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Review Article

# Ultrastructures of mechanoreceptors in the oral mucosa

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**Abstract**

The present review describes the fine structures of lamellated mechanoreceptive corpuscles, Merkel cell–neurite complexes and free nerve endings in the oral mucosae of mammals, with special attention to axon terminals and lamellar cells. The mechanoreceptive nerve endings of the oral mucosa were studied using histochemistry, immunohistochemistry and transmission electron microscopy techniques. The organized mechanoreceptive corpuscles are present in the mucosae of gingiva, cheek, tongue and soft and hard palate. They are elongated or globular in shape, being located in the connective tissue papillae. The capsule is composed of several layers of cytoplasmic extensions of perineural cells. Numerous bundles of collagen fibers are noted at the periphery of the corpuscle. The lamellated corpuscles are surrounded by several layers of superimposed flattened capsular cell processes. The interlamellar spaces are 0.2–0.4 μm in width and filled with thin fibrillar collagen fibers embedded in the amorphous substance. The lamellar cells contain rich microtubules and are characterized by the presence of caveolae on the surface plasma membrane. The terminal axon contains an abundance of mitochondria and small clear vesicles (20–50 nm in diameter). There are neurofilaments in the center of the axon terminal. Intermediate-type junctions are seen between the adjacent lamellar cells and between the axon and adjacent lamellae. The free nerve endings are found in the subepithelial regions, very close to the basal laminae of mucosal epithelium. They are surrounded by a thin cytoplasm of Schwann cells. Sometimes Schwann cell basal laminae become multilayered. Merkel cells are present within the basal layer of mucosal epithelium and contain characteristic electron-dense granules that are located almost exclusively at the side of cytoplasm in contact with axon terminals. Intermediate-type junctions are noted between axon terminals and Merkel cells.

**Key words:** free axon terminal, lamellated corpuscle, mechanoreceptor, Merkel cell, oral mucosa, ultrastructure.

## Lamellated mechanoreceptive corpuscles

Usually the lamellated corpuscles are located in the transitional area between the lamina propria and epithelial layer of the mucosa. The density of the lamellated corpuscles is variable, depending on the sites of oral tissue. They measure from 18 to 30 μm in diameter and have several layers of asymmetrically arraged lamellae of lamellar cells (modified Schwann cells) around axon terminals. The lamellae measure 0.5–1 μm in width and contain an abundance of intermediate filaments, as reported for other similar corpuscles (Watanabe & Yamada, 1983). Few endoplasmic reticulum are noted in the cytoplasmic processes of the lamellae.

The lamellae are characterized by numerous caveolae on the plasma membrane. The peri-axonal space between the axon terminal and their adjacent lamellae or interlamellar spaces between neighboring lamellae measure from 0.1 to 0.3 μm in width. There are fine filamentous or amorphous materials in the interlamellar spaces. The amorphous material is electron opaque near the plasma membrane of the lamella, suggesting that it is what is known as basal lamina-like material.

Sensory nerve endings found in the lamina propria of cheek mucosa of mouse and rat are encapsulated and composed of the axon terminals and associated lamellae of cytoplasmic processes of lamellar cells (Watanabe & Semprini, 1985; Watanabe & Yamada, 1985). The fine structures of the sensory nerve endings were reported in the rat gingiva by Martinez and Pekarthy (1974) and Watanabe and Yamada (1979, 1983), in the rat lip by Tachibana *et al*. (1987) and Watanabe and Ide (1987), in the cat cheek by Watanabe and Yamada (1985), and in the tongue fungiform papillae by Toyoshima *et al*. (1987) and Watanabe and Ide (1991).

