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Ultrastructure of the Taste Bud of the Human Fungiform Papilla

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Summary. The taste bud of the human fungiform papilla was examined by electron microscopy. Typical type I, type II, and type III cells were found along with contact sites with nerve endings. Vesicles in nerve fibers contacting type I and type II cells suggest that these cells may receive efferent impulses, whereas vesicles and granules in type III cells adjacent to (afferent) nerve fibers support the view that type III cells are sensory receptors. All of these features are virtually indistinguishable from those previously reported in fungiform taste buds of other mammals.

Key words: Human fungiform papilla — Taste bud — Ultrastructure.

Introduction

Most ultrastructural studies of mammalian taste buds refer to circumvallate or foliate papillae (see Murray, 1973; Jahnke, 1972). Only a few reports exist on fungiform buds of the rat (Farbman, 1965a, 1965b; Beidler, 1969, 1970; Murray, Murray and Hellekant, 1972), mouse (Mattern and Paran, 1974) and rabbit (Murray, 1969, 1971, 1973; Murray and Murray, 1970, 1971; Graziadei, 1969).

Farbman discussed four cell types in the rat fungiform bud, two of which, the peripheral and basal cells, were postulated to be precursors of the remaining two cell types. The latter, designated type I and type II cells, are centrally located within the bud, extending from the pore, where they terminate in microvilli, to the base of the bud which is penetrated by unmyelinated nerve fibers. Type I cells were thought to be the receptor cells described in earlier studies. Type II cells were believed to function in the development and maintenance of the taste pore.

Murray and Murray (1970) and Murray (1971) observed similar type I and type II cells in rabbit fungiform buds. In addition they observed type III cells as previously described in foliate buds (Murray, Murray and Fujimoto, 1969). Type III cells characteristically contain both dense-cored vesicles and clear-cored, synaptic-like vesicles near nerve fibers contacting their basal halves. Although type III cells could not be identified in the apical part of fungiform buds, as were their counterparts in foliate buds, they are, nonetheless, considered likely to be receptor cells.

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Beidler (1969, 1970) and Graziadei (1969) described the morphology of the lingual surface of fungiform papillae as seen in the scanning electron microscope. The pore is situated in the middle of a conical depression formed by overlapping squamous epithelial cells. Recently, Mattern and Paran (1974) studied mouse fungiform papillae *in vivo*, and observed fluid to well up from the pore in response to puffs of HCl vapor.

The present report will describe the ultrastructure of the taste buds of human fungiform papillae which are anatomically similar to those previously reported from rat, mouse and rabbit.

Materials and Methods

Fungiform papillae were excised from human volunteers who had normal taste acuity for the four primary taste qualities (Henkin and Christiansen, 1967) and who received general anesthesia for reasons other than papilla excision. Papillae with adequate epithelial margins were excised with a Hoyes-Martin biopsy punch, the bases being carefully severed with fine iridectomy scissors. Papillae were immediately immersed in 2.5% glutaraldehyde in Millonig's (1962) buffer pH 7.3 and fixed at least 24 hr. at 4C. Subsequently they were washed in the same buffer, post-fixed 1 hr. in buffered 1% OsO_4, dehydrated in graded alcohols, terminating in propylene oxide, and embedded in Epon-Araldite. Thin sections, stained with lead citrate followed by uranyl acetate, were examined in a JEM 100B electron microscope.

Generally 3 to 5 papillae were removed from a total of 11 normal volunteers. However, satisfactory preservation and success in finding buds by electron microscopy were limited to fungiform papillae of 3 persons. One-3 buds were examined from each of 10 papillae of these 3 volunteers.

Results

In the dorsum of human fungiform papillae we have usually encountered 2–5 buds embedded in the epithelium. These buds are somewhat more elongated than the pear shaped or thick, oval circumvallate taste buds.

