

THE ULTRASTRUCTURE OF TASTE BUDS IN THE NEWBORN PIG

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University of Veterinary Science*Received***Abstract**Tichý, F.: *The Ultrastructure of Taste Buds in the Newborn Pig*. Acta vet. Brno, 61, 1992: 171–177.

Taste buds localized on circumvallate papillae of the porcine tongue were investigated for the occurrence of dark, light and receptor cells and the stage of their differentiation, the morphology of the taste pore area, the occurrence and distribution of intragemmal nerve endings and the way in which these are connected with each cell type.

It was observed that, as early as two days after birth, the porcine taste buds included all three cell types. These were elongated towards the taste pore. Their apical parts, however, did not come up to level with the epithelial surface nor were they shaped into microvilli typical of the bud ultrastructure described in adult animals of other mammalian species. The cytoplasm of the dark cells had only a low amount of dark secretory granules and the receptor cells showed only occasional occurrence of dark vesicles. The dark, light and receptor cells were connected with nerve fibres and the way of contact was different in each cell type.

Taste bud, taste pore, gustatory nerve, ultrastructure

The ultrastructure of taste bud has been studied and thoroughly described in a number of amphibian and avian species (Farbman and Yonkers 1971; and others), in laboratory mammals (Farbman 1965a; Murray et al. 1969, 1972; Fujimoto and Murray 1970; Takeda and Hoshino 1975; Takeda 1976; and others) and also in man (Takeda 1972; Paran et al. 1975; etc.) The results of ultrastructural studies of taste buds have revealed considerable differences which are species-specific and also related to the position of the bud in the lingual mucosa (Beidler 1969; Murray 1971, 1973; Mattern and Paran 1974; Takeda and Hoshino 1975; and others).

Farbman (1965a, b), Murray and Murray (1967) and others showed the existence of two basic cell types constituting the taste bud, which they called dark and light cells. Later it was (Murray et al. 1969) that the taste bud contains one more cell type which was designated the receptor cell. Although the functions of these three cell types have not been clearly determined, the evidence so far obtained suggests that their respective roles are similar in all the taste buds (Mattern and Paran 1974; Paran and Mattern 1975; Takeda 1977; and others). The dark cells are implemented in secretory and supportive function, light cells mediate contact between the taste stimuli and receptor cells, the true receivers of the stimulus.

Still incomplete is the information on the mechanism by which each cell type in the taste bud is replaced or regenerated. The view of some authors (Beidler and Smalman 1965; Farbman 1965b) that the cells are differentiated by a continual process from so-called perigemmal cells of the surrounding epithelium is likely to hold only for the dark cells (and possibly also for the light ones). Later investigations by Takeda (1977) and Farbman (1980) indicate that in the receptor cells the presence of some specific structures in the cytoplasm relates the cells to nervous tissue. It is not known whether the light cells develop from the dark or the receptor cells or are an independent cell type. In association with this some authors discuss the process of taste bud formation in the lingual epithelium (Beidler and Smalman 1965; Farbman 1965b, 1980; Fujimoto and Murray 1970; Takeda 1976). They suggest that the origin of a taste bud and its localization are both determined and initiated by contact of epithelial cells with a nerve fibre. Some observations on the development of taste buds in relation to age of the animal have been

made in the tongues of sheep and pigs (Tichý and Černý 1987; Tichý 1991a, b, c, d, 1992a) and the bud ultrastructure has been described (Tichý 1992b).

In addition to studying the ultrastructure of the bud and the process of its development, some authors were interested in the way gustatory stimuli are perceived (Adatia and Gehring 1971; Paran and Mattern 1975; Schiffman 1986) particularly in the first phase which occurs in the gustatory pore region.

The data presented here show a considerable diversity of opinions on the structure, function and origin of each cell type involved in the taste bud. Moreover, the majority of studies have used laboratory animals or human material. Adequate data on farm animals, however, are missing. It is the aim of this study to add new facts to the understanding of the development of taste buds in the pig at an important stage of ontogenesis.

Materials and Methods

Samples of circumvallate papillae were collected from the tongues of three piglets two days after birth. The tissues were immediately fixed with glutaraldehyde in 0.1 M phosphate buffer (300 mmol/l) for 4 h, washed with 4 changes of 0.1 M phosphate buffer and postfixed with OsO₄ (40 mmol/l) in 0.1 M phosphate buffer for 1 h. After dehydration with a graded acetone series (25%, 50%, 75%, 90%, 100%) the samples were embedded in Durcupan ACM and polymerized at 60 °C for 3 days. Fixation, dehydration and embedding were performed at room temperature. All buffers were at a pH range of 7.4 to 7.42.