The lamellated mechanoreceptive corpuscles consist of axon terminals and associated lamellae, which are successively stacked thin cytoplasmic processes of lamellar cells (Cauna & Ross, 1960; Chouchkov, 1973; Ide, 1976, 1977, 1982; Castano & Ventura, 1978). Axon terminals of Meissner corpuscles are branched within the corpuscle, with each branch terminating as

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flattened or discoid extremities sandwiched by layered lamellae. These corpuscles usually receive one to three myelinated nerve fibers and are surrounded by a capsule, as observed in the gingiva of the *Cebus apella* monkey (Watanabe, 1982). The fine structures of Pacinian corpuscles were first studied by Cauna and Mannan (1959), Andres (1969), Chouchkov (1971), and Zelená (1978, 1980, 1981). The Pacinina corpuscle has a single straight axon terminal at the center of the corpuscle, which is sandwiched by the paired halves of densely stacked laminae (i.e. the inner bulb). The inner bulb lamellae are formed by thin cytoplasmic extensions of terminal Schwann cells. Details of these structures have been reported by Munger and Ide (1988), Munger *et al*. (1988) and Ide *et al*. (1988).

The fine structures of mechanoreceptive corpuscles in stomatognatic apparatus like rhinarium have been reported in rats (Silverman *et al*., 1986) and in cats (Halata, 1970). Nerve endings were reported in the gingiva by Barker (1967), Martinez and Pekarthy (1974) and Watanabe and Yamada (1979, 1983), and in the periodontal ligament by Griffin and Harris (1974a, 1974b), Harris and Griffin (1974a, 1974b), Berkovitz *et al*. (1983), Maeda *et al*. (1990) and Lambrichts *et al*. (1992). Various kinds of mechanoreceptive endings, including small lamellar corpuscles, Merkel cells and Meissner-type corpuscles, have been described in the hard palate by Watanabe and Yamada (1984), Watanabe *et al*. (1985) and Halata *et al*. (1999).

Usually, the corpuscular endings within the connective tissue papillae are formed by a grouping of two to several small corpuscles, depending on the size of the papillae. Intraepithelial axon terminals are described in the mucosae of soft palate, tongue, cheek and gingiva (Munger, 1965; Watanabe & Yamada, 1979, 1985; Muller, 1996) (Fig. 1). There are many variations in morphology of axon terminals within the epithelium (Fig. 2). Intraepithelial axon terminals contain mitochondria, neurofilaments and clear vesicles.

## Merkel Cells

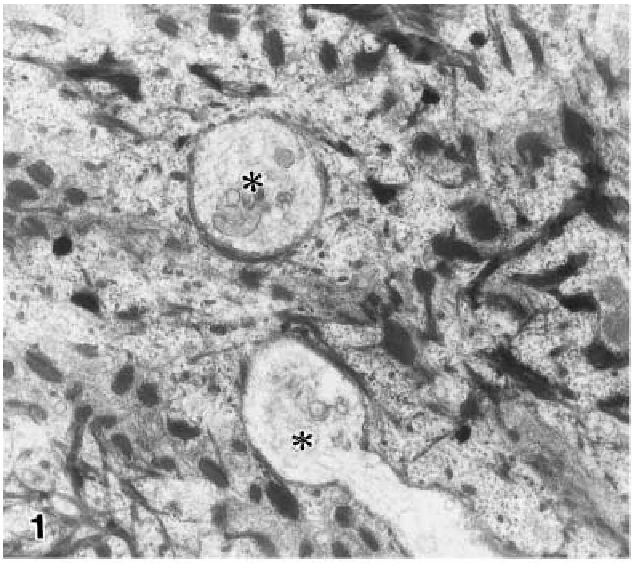
The Merkel cells are in close contact with axon terminals and the characteristic granules are located almost exclusively in the half of the cytoplasm where the axon terminal is attached (Fig. 3). They contain characteristic electron-dense granules and have finger-like protrusions on the cell surface, which are considered to be involved in the mechanoreceptive function of the Merkel cell–neurite complexes (Fig. 4). Andres and During (1973) reported similar protrusions in birds that extend from the Schwann cell cytoplasm. The phenomenon of Merkel cell degeneration has been reported (Kurosumi *et al*. (1969; I Watanabe, pers. obs.): degenerative Merkel cells have an electron-dense nucleus and only several dense granules (Fig. 5). The function of characteristic electron-dense granules of the Merkel cell has been the subject of many studies (Tachibana, 1995; Tachibana *et al*., 1997, 2000; Tachibana & Nawa, 2002).

