: +420 541 562 207
Fax: +420 541 562 217
E-mail: kocianovai@vfu.cz
<http://www.vfu.cz/acta-vet/actavet.htm>

individual aged 730 days. The samples were collected always from three individuals of the respective age category. The age of the foetuses was determined as described by Evans and Sack (1973).

The samples were fixed immediately after withdrawal in 300 mmol/L solution of glutaraldehyde in 100 mmol/L phosphate buffer for 4 h, washed four times in 100 mmol/L phosphate buffer, and post-fixed in 40 mmol/L osmium tetroxide dissolved in 100 mmol/L phosphate buffer for 1 h. After dehydration in increasing acetone series (0.25, 0.5, 0.75, and 1.0 mmol/L), the tissue samples were embedded in Durcupan ACM and let to polymerise at 60 °C for 3 days. All the fixation, dehydration, and embedding procedures were carried out at room temperature. pH of buffers was 7.4 to 7.42.

Semithin sections (1 µm) were stained with a 1:1 mixture of methylene blue and Azur II on a heated (50 °C) plate for 1 min.

Ultrathin sections were prepared using the ultramicrotome Ultra-cut Reichert-Jung, stained on carrier wire mesh (No. 100) with uranyl acetate and lead citrate, and viewed in the electron microscope Tesla BS 500.

Results

Ovine foetus, age 74 days

At this developmental stage, the olfactory epithelium already comprised the three characteristic cell types: sensory, supporting, and basal cells. Ongoing structural differentiation was apparent in many cells.

Sensory cells

Most of the sensory cells were spindle-shaped and formed a knob-like termination on the epithelial surface. Spherical nuclei were situated in the widest part of the cells and two to three compact nucleoli were regularly present. Uniform distribution of chromatin and annular nuclei, or absence thereof, were observed in some nuclei.

Perinuclear cytoplasm contained cisterns of granular endoplasmic reticulum, free ribosomes, and a small amount of oval mitochondria.

The supranuclear part of the cells formed a slim projection containing mitochondria, cisterns of granular endoplasmic reticulum, solitary microtubuli and, in some cases, also groups of centrioles. Cupola-like endings of the projections at the epithelial surface had a diameter of 2 to 3 µm. Their surface was smooth or irregularly rugged (Plate I, Fig. 1), or coated by olfactory cilia. The diameter of most of the cilia-free endings was somewhat larger than that of ciliated endings. Replication figures of centrioles were sporadically observed in the endings.

The per-ending number of cilia varied, but not more than 4 cilia, the length of which did not exceed 3 µm, were observed in one transversal section. The internal structure of the cilia was as usual.

Small prominences developed on the surface of the olfactory ending in some cells (Fig. 1). The infranuclear part of the olfactory cells narrowed towards the basal membrane. Although we failed to detect the origin of the axon, its parts were seen among the basal cells and in the mucosal fibrous tissue. Mitochondria and numerous light vesicles were present in axolemma. Sensory cells of the olfactory epithelium were separated from each other by the supporting cells. Groups of 2 to 3 nerve endings contacting each other directly were found sporadically. Regular alternation of olfactory and supporting cells was not typical of this stage of development.

Supporting cells

Prismatic supporting cells contained oval nuclei with diffusely distributed chromatin. Mitoses were found sporadically.

The cytoplasm around nuclei contained sporadic cisterns of endoplasmic reticulum, a small amount of mitochondria and glycogen inclusions, the amount of which varied in the individual cells. A larger amount of endoplasmic reticulum was found in apical cytoplasm (Plate I, Fig. 1) and sporadic lysosomes 0.5 to 1.0 µm in size were present in supranuclear parts of the cells.

Various degrees of differentiation were recognisable in apical segments of the supporting cells. In most of them, this segment was rugged and approximately 1-to-1.5 μm long projections protruded from the prominences. Up to 10 μm high bag-like structures formed endings of cells containing a larger amount of glycogen. The basal narrow part of the supporting cells adjoined the basal membrane.

Supporting cells contact sensory cells and each other. Numerous desmosome-like links were found among apical segments of supporting cells.