Ultrathin sections were made with an Ultracut Reichert-Jung ultramicrotome. They were stained on grids (MESH 100) with uranyl acetate and lead citrate and examined and photographed with a Tesla BS 500 electron microscope.

Semithin sections taken from the collected material were stained with methylene blue and Azure II (mixed 1:1) on a plate 50 °C warm for 1 min.

Results

Taste buds in the epithelium of circumvallate papillae in two-day old piglets tapered towards the taste pore forming a thin neck. They consisted of three cell types distinguished by electron microscopy as dark, light and receptor cells. Each type was different as for their appearance, and organelles and inclusions present in the cytoplasm.

Dark cells (type I) were slim, running from the bud base up to the pore where they terminated in a narrow uneven area not extending above the level of the surrounding epithelium. The nucleus was usually elongated in shape and its nuclear envelope consisted of many irregular invaginations and the karyoplasm included regularly distributed minute clusters of heterochromatin (Plate II.)

The cells were characterized by dark cytoplasm and frequent vacuoles, varying in size and shape, which were accumulated mainly in the area below the nucleus and in variable amounts the apical part. The cytoplasm of the basal part contained numerous bundles of filaments which were less frequent in the supranuclear region (Plates II.—V., Figs 2, 3, 4, 5). Only some of the dark cells, mostly those at the bud periphery, had large quantity of glycogen particles in the cytoplasm (Figs 2, 3). The granular endoplasmic reticulum was seen predominantly in the perinuclear area. A well developed Golgi complex was situated close below the nucleus surrounded by numerous mitochondria. These were elongated or elliptical with numerous cristae (Fig. 5). The apical part of the cytoplasm included infrequent granules (100—200 nm) with dark homogeneous content, and fine bundles of parallel filaments. Areas of dark matter in the taste pore were limited in extent and few in number (Plate I., Fig. 1).

This cell type made frequent contacts with nerve fibres, entering the taste bud in its bottom part. Some thin nerve fibres were often found encircled with cytoplasm of the dark cells; if in greater accumulation, these connections imitated

Schwann's sheath. Structures indicating synaptic junctions were not observed but some wider nerve fibres contained minute light vesicles reminiscent of synaptic vesicles.

Light cells (type II) were larger than the dark cells, had lighter cytoplasm and nucleus and, like dark cells, ran from the base of the bud to its pore. The nucleus usually had an irregular oval shape, low content of chromatin, and a nucleolus of the reticular type (Figs 2, 5, 6).

The cytoplasm contained numerous light vesicles, varying in shape and size (60 to 200 nm), which were situated in the basal part as well as above the nucleus, small round or oval mitochondria and smooth endoplasmic reticulum distributed in the supranuclear region (Figs 2, 6). The Golgi complex was regularly larger than in the dark cells. Small glycogen inclusions dispersed in the cytoplasm and rare lysosomes were also seen. The apical part of the cell showed small light vesicles and very fine, infrequently occurring bundles of filaments. The terminal narrow part of the cell entered the taste pore but did not come up above the epithelial surface.

Contact of the light cells with nerve fibres occurred over considerably large areas (Figs 5, 6) but never was a nerve fibre found to penetrate into the cytoplasm to form a „mesaxon“ or synaptic junction even though some small vesicles were occasionally present in the axoplasm.

Receptor cells (type III) were found sporadically in the central part of the taste bud. Their appearance, density and the shape of the nucleus were similar to the light cells (Fig. 6). They were seen as elongated, rather large cells; their oval nuclei showed shallow invaginations all over the surface (Figs 2, 4). Chromatin content was usually higher than in the light cells and clusters of heterochromatin were usually found close below the karyolemma (Fig. 6). As a rule, the cells were in contact with the dark cells through intercellular connections, appearing as small interdigits, producing numerous desmosomes. The cytoplasm was rich in cisternae of the granular endoplasmic reticulum, in round, rather large mitochondria and in irregularly dispersed fine bundles of filaments (Fig. 4). The Golgi complex was small and placed close to the nucleus. The cytoplasm also contained clusters of small light vesicles (30–60 nm) and occasional larger vesicles (100–150 nm) with dark content. A more conspicuous accumulation of these structures was frequent near the area of cell-nerve fibre contact. The relation of nerve fibres to these cells was similar to that seen in type II cells. A connection resembling desmosome was occasionally found between the axolemma of an intragemmal nerve fibre and the membrane of a receptor cell (Fig. 4). The apical parts of receptor cells included minute light vesicles and numerous fine bundles of filaments.

Nerve fibres found in the lamina propria mucosae under the taste bud were covered only with the cytoplasm of Schwann's cells and comprised varying amounts of neurotubules, vesicles and mitochondria. The intragemmal parts of the nerve fibres were of two kinds, one thinner with neurotubulus and few mitochondria, and the other thicker with numerous mitochondria and small vesicles (about 50 nm). The thinner fibres were in contact with the dark cells while the thicker fibres connected with the light and receptor cells.

