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Fine Structure of the Canine Olfactory Hairlets.

犬の嗅小毛の微細構造について.

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The construction of the olfactory epithelium was explored by BLOOM (1952) and BLOOM and ENGSTRÖM (1952) first using the electron microscope. In later studies ENGSTRÖM and BLOOM (1953) published the detailed structure of the olfactory region in man. In 1954 BLOOM made another contribution to light and electron microscopy of the frog and the toad olfactory region. In 1955 GASSER published his study on the olfactory nerve fibers of the pike. DE LORENZO (1957), BRETTSCHEIDER (1958), YAMADA and YASUTAKE (1959), YASUTAKE (1959), DE LORENZO (1960) and REESE (1964) published papers describing the fine structure of olfactory epithelium in the albino rat, the guinea pig, the rabbit, the frog, and other species. In 1964 WEBER and OKANO reported on the subject from the dog. They observed unique structures which could not demonstrate in other species. The microtubules, the multivesicular bodies, the basal foot, the striated rootlet fibers of the olfactory cilia and an apparent 4th cell type were discussed which might be the characteristic for the dog. However, to the knowledge of the author no detailed studies on the olfactory cilia or hairlets of the dog have been reported. Thus the purpose of this work was to elucidate the characteristic fine structures of the olfactory hairlets previously overlooked by other researchers.

I. Materials and Methods.

The materials used in this study were obtained from the clinically normal dogs. The entire mass of ethmoturbinates was rapidly excised and immersed in the glutaraldehyde fixative in toto, and later the mucous membrane was carefully removed from the turbinate bone. Small pieces of the tissue were transferred to fresh glutaraldehyde fixative and allowed to further fix for two hours (SABATINI et al. 1963). After glutaraldehyde fixation the tissue was further sliced to the proper size for embedding. The blocks were subjected to fixation with buffered osmium sucrose at pH 7.2 to 7.4 for two hours according to the method of CAULFIELD (1957), dehydrated in a graded series of alcohols and embedded in a Maraglas-Cardalite mixture according to SPURLOCK et al. (1963). During dehydration the tissues were passed through 1% potassium permanganate in acetone and a reducing agent in acetone to increase contrast in sections (PARSONS 1961). Sections were cut on a PORTER-BLUM microtome with glass knives, and mounted on collodion covered copper grids. After double stain-

ing with uranyl acetate according to WATSON (1958) and lead citrate according to REYNOLDS (1963) they were examined with an JEM-6C electron microscope.

II. Observations.

A. Olfactory epithelium.

It is composed of 4 different kinds of cell types. They are the olfactory cell, the supporting cell, the basal cell and an apparent 4th cell type. The olfactory cell was found to contain 6 to 16 characteristic hairlets. The basal corpuscles of the olfactory hairlet contained two accessory structures, namely the basal feet and the cross-striated rootlet fibers. The rootlet fibers consisted of a striated bundle of several fine, closely adherent filaments. Microtubules and multivesicular bodies were found in the olfactory cells. The supporting cells were easily recognized by their remarkable unique bushy microvilli, and electron opaque cytoplasmic organelles, and smaller sized multivesicular bodies. In addition to the usual supporting cell type, an apparent 4th cell type was observed. It contained short and sparse microvilli. This cell type was easily identifiable by its less electron opaque cytoplasm and was speculated to be a precursor of the usual supporting cell type though no intermediate stages have been encountered between the 4th cell type and the supporting cells (WEBER and OKANO 1964).

Fig. 1. A schematic drawing, which, based on the present observations, shows the structures of the olfactory hairlet, basal body and its apparatuses. A figure put in a frame is cross-section of hairlet shaft at the original region. Arrows indicate microtubules in the olfactory rod. *BB1* longitudinal section of the basal body, *BB2* cross-section of the basal body which displays pin-wheel pattern, *BF* basal foot, *OH* olfactory hairlet, *OR* olfactory rod, *RF* rootlet fiber, *SUP* supporting cell, *TK* thick portion, *TN* thin portion, *TP* tip of the olfactory hairlet, *TR* transitional region from the thick portion to the thin portion, *VI* microvilli, *ZVI* zone of the microvilli.