Electron microscopic studies of Merkel cells were made by Munger (1965), Kurosumi *et al*. (1969), Robins (1970), Smith (1970), Andres and During (1973) and Breathnach and Winkelmann (1973). Merkel cells have been reported in the oral mucosa of several animal species by Halata (1970), Tachibana (1978, 1979), Watanabe (1979/80), Tachibana and Nawa (1980) and Tachibana *et al*. (1983). Nikai *et al*. (1971) reported the fine structure of Merkel cells in the rat gingiva. Watanabe (1979/80) described Merkel cells in the gingiva and palatine mucosae of rats and mice (Fig. 6). Watanabe (1988) showed that the fine structures of Merkel cells and associated nerve endings in the lizard gingiva were similar to those of Merkel cell–neurite complexes in mammals**.** Tachibana (1978) studied the presence of Merkel cells in the labial ridge epidermis of anuran tadpoles, describing that the fine structure of these cells was not different from that of other vertebrates. Merkel cells are frequently seen in the labial ridge epidermis and arranged in a line at a uniform level of the triangular epidermis. Hashimoto (1972) studied Merkel cells in human oral mucosa and Garant *et al*. (1980) reported Merkel cells in the palate mucosa of the squirrel monkey. Andersen and Nafstad (1968) and Saxod (1978) reported the presence of Merkel cells in some species of birds.

## Free nerve endings

The sensory nerve fibers are myelinated but lose their myelin sheets beneath the epithelial layer. These

