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The Fine Structure of the Olfactory and Vomeronasal Organs of a Lizard *(Tiliqua scincoides scincoides)*

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Summary. Olfactory epithelium in *Tiliqua scincoides scincoides* is of a loosely packed pseudostratified type. It receives secretion from the supporting cells and the underlying glands of Bowman. Its surface bears microvilli and cilia from sensory cells and microvilli from supporting cells. The vomeronasal epithelium is also pseudostratified but higher and more closely packed. Its surface carries microvilli from sensory and supporting cells but lacks cilia. Vascular connective tissue penetrates it almost to the epithelial surface but is always outlined by basal cell processes and a basal lamina. There are no secretory cells in or under the sensory epithelium but some cells in the epithelium of the mushroom body contain secretion granules.

Sensory cells of both epithelia are bipolar neurons. The perikarya of the vomeronasal cells are more neuronal in character. Axonic processes are similar in both, dendrites are distinctive. Olfactory dendrites end in rounded rods bearing microvilli and cilia of an unusual type. Microvilli with filamentous cores occur on vomeronasal dendrites. There are no cilia, but 2–6 centrioles appear below the cell surface.

Basal cells are structurally similar in both epithelia, but axonic processes of olfactory cells are surrounded by supporting cell processes, while vomeronasal axonic processes are surrounded by basal cells before they leave the epithelium.

The presence of cilia and microvilli on the surface of the sensory cells is discussed in relation to the physical conditions surrounding them.

Key words: Olfactory mucosa — Sense organs — Reptilia — Electron Microscopy.

Snakes and lizards provide excellent material for the study of olfactory and vomeronasal organs, since both organs are present and well developed. It is generally assumed that the functions of these two chemoreceptors are similar (Negus, 1958; Parsons, 1970). Studies on reptiles (Bannister, 1968; Bannister and Cuschieri, 1971; Altner, Müller & Brachner, 1970; Graziadei and Tucker, 1970) and mammals (Kratzing, 1971; Loo and Kanagasuntheram, 1972) have established the distinctive features of the vomeronasal cell, and have made it clear that if differs in some respects from the olfactory cell. A detailed comparison of the two sensory epithelia in the same species appear not to have been carried out. The following study was undertaken to explore the structural similarities and differences of the two types without the complication of species differences. In addition, it provides a description of the fine structure of the olfactory epithelium in the Squamata.

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Material and Methods

Blue-tongued lizards (*Tiliqua scincoides scincoides*) were trapped in the early summer and were made hypothermic in a cold room before perfusion or decapitation. Some difficulty was experienced in achieving satisfactory fixation for electron microscopy and several methods were employed. For immersion fixation the dorsal wall of the nasal cavity was removed and the whole head rostral to the eyes was immersed in ice-cold 4% glutaraldehyde in cacodylate buffer at pH 7.2. The vomeronasal organ was exposed by dissection under fixative. Small strips of epithelium were removed from the olfactory, respiratory, and vomeronasal areas and placed in fresh fixative for one hour.

Some material was obtained from a lizard fixed by perfusion. The perfusate consisted of 1.5% glutaraldehyde in 0.1% cacodylate buffer, pH 7.2, containing 4% polyvinylpyrrolidone (Bohman and Maunsbach, 1970), and was introduced into the ventricle. Specimens were then dissected out in the manner described above. Materials were also obtained from the decalcified head of a recently hatched lizard. The head was fixed by immersion in 4% glutaraldehyde in cacodylate buffer at pH 7.2 and decalcified at 4°C for 14 days in 4.13% EDTA solution (Warshawsky and Moore, 1967). All tissues were post-fixed in osmium tetroxide, dehydrated in graded alcohols and embedded in Araldite. Sections were cut on an LKB Ultratome III, stained with uranyl acetate and Reynold's lead citrate, and viewed in a Sieman's Elmiskop 1 A electron microscope.

Specimens for light microscopy were fixed in 5% formalin and decalcified in a solution of picric acid, formalin, and formic acid. Paraffin sections were cut at 5–6 μ and stained with haematoxylin and eosin (H & E), alcian blue, and periodic acid-Schiff (P.A.S.).

Results

Light Microscopy

Olfactory epithelium lines the nasal septum, the dorsal aspect of the *cavum nasi proprium*, and the dorsal aspect of the concha. The ventral surface of the concha and ventro-lateral part of the cavum is lined with a ciliated epithelium interrupted by small crypts of mucous-producing cells. The vomeronasal organ consists of a pair of dome-shaped structures located in the rostral floor of the nasal cavity. The space occupied by each is defined by the vomer and nasal septum medially, the vomer ventrally, and the septo-maxillary bones dorso-laterally. The cavity of the organ is greatly restricted by an evagination from the floor forming the mushroom body. The organ communicates with the oral cavity ventrally by a short duct; there is no communication with the nasal cavity (Fig. 1).

The olfactory epithelium is pseudostratified, with cells of three types; sensory, supporting (and also secretory), and basal. Olfactory rods, cilia and microvilli extend beyond the surface as a border in which a long and short component are visible. The superficial cytoplasm of supporting cells stains bright red with P.A.S. and a strong blue with alcian blue. Below this there is a wide nuclear region. The superficial nuclei belong to supporting cells, below them the rounded olfactory nuclei are more numerous, and have an open scattered chromatin pattern. Basal cell nuclei are separated from the rest by a narrow cytoplasmic zone. They are the least frequent cells in the epithelium. The epithelial base is irregular since small bundles of olfactory axons leave it at intervals to join larger groups in the lamina propria.