B. Olfactory hairlets.

The olfactory rod or the olfactory vesicle is a projection from the olfactory cell beyond the free surface of the epithelial lining, it is usually columnar, with a swollen end. The dimension of the rod or vesicle differs considerably. The projected

Fig. 2. Longitudinal section of an olfactory rod (OR) cut perpendicular to the surface of the epithelium, also showing numerous interwoven hairlets in the zone of the microvilli (VI) and the basal bodies (BB). The longitudinal sections of the olfactory hairlets (OH) cross the bushy microvilli and display several ampullar structures on the thin portion and the tip (indicated by arrows), on the other hand cross sections of the hairlet shafts reveal various numbers of the hairlet tubules. $\times 21,300$

olfactory rod measured about $4\ \mu$ in length and $1.2\ \mu$ in width.

The olfactory hairlets protrude from different parts of the olfactory rod which is enclosed with bushy microvilli of the supporting cell (Fig. 2). They are oriented at right angles to the surface of the olfactory rod which is located in the center like a core and extend radially from the rod on the cross-section cut parallel to the surface of the epithelium (Fig. 3). The olfactory hairlet could be divided into four regions according to the structural characteristics, that is, 1. the basal body and its apparatuses, 2. the thick portion of the hairlet shaft, 3. the transitional region where the majority of the peripheral tubules terminate, and 4. the thin portion and the tip of the hairlet. However a sheath or a membrane covering the hairlet throughout the

Fig. 3. A cross-section of an olfactory rod (OR) cut parallel to the surface of the epithelium. Five hairlets (OH) are oriented at the right angles to the surface and diminish their diameter abruptly. Notice the interwoven hairlets and the cross-sections of microvilli (VI) which surround the receptor cell. Ampullar structure (indicated by an arrow) in the thin portion of the hairlet is seen. $\times 30,000$

different portion of it is a same continuous unit membrane which is $100 \text{ \AA}$ thick and is a direct continuation of the rest of the plasma membrane covering the olfactory rod. The stroma of the hairlet is of the same object as the ground substance of cytoplasm which consists of very fine homogenous substance in the rest of the cell.

a) *The basal body and its apparatuses.*

In the thick portion of the hairlet it contains nine pairs or doublets of fine tubular structure arranged peripherally in a regular circle about a central pair of the tubule. The nine peripheral doublets are continuous with the basal body of a hairlet, while the central two disappear at the level of transition (the original region of the hairlet shaft) between the shaft and the basal body of which nine peripheral doublets transformed into nine triplets in the matrix of the olfactory rod (Fig. 7). The basal body can be followed for the distance of about $260 \text{ m}\mu$ into the cytoplasm of the olfactory rod. The transverse section of the basal body which was cut perpendicular to the surface of the epithelium displays the triplets of subtubule A, B and C. Each tubule is tilted inwards and all in same direction. It is the two inner elements, subtubules A and B in each triplet, that are continuous with the two subunits of the corresponding double tubule of the hairlet shaft. The outermost element, subtubule C, is an additional structure not represented in the hairlet shaft. The delicate linear densities joining subtubule A of each triplet to subtubule C of the adjacent one can be seen also (Fig. 7). From the proximal end of the basal body the rootlet fibers which appear to consist of a striated bundle of several fine, closely adherent filaments, intrude longitudinally into the olfactory rod for a distance of about 1.6μ . From the lateral wall of each peripheral triplet a tiny basal foot which measured $130 \text{ m}\mu$ in length and $40 \text{ m}\mu$ in width emanates into the cytoplasm all in same plane and direction, thus forming a 'pin-wheel' fashion in cross sections (Fig. 7).

Near the original region of the hairlet shaft where the subtubule C had terminated the subtubule A and the subtubule B of an antecedent doublet are connected with a linear density. Moreover each doublet is anchored to the hairlet membrane with a 'Y-figure' density. Here in the matrix between the nine peripheral doublets and the two centrals there is a electron opaque circular structure which encircles two central tubules (the framed figure of Fig. 1 and 8).

b) *The thick portion.*

The thick portion of the hairlet shaft measures about $250 \text{ m}\mu$ in diameter and keeps this diameter for a distance of about 1.5μ , where it diminishes the dimension of the hairlet shaft abruptly to one third ($80\text{--}90 \text{ m}\mu$) of the thick portion (Fig. 4). The cross-section of the thick portion displays a typical nine plus two pattern of the tubular arrangement, consisting of subtubule A and B. The both subtubule A and B are, about $200 \text{ \AA}$ in diameter, continuous with the subtubule A and B of the basal triplet and have a wall which measured $60 \text{ \AA}$ in thickness. The peripheral subtubule A and B and central pair are homologous and have light and homogeneous interior. The peripheral tubules thus have a 'double-barreled' or 'figure-of-eight' appearance in the section (Fig. 8). However they appear rather a single oval canaliculus separated with septum into two rather than two canaliculi adhered together. Unlike the peripheral doublets the central tubules are not in contact with each other, but are about

