Electron Microscope Study of the Grandry and Herbst Corpuscles in the Palatine Mucosa, Gingival Mucosa and Beak Skin of the Duck*

Ii-sei WATANABE,** Jiro USUKURA and Eichi YAMADA***

Department of Anatomy (Prof. E. YAMADA), University of Tokyo Faculty of Medicine, Tokyo, Japan

Received October 24, 1984

Summary. Grandry and Herbst corpuscles of the palatine mucosa, gingival mucosa and beak skin were studied with the electron microscope.

Typical Grandry corpuscles are surrounded by thick bundles of collagen fibers and composed of a terminal axon sandwiched between Grandry cells. Occasionally, two or three nerve endings are found within one corpuscle. The Grandry cell contains numerous electron-dense granules similar to those of a Merkel cell. The cell extends protrusions at the poles and the opposing faces. Desmosome-like attachments are noted between interdigitated protrusions, and between the axon and Grandry cell.

Herbst corpuscles are composed of an outer capsule, inner core and central nerve ending. The outer capsule consists of 15 to 20 concentric lamellae, while the inner core possesses 60 to 70 sheets of cytoplasmic extensions. Under the scanning electron microscope, the corpuscles appeared as an elongated oval form surrounded by dense fibrous connective tissue, and each lamella of the outer capsule was composed of a dense network of thick and thin fibrils. These were seen under the transmission electron microscope as thick fibrils about 50 nm in diameter and peripheral thin fibrils about 10 nm in diameter. In some portions, a periodic increase of cytoplasmic density about 20 nm in width located in neighboring sheets was noted.

The terminal axons of both corpuscles contain numerous neurofilaments, slender mitochondria, neurotubules, smooth endoplasmic reticulum and vesicles. Both corpuscles are limited by several flat cells which are arranged in parallel and probably correspond to the perineural cells of the peripheral nerve. Tight junctions were observed between these cells.

The fine structure of the Pacinian corpuscle has been studied by Pease and Quillian (1957), Cauna and Mannan (1958), Shanthaveerappa and Bourne (1963), Nishi et al. (1969), Santini (1969), Kanagasuntheram et al. (1971), Spencer and Schaumburg (1973) and Halata (1977).

On the other hand, the afferent axon and the cellular organization of the Herbst
corpuscle were described by Andres (1969), Nafstad and Andersen (1970), Saxod (1970b, 1978), Halata (1971) and Halata and Munger (1980). Concerning the characteristics of the Grandry corpuscle, there have been only a few reports by Saxod (1968, 1970a, 1978), Andres (1969) and Ide and Munger (1978).

This study aims to elucidate the fine structure of Herbst and Grandry corpuscles found in the palatine mucosa, gingival mucosa and beak skin of the duck, presenting

Fig. 1. Unstained frozen section examined by Normarski-optics. Grandry cells (*) and nerve endings (**) are observed. ×340
Fig. 2. Semithin section stained with toluidin blue. It denotes a large Grandry cell in hemispherical shape (*) containing a nucleus and nucleolus. One terminal axon (**) in central portion can be noted. ×340
Fig. 3. Semithin section stained with toluidin blue. Two nerve endings (*) are observed within one corpuscle. ×340
Fig. 4. Semithin section stained with toluidin blue. Three nerve endings (*) are noted within one corpuscle. ×250
Fig. 5. Transversal section of a Grandry corpuscle (TEM). The terminal axon (*) is located in the intercellular space between Grandry cells. Several lamellae of capsular elements are noted (arrows). ×2,100
Fig. 6. A part of the cytoplasm of a Grandry cell with electron-dense granules of 50–100 nm (small arrow), filaments (large arrow) and rough endoplasmic reticulum (*) ×36,000
Fig. 5 and 6. Legends on the opposite page.
some new findings on the cellular components, terminal axon and capsule of both corpuscles.

A portion of this paper was previously reported in an abstract form (WATANABE, USUKURA and YAMADA, 1980).

MATERIALS AND METHODS

For transmission electron microscopy (TEM)
Duck palatine mucosa, gingiva and beak skin were fixed for 3-4 hrs in 2.5% glutaraldehyde and 2% paraformaldehyde in 0.1 M (pH 7.4) phosphate buffer at room temperature. They were post-fixed in 1% osmium tetroxide in 0.1 M phosphate buffer (pH 7.4) at 4°C for 2 hrs.