Basal cells

Basal cells were scattered on the basal membrane (Plate I, Fig. 2). Their shape varied; most of them were pyramidal or conical. Nuclei with chromatin aggregations occupied most of the cellular contents (Fig. 2). The cytoplasm further contained spherical mitochondria, a small amount of granular endoplasmic reticulum, and glycogen inclusions. Centrioles were usually situated near the nuclei (Fig. 2). Axons of sensory cells and basal segments of supporting cells penetrated into cytoplasmic folds of basal cells.

Ovine foetus, age 79 days

Sensory cells

An approximately 2 μm thick dendrite protruded from the cell body to the surface ending in a hemispherical swelling 1.5-to-3 μm in diameter. In most cells, this swelling carried several 0.5-to-2 μm long cilia with a usual structure (Plate II, Fig. 3). Cilia-free endings were observed less frequently than in foetuses aged 74 days, but their appearance and structure were similar.

Nuclei of sensory cells were light and chromatin was concentrated at the nucleus membrane. A compact nucleolus was present regularly. Perinuclear cytoplasm contained numerous cisterns of granular endoplasmic reticulum, mitochondria of various shapes, a small Golgi complex, and groups of approximately 100 nm large light vesicles.

The dendrite cytoplasm contained mitochondria, cisterns of granular endoplasmic reticulum, neurotubuli, aggregations of light vesicles, and many centrioles (basal bodies) concentrated beneath plasmalemma of olfactory ending, or in groups in the cytoplasm (Fig. 3).

The axon structure and appearance were the same as described for the 74-day-old foetuses.

Sensory cells along with supporting cells formed extensive close connections (Fig. 3). Semidesmosomes were often observed between the dendrite and the supporting cell membranes (Fig. 3).

Supporting cells

Cylindrical supporting cells widen somewhat towards the epithelial surface and their apical surface is rugged forming protrusions of irregular shape and size (Fig. 3). The bag-like structures on the apical segments of supporting cells were seen only exceptionally.

Oval nuclei containing diffusely distributed chromatin were situated in the upper third of the cytoplasm. Compact or reticular nucleoli were observed frequently (Plate II, Fig. 4).

The nucleus-surrounding cytoplasm contained subtle granular endoplasmic reticulum and smooth cisterns were present in apical cytoplasm. Lysosomes and aggregations of glycogen inclusions were sporadic only. A continuous strip of dark, fine granular material was found in the cytoplasm immediately beneath the apical surface (Fig. 3). Compared with the preceding developmental stage, the glycogen content in the supporting cells was lower.

Supporting cells contacted sensory cells forming with them typical connection complexes.

Basal cells

The basal cells formed a layer at the basal membrane. Their shape was mostly irregular with many cytoplasmic projections. The cells contained dark nuclei with karyosomes and a reticular nucleolus. Granular endoplasmic reticulum, mitochondria, and 0.5-to-1 μm large lysosomes with dark contents were situated in the cytoplasm.

Intraepithelial segments of olfactory gland ducts were lined with flattened cells with oval nuclei. The cytoplasm contained cisterns of granular endoplasmic reticulum, mitochondria, and a centriole situated near the nucleus. The cell surface facing the duct lumen carried short and rare microvilli.

Lamb, the day of birth

Sensory cells

Spherical nuclei contain a small amount of chromatin and mostly reticular nucleoli (Plate III, Fig. 5). The cytoplasmic structure was similar to that seen in foetuses aged 79 days. Cell bodies sent approximately 1-to-1.5 μm thick dendrite with club-shaped ending 1 to 2 μm in diameter. The dendrite cytoplasm contained mitochondria, small vesicles, neurotubuli, and groups of centrioles including replication figures. Cilia-free endings were rare. The structure of approximately 2 μm long olfactory cilia was usual.

Cell bodies further sent thin ($\leq 5 \mu\text{m}$) neurites towards the basal membrane. Axoplasma contained numerous small vesicles with light contents.

Contacts between sensory and supporting cells were the same as described for foetuses aged 79 days.

Supporting cells

Supporting cells were cylindrical with oval nuclei containing a larger amount of chromatin. Their cytoplasm contained numerous mitochondria, vesicles of smooth endoplasmic reticulum, glycogen inclusions and supranuclearly situated extensive Golgi complex (Plate III, Fig. 6). The free cell surface was divided into numerous up to 3 μm -long microvilli, which often formed shrubby structure (Fig. 6). A dark granular line was observed in the cytoplasm beneath them.