Fig. 7. A few favorable cross-sections of the basal bodies and the three original region of the hairlet shaft indicate the presence of what appears to be a complex pattern of thin fibrillar densities. Each of three cross-sections of the original region of the hairlet shaft shows nine peripheral doublets and two central tubules which are missing partially, all the tubules are sheathed in a hairlet membrane at this site. Each of the cross-sections of the five bodies consists of nine triplets. Note two cross sectioned hairlet shafts (thin portion) indicated by arrows 1 and 2, each contains four tubules, however one indicated by an arrow 1 contains four independent single tubules and the profile of the shaft is rather square, the other indicated by an arrow 2 contains two doublets and it is rather oval. $\times 60,000$

Fig. 4. Longitudinal section of two olfactory hairlets showing the transitional region from thick portion to thin portion, where the majority of the hairlet tubules terminated in the matrix as the shaft reducing its diameter. The hairlet membrane is not smooth, instead numerous vesicular structures swell out. $\times 60,000$

Fig. 5. Longitudinal section showing the transitional region also. Notice the rather gradual reduction of the number of the tubules and the diameter of the hairlet shaft compared with the abrupt change in the figure four. $\times 60,000$

Fig. 6. Longitudinal and cross-sections of the thin portion showing the thick population of the olfactory hairlets (OH) in the zone of the microvilli (VI). The hairlets reveal two or four hairlet tubules on the cross-section. $\times 60,000$

200 Å apart and have a simple circular profile.

The sheath enveloping the hairlet shaft is wavy and rough due to the swellings of the matrix in the longitudinal section, they resemble a vesicle, measuring about 70 m μ in diameter and their interior is electron less opaque than the matrix of the hairlet (Fig. 4). Frequently the vesicular structure is observed also in the matrix.

c) *The transitional region.*

At the transitional region the first detectable changes seem to be that the peripheral tubules approach each other more closely. The two central tubules tend to lose their central position and even spacing of the peripheral tubules is partly lost. Some of the peripheral double tubules then become single, this seems to result from the rather abrupt termination of one subtubule. Both the change from doublet to singlet

Fig. 8. The 'Y-figure' linear densities are shown at the original region of the hairlet shaft where the two central tubules terminate. This 'Y-figure' structure seems to transform into comma-like shape, the basal foot, which composes pin-wheel pattern in the olfactory rod (cf. Fig. 7). $\times 100,000$

Fig. 9. Cross-section of the transitional region from the thick portion to the thin portion cut perpendicular to the surface of the epithelium, showing reduced number of hairlet tubules, they are twelve isolated single tubules and one doublet. The cross-section of the thin portion which maintains two single tubules is also shown, it has rather oval profile. $\times 100,000$

Fig. 10. Cross-section of the transitional region in which seven single tubules are seen. Cross-section of the thin portion which has two single tubules is shown also. $\times 100,000$

Fig. 11. Six single tubules are seen on the cross-section of the transition. $\times 100,000$

Fig. 12. Three single tubules are seen on the cross-section of the thin portion. $\times 100,000$

Fig. 13. One single tubule is seen on the cross-section of the thin portion. $\times 100,000$

and the ending of the singlets occur at different distance from the original region of the hairlet in different tubules, so that transverse sections show variable numbers of mixed doublets and singlets up to the maximum of eleven (nine plus two) (Fig. 8 to 13). However on transverse section odd numbers of tubules appeared very seldom. The central tubules are not easily identified after they have lost their central position. These dramatic changes in numbers, the dimension of hairlet shaft, and arrangement of the tubules occur all of a sudden within the distance of about 0.3μ in most cases (Fig. 4), but in some case this transitional region is extended for the distance of about 1μ (Fig. 5). After the majority of the tubules disappeared at this region, usually four or two single tubules remain in the matrix of thin portion but doublets are observed also in transverse section (Fig. 7) and longitudinal section (Fig. 16), however three (Fig. 12) or one (Fig. 13) single tubules are observed very rarely.

d) *The thin portion and the tip of the hairlet.*

The characteristics of the hairlet tubule, its wall and the hairlet membrane seem to remain unaltered except the dimension of the over-all hairlet diameter. The profile of the transverse section appeared oval (Fig. 9), rather triangular (Fig. 12) or square (Fig. 7) when two, three or four tubules remained respectively in the matrix of the hairlet shaft.

