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# THE PILARY END-ORGAN OF QUIESCENT FACIAL VELLUS HAIR FOLLICLES IN THE MOUSE

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## ABSTRACT

The pilary end-organ is a sensory receptor which is located around the upper part of a hair follicle. It lies between the outer root sheath of the follicle and its sebaceous gland, below the orifice of the sebaceous gland. In quiescent vellus hair follicles in the facial region of the mouse, the pilary end-organ consists of a collar of longitudinal nerve fibers and a connective tissue capsule containing circular or spiral nerve fibers. The nerve fibers of the pilary end-organ arise from small myelinated nerve fibers which lose their myelin sheaths as they enter the pilary end-organ. Accompanying the nerve fibers in the pilary end-organ are processes of specialized Schwann cells and processes of laminar cells. The laminar and Schwann cell processes which are adjacent to the longitudinal nerve fibers have foot processes or pedicels facing the basal lamina of the outer root sheath of the hair follicle and sometimes facing the basal lamina adjacent to the capsule. Structural differences in the quiescent follicle and the actively-growing follicle lead one to believe that the quiescent follicle acts as a better receptor for touch stimuli than does the actively-growing follicle. The pilary end-organ is more prominent in quiescent follicles; this may be related to the fact that the hair follicle is reduced in diameter during telogen (quiescence). The quiescent follicle has much less depth than the actively-growing follicle; any movement of the follicle caused by movement of the hair shaft above the surface of the skin would be more effective in pressing against the pilary end-organ (as a lever) when the follicle is shorter.

## INTRODUCTION

A bilaminar arrangement of nerve fibers consisting of inner longitudinal and outer circular fibers which supply hair follicles has been described by a number of authors (Szymonowicz, 1909; Weddell et al., 1955; Winkelmann, 1959; Miller et al., 1960; Straile, 1960; Montagna et al., 1964; & Mann, 1968). The encapsulation of these nerve fibers was first noted in damaged hair follicles of leprosy patients (Dastur, 1955); the structure was referred to as a "trichoneural apparatus" and was said to be homologous to encapsulated nerve endings found in glabrous skin and exposed mucous membranes. The encapsulation was later confirmed in normal hair follicles (Miller et al., 1960); the sensory structure was termed a "neurotrichial end-organ" and was said to be homologous not only to encapsulated nerve endings of glabrous skin but also to those of deeper tissues. Histochemical studies showed that the sensory end-organ encircles part of the hair follicle like a napkin ring (Winkelmann, 1968) or collar (Montagna & Parakkal, 1974) and is located below the junction of the sebaceous gland orifice with the hair follicle (Winkelmann, 1968). Terms introduced to describe this sensory structure were "hair follicle nerve end-organ" (Winkelmann, 1968), "hair nerve tube" (Seto, 1963) and "hair nerve shield" (Seto, 1963). The terms "end-organ proper" (Montagna et al., 1964) and "follicle end-organ" (Montagna & Parakkal, 1974) have been used to describe the collar of vertical fibers only.

Fine structural studies of this sensory structure have dealt primarily with the vertical (longitudinal) nerve fibers and their relationship to the outer root sheath of the hair follicle and to the specialized Schwann cell processes which accompany them (Yamamoto, 1966; Orfanos, 1967; Orfanos, 1968; Cauna, 1969; Hashimoto, 1973a). The term "starter organs" (Orfanos, 1967) and "mechanoreceptors" (Orfanos, 1967; Hashimoto, 1973a) have been used to describe these fibers, which apparently can detect movement of hair. The junction of these nerve fibers and epithelial cells of the outer root sheath, with only a basal lamina between them, has been called an "epithelio-neural junction" (Orfanos, 1967).

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In the present study, the term "pilary end-organ" is used to refer to the palisade of longitudinal nerve fibers, the circular or spiral nerve fibers and the connective tissue capsule, which are located below the junction of the sebaceous gland with the hair follicle. This study includes a light and electron microscopic study of the pilary end-organ in vellus hairs (down, hairlets) in mice which are in the telogen (quiescent) stage. Some new findings concerning the nerve fibers, their sheaths and the connective tissue capsule are presented.

## Materials and Methods

Skin containing vibrissa and vellus hair follicles was removed from the upper lip of male and female mice. Some of the mice were albino and some were black-and-white mice of unknown strain.

For light microscopy, tissue was fixed in 10% formalin, washed in tap water, dehydrated in ethanol, embedded in paraffin and sectioned at 8 microns. Some of the sections were stained with Holmes' silver stain and counterstained with luxol fast blue (Humason, 1962). The sections were stained briefly instead of overnight in luxol fast blue. This gave the connective tissue a light blue color. No destaining was necessary. Other sections were stained with a triple stain for DNA, polysaccharides and proteins (Humason, 1962).