The Taste Pore. The taste pore of the fungiform bud is on the lingual surface of the papilla and communicates directly with the oral cavity. The microvilli[1] of the taste cells lie deep within the pore which consists of a channel in the lingual epithelium of the papilla (Fig. 1), the channel being longer than that of other bud types. The channel area contains a mixture of a few clear-cored vesicles which resemble the apical vesicles of type I cells and more numerous, somewhat smaller, and frequently uniformly staining granules. Large masses of dense extracellular material characteristic of the pores of other taste bud types (Murray and Murray, 1971) are absent from human fungiform buds.

This appearance is similar to that of fungiform buds of other mammalian species (see Introduction for references).

As is the case with other taste buds we can distinguish three major cell types within the human fungiform bud.

Type I Cells. Type I cells constitute the majority of cells. They originate near the base of the bud (Figs. 3, 7) and terminate distally in microvilli (Fig. 1). These cells have a lightly staining cytoplasm and a paucity of dense apical granules

1 Under the biopsy conditions employed in removing papillae, the microvilli appear somewhat swollen and less well preserved than those of other species which can be fixed *in situ*.

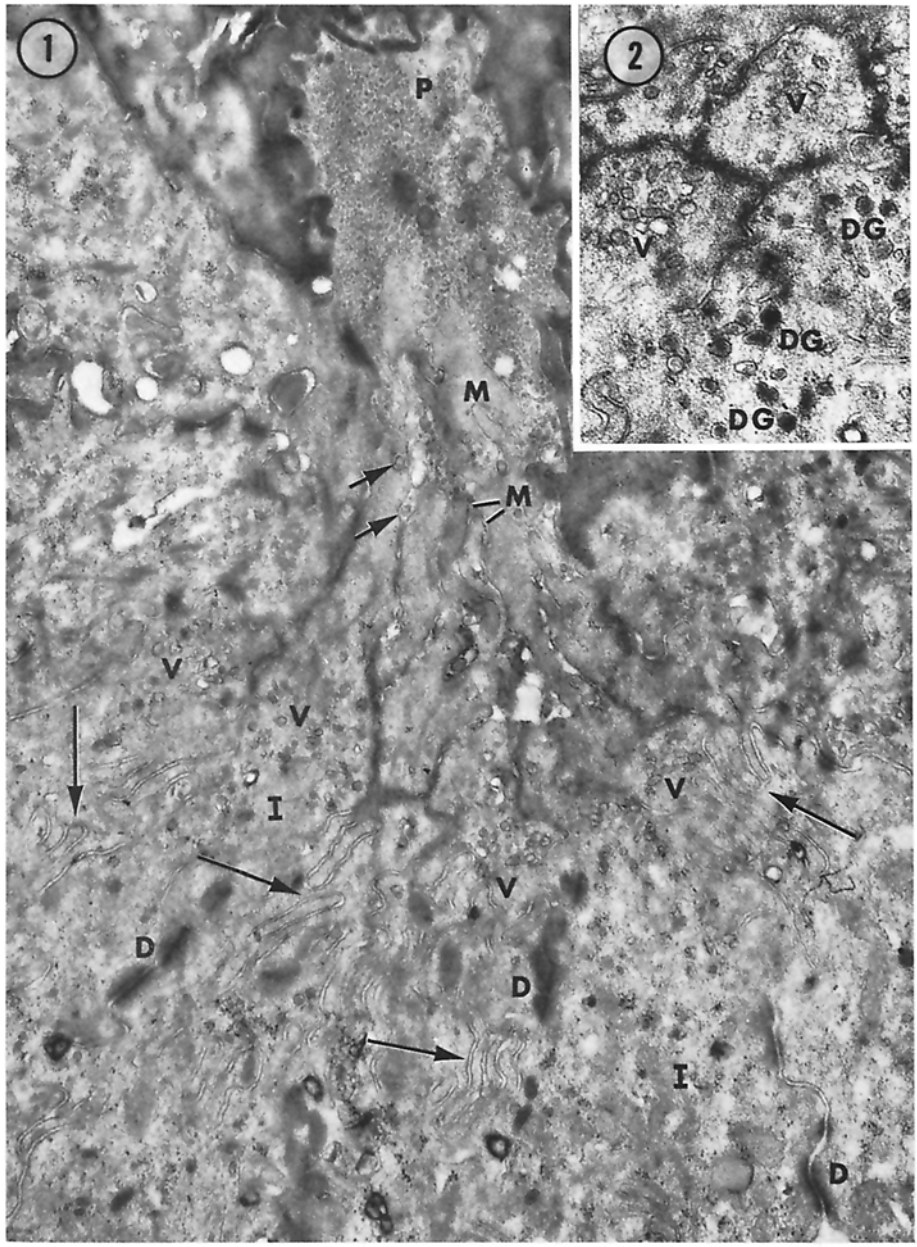

Fig. 1. Apical part of human fungiform taste bud. Type I cells (*I*) with clear-cored vesicles (*V*) and lateral interdigitations (long arrows), largely free of desmosomes (*D*), are dominant. Note terminal microvilli (*M*) surrounded by few clear-cored vesicles (small arrows) and numerous granules filling the pore (*P*). × 18300

Fig. 2. Near cross section of apical region of bud showing many clear cored vesicles (*V*) and fewer dense cored granules (*DG*) in type I cells. × 27600