Simple tubulo-alveolar glands of Bowman lie in the loose collagenous lamina. They are PAS-positive but do not stain with alcian blue. In the respiratory area,

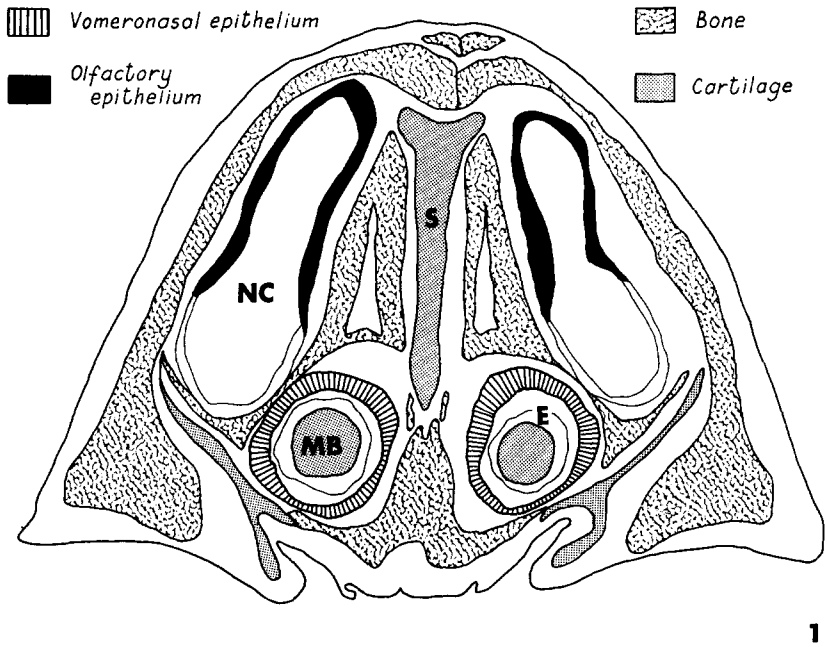

Fig. 1. Diagrammatic cross section of snout of *T. scincoides* showing areas of olfactory and vomeronasal epithelium. *E* epithelium of mushroom body; *MB* mushroom body; *NC* nasal cavity; *S* nasal septum

goblet cells in small crypts, give a strong magenta with P.A.S. and a bright blue with alcian blue; the lateral nasal gland which is housed mainly in the concha gives only a slight red colour with PAS.

In contrast to the nasal area, the vomeronasal organ shows little evidence of secretory activity. There are no glands under the sensory epithelium, and the supporting cells are not secretory. There are no goblet cells in the non-sensory epithelium over the mushroom body, but some cells are stippled with small granules which are PAS- and alcian-blue positive.

Sensory epithelium lines the roof and sides of the dome of the vomeronasal organ and reaches maximal height on the medial aspect, where as many as 30 nuclei may be stacked from base to surface. An unusual feature is the intrusion of columns of connective tissue that carry blood vessels almost to the epithelial surface. These columns are flanked by bundles of nerve fibres which are the proximal extensions of the sensory cells. Only two epithelial cell types are clearly evident, vomeronasal and supporting; there is no distinctive line of basal cell nuclei. The epithelial base is frequently interrupted by the connective tissue columns and large bundles of axons. Pale, ovoid, supporting cell nuclei form a superficial nuclear layer about three nuclei in depth. Vomeronasal nuclei are rounded, stain deeply, and occupy most of the depth of the epithelium. The surface of the sensory epithelium ends in a fine brush border, but there are no cilia.