The tissues were dehydrated in a series of ethanol and embedded in Spurr’s epoxy resin.

Sections of 1-3 μm in thickness were stained with toluidine blue for light microscopy. Thin sections made by using glass knives were stained with 4% uranyl acetate in 50% ethanol followed by 0.4% lead citrate and examined in a Hitachi-12A TEM.

Frozen sections for light microscopy
The unfixed material was immersed in the phosphate buffer, and then frozen sections about 30 μm thick were cut with a freezing microtome. The sections were mounted with the buffer solution on glass slides and examined by Nomarski-optics.

For scanning electron microscopy (SEM)
The samples were fixed by immersion in a modified Karnovsky fixative containing 2.5% glutaraldehyde, 2% paraformaldehyde in 0.1 M phosphate buffer (pH 7.4) for 12 hrs. After postfixation with 1% osmium tetroxide, the specimens were dehydrated in graded ethanol. Following dehydration, the samples were submerged in liquid nitrogen and fractured with the aid of a chilled scalpel. The samples were transferred to ethanol at room temperature followed by amyl acetate, and then criticalpoint dried with liquid CO₂. The specimens were mounted on aluminum stubs with silver conductive paint and vacuum-coated with gold paladium. Observations were made in a Hitachi S-700 SEM at 15 kV.

RESULTS

Both Grandry and Herbst corpuscles are found within the subepithelial connective tissue layers of the palatine mucosa, gingival mucosa and beak skin.

Grandry corpuscles
Light microscopy: Typical Grandry corpuscles are found in the subepithelial layer surrounded by thick bundles of collagenous fibers, and composed of Grandry cells and nerve endings. The Grandry cells are large and hemispherical in shape, and contain a large spherical nucleus with a prominent nucleolus (Fig. 1, 2). The cytoplasm is granular in appearance. The nerve ending is usually single, and enclosed between medial surfaces of two Grandry cells. Occasionally, however, two or three nerve endings are found within one corpuscle. In this instance, more than two Grandry cells
Fig. 7. Peculiar concentric bodies in a transversal section and an arrangement of bundles of 10 nm filaments (arrows). $\times 10,000$

Fig. 8. Peculiar concentric bodies in a longitudinal section. $\times 21,000$
form one corpuscle and each nerve fiber is sandwiched between two Grandry cells (Fig. 3, 4). In addition, several small cells are noticed, being concentrically applied on the surface of the corpuscle (Fig. 1–4).

**TEM observation**: The corpuscle is constituted usually of two giant Grandry cells whose flat medial surfaces are opposed in parallel. The terminal axon is located in this intercellular space between the Grandry cells (Fig. 5). The cytoplasm of a Grandry cell is characterized by the presence of numerous electron-dense granules. They are 50–100 nm in diameter and are limited by a single membrane (Fig. 6). Sometimes a clear space is noticeable between the granule and membrane (Fig. 7). The granules

---

**Fig. 9.** Several cytoplasmic protrusions of Grandry cells which interdigitate with satellite cells. Note microfilaments crossing (*MF*) and dense granules in the Grandry cell. ×10,000

**Fig. 10.** Cross section of a terminal axon. Abundant mitochondria (*M*), neurotubules (*NT*) neurofilaments (*NF*) and vesicles (arrow) are shown. ×12,000

**Fig. 11.** A terminal axon enters into a Grandry corpuscle losing its Schwann cell covering (arrow) and is sandwiched between Grandry cells. ×4,800
Fig. 10 and 11. Legends on the opposite page.
are scattered throughout the cytoplasm apparently at random, and are similar to those found in the Merkel cell.

Another feature of the cytoplasm is the presence of moderate amounts of 10 nm filaments. These filaments are usually in bundles, and run in various directions, sometimes in a whirling arrangement (Fig. 8). In particular, they tend to arrange themselves perpendicularly to the medial surface of the cell (Fig. 5). The opposing contact surfaces of the Grandry cell, except the area applied on the nerve ending, show finger-like protrusions. They interdigitate with each other and those of modified Schwann cells which will be described below. These protrusions are also found at the pole of the corpuscle. The bundles of filaments extend into these protrusions (Fig. 9). Desmosome-like attachments are recognized between interdigitating protrusions.

In addition, the cytoplasm contains slender mitochondria, microtubules, a small amount of rough surfaced endoplasmic reticulum, free ribosomes, and a peculiar cylindrical complex similar to the Kolmer's crystalloid found in the horizontal cell of the human retina (Fig. 7, 8).