Discussion

The ultrastructure of taste buds on the porcine circumvallate papilla, particularly in the areas of the taste pore and below it, was very similar to that described by Takeda and Hoshino (1975) on fungiform papillae or on in the buds the exposed regions of foliate papillae. The deep and relatively narrow taste pore, small amounts of dark granules in the cytoplasm of type I cells, infrequent and small areas of dark matter in the pore and the fact that the terminal parts of both dark and light cells did not project above the surface epithelium indicate that the buds localized in the wall epithelium of circumvallate papillae in the pig are exposed to greater strain than those in the sheep in the same postnatal period (Tichý 1992b). This assumption is supported by the finding that the furrow encircling the circumvallate papilla is noticeably larger in the piglet than in the lamb (Tichý and Černý 1987; Tichý 1991b, c), which means that the porcine taste buds are exposed to physical and mechanical factors to a great extent. Alternatively, the bud morphology may reflect the fact that differentiation in this area of the bud was not completed at the developmental stage studied. The supportive function of the dark cells is apparent from the presence of large numbers of filaments in the cytoplasm, which is higher than in the lamb (Tichý 1992b), and their secretory activity is evidenced by a rare occurrence of granules in the apical cytoplasm. The presence of vacuoles varying in size, mitochondria and glycogen particles in the cells of taste buds was reported in man by Paran et al. in 1975. It is apparent that this organelle content is related to high metabolic activity. Of interest was the finding of dark cells whose cytoplasm in the basal part was completely filled with many glycogen inclusions. Because these cells were found predominantly at the bud periphery, they may be considered transitional forms between perigemmal and type I cells and compared to the cells which Farbmann (1965a) referred to as peripheral. The terminal portions of dark cells extending into the taste pore were markedly thinner than the corresponding cell parts in the ovine buds (Tichý 1992b) and were broken into irregular projections. However, the typical microvilli described in other mammalian species (Murray 1977; Paran et al. 1975; Takeda and Hoshino 1975; Takeda 1977) were missing. This may be either due to an incomplete process of differentiation of this cell type or a species-related difference in the shape of this part of the dark cell. Contact between these cells and nerve fibres is similar to that found in ovine taste buds (Tichý 1992b), i. e., the cytoplasm envelopes the fibre in the way Schwann's sheath is formed, which gives rise to a structure imitating a mesaxon. The presence of minute vesicles, known as synaptic vesicles (Paran and Mattern 1975; Paran et al. 1975), in the axoplasm of some larger fibres can be taken as evidence of the effector (secretory) function of these cells.

The views on the function and role of the light cells in taste buds are very varied and were discussed earlier (Tichý 1992b). The small vesicles present in their apical cytoplasm and a rather large Golgi complex suggest secretory function. On the other hand, their generation by endocytosis should also be considered (Murray and Murray 1967), in which case the cell would serve as a mediator leading stimuli to the receptor cell (Farbman and Yankers 1971). The nerve endings found to connect with the membranes of light cells seem to give support to this view. The occasional occurrence of small vesicles in the axoplasm of fibres in contact, however, does not give enough grounds for the assumption (Paran et al. 1975) that this is the ending of effector cells. From

this point of view it will probably be more important to look for explanation of interconnected intragemmal nerve fibres observed by Takeda (1977).

The receptor cells, resembling the light ones, are localized in the central part of the taste bud. In comparison with the ovine receptor cells (Tichý 1992b), their karyolemma shows only shallow and indistinct invaginations and the cytoplasm includes vesicles with dark matter and clusters of minute vesicles only on rare occasions. These two kinds of structures were more frequent in the basal extended parts of the cells which were the sites of contact with nerve endings similar in appearance to those seen in the light cells. The occasional occurrence of dark vesicles in the cytoplasm of receptor cells, observed also in the sheep (Tichý 1992b), was in contrast with the data of some authors (Takeda and Hoshino 1975; Takeda 1977) who found clusters or aggregations of these structures in the close vicinity of the area where a nerve ending contacts with the cell. A likely explanation is that the amount of dark vesicles increases with their involvement in transferring stimuli from the cell to a sensory fibre. It has been suggested (Takeda 1977; Farbman 1980; Shepherd et al. 1986) that the process of transmission is mediated by neurotransmitters contained in the dark vesicles. The regular finding of a majority of small light vesicles in the area of contact between nerve fibres and the cells points to their role as synaptic vesicles (Murray 1973; Paran et al. 1975; Takeda 1977). As in the sheep (Tichý 1992b), the synaptic connection failed to show the outlines of the cell membrane, a fact also noted by some other authors (Murray 1973; Paran et al. 1975). The desmosome-like contacts between intragemmal nerve fibres and the receptor cells observed on rare occasions seem to be analogous with the connections reported in other sensory organs of some mammals (Malinovský and Páč, 1978; Malinovský et al., 1982; Malinovský, 1984). In the sheep, however, such structures were not recorded (Tichý 1992 b).