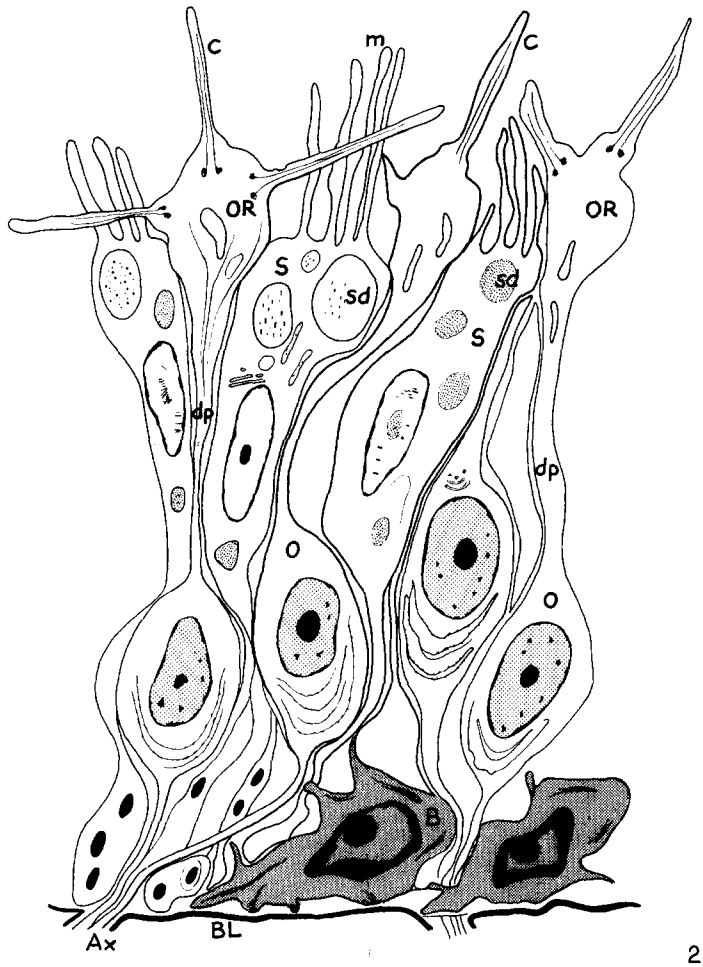

Fig. 2. Diagrammatic view of the olfactory epithelium. The height of the epithelium has been reduced. *Ax* axonic process; *B* basal cell; *BL* basal lamina; *C* cilia; *dp* dendritic processes; *m* microvilli; *O* olfactory cell; *OR* olfactory rod; *S* supporting cell; *sd* secretion droplet

The mushroom body has a central core of hyaline cartilage covered by a thin perichondrium and a pseudostratified, ciliated epithelium which is lower than its sensory counterpart and does not have invasive blood vessels.

Fine Structure

General Characteristics of the Olfactory Epithelium. The structure and relationships of the three cell types are shown diagrammatically in Fig. 2. The appearance of the surface of the epithelium varies considerably, important factors being age of the specimen and the amount of secretory activity in supporting cells. The cytoplasm of supporting cells increases in electron density with age of the animal but may contain such a large number of secretion droplets as to give an overall

light appearance. The narrow dendritic processes of olfactory cells have an electron-lucent cytoplasm in which mitochondria and microtubules are readily seen. The dendrites end in rounded olfactory rods that extend beyond the surface and carry long cilia, and, at least in some cases, microvilli. The cilia form the longer element of the ciliated border evident in light microscopy. The shorter component is made up mainly of the microvilli on the surface of supporting cells (Fig. 4).

Below the surface, throughout the nuclear zone and down to the basal lamina, the epithelium is loosely knit with a considerable amount of intercellular space. There is a change in electron density of the cytoplasm in the supporting cells deeper in the epithelium so that their basal processes are much lighter than their surface cytoplasm. Basal cells stand out clearly, especially in mature specimens, as they have a greater electron density than the basal processes of the other cells (Fig. 10).

General Characteristics of the Vomeronasal Epithelium. The epithelium is deeper and more complex than its olfactory counterpart, with less intercellular space, and with columns of vascular connective tissue extending into it. The general structure is shown diagrammatically in Fig. 3. Basal cells, which are difficult to distinguish in the light microscope, are readily identified by their dense cytoplasm. The surface of the epithelium is covered by microvilli produced by both sensory and supporting cells (Fig. 7).

Electron microscopy makes it clear that the connective tissue columns are always separated from the epithelial cells by processes of basal cells and the basal lamina. Large bundles of axonic processes frequently flank these columns but remain above the basal lamina. They are surrounded by fine processes of basal cells until they interrupt the lamina near the true base of the epithelium to join the vomeronasal nerves in the lamina propria.

Olfactory Cells. The receptor cells are bipolar, with most of their cytoplasm in the perinuclear area, narrowing to a fine proximal process towards the epithelial base and a distal dendritic process extending to the surface where it ends by forming a rounded olfactory rod carrying the olfactory cilia (Fig. 4). In the perinuclear region there is a prominent Golgi apparatus and an extensive array of parallel rows of rough endoplasmic reticulum, often with enlarged cisternal space between the rows (Fig. 6). Smooth-surfaced vesicles are numerous near the Golgi area but are frequent throughout the perikarya, and mitochondria occur but are more numerous in the dendrite. The nuclei have a dark peripheral chromatin band and a single nucleolus. Nucleopores are frequent, usually filled with a light amorphous material.

Below the nucleus the cell tapers rapidly to the narrow axonic process. Bundles of these among the basal cells are surrounded by the proximal processes of supporting cells. At intervals, bundles of axons interrupt the basal lamina to become olfactory nerve fibres in the lamina propria. Microtubules, vesicles and occasional mitochondria can be seen in the cytoplasm of axonic processes.

Mitochondria are numerous in the dendritic process of the olfactory cell, and microtubules extend throughout and into the terminal rod. Mitochondria do not always appear in the rods, but vesicles are a constant feature. The olfactory cilia and their basal bodies are the most distinctive feature of the rods. The cilia vary in number but there are usually about ten, arranged in a basal ring of six and a