The axon shows a clearer cytoplasm than the Grandry cell. The cytoplasm contains relatively abundant mitochondria, microtubules, neurofilaments, secondary lysosomes and vesicles. Microtubules are usually found near the mitochondria and lysosomes (Fig. 10). The naked nerve fiber enters into the corpuscle and expands to the terminal ending in discoidal form (Fig. 11).

The Schwann cells around the nerve fiber modifies their shape as they approach the corpuscle. They extend complicated flat processes arround the corpuscle. They also send their processes from the poles towards the area between the Grandry cells.
Grandry and Herbst Corpuscles in the Duck

Their surfaces are covered by a basement membrane, except for an area which directly contacts the Grandry cell or another Schwann cells (Fig. 12). Thus, the outer surfaces of Grandry cells are completely covered by these sheet-like extensions of Schwann cells. The covering is laminated, and 10-15 laminae are usually found. Each extension contains microtubules and filaments. In addition, they show abundant caveolae, and some coated pits and vesicles (Fig. 12).

Several layers of fibroblasts enclose the whole corpuscle (Fig. 5). The cells are flat and their nuclei are elongated. Their cytoplasm contains a moderate amount of granular endoplasmic reticulum, small mitochondria and filaments which run along the cell surfaces. A lipid droplets area is often recognized. Between layers of fibroblasts, collagen fibrils and homogeneous matrix are observed. However, the basement membrane is not prominent along the cell surfaces of each fibroblast.

**Herbst corpuscles**

*Light microscopy:* Observations show that the Herbst corpuscles are distributed rather regularly within the subepithelial connective tissue layers of the palatine mucosa, gingival mucosa and beak skin (Fig. 13). They are composed of an outer capsule, inner core and central nerve ending. The outer capsule is formed by a large number of concentric layers while the inner core appears rather homogeneous in both longitudinal (Fig. 14) and cross (Fig. 15) sections. Nuclei are usually recognized at the opposite poles of the inner core (Fig. 15). The single naked nerve fiber enters through the outer capsule into the inner core (Fig. 14).

*SEM observation:* In successful preparations of freeze-cracked specimens, the Herbst corpuscles appear as elongated oval bodies separated from the surrounding dense fibrous connective tissue (Fig. 16). They are generally about 100 μm in length, and, in some instances, an efferent nerve fiber can be observed as shown in Figure 16. When the Herbst corpuscle is fractured transversely, the lamellated outer capsule and the inner core with nerve endings are distinguishable (Fig. 17). Furthermore, it becomes evident that each lamella of the outer capsule is composed of a dense network of thick and thin fibrils which are arranged roughly parallel to the plane of the lamella (Fig. 17).

*TEM observation:* Figure 18 shows a cross section of the Herbst corpuscle under low magnification, and the outer capsule, inner core, as well a central nerve fiber are clearly recognizable. The outer capsule is composed of 15 to 20 concentric lamellae and interlamellar spaces. In each lamella, one can observe 2 kinds of fibrils, namely thick fibrils about 50 nm in diameter with typical collagen striation, and thin fibrils about 10 nm in diameter with fine striation (Fig. 19). The interlamellar space is occupied by a loose network of fine filamentous structure. The filament frequently shows local thickenings which give it a bead-like appearance. The network is continuous with the lamellae and throughout the outer capsule (Fig. 18, 19). Flat sheet-like extensions of fibroblasts are occasionally found along the lamellae in the interlamellar space. They are more often encountered around the inner core. However, these cells are distinguishable from the cells of the inner core by the absence of a basement membrane along their surface (Fig. 20).

The inner core of the Herbst corpuscle presents a bilateral and symmetrical organization. On each side of the corpuscle, there are 60 to 70 sheets of cytoplasmic extension derived from the inner core cell. The inner core cell probably represents a modified Schwann cell with its perikaryon located at the opposite two poles. A Golgi apparatus, granular endoplasmic reticulum and mitochondria are usually found in the
I. WATANABE, J. USUKURA and E. YAMADA:

perikaryon (Fig. 20, 22). The cells send out numerous thin extensions bilaterally. These sheets of cytoplasmic extensions do not usually branch nor turn back, but reach the other pole and end with a slight dilatation. The thickness of the sheet is about 0.1 μm and contains a few organelles, such as filaments, microtubules and vesicles. Between these sheets there exist a basement membrane-like substance and fibrils about
10 nm in diameter. In some portions, a periodic increase of cytoplasmic density about 20 nm in width is observed. The space between these densities is about 0.1 μm in width. Often, the periodic densities of neighboring sheets are aligned side by side (Fig. 20, 23). In addition, the perikaryon also extends relatively short finger-like processes which sometimes divide, and some of them end on the nerve terminal with a flat surface at the same pole.