The lower cell segments narrowed and contacted the basal membrane.

The supporting cells are regularly arranged among sensory cells forming with them close connections.

Basal cells

Basal cells were usually polygonal with surface cytoplasmic projections, between which bundles of sensory cell axons were situated (Plate IV, Fig. 7).

Nuclei were dark and lobular with numerous karyosomes. The cytoplasm contained granular endoplasmic reticulum, mitochondria, and glycogen inclusions.

The structure of intraepithelial parts of olfactory gland ducts was similar to that observed in the preceding developmental stage.

Lamb, age 30 days

The olfactory epithelial surface was covered by an up to 1 μm high tangle of olfactory cilia, microvilli, and light vesicles (Plate IV, Fig. 8).

Sensory cells

The structure of sensory cells was comparable with that seen in newborn lambs. Dendrite endings of olfactory cells had the form of club-shaped structures 1-to-1.5 μm in size with dark cytoplasm (Fig. 8). The cytoplasm contained light vesicles 50 to 100 nm in diameter,

mitochondria, and basal bodies of cilia. Proximal segments of olfactory cilia showed the usual structure; the distance between them and the endings was approximately 2 μm . Distal segments had the form of thin, moderately undulated fibres running parallel to the epithelial surface. The distal and proximal segments contacted closely clumps of microvilli originating from apical parts of supporting cells.

Bodies of sensory cells showing signs of degeneration were seen exceptionally in the basal layer of the olfactory epithelium.

Supporting cells

The structure of cytoplasm and nuclei was similar to that seen in newborn lambs.

Apical cytoplasm contained extensive Golgi complexes, light vesicles, mitochondria, lysosomes with dark contents, and a marked horizontal strip of fine granular material (Fig. 8). The supporting cells were interspersed regularly with the sensory cells (Fig. 8) forming with them close connections. Numerous 3-to-5 μm long microvilli originating from the surface of the supporting cells branched out sometimes (Fig. 8).

Basal cells

Basal cells were polygonal with cytoplasmic projections varying in length, which surrounded bundles of sensory cell axons.

Basal cells contained lobular dark nuclei, mitochondria, glycogen granules, and solitary cisterns of granular endoplasmic reticulum.

Intraepithelial parts of olfactory gland ducts were usually filled up with light secretion vesicles 70 to 100 nm in size immediately before their ends.

Adult sheep, age 730 days

The surface of the olfactory epithelium was covered by a dense tangle of microvilli, cilia, vesicles, and numerous distal segments of olfactory cilia characteristic by a reduced number of microtubuli. The cilia are tangled up into dense 3-to-4 μm long microvilli originating in clumps from the surface of supporting cells.

Sensory cells

The appearance, structure, and ultrastructure of sensory cells did not differ from those described for 30-day-old lambs. Only solitary degenerating olfactory cells were found. No cilia-free dendrite endings were observed.

Supporting cells

The structure of most of the supporting cells was the same as described for 30-day-old lambs. Typical supporting cells were irregularly interspersed by cells with a lighter cytoplasm and numerous mitochondria in the apical segments. The free surface was covered by numerous microvilli. The cytoplasm contained glycogen inclusions, and fine bundles of tonofibrils. The nuclei contained circular nucleoli.

The cytoplasm of some supporting cells was vacuolised. The cytoplasm also contained dark lysosomes 0.5 to 1.5 μm in size and pigment inclusions.

Basal cells

Basal cells were arranged in one layer at the basal membrane of the olfactory epithelium and their structure corresponded to the pattern seen in 30-day-old lambs. The cytoplasm formed long filamentous projections between which bundles of sensory cell axons were situated.

Intraepithelial segments of olfactory gland ducts often contained aggregations of minute (100 nm) light vesicles.

Discussion

Sensory, supporting, and basal cells are recognisable by transmission electron microscopy already in 74-day-old sheep fetuses. Changes occurring at the submicroscopical level during the subsequent ontogenetic development were seen above all in apical parts of the sensory and supporting cells.