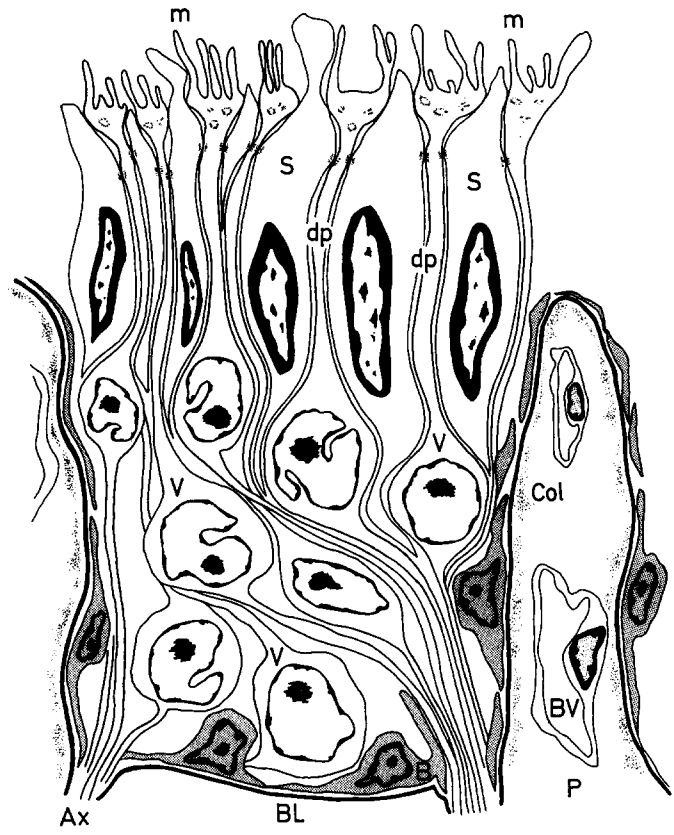

Fig. 3. Diagrammatic view of the vomeronasal epithelium. The height of the epithelium has been reduced. *Ax* axonic processes; *B* basal cell; *BL* basal lamina; *BV* blood vessel; *Col* collagen; *dp* dendritic process; *m* microvilli; *P* areas of vascular connective tissue; *S* supporting cell; *V* vomeronasal cell

smaller ring of four towards the tip. However, not all rods fit this pattern, and many have a single terminal cilium with a single ring of cilia below it. The total length of cilia is difficult to estimate, since few are sectioned throughout their length; the longest seen was 5 μ. The rods themselves project 0.8 to 1.5 μ beyond their junction with neighbouring cells. The shaft of the cilium consists of a ring of 9 double filaments and a central pair of single filaments (Fig. 5e), the typical pattern of motile ciliary structure. The double filaments of the cilia become triple in the basal bodies, and each triplet ends in a dense rounded footplate. The basal body is usually situated in an elevated area of cytoplasm ending quite abruptly in a "shoulder" where it narrows to the base of the cilium. The cell membrane in this region and the basal 0.25 μ of the ciliary shaft carries longitudinally orientated rows of short rods or setulae about 30 nm in length. In transverse section the rows can be seen to correspond to the peripheral filaments of the basal body and

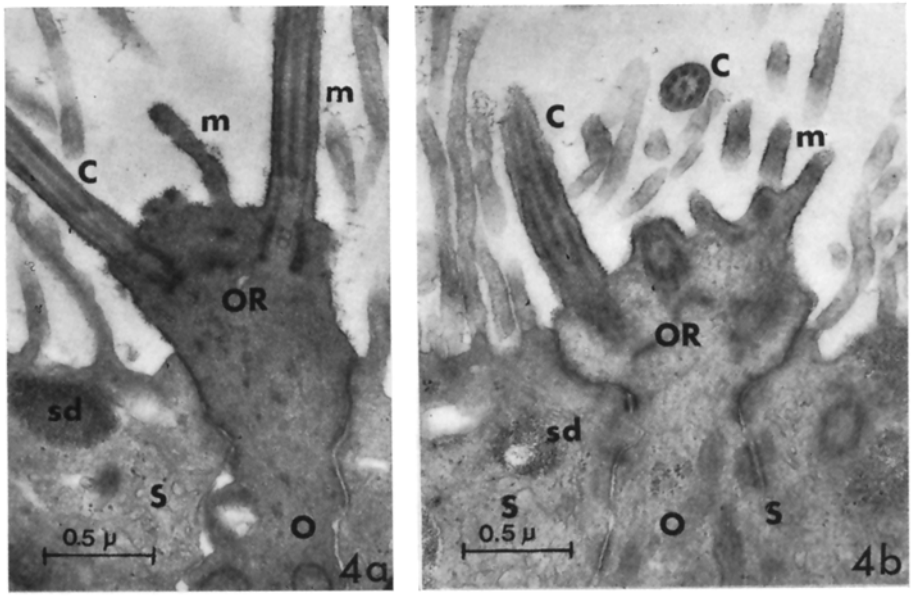

Fig. 4a and b. Surface of the olfactory epithelium. Olfactory cell dendrites (*O*) end in olfactory rods (*OR*), carry cilia (*C*) and microvilli (*m*). Supporting cells (*S*) contain secretion droplets (*sd*) and carry microvilli

cilium, so that there are 9 rows, each about 5 or 6 separate setulae in width (Fig. 5a–d). After the initial length of 0.25 μ they cease abruptly and the cell membrane is smooth over the remainder of the cilium. The two central filaments of the cilium begin at the point of transition to a smooth membrane, so that the initial pattern of the cilium is 9 +0.

Microvilli occur on the olfactory rods in a significant number of sections (Fig. 4). They are much shorter than cilia and do not appear to have any internal organization.

The Vomeronasal Cell. The general structure of the vomeronasal receptor resembles its olfactory counterpart. It is a bipolar cell, enlarged in the nuclear region and extended into a thin dendritic and thinner axonal process; the latter continues as an axon of the vomeronasal nerve. The nucleus is rounded and pale, with a light stippling of chromatin which does not usually form a condensed band inside the nuclear membrane. The nucleolus is large (Fig. 8b). Around the nucleus closely packed parallel rows of endoplasmic reticulum occupy most of the cytoplasm. Rough and smooth reticulum both occur and are continuous at some sites, but the latter is more extensive and the rough reticulum is often only lightly studded with ribosomes. The Golgi complex lies close to the nucleus and in cells from mature animals, it is usually associated with one or more dark bodies of a complex, laminated and vacuolated internal structure enclosed in a limiting membrane (Fig. 8a, b).