For electron microscopy, the tissue was cut into small pieces, fixed in 4% glutaraldehyde in sodium cacodylate buffer (pH 7.6), postfixed in 2% osmium tetroxide, dehydrated in methanol and embedded in epon. One-half micron sections were stained with toluidine blue (½% in ½% solution of borax) and used for orientation, using the light microscope. Thin sections (about 500 Angstroms) were stained with saturated aqueous uranyl acetate and 0.4% lead citrate in 0.2N NaOH and were studied with an RCA EMU 3F electron microscope.

## Light Microscopy

The vellus hair follicles included in this study are located between the mystacial vibrissa (sinus hair) follicles in the upper lip of the mouse. The vellus hair follicles are much smaller in diameter and in depth than the vibrissa follicles. Most of the vellus hair follicles are in the telogen (quiescent) stage and are about 250 microns in depth and 20-25 microns in diameter; those in anagen (active growth stage) are about 500 microns in depth and are 30-35 microns in diameter. The depth of the vibrissa follicles ranges from one to two millimeters, and the diameter from about 150-250 microns.

The diameter of the vellus hairs decreases during catagen (stage in which the follicle is becoming quiescent). The diameter of the vellus hair formed during anagen is about 12-14 microns; that formed during catagen tapers down to 5-6 microns in diameter, with the root of the quiescent hair being 5-6 microns in diameter. The tip of the root may taper to a point or fan out slightly. There is no inner root sheath in the telogen hair follicle and the hair in this stage contains no living cells.

The vellus hairs have no smooth arrector pili muscles. However, skeletal muscle fibers of the facial muscles often come in close contact with the vellus follicles as they pass to their insertion in the skin.

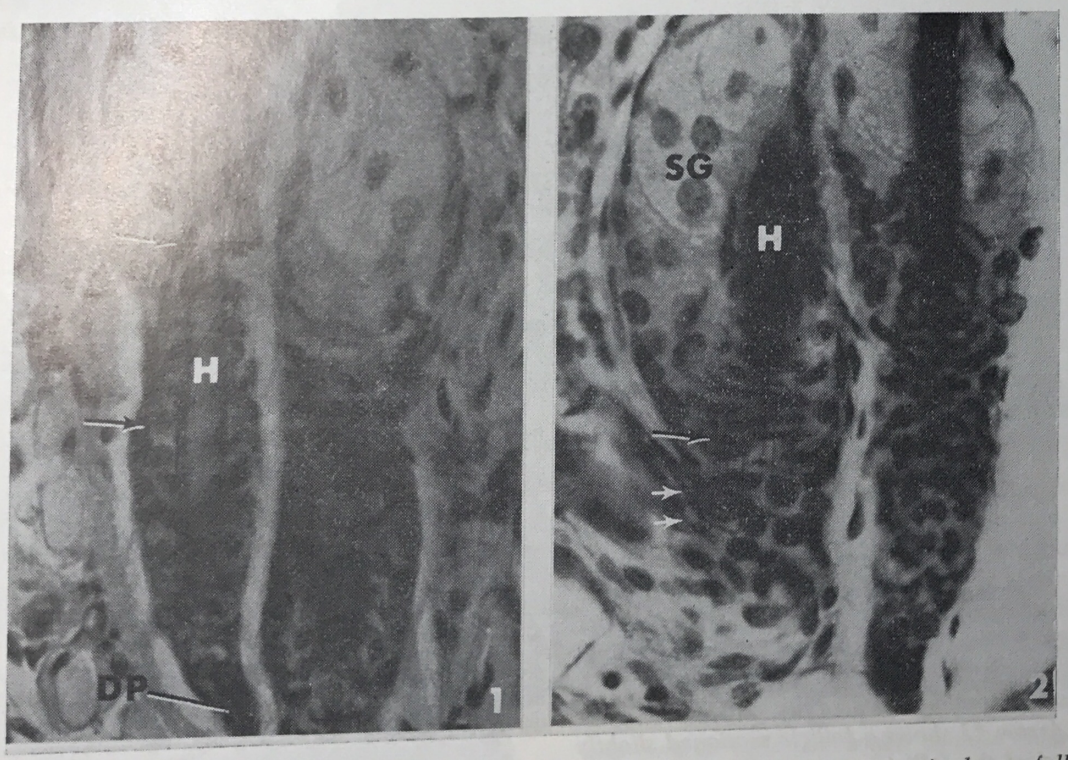


FIG. 1. *Longitudinal section of telogen follicles. Approximate upper and lower limits of pilary end-organ are shown by arrows. SG, sebaceous gland in direct contact with hair; H, telogen hair; DP, dermal papilla of follicle. PAS, Azure blue and Naphthol yellow stain. 570x.*

FIG. 2. *Longitudinal section of telogen follicles. Longitudinal nerve fibers of the nerve collar are shown to the right of the upper arrow. Lower (white) arrows show nerve fibers passing into the pilary end-organ. SG, sebaceous gland; H, telogen hair. Holmes' silver stain. 570x.*

A sebaceous gland, at the level of its orifice (SG, Figs. 1 and 2) encircles the hair, there being no outer root sheath or connective tissue between them at this point. Below this level, the gland usually divides into two lobes of unequal length which extend downward, covering most of the pilary end-organ. The sebaceous gland covers one-third to one-half of the quiescent hair follicle.