Our results do not warrant a conclusion on whether the development in function of taste buds will result in further differentiation of their components or whether the observed structures are final, species-specific or site-specific structures of porcine lingual mucosa. All three aspects can be manifested in the ultrastructure of the taste bud (Murray 1973; Mattern and Paran 1974; Paran and Mattern 1975). In our view the findings suggest that, similarly to the sheep (Tichý 1992b), at this stage of development the process of differentiation has not been completed and therefore the taste bud cannot function in its full capacity.

Ultrastruktura chuťových pohárků u prasete po narození

V chuťových pohárcích, lokalizovaných na hrazených papílách jazyka tří selat stáří dva dny po narození, byl sledován výskyt a stupeň diferenciacie tmavých, světlých a receptorových buněk, utváření oblasti chuťového póru, výskyt a distribuce intragemálních nervových vláken a způsob jejich kontaktu s jednotlivými buněčnými typy.

Ze získaných výsledků vyplývá, že v chuťových pohárcích selete jsou již těsně po narození zastoupeny všechny tři sledované typy buněk. Jsou vřetenovitě protaženy směrem k chuťovému póru, avšak jejich apikální úsek není členěn v typické mikrokly, uváděné v popisech ultrastruktury pohárků dospělých jedinců jiných druhů savců. Další zjištěné odlišnosti spočívají v nepřilíh čítném výskytu tmavých sekretorických granul v cytoplasmě tmavých buněk a v ojedinělém zastoupení tmavých vesikul v buňkách receptorových. Apikální úseky buněk

chutového pohárku nedosahují úrovně povrchu okolního epitelu. Všechny typy buněk jsou v kontaktu s nervovými vlákny, avšak uspořádání kontaktů je odlišné u buněk tmavých, světlých a receptorových.

Ультраструктура вкусовых луковиц поросят после рождения

В расположенных на желобоватых сосочках трех поросят в возрасте двое суток после рождения вкусовых луковицах проводили исследования наличия и степени дифференциации темных, светлых и рецепторных клеток, формирования области вкусовой поры, наличия и распределения интрагемальных нервных волокон и способа их контакта с отдельными типами клеток.

Из полученных результатов вытекает, что во вкусовых луковицах поросенка представлены уже непосредственно после рождения все три исследуемые типы клеток. Они веретенообразно вытянуты по направлению вкусовой луковицы, однако их верхушечная часть не разделена характерными микроворсинками, приводимыми в описаниях ультраструктуры луковиц взрослых особей других видов млекопитающих. Следующее установленное различие заключается в редком наличии темных секреторных гранул в цитоплазме темных клеток и в единичном наличии темных пузырьков в рецепторных клетках. Апикальные участки клеток вкусовой луковицы не достигают уровня поверхности окружающего эпителия. Все типы клеток находятся в контакте с нервными волокнами, однако расположение контактов темных, светлых и рецепторных клеток отличается.

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Fig. 1: Apical part of a porcine taste bud. The regions of dark matter in the porus gustatorius (s), secretory granules in a dark cell (g) and part of a light cell (L). A perigemmal cell (P). $\times 8\ 000$.