The structural development of sensory cell and dendrite cytoplasm including its ending has been characterised by Cuschieri and Bannister (1975) as the final maturation of receptor cells. Particularly apparent are an increasing number of microtubuli and progressive redistribution of organelles, above all mitochondria and centrioles, from the dendrite into the nerve ending at the epithelial surface. Assuming that the differentiation of sensory cells is characterised particularly by morphogenesis of nerve endings (Cuschieri and Bannister 1975; Menco 1977; 1988), our observations indicate that cells at various stages of development are present simultaneously in the olfactory epithelium of sheep fetuses. We could observe here ciliated and cilia-free endings and the structure of the cilia corresponded to descriptions published by other authors (Kerjaschki and Hörander 1976; Menco et al. 1978). The presence of cilia-free olfactory endings is indicative of continuous renewal of olfactory cells. As demonstrated by scanning electron microscopy, the renewal is more frequent in caudal parts of the olfactory epithelium (Tichý et al. 1995). Local differences in the conformation of the olfactory epithelium surface and a higher heterogeneity in adults than in young individuals were also described by Menco (1977).

The length of olfactory cilia only rarely exceeded 2 to 3 μm . This observation corresponded to data on the length of proximal segments in various animal species as published by Moulton and Beigler (1967), Kerjaschki and Hörander (1976), Menco (1977) and other authors. Their conformation was found to be identical with the usual ciliar structure. Distal segments were seen as late as in 30-day-old lambs and it is apparent that the occurrence of these structures was only sporadic at the prenatal and early postnatal stages of development. It can therefore be concluded that the receptor capacity of the olfactory epithelium of young individuals is incomplete. This opinion is supported also by data published by Kerjaschki and Hörander (1976), Menco et al. (1978) and Getchell (1986). Proximal segments of olfactory cilia are embedded in basal bodies in the cytoplasm of olfactory endings (Seifert 1970; Yamamoto 1976). Our observations indicate that the distribution of the basal bodies depends on the degree of differentiation of sensory cells. The role of centrioles in ciliogenesis has been generally emphasised in association with replications occurring in the cytoplasm of olfactory endings (Menco 1977; 1988).

The degree of maturation of receptor cells is characterised by their arrangement relative to other cells of the epithelium. As observed by Graziadei (1971; 1972), the bodies of olfactory cells and their dendrites often contacted each other without being separated by supporting cells. A similar arrangement was found in early developmental stages by Cuschieri and Bannister (1975). In our investigations, direct contacts between groups of neighbouring were observed only in 74-day-old fetuses and invariably in cilia-free cells. Hence, the role of such connections is open to discussion. Cuschieri and Bannister (1975) described the grouping of olfactory cells as a regularly occurring process.

The differentiation of supporting cells is closely associated with the development of sensory cells. Microvilli on their free surface develop most rapidly in the perinatal stage, i.e. at the time of distinctive formation of distal segments of olfactory cilia.

The differentiation of supporting cells is closely associated with the development of olfactory cells. Microvilli on the free cell surface develop most rapidly in the perinatal period, i.e. at the time of the most distinctive formation of distal segments of olfactory cilia. Menco et al. (1978) described numerous contacts of microvilli with cilia and the presence

of intermembrane particles on microvillous membranes similar to those found on ciliated membranes. Referring to the recognised responsiveness of supporting cells to certain odorants (Okano and Takagi 1974), we can speculate on functional significance of such connections.

Remarkable and hitherto not described finding were the bag-like structures in apical segments of supporting cells in 74-day-old foetuses. We assume that they represent the initial stage of differentiation of cell surface structures that are characterised by a high glycogen content in the cytoplasm. Although it can be assumed that supporting cells, like sensory cells, undergo permanent renewal (Menco 1977), no bag-like structures were observed in the older age categories (except for sporadic findings in 79-day-old foetuses).

Rather extensive close connections of apical parts of the supporting and the sensory cells were found already in the 74-day-old foetuses. Numerous semidesmosomes between the sensory cell dendrites and adjacent parts of the supporting cells were observed at day 79 of the ontogenetic development. Considering the numerous and extensive connections, the assumption of Menco et al. (1978) of communication not only between neighbouring cells, but also between various areas of the olfactory region is probably right. In this regard, Moulton and Beigler (1967) attribute to the supporting cells a role similar to that of Schwann cells.