The pilary end-organ is adjacent to the outer root sheath and extends from just below the sebaceous gland orifice to the area just below the lower limit of the sebaceous gland (area between arrows, Fig. 1). The pilary end-organ consists of a collar of longitudinal nerve fibers, which encircles the upper part of the outer root sheath (Fig. 4, Follicles #1, small arrows), surrounded by a connective tissue capsule (Fig. 4, Follicle #1, large arrow). The connective tissue capsule contains some circular (or spiral) nerve fibers (CF, Fig. 3). The longitudinal nerve fibers are seen in longitudinal section in Fig. 2 (to the right of the black-on-white arrow) and in cross section in Fig. 3 (labeled NF) and Fig. 4 (shown by small arrows).

The nerve fibers which supply the pilary end-organ pass below the sebaceous gland (Fig. 2, white arrows, and Fig. 3, black-on-white arrows) and branch to form the collar of longitudinal fibers and the circular (or spiral) fibers. Just before reaching the follicle, the nerve fibers lose their myelin sheath and become associated with specialized Schwann cells which have large amounts of light-staining cytoplasm. Schwann cell processes accompany the longitudinal nerve fibers and some of the circular fibers. These processes are seen as clear areas on each side of the longitudinal nerve fibers in Figs. 3 and 4. Thin processes of laminar cells accompany some of the nerve fibers but are not seen with the light microscope.

Above the upper ends of the longitudinal nerve fibers (Fig. 4, Follicle #2) a space is seen between the outer root sheath and the connective tissue capsule. This space is probably filled with tissue fluid (in the intact mouse). Electron microscopy reveals the presence of a few filaments in this area. Above this level (Fig. 4, Follicle #3) the connective tissue capsule moves closer to the follicle. A short distance above this level both the capsule and the outer root sheath disappear as the sebaceous gland opens directly onto the hair (SG, sebaceous gland, and H, hair, in Figs. 1 and 2).

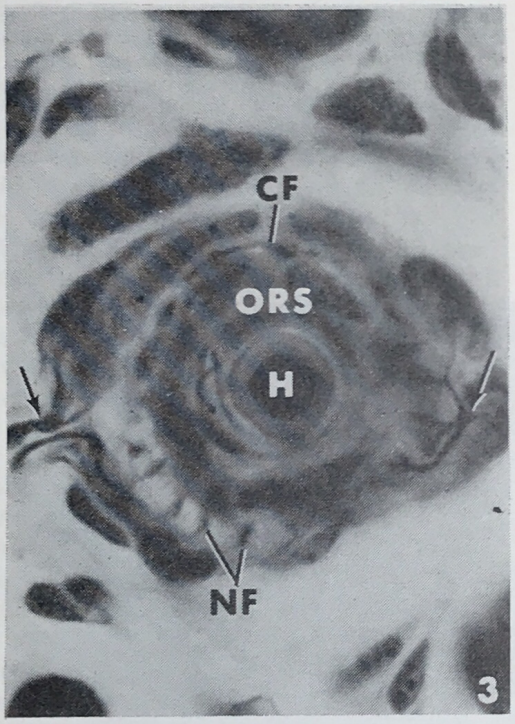


FIG. 3. *Cross section of vellus hair follicle. Arrows show nerve fibers entering the pilary end-organ from two sides, accompanied by light-staining specialized Schwann cell processes. CF, circular or spiral nerve fiber; NF, longitudinal nerve fibers which run parallel to the axis of the follicle; ORS, outer root sheath of hair follicle; H, telogen hair. Holmes silver stain. 1420x.*

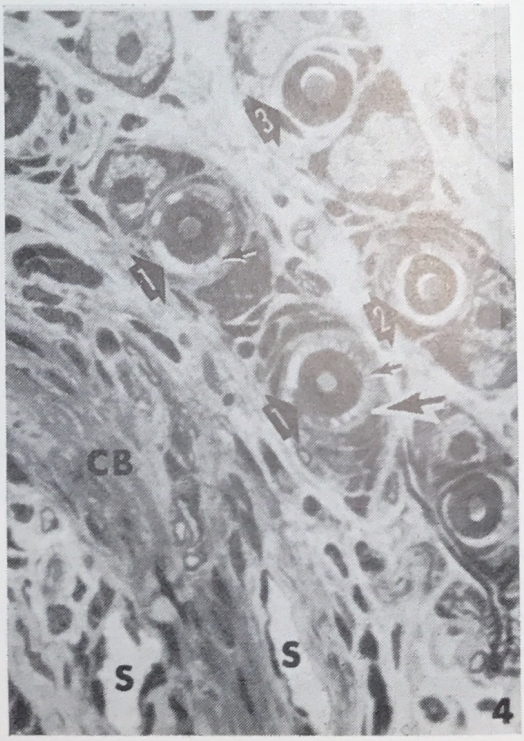


FIG. 4. *Cross sections of vellus hairs and part of conical body, CB (a part of the much larger sinus hair follicle). Follicles designated by #1 arrows contain a collar of longitudinal nerve fibers (small arrows) surrounded by a connective tissue capsule (large arrow). Arrow #2 shows a follicle sectioned just above the collar of longitudinal nerve fibers. An empty-looking space, surrounded by a connective tissue capsule, is located just outside the outer root sheath. Arrow #3 shows a follicle sectioned slightly above the level of the follicle at arrow #2. The connective tissue capsule has filled most of the "empty space" above the nerve collar. S, venous sinus of conical body. Epon section. Toluidine blue stain. 570x.*