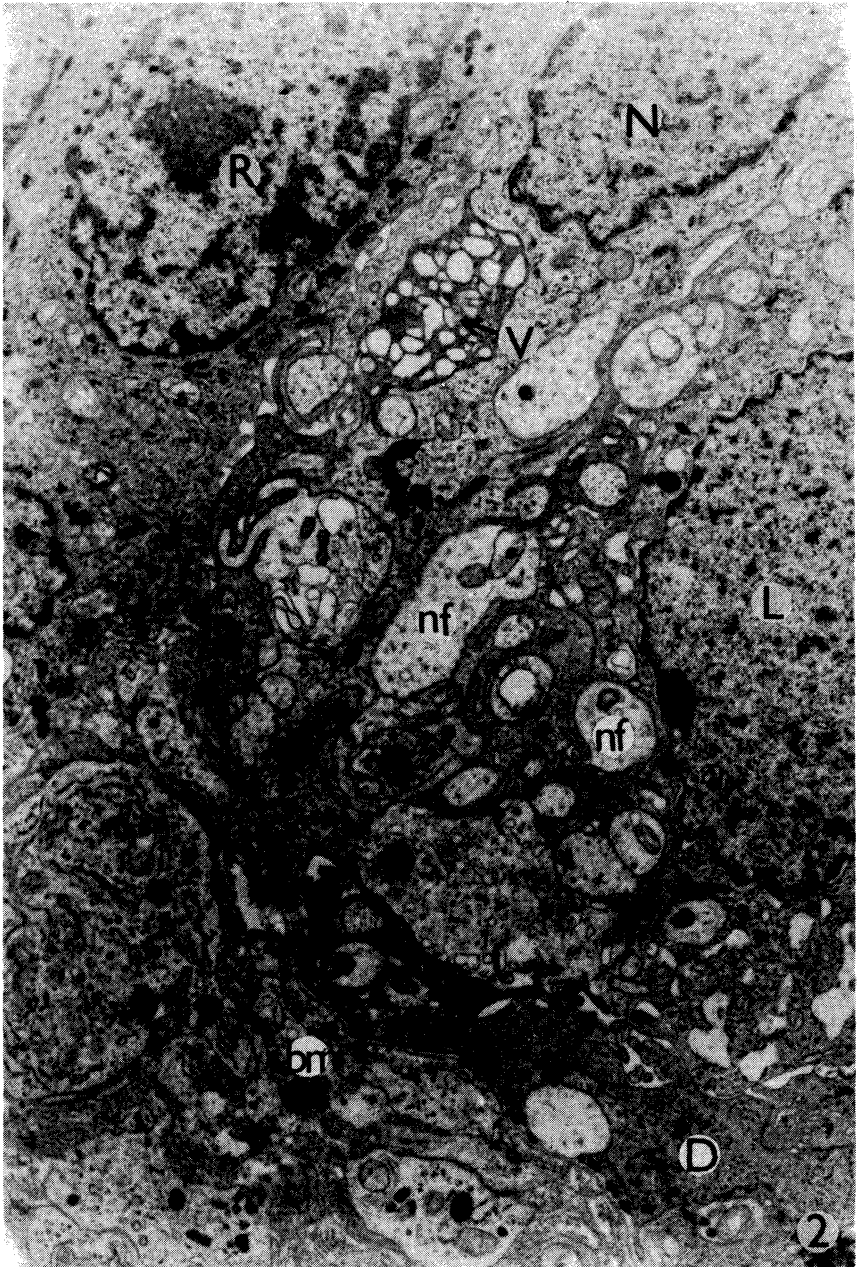


Fig. 2: Basal part of a porcine taste bud. Basement membrane (bm). Extension of a peripheral dark cell (D) with numerous glycogen inclusions in the cytoplasm. Receptor cell (R), light cell (L), nucleus of a dark cell (N). Intragemmal nerve fibres. Vacuoles in the dark cell cytoplasm (V). $\times 8\ 000$.