**Figures 1–6. 1.** Intraepithelial axon terminals (asterisks) in the palatine mucosa. Original magnification ×17 100. **2.** An intraepithelial axon terminal in the tongue mucosa. This axon terminal contains many mitochondria (M). Tonofilaments (small arrows) and basal lamina (large arrow) of epithelial cells are seen. Original magnification ×13 500. **3.** High magnification of part of the Merkel cell. Electron-dense granules (arrows) and mitochondria (M) are seen in the Merkel cell cytoplasm, as well as in the axon terminal (A). Original magnification ×39 000. **4.** Cytoplasmic protrusions from the Merkel cell extending into spaces between epithelial cells. Bundles of filaments (P) are extending through the protrusions. Original magnification ×62 000. **5.** This micrograph shows the presumable degenerating Merkel cell in the basal layer of the epithelium. Arrows point to dense granules. M, mitochondria; N, nucleus. Original magnification ×15 000. **6.** A Merkel cell located in the basal layer of the epithelialium. An axon terminal (A) is seen in association with the Merkel cell. Electron-dense granules are deviated in the cytoplasm towards the side of the axon attachment. N, nucleus. Original magnification ×15 000.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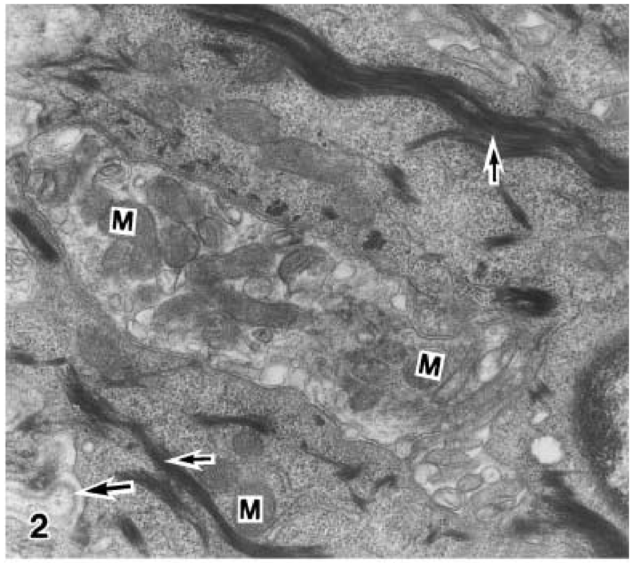
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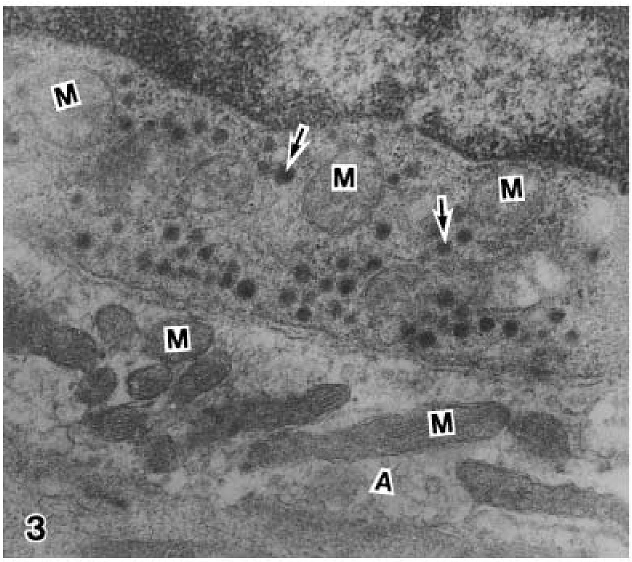
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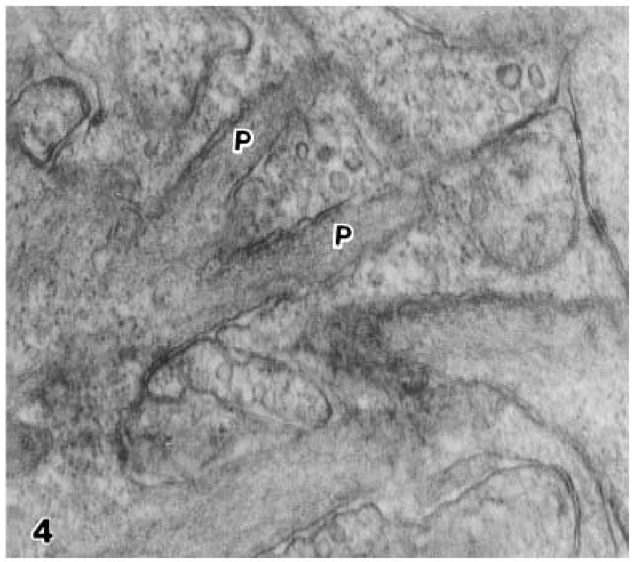
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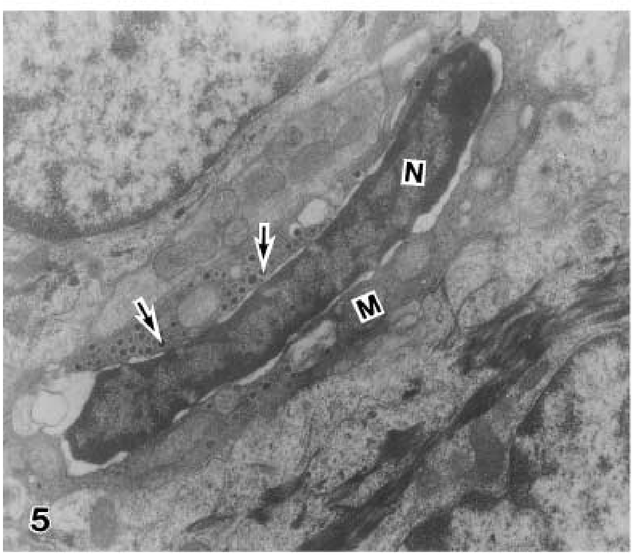
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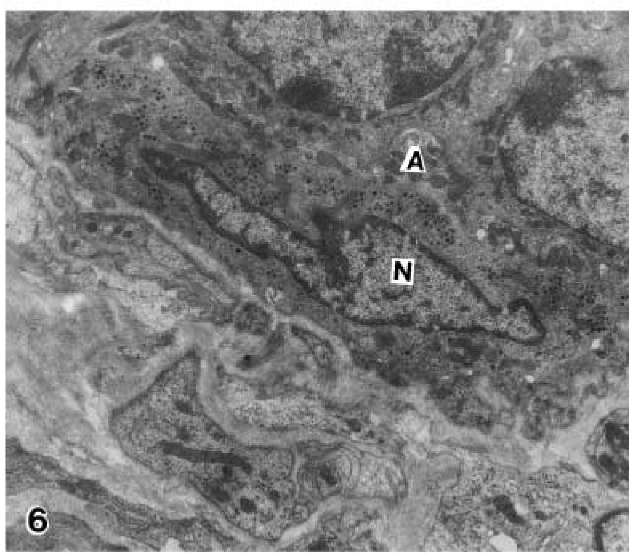
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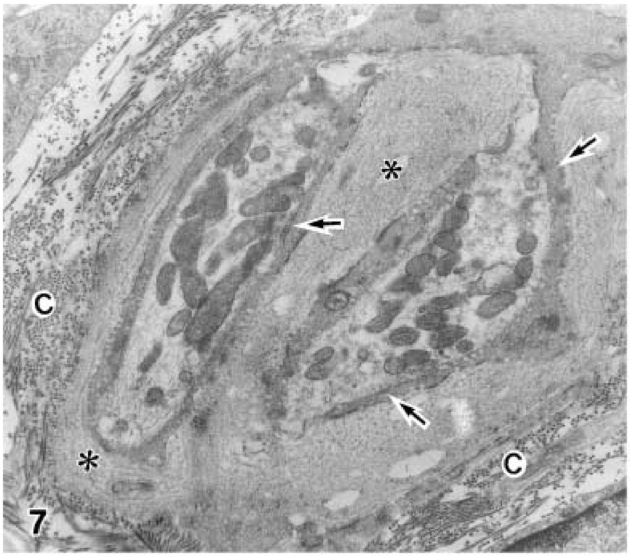