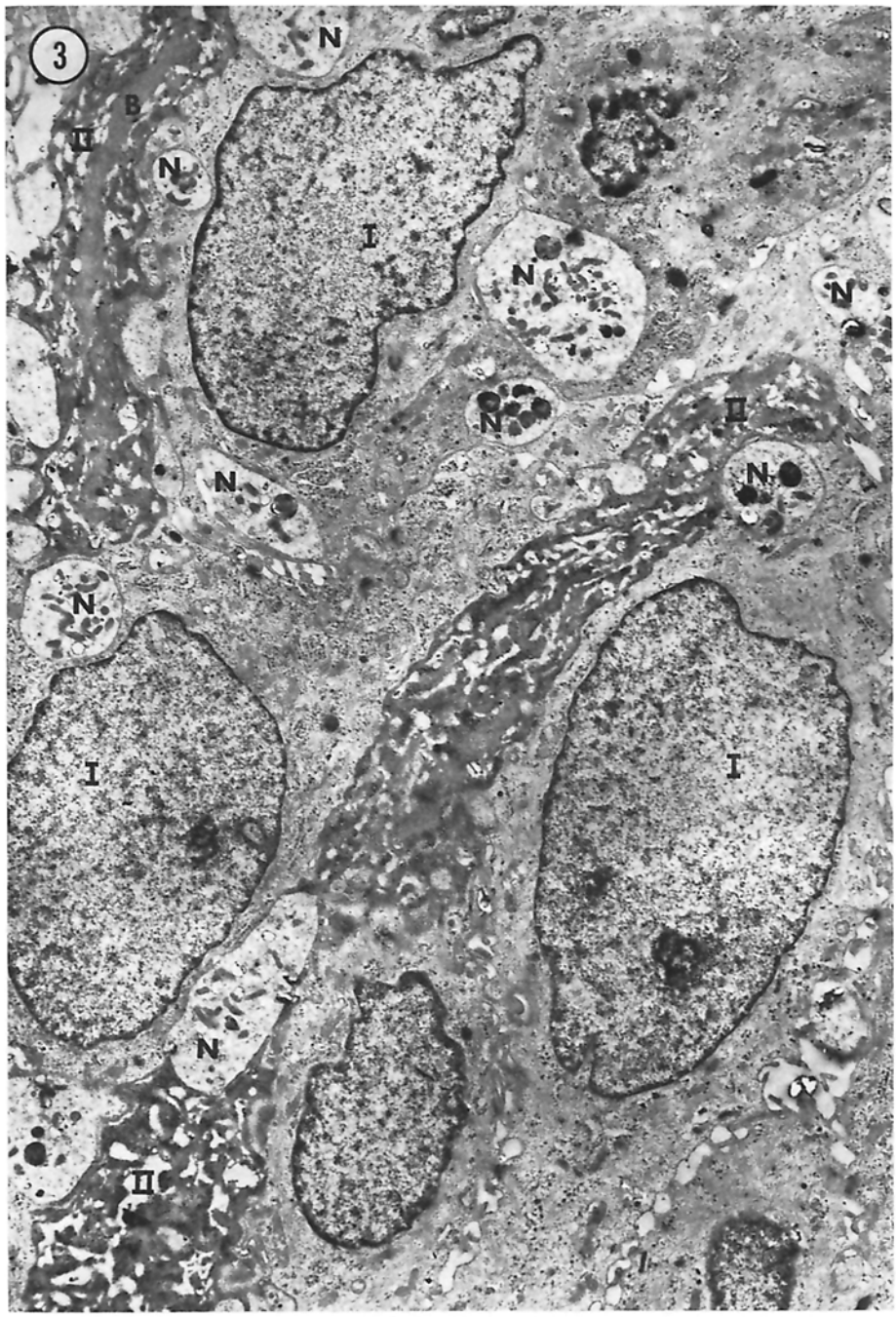

Fig. 3. Longitudinal section of fungiform bud. Note two type II cells and some type I cells. Numerous nerve fibers (*N*) in intimate contact with these cells. Note tonofilament bundle (*B*) in type II cell (upper left). × 7000