Above the nucleus, the cell body narrows to a dendritic process about 0.75 μ in diameter which extends to the surface and contains longitudinally orientated

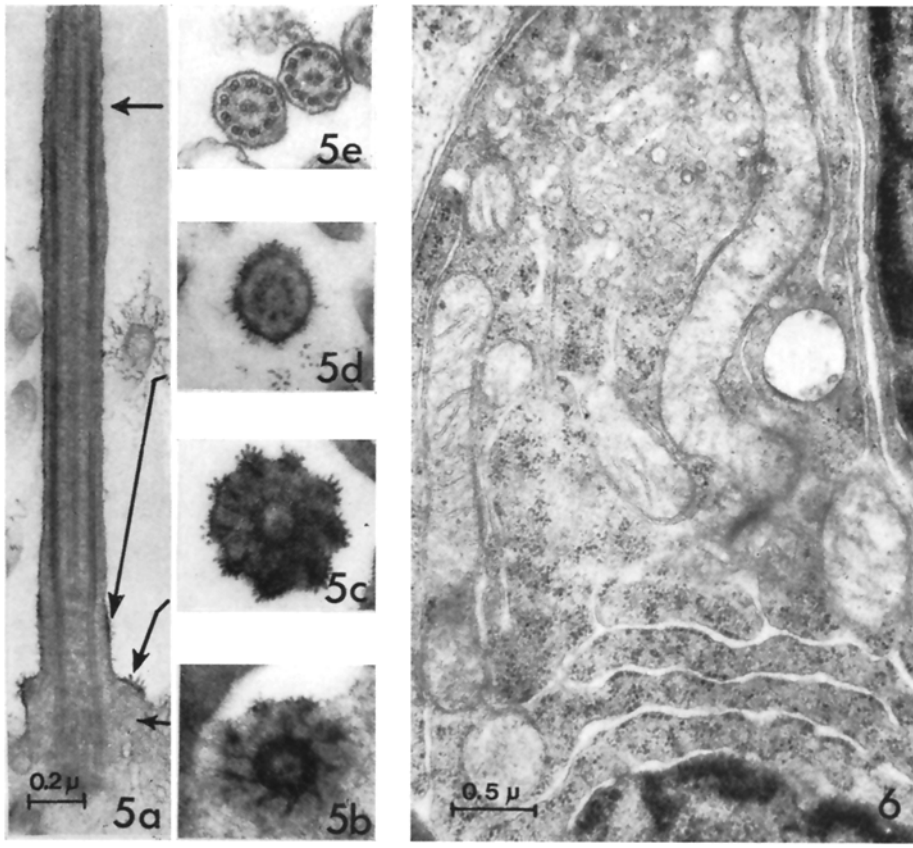

Fig. 5a—e. Sections of an olfactory cilium. a longitudinal section; b—e transverse sections at levels indicated on (a)

Fig. 6. Olfactory epithelium: perinuclear cytoplasm of olfactory cell. Rough endoplasmic reticulum, elongate mitochondria, and numerous vesicles characterize the cytoplasm

microtubules and mitochondria. Two or three dendrites may lie side by side without intervening processes of supporting cells, but no junctional specializations occur between them. The dendrite expands just below the surface and typically ends at, or just beyond, the general epithelial surface. Two to six centrioles occur in the expanded area or deeper in the dendrite. Basal feet or transitional fibres were not observed in association with the centrioles. Smooth surfaced vesicles occur near the surface of the cell and are probably pinocytic in origin since indentations of the cell membrane are often observed at the base of the microvilli. Sensory cells carry 2–10 microvilli which are sometimes branched (Fig. 7a, b). A central core of fine fibrillar material in the microvillus extends down some distance into the apical cytoplasm. The expanded terminal regions of the dendrites are separated from one another by processes of supporting cells, and junctional complexes occur between the two cell types. The desmosomes that form part of the complex lie well