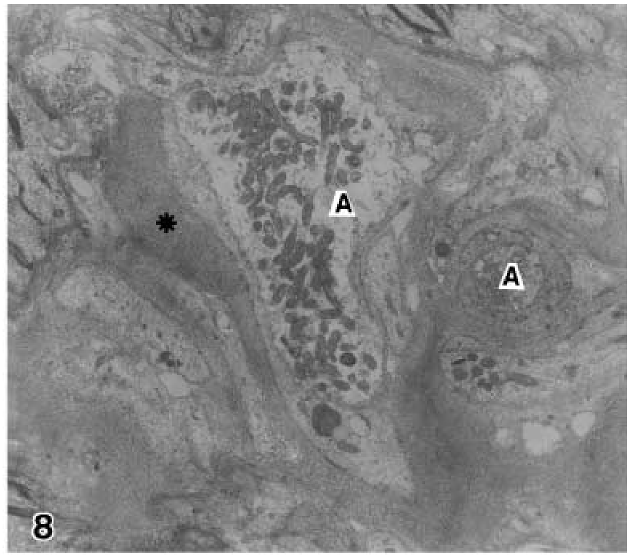


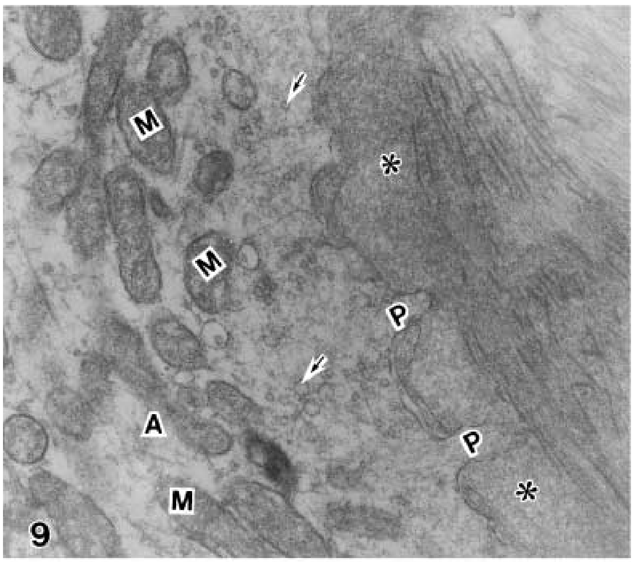


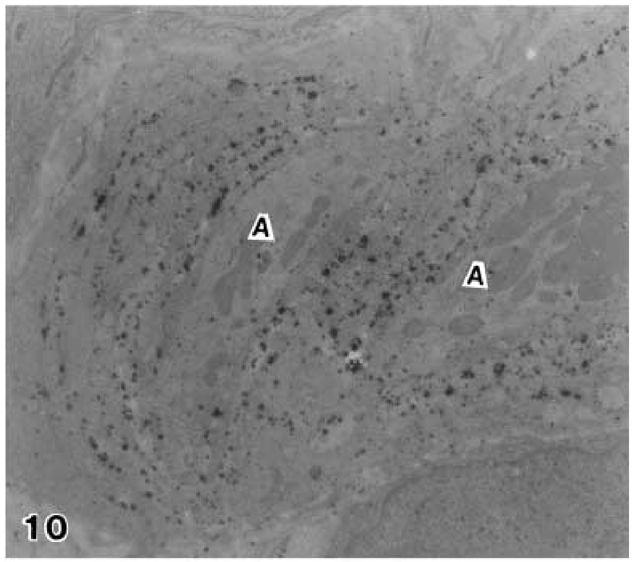


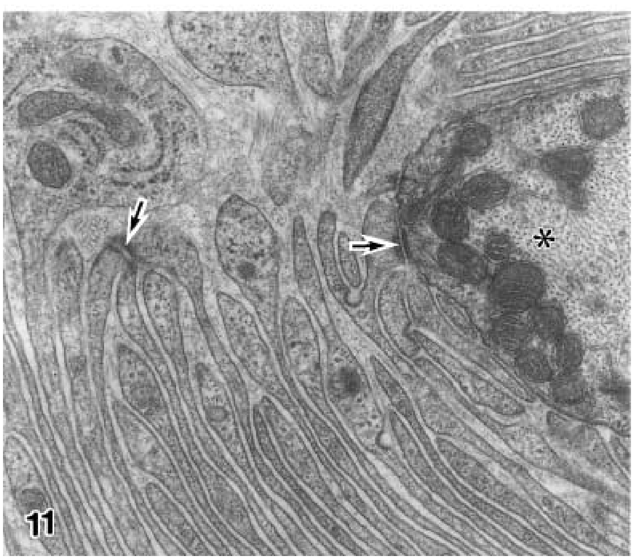


**Figures 7–11. 7.** Free nerve endings located in the subepithelial connective tissue. The thin cytoplasmic processes (arrows) of Schwann cells are associated with the axons. Extensive basal lamina-like afibrillar substance (asterisk) and collagen fibers (C) are seen around Schwann cell processes. Original magnification ×13 000. **8.** This micrograph shows an extensive afibrillar substance (asterisk) enveloping the axon terminal (A) surrounded by Schwann cell cytoplasm in the palatine mucosa. Original magnification ×11 000. **9.** High magnification of a part of the axon terminal. Small axoplasmic protrusions (P) are seen. There are clear vesicles (arrows) and numerous mitochondria (M) in the axon terminal (A). Original magnification ×52 000. **10.** Reaction products of histochemistry for non-specific cholinesterase activity are seen in the spaces between neighboring lamellae. A, axon terminal. Original magnification ×9000. **11.** Intermediate-type junctions (arrows) are formed between lamellar cell processes, and between the lamellar cell process and terminal axon (asterisk). Original magnification ×46 000.