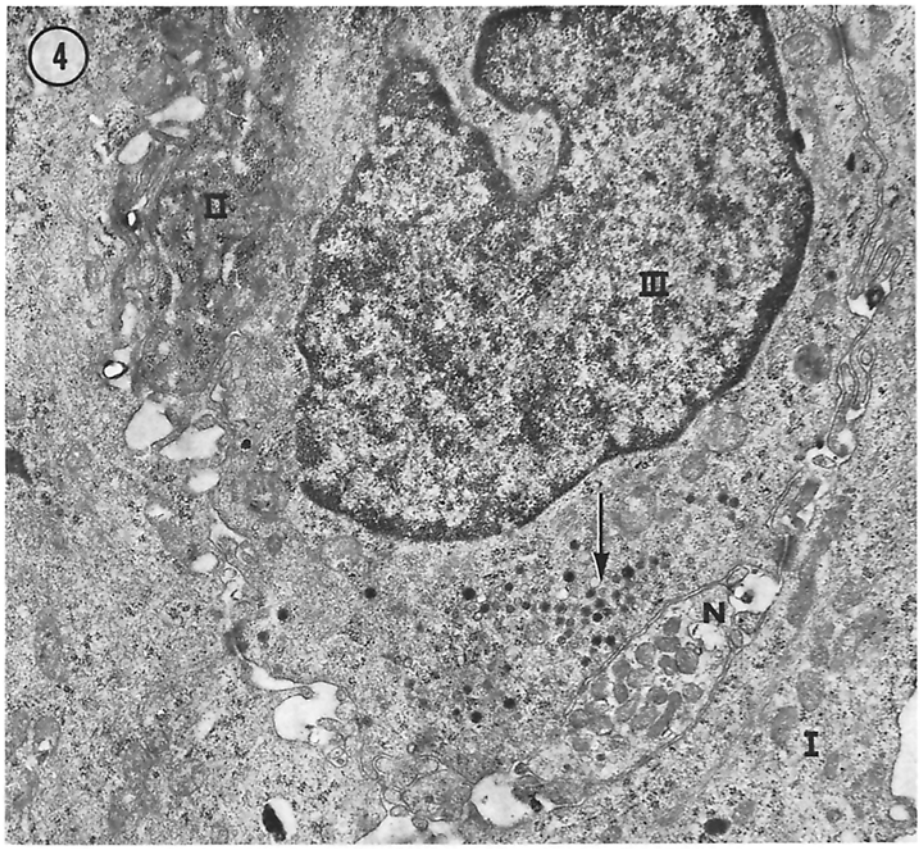

Fig. 4. Longitudinal section through bud showing cell types I, II, III. Type III cell recognized by dense cored granules (arrow), type II cells by dense cytoplasm and vacuoles. × 14100