The terminal axon runs through the center of the corpuscle. Its cytoplasm contains numerous neurofilaments which are arranged in longitudinal direction with a rather regular space. They occupy the major part of the cytoplasm. A considerable number of slender mitochondria are recognized adjacent to the fibers. They run longitudinally and are accompanied by neurotubules, smooth endoplasmic reticulum and vesicles. The cytoplasm surface of the cell membrane shows a somewhat increased density. The terminal ends of extensions derived from the inner core cell are applied
Fig. 17 and 18. Legends on the opposite page.
on the axon surface, and desmosome-like attachments are observed between them (Fig. 21, 22).

The corpuscles are limited by a series of flat cells from the surrounding dense fibrous connective tissue. These cells are arranged in parallel and probably correspond to the perineural cells of the peripheral nerve. There are generally 10-15 sheets of cells. Two or three sheets come close together and, consequently, several groups are formed. Between groups, a small amount of connective tissue with collagenous fibrils and elastic fibers are present. The cells are characterized by the presence of numerous caveolae along their cell surfaces (Fig. 24, 25, 26). The cytoplasm shows microtubules, filaments, granular endoplasmic reticulum, mitochondria and occasional coated vesicles. Two types of junctions between adjacent cells are distinguished, namely, desmosomes and tight junctions (Fig. 24). The latter are demonstrated more clearly in a freeze-fractured preparation (Fig. 26), especially for the network of strands characteristic to this type of junctions.

DISCUSSION

The present investigation clearly demonstrates the characteristics of the Grandry corpuscle located in the palatine mucosa, gingival mucosa and beak skin of the duck. As

Fig. 17. Freeze-cracked preparation. Transversely fractured image of a Herbst corpuscle shows the lamellated outer capsule (⋆) and compact inner core (★★). × 3,000

Fig. 18. Low magnification of a Herbst corpuscle in cross section (TEM). The inner core (⋆), outer capsule (★★) and nerve endings (arrow) are noted. × 3,000
shown by our results, the Grandry corpuscle is formed of two large specialized cells which present flat surfaces and enclose a discoidal terminal axon. Each corpuscle is surrounded by a capsule formed by dermal fibroblasts and collagen fibers. In our results, however, there were corpuscles which contained two or three terminal axons sandwiched by several Grandry cells. These aspects were described only by Saxod (1968, 1970a) and Halata (1971) respectively, in Canard and aquatic birds, and Ide and Munger (1978) in chicken toe skin.

The electron-dense granules of the Grandry cell are generally smaller than those described by Saxod (1978). Saxod maintained that granules are 120–180 nm in diameter and originate from the Golgi apparatus. These granules in our present data are 50–100 nm in diameter and are limited by a single membrane. Sometimes showing a clear space between the granule and membrane, the granules are very similar to those in the Merkel cell described by Smith (1967), Kurosuni et al. (1969), Nikai et al. (1971), Hashimoto (1972), Saxod (1978) and Watanabe and Yamada (1979). Although the chemical nature as well as physiological meaning of the granules are not known yet, it is possible that they contain some chemical transmitter.

The structural features of the terminal axon in the corpuscle observed in this study are similar to those described by several authors (Saxod, 1968, 1970a; Halata, 1971; Ide and Munger, 1978).

The contact faces of the Grandry cells and their peripheral surface show many protrusions which are interdigitated with those of the subjacent cells. According to our results, the protrusions are more numerous in the poles and in the contact faces with opposing cell. These features may reflect their function which suggests some role in supporting the axon terminal.
Fig. 21. At high magnification, the desmosome-like attachments (arrows) between lamellar processes and terminal axon. ×18,000

Fig. 22. Desmosome-like attachments (arrows) between axon and processes of inner core cell. Golgi apparatus (⁎), mitochondria (M), granular endoplasmic reticulum (**) are observed. ×18,000
Fig. 23. Periodic cytoplasmic densities of lamellar inner core cell. They are disposed about 20 nm apart and aligned side by side between two neighbouring sheets (arrows). $\times 33,000$