free nerve endings extend through the subepithelial connective tissue of the oral mucosa, forming tortuous courses and swellings. Each bulbous terminal (Fig. 7) is located close to the basal surface of the oral epithelium and is surrounded by a thin laminar cytoplasmic extension of Schwann cells. Usually, the endings contain numerous mitochondria, neurofilaments and clear vesicles. Desmosomal junctions are formed between Schwann cells and axoplasmic membranes. The cytoplasm of Schwann cells has numerous intermediate filaments. The basal laminae of Schwann cells are multilayered and irregular, presenting an extensive afibrillar layer (Figs 7–9). A number of small collagen fibrils is inserted into this layer. In some areas facing the basal surface of the epithelium, the Schwann cell cytoplasm covering the terminal branches becomes very thin. Intraepithelial axon terminals were reported by Munger (1965), Luzardo-Baptista (1973) and Watanabe and Yamada (1979, 1984, 1989). Axonal endings are surrounded by thin laminae of cytoplasmic extensions of Schwann cells. An extensive afibrillar substance (Fig. 8) may surround the nerve endings, as noted by Watanabe and Yamada (1984, 1989). The intraepithelial endings without Schwann cell association are observed in the intracellular space of the palate and tongue mucosae (Fig. 2). The fine structure of free nerve endings have been studied in the soft and hard palate mucosa of mouse and rats by Watanabe and Yamada (1984, 1985, 1989).

## Morphology of axon terminals and associated Schwann cells

The axon terminals of the sensory corpuscle and free nerve endings are oval in cross-section and measure approximately 2.5–3 μm in diameter. It has been revealed that axon terminals in the sensory corpuscles contain many mitochondria and small clear vesicles of approximately 50 nm in diameter, especially at the base of fine axoplasmic protrusions (Fig. 9). The fine structures of intraepithelial axon terminals have been reported by Munger (1965) and by Watanabe and Yamada (1979, 1983). The findings are similar to those reported in the sheep oral mucosa by Jayaraj *et al*. (1973) and in the rat oral mucosa by Watanabe and Semprini (1985), Tachibana *et al*. (1987) and Watanabe and Ide (1987). The axon terminals exhibit fine axoplasmic protrusions on the surface, which are considered to be the receptive sites for mechanical stimuli, including mastication (Watanabe & Yamada, 1985; Toyoshima *et al*., 1987). The same types of axoplasmic protrusions are seen on axons terminals of lamellated corpuscles, which are of the property of rapidly adapting mechanoperception (Watanabe & Yamada, 1983; Watanabe *et al*., 1985; Malinovsky, 1986; Malinovsky *et al*., 1986; Maeda *et al*., 1990).

The terminal Schwann cells associated with the lamellated corpuscle and with free endings have many caveolae on the surface plasma membrane. The interlamellar spaces are filled with amorphous material and fine filaments (Fig. 11). These characteristic features of terminal Schwann cells were also observed with the nerve endings in the oral mucosa by Watanabe and Ide (1987) and by Tachibana *et al*. (1987). Non-specific cholinesterase activity was demonstrated in lamellar corpuscles (Ide & Saito, 1980a, 1980b), as was ATPase activity (Ide & Saito, 1980c). Histochemical reaction products of non-specific cholinesterase activity are deposited in the peri-axonal spaces between the axon terminals and adjacent lamellae, as well as in the interlamellar spaces between neighboring lamellae and within the caveolae of lamellar cells. It cannot be determined whether the reaction products are situated on the plasma membranes of lamellae or on the amorphous material in the interlamellar spaces. Although the functional implication is not known, non-specific cholinesterase activity is a marker of the nerve ending having terminal Schwann cells. Non-specific cholinesterase is produced by lamellar cells, as clearly demonstrated by transmission electron microscopy (Fig. 10). The intensity of the reaction products is higher in the center than in then peripheral regions of the corpuscles. Reaction products are found in caveolae, cisternae of the rough endoplasmic reticulum and nuclear envelope of lamellae cells.

The presence of intermediate-type junctions between the axon terminal and adjacent lamellae and between neighboring lamellae (Fig. 11) has been reported by several authors (Martinez & Pekarthy, 1974; Watanabe & Yamada, 1983, 1985, 1989; Watanabe *et al*., 1985; Tachibana *et al*., 1987; Halata, 1970). These intermediate-type junctions are considered to function for the structural stabilization of the corpuscles.

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