## Electron Microscopy

The longitudinal nerve fibers which run parallel to the axis of the follicle usually appear compressed from side to side, giving them a spindle-shaped appearance when viewed in cross section (Fig. 5, arrows point to some of the nerve fibers; Fig. 6, nerve fibers $N^1$-$N^5$; Fig. 7, nerve fibers $N^1$ and $N^2$; Fig. 9, nerve fiber N). They are characterized by large mitochondria (Fig. 7, in nerve fiber $N^1$; Fig. 9, in nerve fiber N) which are sometimes seen to have tubular cristae (Fig. 6, nerve fiber $N^5$). These nerve fibers also contain some filaments and microtubules, some irregular-shaped vesicles and some dense-cored vesicles (Figs. 7-9, in nerve fibers labeled $N^1$, $N^2$ and N). The axolemma often has a ruffled appearance (Fig. 8, on nerve fiber N), with these ruffles sometimes appearing to be forming pinocytotic vesicles. The medial and lateral edges of the longitudinal nerve often exhibit a thickening of the axolemma and increased electron density of the subjacent neuroplasm (Fig. 9, asterisks). The outer root sheath cells facing the medial edge of the nerve fibers have many hemidesmosomes (Fig. 9, white arrows).

Each side of the nerve fibers is flanked by either a process of a specialized Schwann cell or a laminar cell. The Schwann cell processes are usually thick and relatively electron-lucent (Fig. 6, S; Fig. 7, S) while the laminar cell processes are thinner and more electron-dense (Figs. 6-9, L). Both types of processes contain secondary foot-like processes or pedicels which face the basal lamina of the follicle; sometimes they contain pedicels which face the capsule, as well. These pedicels are clearly seen on a Schwann cell process, S, in Fig. 7. They may also be seen on Schwann cell processes and laminar cell processes in Figs. 5, 6, 8 and 9. An increased electron-density of the cell membrane and subjacent cytoplasm occurs in the pedicels facing the basal laminae. The inner and outer basal laminae are shown by the upper and lower arrows, respectively, in Fig. 7. Increased electron density is seen in the pedicels of the Schwann cell process, S, in this Figure. In addition to the pedicels, the laminar and Schwann cell processes contain many filaments, occasional small mitochondria, some microtubules, some dense-cored vesicles and pinocytotic vesicles.

The laminar and Schwann cell processes may extend completely around the lateral (capsular) edge of the longitudinal nerve fibers, but usually are separated at this edge by a distance of up to one micron. In Fig. 6 the arrows show the small space between the laminar and Schwann cell processes at the capsular edge of the longitudinal nerve fibers. These processes never completely surround the medial (follicular) edge of the longitudinal nerve fibers. The medial edge comes in contact with the (inner) basal lamina surrounding the outer root sheath (Fig. 7, upper arrows), while the lateral edge usually comes in contact with the irregular (outer) basal lamina between it and the capsule (Fig. 7, lower arrows). The lateral edge of the nerve fibers often extends beyond the laminar and Schwann cell processes. In Fig. 7, the lateral edge of nerve fiber $N^1$ extends beyond its processes and connects with a nerve fiber in the connective tissue capsule, C (collagenous fibers of capsule).