Rather outstanding structure in the thin portion is a spindle shaped swelling which measured $150 m\mu$ in diameter at the most stout site whereas both the proximal and distal thin portions to it measured $50-70 m\mu$. The longitudinal section of this part, cut perpendicular to the surface of the epithelium, displays two single tubules running side by side in the center of the ampullar structure (Fig. 3 and 14).

The tip of the hairlet shaft. The termination of the thin portion is characterized with a vesicular formation, which appears like an Indian club or a pear at the last half micron of the hairlet tip. The size and shape vary very much. For example the vesicle in the figure 14 measured about $710 m\mu$ in length and $40 m\mu$ in diameter, and rather compact one in the figure 16 measured about $430 m\mu$ in length and $14 m\mu$ in diameter. And usually the vesicle at the tip contains smaller vesicles (Fig. 15). The mode of the tubular termination in the vesicle varies remarkably, first of all the number of the tubule, two or four tubules remains as far as the end in many cases and some of them makes a simple glomerular termination, sometimes two tubules form a loop-like configuration (Fig. 15) or two isolated wavy tubules just cross the center of the vesicle (Fig. 14).

C. Atypical olfactory hairlet.

During the observation two olfactory hairlets which seem to be abnormally gigantic are found. No particular attention was paid to appearance frequency of this cell type, however the presented electron micrographs are taken from the very two atypical hairlets which were found out of the countless olfactory cells. On the longitudinal section cut perpendicular to the surface of the epithelium, several nine-plus-two patterns of hairlet tubules in a common hairlet membrane are observed, thus forming a gigantic hairlet but, in other respects, the olfactory rod and the other hairlets are entirely normal (Fig. 17). There is a different type of hairlet deformity (Fig. 18), in

this case all the nine-plus-two patterns of hairlet tubules are bundled together in a common hairlet membrane and many vesicles are observed in a matrix, moreover the olfactory rod resembles the ciliated cell found in the respiratory region of canine nasal cavity.

III. Discussion.

The electron microscopic study to epithelial cilia of animals was first undertaken by ENGSTRÖM (1951) using tracheal epithelium from guinea pig and dog, and later BLOOM and ENGSTRÖM (1953). However the first indication of uniformity of ultrastructure in a wide range of different forms came from the work of MANTON and her associates (1953 a, 1953 b, 1955) who carried out an extensive series of comparative investigations on plant cilia.

FAWCETT and PORTER (1954) published an elegant paper on ciliated epithelia from mollusks and amphibians and established unique ultrastructures on ciliary complex and its apparatus, especially FAWCETT (1961) edited conclusive article on 'cilia and flagella' which covers few different species from the plant and the animal kingdom. STINSON et al. (1962) described the structure of cilia from the bovine endometrium. On the other hand YAGIU and SHIGENAKA (1960) published fine article on the studies of the fibrillar system in the protozoan ciliates and FUJIMOTO (1964) described the fine structure of the cilium and the ciliary apparatus of the epithelium of the renal tubule in urodele, in which they presented the fact that the basic ultrastructures were similar to other species fundamentally.

RHODIN and DALHAMN (1956) contributed detailed studies of the tracheal ciliated mucosa in rat, in which he has founded the basic morphology of the motile cilia. And also YAMADA (1962), RHODIN (1963) and HAMA (1964) described the ciliated epithelium of the mammalian trachea. The studies of ependyma in the brain of the rat by BRIGHTMAN and PALAY (1963), and of the respiratory mucous epithelium of the canine nasal cavity by OKANO and SUGAWA (1965) brought similar results to their findings on the main point. However the study on the ciliated secretory cells in the pars distalis of the mouse hypophysis has demonstrated the motile cilia possessing a 9+0 fibril pattern (BARNES 1961).