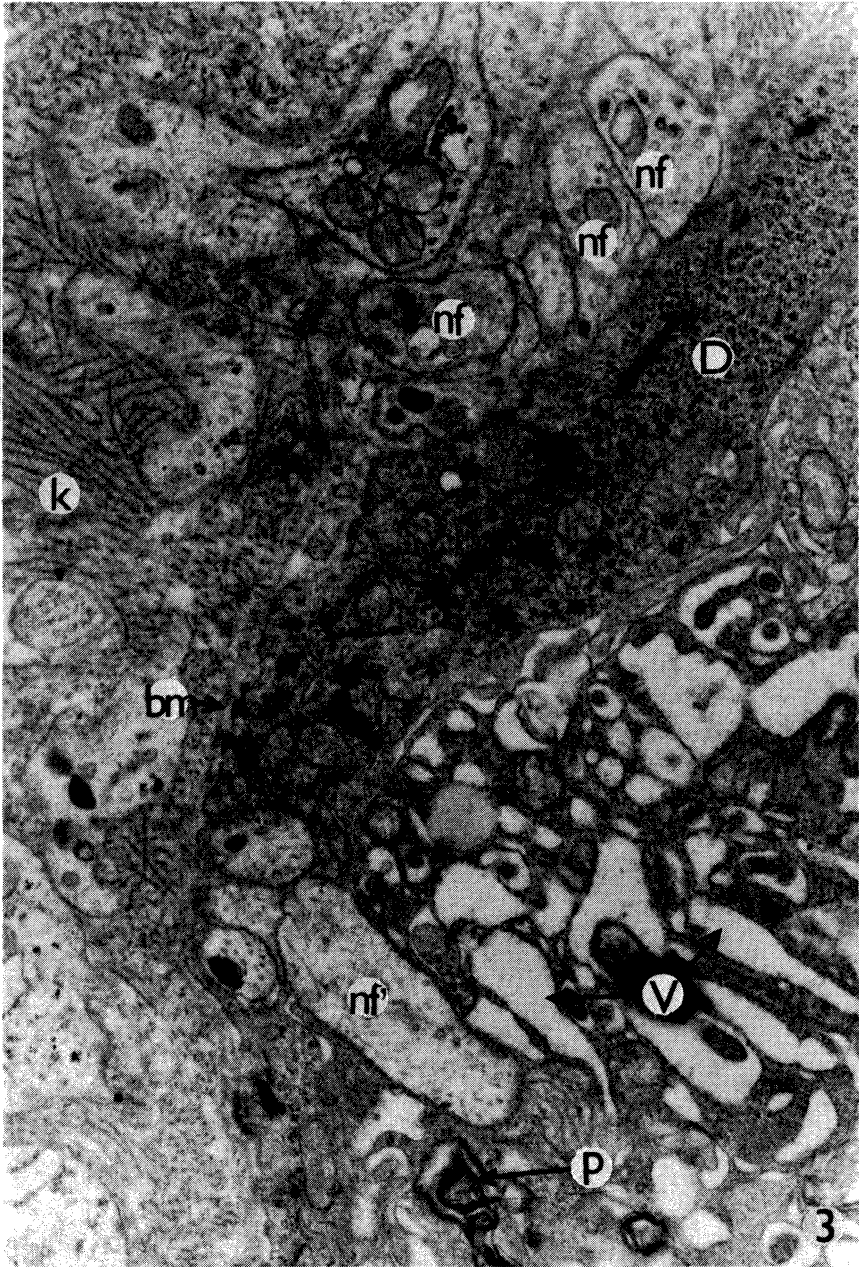


Fig. 3: Central region of a porcine taste bud base. Basement membrane (bm). Lamina propria mucosae with collagen fibres (k). Nerve fibres running under the basement membrane (nf) and fibres entering the bud (nf'). A great amount of glycogen inclusions, filaments and mitochondria in the cytoplasm of a peripheral dark cell (D). Vacuoles in the basal part of a adjacent dark cell (V). Pseudomyelin formations (p). $\times 16\ 000$.