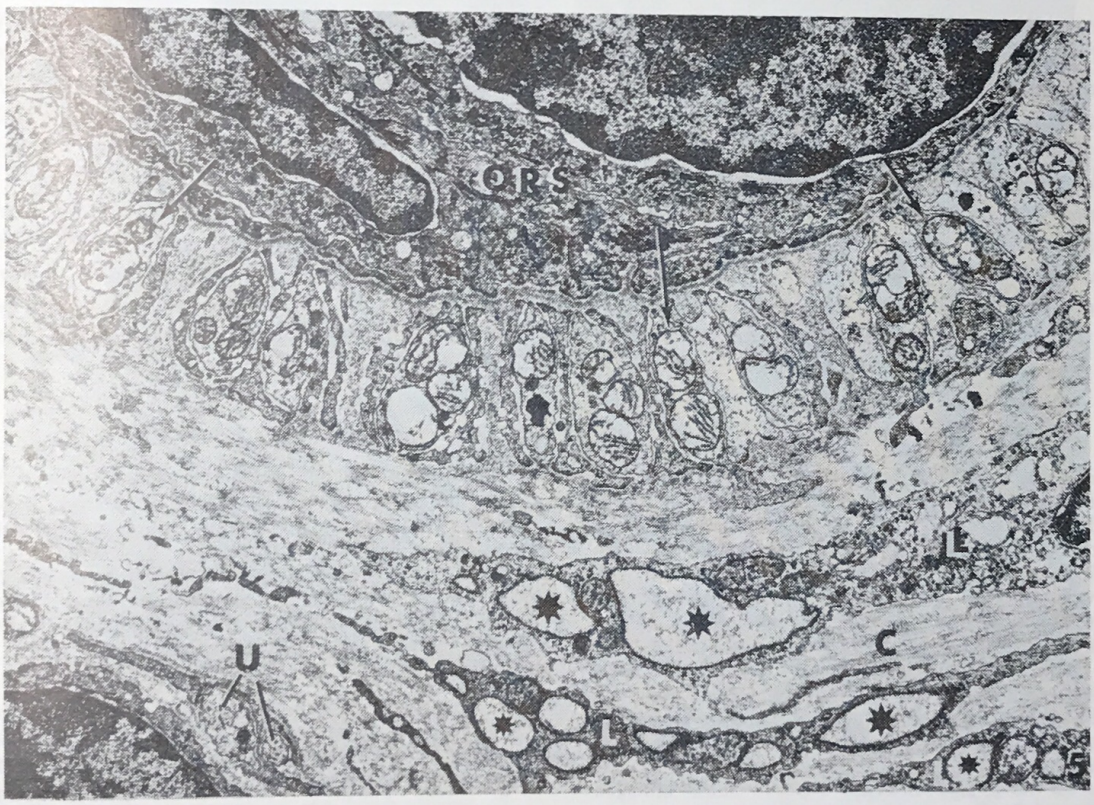


FIG. 5. *Cross section showing part of hair follicle and pilary end-organ. Some of the longitudinal nerve fibers are designated by arrows. These nerve fibers are flanked by processes of specialized Schwann cells or laminar cells. The connective tissue capsule outside the collar contains collagen fibrils (C) oriented in a spiral direction and laminar cells (L), which contain enlarged cisternae of granular endoplasmic reticulum (asterisks). Some unmyelinated nerve fibers (U) accompanied by laminar cell processes are seen in the outer part of the capsule. ORS, outer root sheath of hair follicle. 6300x.*