The remarkable observations in this field were made by AFZELIUS (1959, 1960, 1961 a, 1961 b, 1963) utilizing the sea urchin sperm and the ctenophore swimming-plates, in which AFZELIUS reported several new structures found in the cilium and the flagellum. The studies of the sperm tail, by YASUZUMI (1956, 1957, 1964), by

Fig. 14. Higher magnification of the part of the figure two showing the longitudinal sections of the ampullar structures of the thin portion and the tip which were cut perpendicular to the surface of the epithelium. Two tubules in the vesicular tip isolated apart themselves and came together at the tip. $\times 60,000$

Fig. 15. Two swollen tips are sectioned longitudinally, it was cut perpendicular to the surface of the epithelium. The upper vesicle has two split tubules and one smaller vesicle located in the center of the tubular loop. The lower one seems to contain four tubules and they form simple glomerular termination. $\times 60,000$

Fig. 16. Relatively compact type of the hairlet tip. At least four tubules are distinguishable in this particular tip. $\times 60,000$

FAWCETT (1962) and by NAGANO (1962) revealed additional fact that all these sperm flagella have rather similar structures, especially the array of the fibers, nine peripheral doublets and two centrals, and also the spokelike arrangement of linear densities in the interfibrillar matrix was identical. LANG (1963) discovered a 9-pointed, star-shaped complex on the cross-section of the original region of a flagellum instead of "Y-figure" linear density found in this canine olfactory hairlet.

Comparing the before mentioned ultrastructures of the motile epithelial cilia, the sperm tail and the other flagella with the olfactory hairlet of the canine olfactory cell, the morphological difference was perceived on the olfactory hairlet. However the study on the flagellar structure in certain flagellates (GIBBONS and GRIMSTONE 1960) presented the remarkable fact that, approaching the tip, the flagella decrease in over-all diameter, the peripheral doublets become single and the central fibers tend to lose their central position. In this respect, the canine olfactory cilia appeared to be similar to the profile on the cross-sections (WEBER and OKANO 1964). REESE (1965) discovered the fine structures on the olfactory cilium in the frog. They are a large vesicle in the distal segment, a group of small vesicles in the proximal segment of an olfactory cilium and a transition between a proximal and a distal segment where a sudden decrease in the diameter of the cilium is accompanied by a change from double to single outer fibers. The findings from this canine material correspond basically with the above mentioned olfactory cilia in the frog.

As for the terminology used in this study, hairlet is chosen rather than cilia and flagella though author used olfactory cilia once in the previous study (WEBER and OKANO 1964), the thick portion instead of a proximal segment and the thin portion instead of a distal segment are applied preferably, because a olfactory hairlet, though it is a common single shaft covered with a common hairlet membrane, has no akin structure to a ordinary motile cilium or a flagellum and displays entirely different morphology according to its portion. Especially the structure of the thin portion is unique in the canine olfactory hairlet, namely four or two hairlet tubules appear with the very few exception of three and one on the cross-section of the thin portion. And there is an ampullar structure in a midway and a tip of a hairlet in which a small vesicle is contained, but there is no electron opaque granular structure at the tip reported by ROTH and SHIGENAKA (1964).

The evidence of irritable properties in a modified cilium is of interest in relation to hair-like processes on other sensory cell such as those of the photoreceptors in the ocellus of hydromedusan (EAKIN and WESTFALL 1962), the rod cells of the vertebrate retina (DE ROBERTIS 1956, TOKUYASU and YAMADA 1959, EAKIN and WESTFALL 1960), taste buds (DE LORENZO 1963, RHODIN 1963), lateral-line organs (HAMA 1965), insect ear (GRAY 1960), some olfactory cilia from insects (SLIFER 1961, SLIFER and SEKHON 1964, SLIFER, SEKHON and LEES 1964), etc. Especially it is of great interest to compare the expanded tip of each of these

Fig. 17. Longitudinal section of an olfactory rod and an atypical gigantic olfactory hairlet which contains few complete sets of nine-plus-two pattern of tubules in a common hairlet membrane. $\times 30,000$

Fig. 18. An atypical gigantic olfactory hairlet which seems to be similar to that of the Fig. 17. However the olfactory cell itself seems to be atypical in this case. $\times 24,000$

olfactory hairlets with the crown cell processes of the saccus vasculosus. The processes forming the apical tuft are found to be modified cilia and the fibrils can be traced upward a short distance into the process, but there they seem to end blindly. The swollen tip is occupied by mass of small vesicles (BARGMAN and KNOOP 1955, FAWCETT 1961). Similar vesicles were found along the cilia-like shaft of the receptor cell in the ocellus of the hypomedusan (EAKIN and WESTFALL 1962). However the ampullar structure at the tip of the olfactory hairlet contains very few small vesicles and no vesicles are found in it sometimes, instead always two or four hairlet tubules can be traced from the thin portion to the expanded tip where the tubules end forming a simple glomerular or a free termination. Moreover there are several different types of the expanded tip in which the few remaining tubules terminated in various ways. The fact that there are several different types of the hairlet ending leads one to speculate upon their functional significance. The odorous substance may be discriminated by different hairlet tips.