Rich organelles in the apical cytoplasm of supporting cells are indicative of their secretory activity (Moulton and Beidler 1967; Yamamoto 1976 and other authors).

We assume that the strip of granular material in the apical cytoplasm of supporting cells is identical with the terminal tissue of microtubuli and filaments described by Moulton and Beidler (1967), that has a supportive role and is related to connection complexes between neighbouring cells.

Our findings in basal cells are identical with those published by numerous authors (Moulton and Beidler 1967; Menco 1977). Moran et al. (1982) regards basal cells as precursors for the regeneration of the olfactory epithelium.

Ultrastruktura čichového epitelu ovce v průběhu ontogeneze

Ultrastruktura čichového epitelu ovce byla studována u fétů stáří 74. a 79. dnů intrauterinního vývoje, jehňat v den narození a 30 dnů po narození a u dospělce stáří 730 dnů. V 74. den intrauterinního vývoje probíhala diferenciace apikálních úseků podpůrných buněk. Na zakončeních dendritů smyslových buněk se objevily řasinky a probíhala redistribuce centriolů z dendritu do jeho zakončení. Podpůrné buňky obsahovaly značné množství glykogenových inkluzí. V 79. den intrauterinního vývoje byly v čichovém epitelu nejpočetněji zastoupeny buňky podpůrné. Na povrchu epitelu se nacházela hustá spleť řasinek, jejich distální segmenty byly přítomny pouze sporadicky. V cytoplasmě dendritů se zvyšovalo množství mikrotubulů. V době narození obsahovala cytoplazma čichových zakončení velké množství světlých vesikul, centriolů a mitochondrií. Volný povrch podpůrných buněk byl členěn v množství mikroklyk. Distální segmenty čichových řasinek byly pozorovány až u jehněte stáří 30 dnů po porodu. Tyto segmenty obsahovaly redukovaný počet osových mikrotubulů a byly v kontaktu s mikroklyky podpůrných buněk. U dospělého jedince se vzhled, uspořádání i ultrastruktura smyslových buněk nelišila od údajů uvedených u jehněte 30 dnů po narození. Pouze ojediněle jsme pozorovali degenerující čichové buňky. V supranukleární cytoplasmě podpůrných buněk byly obsaženy glykogenové inkluze a jemné svazky tonofilament.

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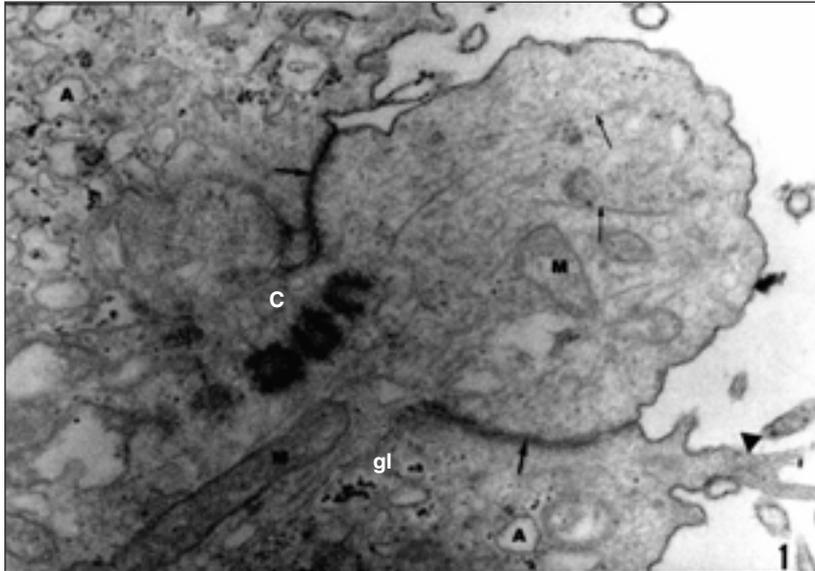