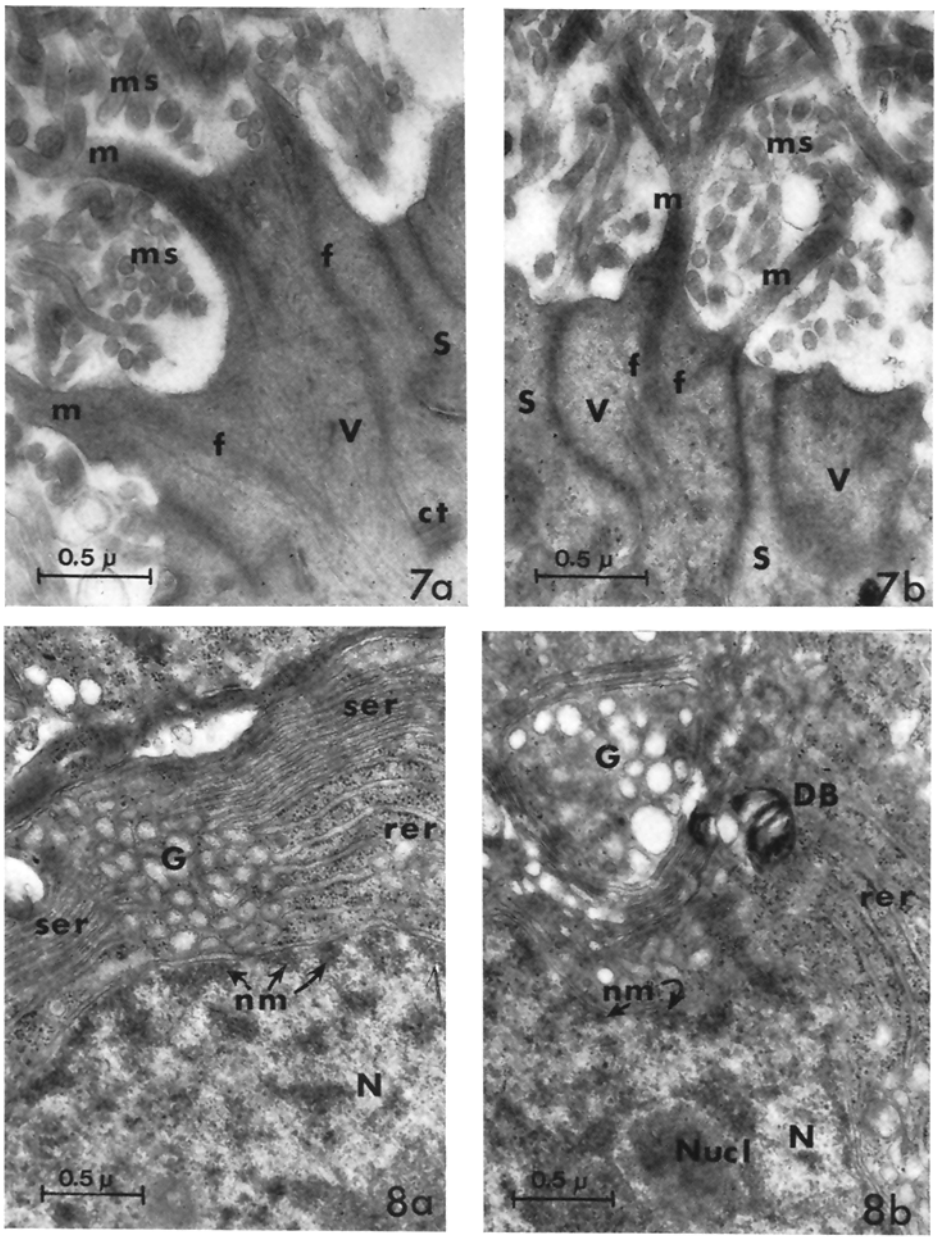

Fig. 7a and b. Surface of the vomeronasal epithelium. Vomeronasal cells (*V*) carry microvilli (*m*) with a core of filaments (*f*) extending into the cytoplasm. A branching microvillus can be seen in b. Narrow processes of supporting cells (*S*) separate vomeronasal cells. Most of the microvilli (*ms*) on the surface are derived from supporting cells. *ct* centriole

Fig. 8a and b. Vomeronasal epithelium: perinuclear cytoplasm of vomeronasal cells. Parallel arrays of smooth (*ser*) and rough (*rer*) endoplasmic reticulum and a Golgi region (*G*) are characteristic. Dark bodies (*DB*) occur more frequently in older specimens. *N* nucleus; *nm* nuclear membrane; *Nucl* nucleolus

below the surface; very little fibrillar material is associated with them in the receptor cells. Although the adjacent cell membranes are close at the cell surface, no tight junctions were observed.

The axonic processes of receptor cells are very fine (about 0.15 μ diameter) and microtubules are their only prominent organelles except for an occasional mitochondrion. Near the epithelial base they are surrounded in groups by processes of basal cells.

Olfactory and Vomeronasal Supporting Cells. Supporting cells in both membranes extend the full height of the epithelium, have most of their cytoplasm above the nucleus and narrow to thin, inconspicuous processes between the nuclei of the sensory cells. These expand slightly into basal regions that form junctional specializations with basal cells and the basal lamina. In both types the nuclei are more peripheral than those of sensory cells, more ovoid, and especially in the vomeronasal membrane, have more condensed chromatin. The nucleus of the vomeronasal supporting cell is often deeply indented. Both types of supporting cells carry microvilli that do not have an obvious central fibrillar core. In the vomereonasal epithelium, these microvilli are difficult to distinguish from the thin terminal part of sensory microvilli.

The two cell types, however, are very different in appearance because of the active secretory function of the olfactory supporting cell, and because of the absence of any evidence of secretion in its vomeronasal counterpart. The surface cytoplasm of the former may be almost completely obscured by secretion droplets. These are variable in density, but usually finely fibrillar in character and bound by a single membrane (Fig. 9). There is an abundance of smooth endoplasmic reticulum and small mitochondria with dense matrix and few cristae. The basal process of the olfactory supporting cell also contains numerous bodies of varying size and density, some of which resemble the secretion droplets of the apical part of the cell, but some have a well developed internal lamination.