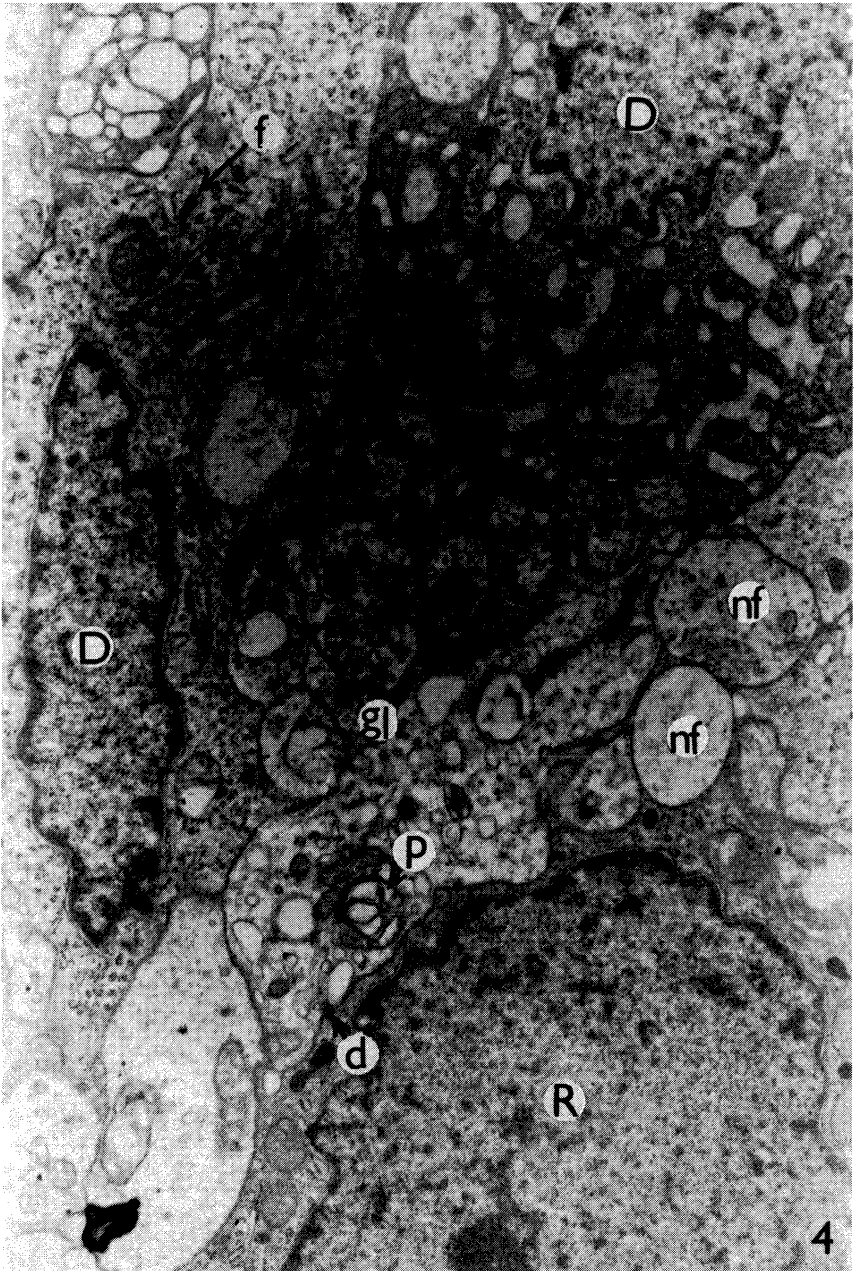


Fig. 4: Middle region of a porcine taste bud. Dark cells (D) with nuclei. Receptor cell (R). Intragemmal nerve fibres (nf). Glycogen particles in the axoplasm (gl). Bundles of filaments in the dark cell cytoplasm (f). Pseudomyelin formation (p). Desmosome between the nerve fibre axolemma and the receptor cell (d). $\times 16\ 000$.