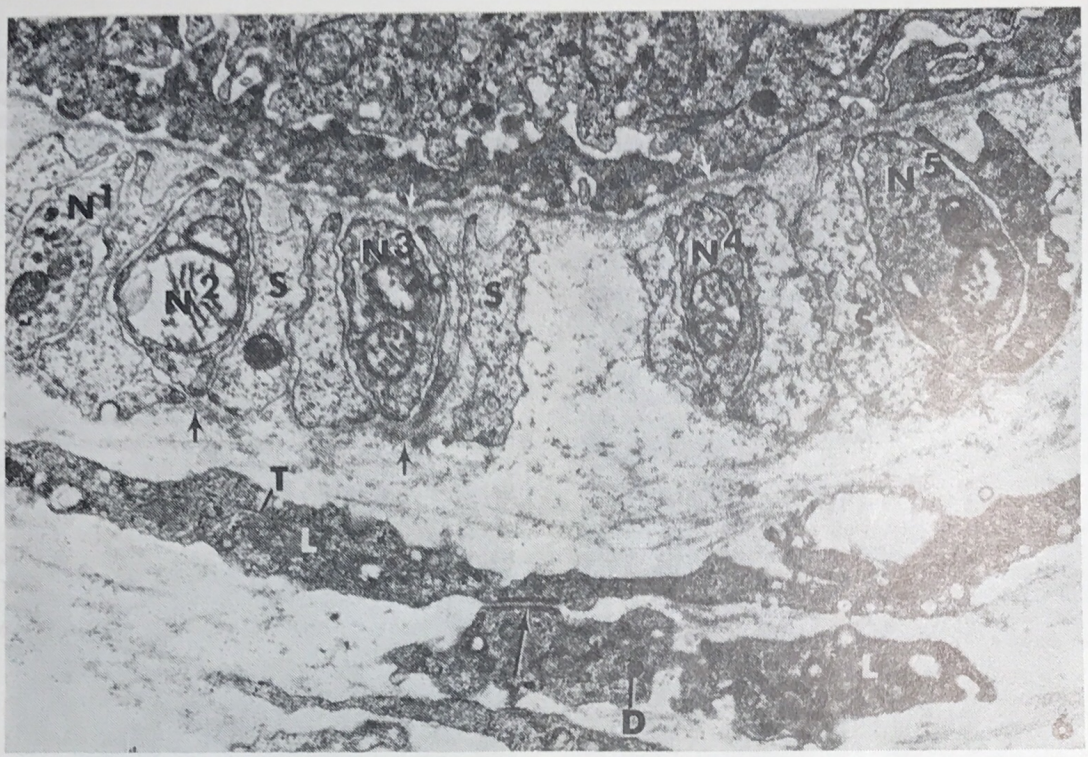


FIG. 6. *Cross section showing edge of hair follicle (above) and part of pilary end-organ. Basal lamina of outer root sheath is indicated by white arrows. The irregular basal lamina between the nerve collar and the connective tissue capsule is shown at black arrows. $N^1$-$N^5$ are longitudinal nerve fibers forming part of the nerve collar. Processes of Schwann cells (S) flank the sides of $N^1$-$N^4$ and one side of $N^5$. Laminar cell process (L) is on the other side of $N^5$. Note the foot-like processes (pedicels) of the Schwann and laminar cell processes that face the basal lamina of the outer root sheath. The cytoplasm near the ends of these processes appears electron-dense. Some of the cristae of the mitochondria are seen to be tubular in shape (in $N^5$). The nerve fibers contain some dense-cored vesicles (in $N^1$) and some irregular-shaped vesicles. Filaments and microtubules are cut in cross section and are not prominent. Pinocytotic vesicles are commonly seen in the laminar cells and their processes (L) and in the Schwann cell processes (S). Black-on-white arrow shows desmosome-like junction between two laminar cells (L) in capsule. T, microtubule; D, dense body. 12,500x.*

The circular or spiral nerve fibers in the connective tissue capsule are smaller in diameter than the longitudinal fibers in the nerve collar. In the medial part of the capsule, the nerve fibers are packed with fine filaments. In Fig. 8, two of these small nerve fibers (NF) are seen. Schwann cell processes (S) and laminar cell processes (L) are also seen. Prominent enlargements are sometimes seen along these nerve fibers. In the outer part of the capsule, the nerve fibers resemble typical unmyelinated nerve fibers, being less densely packed with filaments, and with prominent microtubules (Fig. 5, U). They are accompanied by laminar processes but are not completely enclosed by them; part of their axolemma comes in contact with the connective tissue of the capsule.

The capsule of the pilary end-organ contains spiral collagen fibers (Figs. 7 and 8, C) and the soma of the laminar cells (Figs. 5 and 6, L) in addition to the nerve fibers and processes of the Schwann cells and laminar cells which have already been described. The soma of the laminar cells usually have large vesicles lined by granular endoplasmic reticulum (Fig. 5, asterisks), smaller smooth-surfaced vesicles, mitochondria, dense-cored vesicles (Fig. 6, D), filaments, microtubules (Fig. 6, T) and some pinocytotic vesicles. Desmosome-like thickenings are sometimes seen between adjacent laminar cells (Fig. 6, black-on-white arrow).

The capsule extends about five microns above the collar of longitudinal nerve fibers (Fig. 10, C) enclosing a space (Fig. 10, S) which contains a few laminar cell processes, a few collagen unit fibers and a few fine filaments.

Above the pilary end-organ the sebaceous gland completely encircles the hair and pours its secretion directly onto its surface, there being no connective tissue or epithelial root sheath between them. No nerve fibers pass into this space.

## DISCUSSION

Seto (1963) has noted that the nerve fibers supplying hair in the scalp and face form different-shaped structures. Those in the face region encircle the follicle to form a hair nerve tube, while those in the scalp do not completely encircle the follicle but instead form a shield-shaped structure. In the present study of the facial region, the pilary end-organ completely encircles the hair follicle, as in Seto's description of the facial hair nerve tube. Cauna's study of the rat auricle (1969) showed a semicircular arrangement of unmyelinated nerve fibers