The cytoplasm of vomeronasal supporting cells contains small dark bodies without internal organization, usually above the nucleus. There is no evidence of secretion droplets in their cytoplasm. The few dark bodies in the basal part of the cell are of variable density and contain remnants of other cell organelles, so that they are probably lysosomal in character. A limited amount of rough endoplasmic reticulum appears in both cell types just above the nucleus, and the Golgi apparatus is evident in the olfactory supporting cell. In the basal part of the vomeronasal supporting cell, bundles of fine fibrillar material occur which closely resemble those seen in the basal cells.

Basal Cells of Olfactory and Vomeronasal Epithelia. There is marked similarity in the structure of basal cells in the two epithelial. In both cases, the cytoplasm has a greater electron density than any others in the epithelium particularly in more mature animals. The cells are irregular in shape with long cytoplasmic extensions, especially in the vomeronasal epithelium. The cytoplasm contains numerous bundles of fine fibrils, abundant scattered ribosomes, vesicles, and mitochondria. In addition, those in the olfactory epithelium may contain large vacuoles which have the appearance of lipid droplets. Basal cells are usually orientated with the long axis of the nucleus parallel to the basal lamina. Desmosomes are frequent between basal cell processes and those of supporting cells, and in the

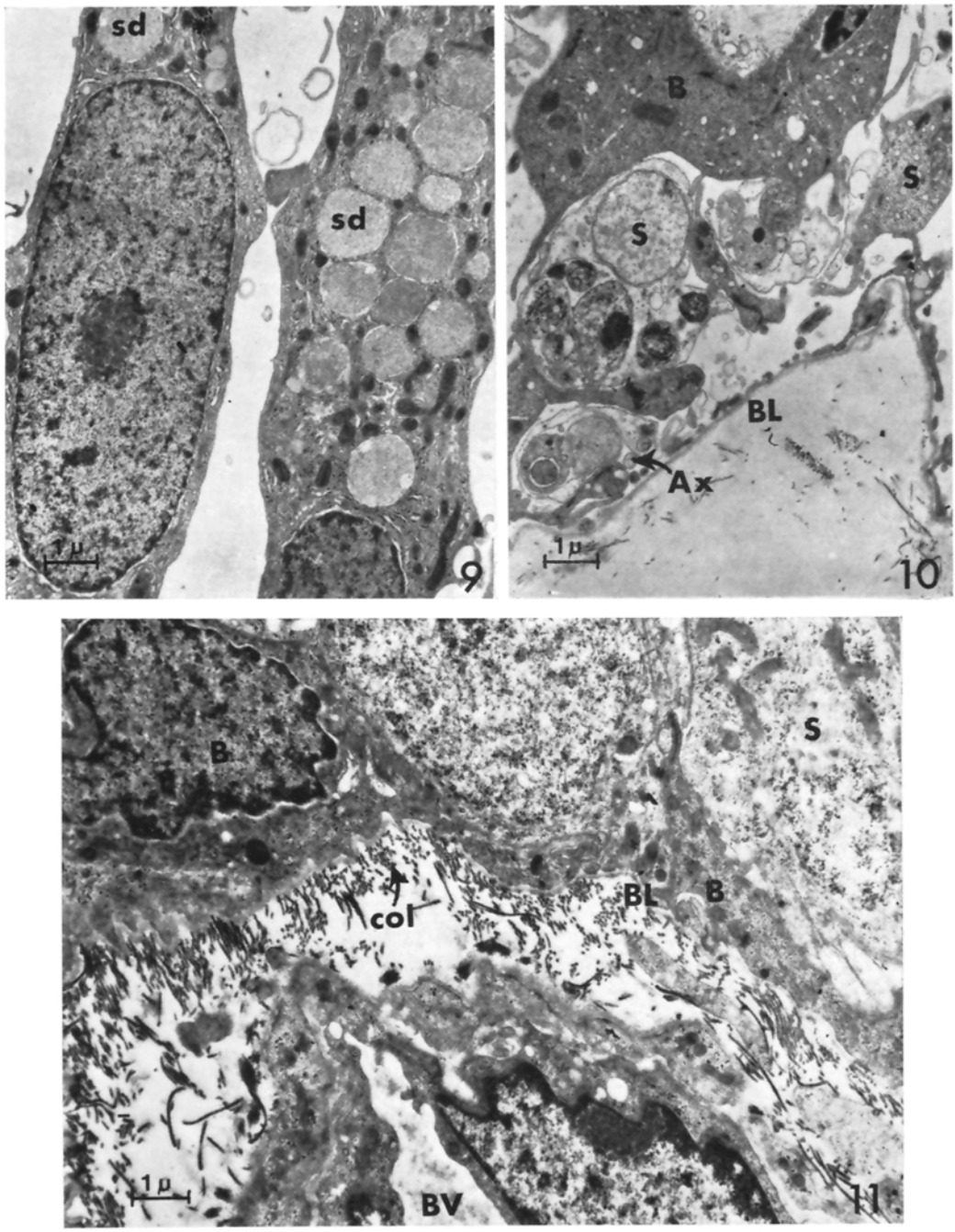

Fig. 9. Olfactory epithelium: nuclear region of supporting cells. Large secretion droplets (*sd*) fill the cytoplasm

Fig. 10. Base of olfactory epithelium. *Ax* axonic process; *B* basal cell; *BL* basal lamina; *S* basal process of supporting cell

Fig. 11. Vomeronasal epithelium. Blood vessel (*BV*) in connective tissue invasion of epithelium. Basal lamina (*BL*) and processes of basal cells (*B*) separate connective tissue elements from vomeronasal (*V*) and supporting (*S*) cells. *Col* collagen

vomeronasal, but not the olfactory epithelium, hemidesmosomes occur where basal cell cytoplasm contacts the basal lamina. There is, however, one point in which the basal cells appear to differ in the two epithelia: in the olfactory epithelium, axonic processes of sensory cells are surrounded by processes of supporting cells until they reach the basal lamina. In the vomeronasal epithelium, basal cells outline and define bundles of axonic processes without any intervening cytoplasm of supporting cells.