(Figs. 1, 2) characteristic of type I cells of circumvallate and foliate taste buds (Murray and Murray, 1971; Jahnke, 1972). Because of the lack of such granules, it is difficult to distinguish between type I and type III cells. Close to the pore, type I cells abound in clear-cored vesicles (Figs. 1, 2), the intracellular site of origin of which has not been determined. At the apex of the bud numerous short lateral projections from type I cells interdigitate with corresponding projections from adjacent cells increasing the area of contact between these cells (Fig. 1). Interdigitations are relatively free of desmosomes which are abundant in other areas of cell to cell contact, particularly at the apex (Fig. 1). Perhaps because of limited sampling, we have only rarely found apical centrioles in type I cells as commonly observed in other taste bud types.

Frequent close contacts are observed between type I cells and nerve fibers, the plasma membranes often appearing deeply indented by the fibers (Figs. 3, 7). No evidence of a synaptic differentiation between nerve fiber and type I cell connections has been found.

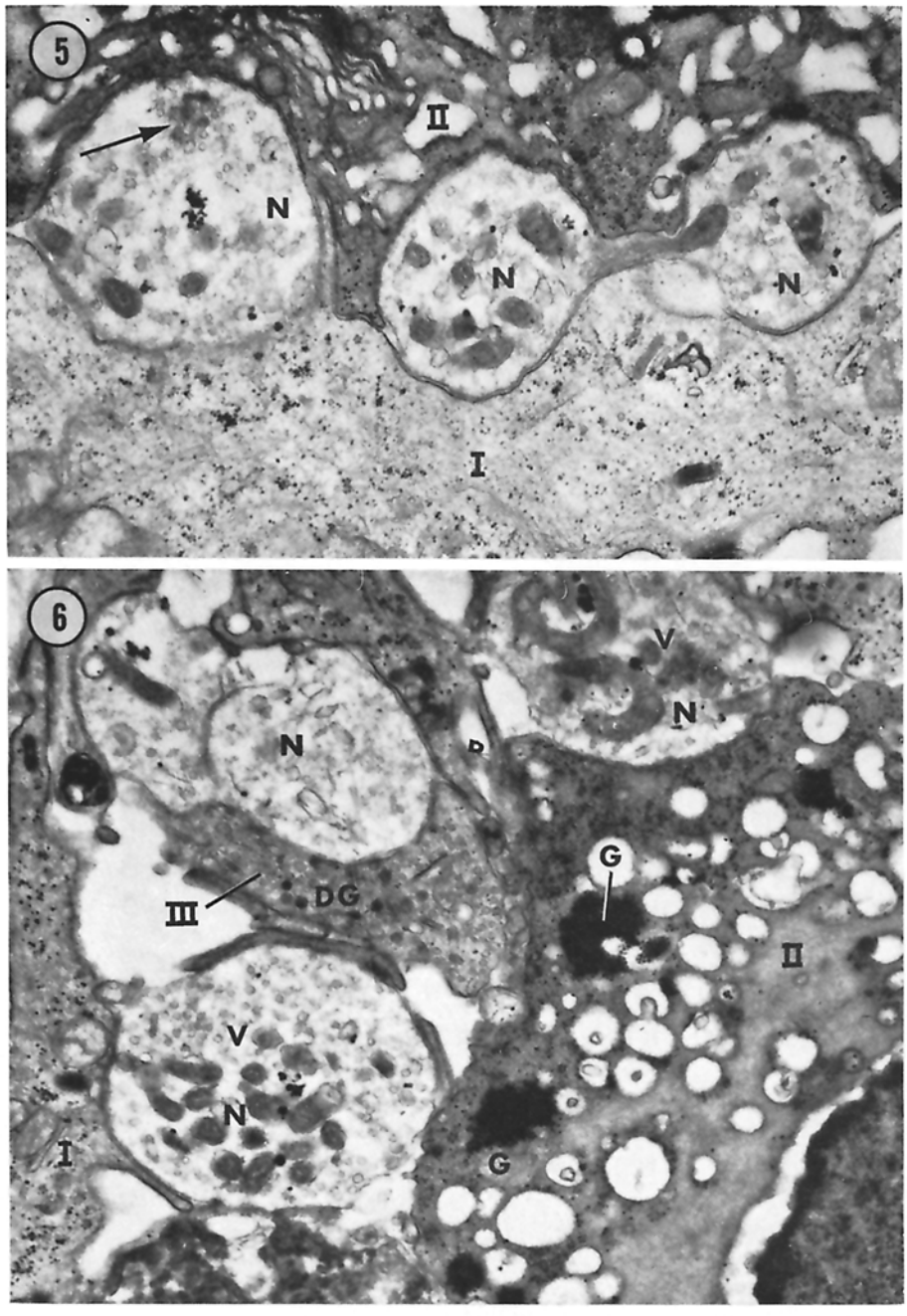

Fig. 5. Contacts between type II cell (*II*) and nerve fibers (*N*) indenting cell. Within nerve fibers many synaptic-like vesicles (*V*) including group (arrow) suggesting possibility of efferent synapse between fiber and type II cell. Lower cell probably type I cell. × 22600