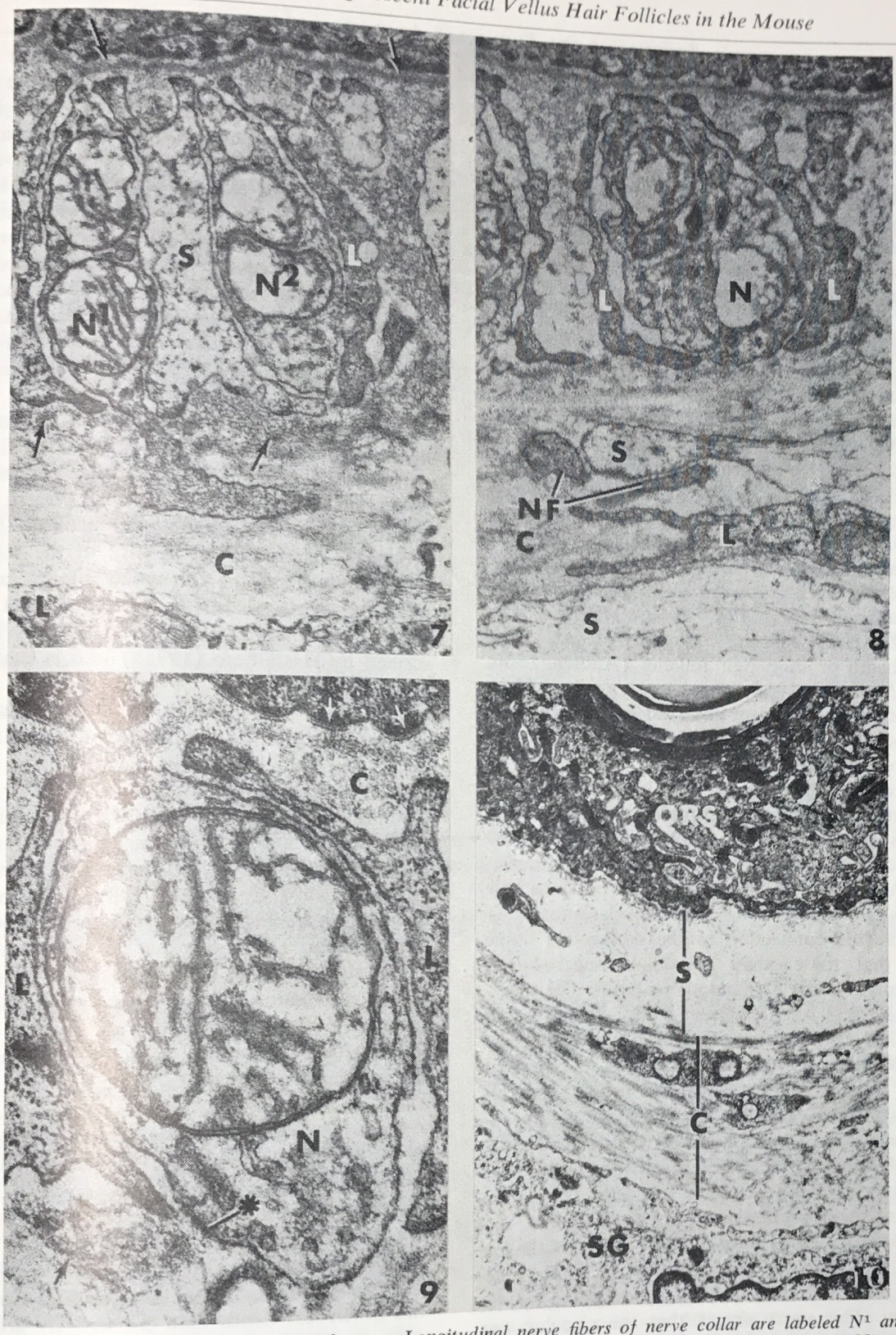


FIG. 7. *Cross section showing part of a pilary end-organ. Longitudinal nerve fibers of nerve collar are labeled $N^1$ and $N^2$. Process of $N^1$ extending into the capsule is seen. It appears to be filled with fine filaments. A few vesicles are seen in $N^1$ and $N^2$. Microtubules and filaments are cut in cross section. Some microtubules and filaments are also seen in the Schwann cell process (S) between the nerve tubules and filaments are cut in cross section. Some microtubules and filaments are also seen in the Schwann cell process (S) between the irregular basal lamina outside the nerve $N^1$ and $N^2$. The basal lamina of the outer root sheath is indicated by the upper arrows; the irregular basal lamina outside the nerve collar (facing the capsule) is shown by the lower arrows. A laminar cell process (L) flanks the right side of $N^2$. Note the increased electron density of the foot-processes (pedicels) facing the basal laminae of the outer root sheath and capsule. Part of the connective tissue capsule is shown; collagen fibrils (C) and a laminar cell (L). 19,880x.*

FIG. 8. *Cross section showing part of a pilary end-organ. A nerve fiber (N) of nerve collar is shown. It contains two irregular-shaped dense-cored vesicles, cross-cut filaments and microtubules, and some irregular vesicles or cisternae. Laminar cell processes are on each side of the nerve fiber. Two circular processes of Schwann cells (S) and a laminar cell process (L) are seen in the capsule. Two small circular or spiral nerve fibers (NF) are seen adjacent to the medial (upper) Schwann cell process. Collagen fibers, C. 19,800x.*

FIG. 9. *Cross section of one longitudinal nerve fiber (N) in pilary end-organ. Increased electron-density of axolemma and subjacent neuroplasm (asterisks) is seen facing the basal lamina of the outer root sheath (upper arrow) and of the capsule (lower arrow). Collagen unit fibrils (C) are seen just outside the basal lamina of the outer root sheath. Hemidesmosomes of the outer root sheath cells are indicated by white arrows. Laminar cell processes (L) show increased electron-density of cytoplasm in the pedicels facing the basal lamina of the outer root sheath and the capsule. 60,000x.*

FIG. 10. *Cross section showing part of hair follicle (ORS, outer root sheath), the space (S) above the nerve collar, the connective tissue capsule (C) and part of the associated sebaceous gland (SG). 6300x.*

around the outer root sheath of the hair follicles, resembling the hair nerve shield of the scalp described by Seto. The complete ring of nerve fibers around facial hair follicles would seem to indicate that they have a greater sensitivity than those of the scalp and auricle.