Fig. 24. Lamellar arrangement of capsular cells. They show microtubules ($MT$), filaments ($F$), granular endoplasmic reticulum ($R$) and caveolae (arrows). $\times 19,000$
Fig. 25. Freeze-fracture replica of capsular cells (TEM) shows numerous caveolae (arrows) along the cell surface. ×36,000

Fig. 26. Freeze-fracture replica of capsular cells (TEM). The tight junction (⋆) with complex network of strands and caveolae are observed. ×
The Herbst corpuscles are observed regularly within the subepithelial connective layers. They are larger (100 μm) than Grandry corpuscles and also much more numerous. Generally, the corpuscles are enveloped by large numbers of concentric layers of cytoplasmic extensions of the inner core cell. The disposition of the lamellated outer capsule and the compact inner core with a terminal axon are revealed by the SEM of freeze-cracked specimens. Similar aspects were reported by Saxod (1978).

The general characteristics of Herbst corpuscle are similar to those described by Saxod (1970b, 1978), who referred to an inner core with sensory nerve terminal, and outer capsule occupied by a lamellar system formed by flat cells in association with collagen fibers. These aspects are also described by Andersen and Nafstad (1968) in the hard palate of the hen; and by Nafstad and Andersen (1970) in the Herbst corpuscle in the chicken.

The outer capsule is composed of 15 to 20 concentric lamellae and interlamellar spaces. It is noted that each lamella is composed of two kinds of fibrils, one about 50 nm in diameter with typical collagen striations and the other about 10 nm in diameter with fine striations.

When comparing the chicken beak corpuscles described by Nafstad and Andersen (1970), these are elongated oval forms and have different dimensions. The chicken inner core is composed of about 50 cells (Saxod, 1978), and the outer capsule possesses less lamellae than observed in our results. The inner core of the Herbst corpuscle in our data presents a very symmetric organization, containing in each side 60 to 70 sheets of cytoplasmic extensions. The sheets measure about 0.1 μm in width and contain a few organelles, such as filaments, microtubules and vesicles. These characteristics have also been reported by Andres (1969), Saxod (1970, 1978), Halata (1971), Halata and Munger (1980). In some portions of cytoplasm of lamellae, a periodic increase in density about 20 nm in width is noted, where the periodic density of neighboring sheets are aligned side by side. They possibly serve for the mechanical support of the cytoplasm sheets.

Polacek et al. (1966) and Malinovsky and Zemanek (1970) reported on Herbst corpuscles in their studies of the joint receptors of birds. The variability in size of the Herbst corpuscles has also been noted by Malinovsky and Zemanek (1971). However, in our results no great variability in the size of Herbst and Grandry corpuscles was noticed.

It has been put forth by Saxod (1970) and Halata (1971) that there are two types of Herbst corpuscles in the pigeon articular capsules. In our freeze-cracked material as well as sectional specimens only one type could be noted.

The corpuscles are surrounded by 10-15 flat cells in parallel which correspond to the perineural cells of the peripheral nerve as also mentioned by Shanthaveerappa and Bourne (1963) and Munger (1971). Halata (1971) mentioned that 6-10 layers of flat cells envelope the corpuscle.

Both Grandry and Herbst corpuscles are considered to work as rapidly adapting receptors. These corpuscles may act in the same conditions as Pacinian corpuscles. However, they are located in different regions. In this paper, we demonstrated the architecture of these corpuscles at the ultrastructural level and presented some peculiar characteristics of these corpuscles found in the palatine mucosa, gingival and skin of the duck beak.
REFERENCES

Andersen, A. E. and P. H. J. Nafstad: An electron microscopic investigation of the sensory organs in the hard palate region of the hen. Z. Zellforsch. 91: 391-401 (1968).

Andres, K. H.: Zur Ultrastruktur verschiedener Mechanorezeptoren von höheren Wirbeltieren. Anat. Anz. 124: 551-565 (1969).

Halata, Z.: Ultrastructure of Grandry nerve endings in the beak skin of some aquatic birds. Fol. morphol. 13: 225-232 (1971).

———: Die Ultrastruktur der Lamellenkörperchen bei Wasservögeln (Herbstsche Endigungen). Acta anat. 80: 362-376 (1971).

———: Ultrastructure of Grandry nerve ending in the beak skin of some aquatic birds. Fol. morphol. 3: 225-232 (1971).