Discussion

In addition to a common origin from the olfactory placode, a structural similarity is imposed on olfactory and vomeronasal cells by their neuronal function and epithelial location. In both, neuronal features predominate in their proximal, axonic extensions. Their structure is essentially that of fine unmyelinated axons even before they interrupt the basal lamina to become olfactory or vomeronasal nerves. Nuclei and perikarya are more typically neuronal in the vomeronasal cell, less so in the olfactory cell. In the more superficial dendritic region in both, epithelial characteristics are more pronounced and it is here that the individual and distinctive structures of the two cell types appear. While microtubules, mitochondria and vesicles are common to both dendrites, olfactory cells are ciliated and have an elaborate terminal structure extending beyond the general surface, while the vomeronasal cells end at about the general surface level and carry microvilli but no cilia.

Modifications of the surface of the two types of sensory cells may be functional specializations, but they may also reflect the physical environment with which they are in contact. Cilia have been regarded as a special modification for chemoreception (Vinnikov, 1965), and in almost all cases, olfactory cells possess cilia. However, vomeronasal cells in various species (Bannister, 1968; Altner *et al.*, 1970; Kratzing, 1971a, b; Loo and Kangasuntheram, 1972) have been found to lack cilia. Physiological studies of the electrical response of olfactory and vomeronasal cells indicate an essentially similar response (Graziadei and Tucker, 1970). Moreover, a number of olfactory cells without cilia have been described. Olfactory cells with microvilli only have been described in *Phoxinus phoxinus* (Bannister, 1965), in *Neoceratodus forsteri* (Theisen, 1972) and *Myxine glutinosa* (Theisen, 1973). Hence it seems probable that cilia are not essential for olfactory reception. The adequate provision of cell membrane on which receptor sites can be located can probably be achieved by microvilli, cilia, or by the long rod-shaped cell tip described by Bannister (1965) in one type of olfactory cell in *Phoxinus phoxinus*.

The presence or absence of cilia on chemoreceptor cells may be related to the physical conditions at the cell surface, for example, the volume and rate of flow of secretions. There are considerable differences on the olfactory and vomeronasal areas of the lizard. The olfactory membrane lines a large cavity exposed to continuous air movement. While the main respiratory air flow is across the floor of the nasal cavity, the olfactory region is only partially separated by the single nasal concha, and a considerable amount of air movement must occur in this region also. The vomeronasal membrane, on the other hand, faces a narrow, restricted cavity since the mushroom body projects from the floor into the dome-shaped

vomeronasal organ. In addition, there is only a single opening, the vomeronasal duct, communicating with the oral cavity, so that a direct current of air through the organ does not occur.

The vomeronasal cell, therefore, occupies a more protected environment than its olfactory counterpart. This appears to be reflected, also, in the supply of secretion that maintains a moist environment for both membranes. The olfactory membrane is provided with the secretions of its own supporting cells and those of Bowman's glands in the lamina propria. Their staining reactions with alcian blue and P.A.S. suggest that the former produce a mixture of acid and neutral polysaccharides, and the latter a neutral polysaccharide secretion. To these may be added a certain amount of secretion from the goblet cells of the respiratory mucosa. The resulting secretions make a thick layer over the olfactory mucosa, into which the cilia project right to the edge of the mucus. It is of interest that the microvilli of the supporting cells only extend for less than half of this distance.

By contrast, the lizard vomeronasal organ is very poorly supplied with secretion. There are no sub-epithelial glands, the supporting cells are non-secretory, and the only cells showing evidence of local production are the non-ciliated cells which occur in some areas of the mushroom body. To this may be added some salivary contribution brought in by the tongue tip when entering the vomeronasal duct, and perhaps some lacrimal secretion since the lacrimal duct is reported to open into or near the duct in some *Scincidae* (Parson, 1967).

In view of these very different surface conditions, the modifications of the two sensory cells may provide an extensive surface area for chemoreception which can be easily maintained in their local conditions. Olfactory cilia have an internal structural framework to help maintain their integrity within the copious mucous covering needed to maintain moist conditions in a large area subjected to air movement, often in hot, dry conditions. The cilia of the olfactory region possess unusual features which have not been described elsewhere; the occurrence of a buttress of rows of short setulae at the ciliary base certainly adds considerably to the total area of surface membrane (Kratzing, 1972), but may also add to the mechanical stability of the cilia. In the narrow, protected space of the vomeronasal organ, microvilli with a core of fine fibrillar material are capable of maintaining an extensive cell surface. It is of interest to note that olfactory cells which lack cilia have been described in aquatic forms. With air-breathing vertebrates, sensory cells in the areas exposed more or less directly to air currents possess cilia on the olfactory cells, and the non-ciliated chemoreceptors are located in the more restricted area of the vomeronasal organ.

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