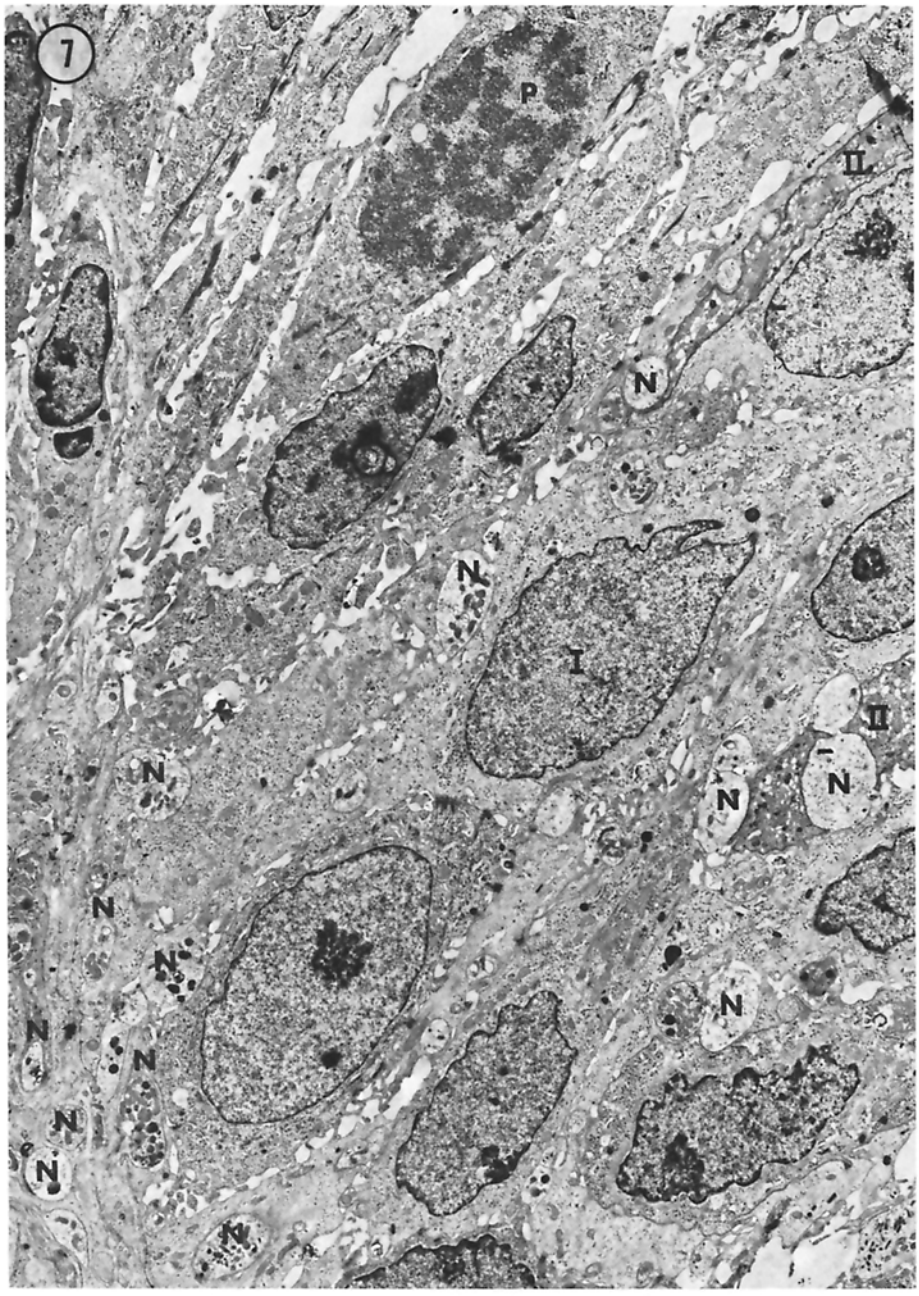

Fig. 6. Contacts between nerve fibers (*N*) and type III cell (*III*). Type II cell (*II*) with masses of glycogen (*G*), and probable type I cell (*I*). Type III cell contains many clear cored vesicles (*V*) and dense-cored granules (*DG*) compatible with type III, being afferent; whereas with type I and type II cells vesicles (*V*) are on nerve fiber side. × 22600

Fig. 7. Section through basal part of bud showing perigemmal cell (*P*) in mitosis. Many unmyelinated nerves (*N*) at base of bud (lower left). × 4400

Type II Cells. In sagittal sections of the bud generally 1 to 3 type II cells are seen (Figs. 3, 7). Like type I cells, they extend from the base of the bud to the pore and terminate in microvilli. These cells are characterized by densely staining cytoplasm, with numerous vacuoles of varying size and shape. The vacuoles appear largely devoid of contents that stain by the methods herein employed. In the apical portions of type II cells there are numerous mitochondria which, along with glycogen and vacuoles, are the dominant cytoplasmic structures. A bundle of tonofilaments is occasionally seen in apical or basal portions of type II cells (Fig. 3).

Type II cells show great variability in morphology. All have dense, vacuolated cytoplasm, but the degree of vacuolization varies (Figs. 3, 7), and not all cells can be shown to have tonofilament bundles. There are other type II cells in which the apical mitochondria are not so numerous.

Nerve fibers are in intimate contact with type II cells, often being deeply embedded in the cytoplasm (Figs. 3, 5, 7), and they occasionally appear as beaded enlargements along the lateral surface of these cells. Occasionally enlargements show narrow connections with continuity of membrane and cytoplasm (Fig. 5). The contact of nerve fiber and type II cell is not characteristic of a typical synaptic junction. On the neural side, however, we often observe numerous clear vesicles (V) which closely resemble synaptic vesicles (Figs. 5, 6) but there is no observable thickening of the plasma membrane suggesting a postsynaptic differentiation. While there may be somewhat more numerous nerve fiber contacts with the basal halves of type II cells, such contacts reach well into the apical portions, even near the pore.