Fig. 1. Differentiation of nerve ending (nz) of an olfactory cell dendrite of an ovine foetus aged 74 days. Neurotubuli (→), centrioles (C), and mitochondria (M) in dendrite cytoplasm. Vesicles of agranular endoplasmic reticulum (A) and glycogen particles (gl) in the cytoplasm of a supporting cell. Developing



Fig. 2. Lower zone of the olfactory epithelium of a sheep foetus aged 74 days. Basal cell nucleus (N), mitochondria (M), centrioles (C), and glycogen particles (gl) the cytoplasm of a basal cell. Basal membrane (▲). Developing collagenous fibres (k). TEM, × 8 000

Plate II

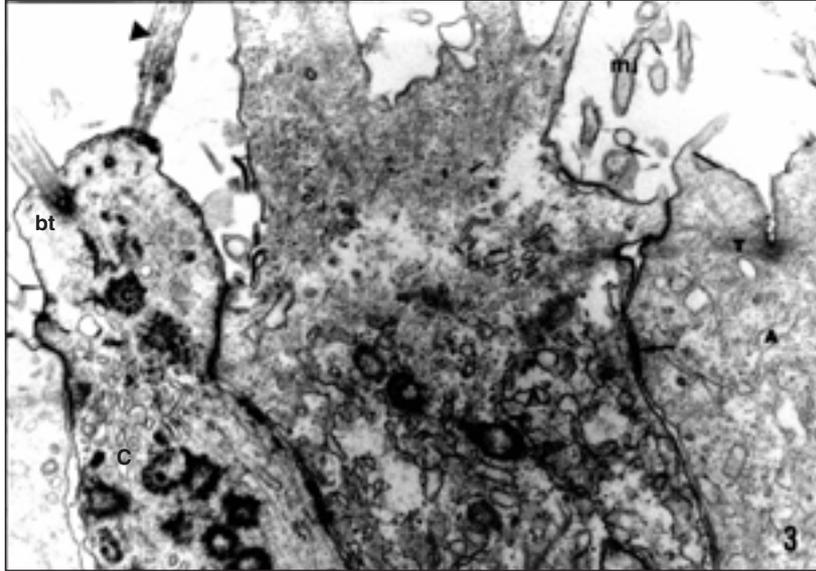


Fig. 3. Apical segments of cells of the olfactory epithelium of an ovine foetus aged 79 days. Nerve ending with cilia (▲) and basal bodies (bt). Centrioles (C) in dendrite cytoplasm. Differentiation of microvilli (mi), agranular endoplasmic reticulum (A) and horizontally running terminal tissue (T) in the cytoplasm of supporting cells. Close links between a supporting cell and a nerve ending. Lining complex (↔) between neighbouring supporting cells. TEM, $\times 20\,000$

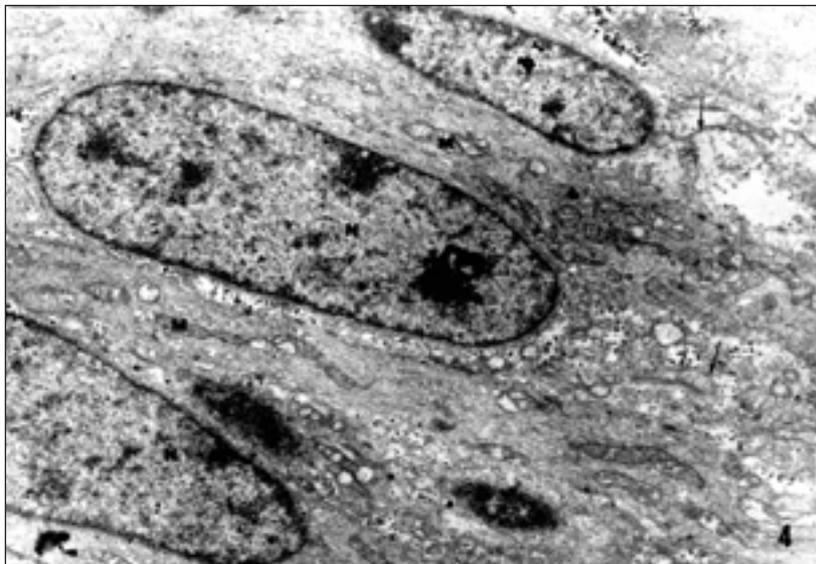


Fig. 4. Upper zone of the olfactory epithelium of a ovine foetus aged 79 days. Supporting cell nuclei (N). Reticular-type nucleolus. Cisterns of granular endoplasmic reticulum (→), in supporting cell cytoplasm. Mitochondria (M) in dendrite cytoplasm of an olfactory cell. TEM, $\times 8\,000$