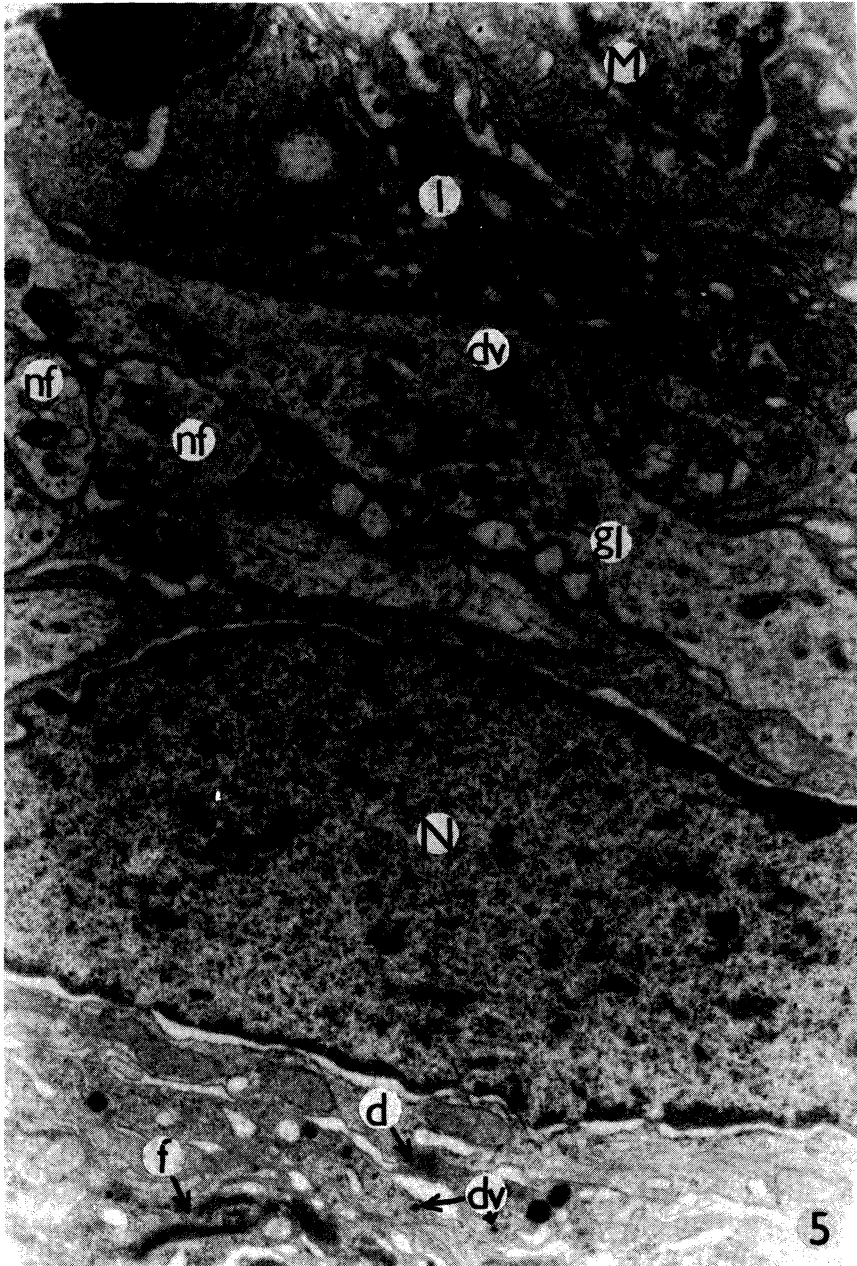


Fig. 5: Peripheral part of the middle region of a porcine taste bud. Mitochondria (M) and filament bundles (f) in the dark cell cytoplasm. Dark vesicles (dv) and lysosomes (l) in the extension of a receptor cell. Intragemmal nerve fibres (nf) with glycogen inclusions (gl). Light cell nucleus (N). Desmosome between the light and the receptor cells (d). $\times 16\ 000$.

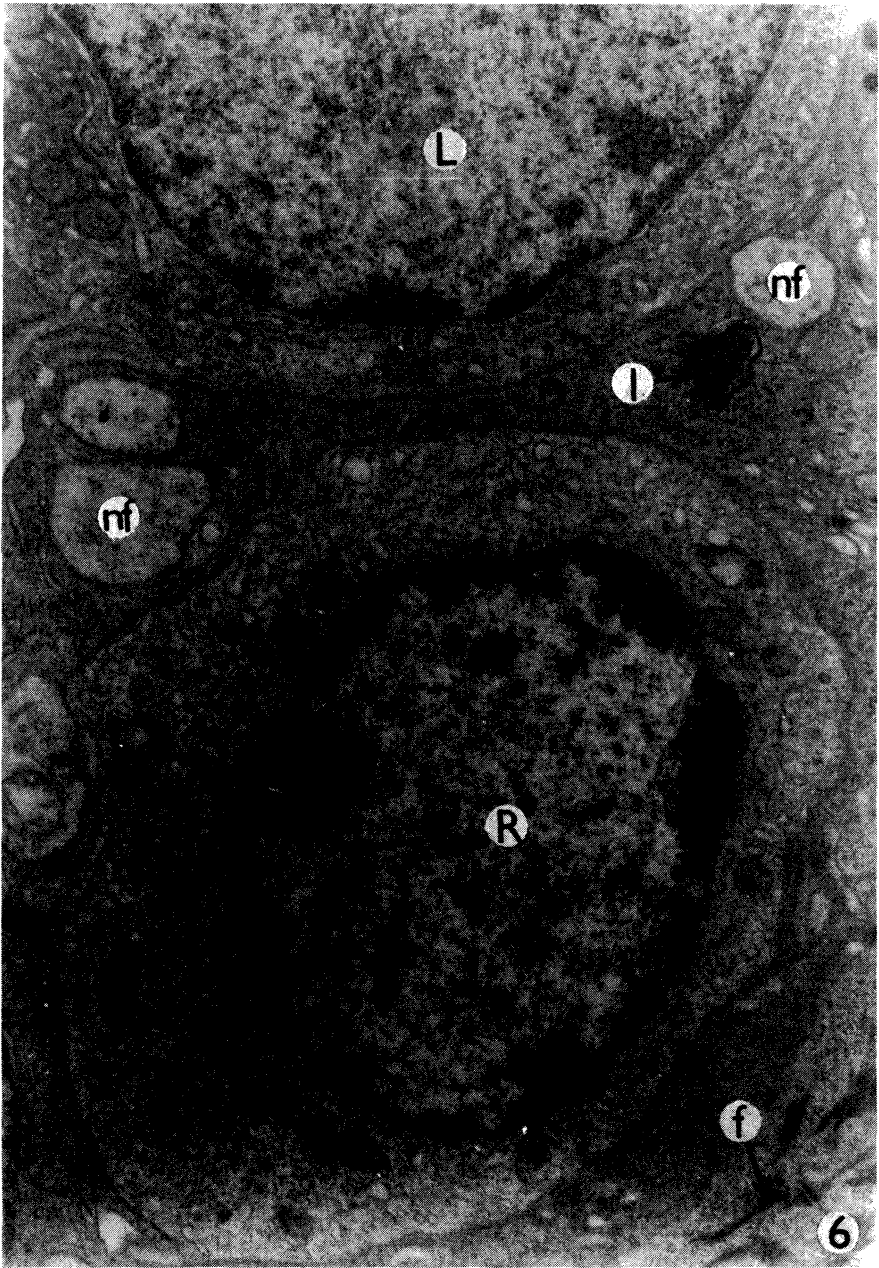


Fig. 6: Nuclei of a light cell (L) and a receptor cell (R) in the middle region of a porcine taste bud. Nerve fibres (nf). Bundles of filaments (f) and a lysosome (l) in the dark cell cytoplasm. $\times 16\ 000$.