In this study, the longitudinal nerve fibers forming a collar around the outer root sheath are not seen to penetrate the outer root sheath, but come into close contact with the basal lamina lying just outside the outer root sheath. This same arrangement has been described by several other investigators (Yamamoto, 1966; Orfanos, 1967; Cauna, 1969; Hashimoto, 1973a). However, it should be noted that some investigators have observed nerve fibers that pass into the outer root sheath (Szymonowicz, 1909; Kadanoff, 1928; Weddell et al., 1955; Miller et al., 1960), and may supply Merkel cells in this location (Szymonowicz, 1909; Kadanoff, 1928; Miller et al., 1960). Kadanoff (1928) has noted that the Merkel cells in the outer root sheath of human hair are present but scarce. Their presence in some human hair follicles has been confirmed by electron microscopy (Breathnach & Robins, 1970; Marle & Orfanos, 1974). Merkel cells are commonly present in the outer root sheath of sinus hair follicles (Andres, 1966; Patrizi & Munger, 1966; Stephens et al., 1973) and in the present study were observed in the sinus hair follicles adjacent to the vellus hair follicles, but were not seen in the vellus follicles.

Stephens et al. (1973) reported that in sinus hair follicles numerous finger-like processes extend from nerve fibers, which are sandwiched by specialized (Schwann) cell processes, into the surrounding connective tissue. Andres (1966) has noted (also in sinus hair follicles) that the edges of the sandwiched (lanceolate) fibers have a free connection to the connective tissue space, and that these edges and their finger-shaped processes contain a fine filamentous material. The longitudinal nerve fibers of the present study are similar to the sandwiched nerve fibers of sinus hair follicles described by Stephens et al. and by Andres, except that they have a more regular arrangement around the follicle. Andres (1966) considers the edges of the lanceolate fibers and their finger-shaped processes to be the site of impulse conduction. These unsheathed processes would certainly appear to be able to act as free nerve endings, sensitive to any movement of the follicle.

The location of circular nerve fibers among collagen fibers of hair follicles, as described by Weddell et al. (1955) and by Miller et al. (1960) is confirmed by the present study. This study shows that the circular (or spiral) fibers, although accompanied by Schwann cell processes or laminar cell processes, still have part of their membrane in direct contact with connective tissue fibers.

Specialized Schwann cell processes have been noted by other investigators around regular hair follicles (Andres, 1966; Yamamoto, 1966; Orfanos, 1967; Cauna, 1969; Hashimoto, 1973a) and sinus hair follicles (Andres, 1966; Stephens et al., 1973). In the pilary end-organ these processes are sometimes replaced by processes of laminar cells. The laminar cells appear identical to the laminar cells in Meissner's corpuscles described by Hashimoto (1973b). The laminar cell processes contain pedicels, pinocytotic vesicles and filaments, as do the Schwann cell processes, but they are thinner and more electron-dense than the Schwann cell processes. While the cell bodies of the laminar cells are located in the capsule of the pilary end-organ and are somewhat flattened, the Schwann cell bodies are rounder and are located adjacent to the lower border of the pilary end-organ. Cauna (1969) noted that the specialized Schwann cell bodies were never in the vicinity of the longitudinal nerve fibers (nerve spindles) in the rat auricle, but were below them.

The large mitochondria of the longitudinal nerve fibers were noted by Orfanos (1968) and Cauna (1969) and the ruffled appearance of the axolemma was noted by Cauna (1969) as well as by the present authors. The thickenings of the cell membrane of the Schwann cell processes and increased density of the subjacent cytoplasm, as well as the thickening of the axolemma and increased electron density of the subjacent axoplasm of the longitudinal palisade of nerve fibers has been described by Hashimoto (1973a) and is confirmed in the present study.

The pilary end-organ is similar in structure to the annular complex of tylotrich follicles (large atypical guard hair follicles containing stiff hairs, described by Straile, 1960, and Mann, 1968); however, the annular complex in rabbits has a capillary network in its outer part (Straile, 1960) while the pilary end-organ is avascular. Most of the tylotrichs are in the telogen phase (Straile, 1960) as are the vellus hairs of this study. Straile (1960) noted that the resting tylotrich follicles of the rabbit are responsive to gentle rubbing, which causes the capillaries of the annulus to dilate, while even severe stimulation of actively growing follicles fails to produce a similar response. This may be partly due to the fact that the annular complex is compressed during the active growth stage (anagen) (Straile, 1960; Mann, 1968).

Factors which contribute to the increased sensitivity of tylotrich follicles during quiescence are also present in the vellus follicles (during quiescence). The decreased diameter of the telogen (quiescent) hair and loss of the inner root sheath relieves compression of the area just outside the outer root sheath, where the annular complex (or pilary end-organ) is located. The quiescent follicle has much less depth than the actively growing follicle; any movement of the follicle caused by movement of the hair shaft above the surface of the skin would be more effective in pressing against the pilary end-organ (as a lever) when the follicle is shorter.

ACKNOWLEDGMENTS

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