Plate III

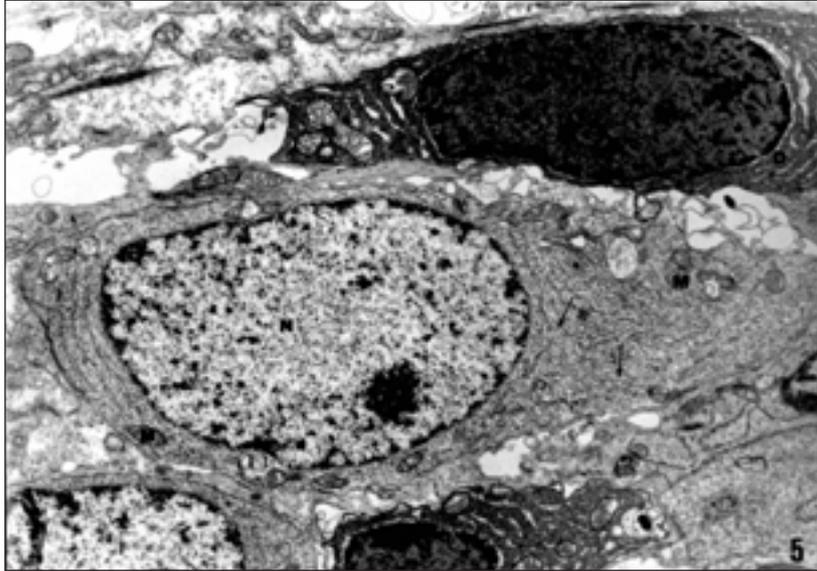


Fig. 5. Medium zone of the olfactory epithelium of a lamb aged 0 days. Olfactory cell nucleus (N) with reticular-type nucleolus. Mitochondria (M) and numerous cisterns of granular endoplasmic reticulum (→) in the cytoplasm. Nuclei (N) of cells with dark cytoplasm. TEM, $\times 8\ 000$

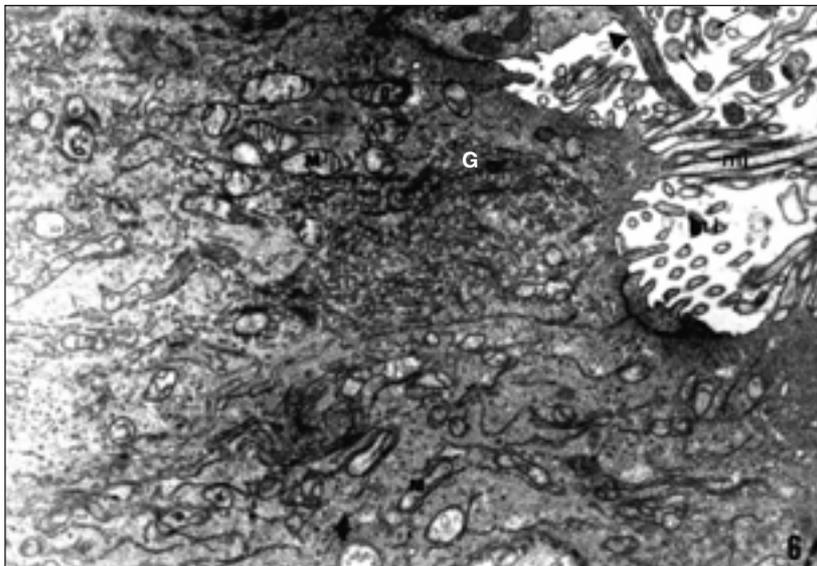


Fig. 6. A part of olfactory epithelium surface of a lamb aged 0 days. Nerve ending of an olfactory cell dendrite with cilia (▲). Cross sections through proximal segments of cilia (→). Mitochondria (M) and extensive Golgi complex (G) in the cytoplasm of supporting cells. Clumps of microvilli (mi) on the surface. TEM, $\times 12\ 000$