———: The ultrastructure of the sensory nerve endings in the articular capsule of the knee joint of the domestic cat. J. Anat. 124: 717-729 (1977).

Halata, Z. and B. L. Munger: The ultrastructure of Ruffini and Herbst corpuscles in the articular capsule of domestic pigeon. Anat. Rec. 198: 681-692 (1980).

Hashimoto, K.: Fine structure of Merkel cell in human oral mucosa. J. Invest. Dermatol. 58: 381-397 (1972).

Ike, C. and B. L. Munger: A cytologic study of Grandry corpuscle development in chiken toe skin. J. comp. Neurol. 179: 301-324 (1978).

Kanagasuntheram, R., A. Krishnamurti and W. C. Wong: The digital Pacinian corpuscle in the slow loris. Observations on the lateral processes of the terminal nerve fibre. Acta anat. 81: 108-112 (1971).

Kurosumi, K., U. Kurosumi and H. Suzuki: Fine structure of Merkel cells and associate nerve fibers in the epidermis of certain mammalian species. Arch. histol. jap. 30: 295-313 (1969).

Malinovsky, L. and R. Zemanek: Sensory nerve endings in the joint capsules of the large limb joints in the domestic hen and the rook. Fol. Morphol. 18: 206-212 (1970).

———: Sensory innervation of the skin and mucosa of some parts of the head in the domestic fowl. Fol. morphol. 19: 18-23 (1971).

Munger, B. L.: Patterns of organization of peripheral sensory receptors. In: (ed. by) W. R. Loewenstein: Handbook of sensory physiology. Springer-Verlag, Berlin-Heidelberg-New York (Chap. 17, p. 523-556) 1971.

Nafstad, P. H. J. and A. E. Andersen: Ultrastructural investigation on the innervation of the Herbst corpuscle. Z. Zellforsch. 103: 109-114 (1970).

Nikai H., G. G. Rose and M. Cattoni: Merkel cell in human and rat gingiva. Arch. oral Biol. 16: 835-843 (1971).

Nishi, K., V. Oura and W. Pallie: Fine structure of Pacinian corpuscles in the mesentery of cat. J. Cell Biol. 43: 539-553 (1969).

Pease, D. C. and T. A. Quillian: Electron microscopy of the Pacinian corpuscle. J. biophys. biochem. Cytol. 3: 331-357 (1957).

Polacek, P. C., A. Skleuska and L. Malinovsky: Contribution to the problem of joint receptors in birds. Fol. morphol. 14: 33-42 (1966).

Santini, M.: Numbers of Pacinian corpuscles of the cat pancreas, mesentery and mesocolon. Anat. Rec. 113: 322A (1969).

Saxod, R.: Ultrastructure des corpuscles sensoriels cutanés de Herbst et de Grandry chez le canard. Arch. Anat. microsc., Morphol. exp. 57: 379-400 (1968).

———: Étude an microscope électronique de l’histogenèse du corpuscle sensoriel cutané de Grandry chez le Canard. J. Ultrastr. Res. 32: 477-496 (1970a).

———: Étude au microscope électronique de l’histogenèse du corpuscle sensoriel cutané de Herbest chez le Canard. J. Ultrastr. Res. 33: 463-482 (1970b).

———: Development of cutaneous sensory receptors in birds. In: (ed. by) Marcus Jacobson: Handbook of sensory physiology development of sensory systems, Vol. 9. Springer-Verlag, (Chap. 8).

Shanthaveerappa, T. R. and G. H. Bourne: New observations on the structure of the Pacinian cor-
puscle and its relation to the perineural epithelium of peripheral nerves. Amer. J. Anat. 112: 97–109 (1963).

Smith, K. R.: The structure of the human Haarscheibe and Merkel cell. J. Invest. Dermatol. 54: 150–159 (1967).

Spencer, P. S. and H. H. Schaumburg: An ultrastructural study of the inner core of the Pacinian corpuscle. J. Neurocytol. 2: 217–235 (1973).

Watanabe, I. and E. Yamada: Light and electron microscopic observations of the nerve endings of the palatine mucous membrane. Acta anat. nippon. 54 (3): 117 (1979).

Watanabe, I., G. Usukura and E. Yamada: Fine structure of the Grandry and Herbst corpuscles in the duck beak. Acta anat. nippon. 55: 545 (1980).