Type III Cells. These represent the smallest number of cells in the fungiform bud, as they do in other taste bud types (Murray and Murray, 1971). They are characterized by dense-cored granules and clear-cored vesicles largely in their basal region (Fig. 5), but occasionally also in the immediate supra-nuclear region. The granules and vesicles are especially numerous in the vicinity of nerve fiber contacts (Figs. 4, 6), a relationship which according to Murray and Murray (1971) suggests synaptic junctions despite the absence of membrane differentiations. The type III cell is, therefore, considered likely to be a true receptor cell, its cytoplasm representing the presynaptic side of the junction.

It is virtually impossible to distinguish between type III and type I cells in the bud apex, since neither contain unique cytoplasmic constituents in this region. Therefore we, as Murray and Murray (1971), are unable to determine whether or not type III cells of fungiform papillae extend all the way to the pore or how they terminate.

Perigemmal Cells. As in other taste bud types, peripherally located perigemmal cells are interposed between the epithelial, cells and the 3 taste bud cell types described above. These cells are occasionally seen in mitosis (Fig. 7) and probably represent an undifferentiated source of one or more of the three types of taste bud cells.

Discussion

The ultrastructure of the human fungiform taste bud is essentially indistinguishable from that of other mammalian species. In fact, all mammalian taste

buds so far studied, whether fungiform, vallate or foliate, appear to consist of the basic three cells, types I, II and III (Murray and Murray, 1971). However, some anatomical differences exist between fungiform buds and the other taste buds. First, microvilli of fungiform buds appear further away from the oral environment than do microvilli of other buds. The microvilli of the fungiform bud appear at the base of a rather lengthy pore channel, which may represent a protective anatomical feature (Mattern and Paran, 1974) because of the exposed nature of the fungiform bud. Second, there are very few typical, round or elongated, dense-cored granules in the apices of type I cells of fungiform buds, although there are numerous clear-cored vesicles in this region. Third, the pore of the fungiform bud is virtually devoid of dense extracellular material characteristically found in other bud types (Murray and Murray, 1971). The fungiform taste pore does, however, contain numerous vesicles also observed in pores of foliate and vallate buds.

The functions of the three major cell types are by no means certain, but there is no reason to doubt that these cells perform similar roles in the different taste bud types, despite minor anatomical variations.

Type I cells of vallate and foliate buds contain large numbers of apical dense granules which are believed to be secreted to form the dense extracellular pore substance (reviewed by Murray, 1973; Mattern and Paran, 1975). In fungiform buds, type I cells may have a similar function, namely to secrete the contents of their apical vesicles into the pore. The lack of synaptic-like vesicles within these cells and the presence of such vesicles in nerve fibers in contact with identifiable type I cells of vallate type buds (deLorenzo, 1958, 1963) are compatible with the hypothetical secretory role (effector cell) for type 1 cells.

The numerous mitochondria within the variably vacuolated cytoplasm of type II cells prompted Farbman (1965a) to suggest that these are the most metabolically active cells in the bud. Bundles of tonofilament-like fibrils course a wavy (or helical) path from the apex to the base of this cell (Mattern and Paran, 1974). The neuronal contact of the type II cell is also compatible with the interpretation of an effector cell. Recently evidence of a contractile mechanism in mouse fungiform buds was presented (Mattern and Paran, 1974), and it was hypothesized that the type II cell with its tonofilament bundle might provide a potentially protective function.

Type III cells are now thought to be the most likely candidates for gustatory receptors (Murray, 1973). This is based upon large accumulations of dense cored granules and synaptic-like vesicles, particularly numerous in the basal halves of these cells where they make contact with nerve fibers. Some thickening of the type III cell membrane has also been noted at these contact sites (Murray, 1973).

The taste pore remains an enigma. It contains microvillous terminations of the three taste cell types and a dense extracellular substance and/or vesicles. Recently acetylcholinesterase has been observed in the pore of the circumvallate bud by ultrastructural histochemistry (Paran and Mattern, 1974). Since the initial events of the gustatory process probably occur in the taste pore (Beidler and Gross, 1971; Murray, 1973) future investigations will have not only to verify or reject the hypothetical functions of the various cells of the bud, but to focus on the contents of the taste pore.

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