Plate IV

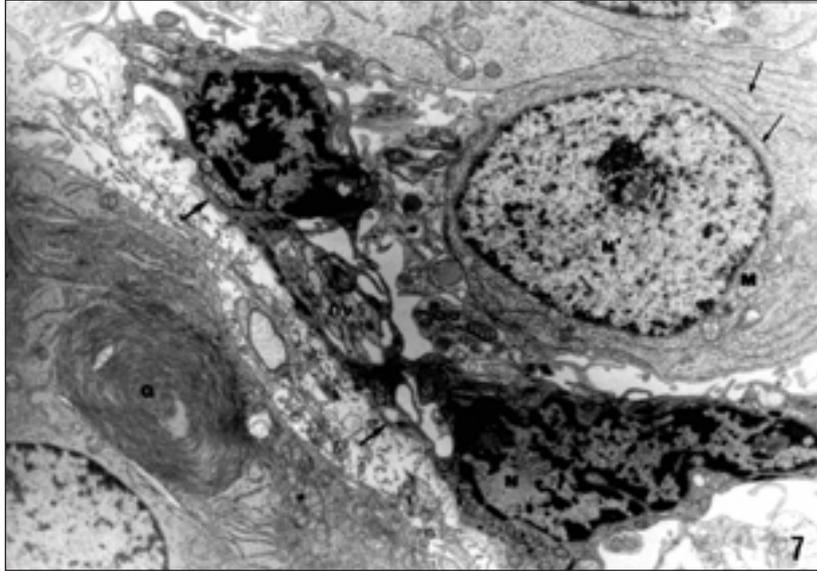


Fig. 7. Lower zone of the olfactory epithelium of a lamb aged 0 days. Basal cell nuclei (N). A group of nerve fibres (nv) (olfactory cell axons). Olfactory cell with a nucleus (N') and reticular-type nucleolus. Cisterns of granular endoplasmic reticulum (→) and mitochondria (M) in the cytoplasm of an olfactory cell. Basal membrane (↔). TEM, $\times 2\,000$

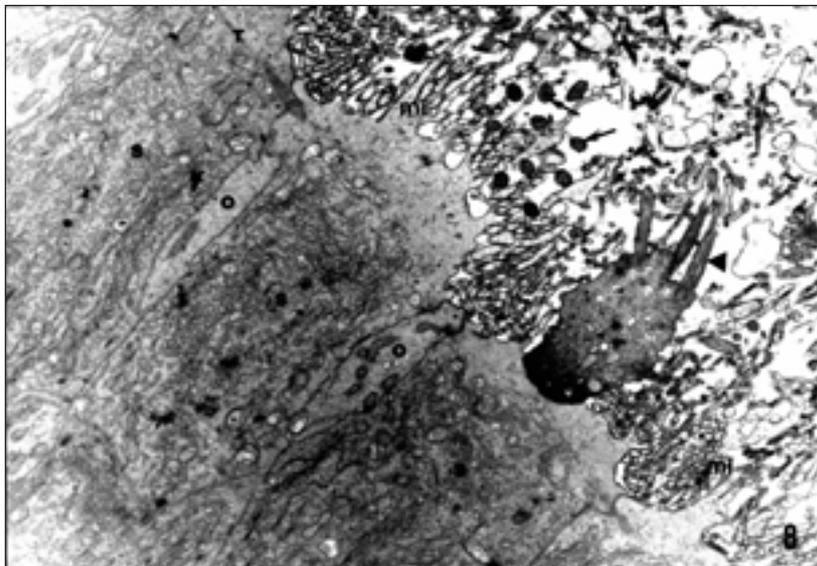


Fig. 8. Surface of the olfactory epithelium of a lamb aged 30 days. Olfactory cells (O) regularly interspersed by supporting cells (S). Olfactory ending with cilia (▲). Cross sections through proximal (↔) segments of cilia. Microvilli (mi) of supporting cells. Terminal line (T). TEM, $\times 8\,000$