Investigation of the electrical responses of olfactory epithelium to odors have shown that the olfactory cilia may be points at which electrical stimulation is initiated by contact with odorous substances (OTTOSON 1963). Cilia or modified cilia are found on sensory cells in sense organs mediating various kinds of stimuli in both vertebrates and invertebrates (DE ROBERTIS 1956, GRAY 1960, SLIFER 1961, SLIFER and SEKHON 1964, TOKUYASU and YAMADA 1959). In this respect the dog olfactory hairlet could not be exceptional.

The construction of the canine olfactory epithelium is not like that in the frog. The olfactory cell, though projecting from the epithelial surface, is thoroughly embedded within bushy seaweed-like microvilli which naturally could hinder odorous molecules in the ambient air from reaching to the receptor cell. The olfactory hairlet also intermingles with microvilli from the supporting cell but a thin portion and a swollen tip of the hairlet occupy the distal surface of the microvillus zone so that more reasonably they can encounter odorous substances earlier than the olfactory rod. The olfactory hairlets are positions which suggest that they are important in the initiation of odorous excitation. In this case the microvilli may provide stationary objects which facilitate the production of eddies and currents as the result of ciliary motion (WEBER and OKANO 1964). The remarkable unique structure of the olfactory hairlets leads one to speculate upon, their functional significance that they play an important role as an olfactory receptor, though morphologically they are something between motile cilia and flagella, still however further investigation is necessary to give any detailed conclusive remarks.

The significance of the atypical olfactory hairlet is not speculated upon, however since the spermatozoon dimorphism (YASUZUMI and TANAKA 1958), a structural abnormality of the sea urchin sperm tail and cilia and flagella that do not conform to the normal nine plus two pattern (AFZELIUS 1959, 1960, 1961, 1963), a double sperm tail (FAWCETT 1961), and twin and triplet ciliary shaft (OKANO and SUGAWA 1965), etc. are reported, it could be concluded as a deformation having no functional significance.

IV. Summary.

The additional fine structure of the canine olfactory hairlet is studied with the electron microscopy. The canine olfactory hairlet is unique in structure and it consists of four main portions, namely, 1. the basal body and its apparatuses, 2. the thick portion which is analogous to the mammalian epithelial cilia, 3. the transitional region where the nine peripheral doublets become single tubule and terminate abruptly leaving few single tubules, 4. the thin portion which has an ampullar structure on the midway and the tip where all the remainders of the hairlet tubules terminated finally. Their position in situ and their characteristic structure lead one to speculate upon their functional significance as a chemoreceptor. An atypical giant olfactory hairlet is found but its functional role is not known.

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内 容 自 抄.

犬鼻腔の篩骨甲介粘膜上皮内の嗅細胞から突出する嗅小毛の超微細構造を観察した。

嗅上皮面に約 4μ 突出した棍棒状の嗅細胞は上皮遊離面に水平，かつ放射状に伸展する10数本の嗅小毛をもち，その形態は一般の繊毛と鞭毛との中間の形態を呈するものと考えられる。嗅小毛は嗅細胞を被う形質膜と同質のもので被覆され，嗅小毛の基底部から約 1.5μ の部位で直径約 $250m\mu$ から急激に細くなり，約 $80m\mu$ の細型となり，先端まで $80m\mu$ 内外の径を保っている。しかし細型の一部と先端はやや膨隆して卵円形をしている。嗅小毛の太い部分は周辺部に9対，中心部に1対の細管を包含しているが，周辺部に配列する9対の細管は細型への移行部で逐次消失し，有対から単独の細管となり，配列も乱れ，横断面に多いものは10数本から，少ないもので，1本観察された。

しかし横断面に2本の細管を保持するものが全体の約80%である。この2本は太い部分に於ける中心部の1対が残存しているものと考えられる。

細管の径は約 $200\text{\AA}$ で管壁は約 $60\text{\AA}$ であった。

化学的受容器の一部であるこれらの嗅小毛がどのような機能を有するかについては，今後の研究にまたねばならないが，その名の示すごとく受容器として極めて重要な役割を演じているものと推察される。なお数本の嗅小毛が集束したもの

のように見受けられる非典型巨大嗅小毛も見られた。

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