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The canine vomeronasal organ

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INTRODUCTION

The mammalian vomeronasal organ is thought to elicit reproductive behavioural responses through the perception of pheromones. In guinea-pigs, the vomeronasal organ functions in the chemoreception of liquid-borne compounds of low volatility (Wysocki, Wellington & Beauchamp, 1980). In the male hamster, where sexual behaviour is dependent upon normal functioning of the vomeronasal complex (Powers & Winans, 1975), fluid is sucked from the ventral nasal meatus into the vomeronasal lumen by constriction of blood vessels within the vomeronasal capsule (Meredith & O'Connell, 1979; Meredith, Marques, O'Connell & Stern, 1980). As demonstrated in the cat, stimulation of sympathetic fibres results in suction of fluid into the vomeronasal lumen (Eccles, 1982).

Ewer (1973) states that Canids generally do not exhibit the Flehmen response ('lip curl'), the coyote, side-striped jackal, and bushdog being exceptions. Although the structure of the canine vomeronasal organ has been reported in several publications (Barone, Lombard & Morand, 1966; Ciges, Labella, Gayoso & Sanchez, 1977; Klein, 1881; Ramser, 1935), the vomeronasal organ of the dog is variously described as reduced, containing no true olfactory receptors (Barone *et al.* 1966) and as being histologically and ultrastructurally similar to that of the cat, guinea-pig, mouse, and rabbit (Ciges *et al.* 1977).

The results of preliminary observations on canine vomeronasal tissue differ somewhat from descriptions of the vomeronasal organs in other mammals and from the illustration and text descriptions by Dellman & Brown (1981) of paraffin sections. The preliminary observations have prompted description both of the 'non-receptor' and 'receptor' epithelium of the canine vomeronasal organ.

MATERIALS AND METHODS

Six mature dogs, four males and two females weighing 15·9–36·4 kg, were anaesthetised with intravenous sodium pentobarbital, heparinized, and exsanguinated. The dogs were sequentially perfused with Tyrode's saline and Karnovsky's paraformaldehyde/glutaraldehyde in 0·2 M phosphate buffer.

Tissue samples containing the vomeronasal complex were removed from a longitudinal ridge of mucosa in the ventral portion of the nasal septum. These samples were prepared for examination by light microscopy, transmission electron microscopy, and scanning electron microscopy.

For light microscopy and transmission electron microscopy, tissues were postfixed for one hour in 1·0% osmium tetroxide in 0·1 M phosphate buffer containing 1·5% potassium ferricyanide. Tissues were rinsed in 0·2 M veronal acetate buffer,

stained *en bloc* with uranyl acetate, dehydrated with alcohol and propylene oxide, and embedded in Epon/Araldite. Sections 1 μm thick were stained with Azure II. Thin sections were mounted on uncoated grids, stained with uranyl acetate and lead citrate, and examined in a Hitachi HU-12A electron microscope.

For scanning electron microscopy, tissues were post-fixed in osmium tetroxide, dehydrated, critical point dried with freon/carbon dioxide, sputter coated with gold/palladium, and examined in a Jeol 35 scanning electron microscope.

RESULTS

Structures peripheral to the vomeronasal epithelium

The length of the mucosal ridge superficial to the vomeronasal organ (Fig. 1) was dependent upon muzzle length; in the animals used in this study, the distance from the oral ostium of the incisive duct, rostrally, to the limit of the mucosal ridge caudally varied from 50–60 mm. Closed caudally, the vomeronasal organ opened rostrally into the incisive duct 13–16 mm caudal to its oral ostium.

For most of its length the vomeronasal organ was crescent-shaped in transverse section and enclosed partially by a J-shaped vomeronasal cartilage. Only the dorsolateral mucosal wall lacked cartilage. The long axis of the crescentic lumen was orientated vertically, with a lateral convex and a medial concave mucosal wall (Figs. 2–4). Two exceptions to this vertical orientation occurred where the vomeronasal complex was interconnected with a more dorsally situated septal 'swell body' (Fig. 1); at these locations, the orientation of the crescentic lumen was more transverse, with the convex mucosal wall lying dorsolaterally,

The lamina propria deep to the epithelia of both the convex and concave surfaces was well vascularised (Figs. 2–4). Veins up to 480 μm in diameter with 3–5 layers of smooth muscle in their walls were more abundant deep to the lateral epithelium than in the lamina propria deep to the medial epithelium. Small veins were present between the larger veins and the vomeronasal epithelium. Microvessels adjacent to

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Fig. 1. The right surface of the canine nasal septum. The mucosal ridge (*mr*) containing the vomeronasal organ is ventral to a large septal swell body (*sb*). The rostral end of the vomeronasal organ, which opens into the incisive duct approximately 20 mm caudal to the nasal vestibule (*nv*), is interconnected with the oral and nasal cavities via the incisive duct (*id*). × 1·1.

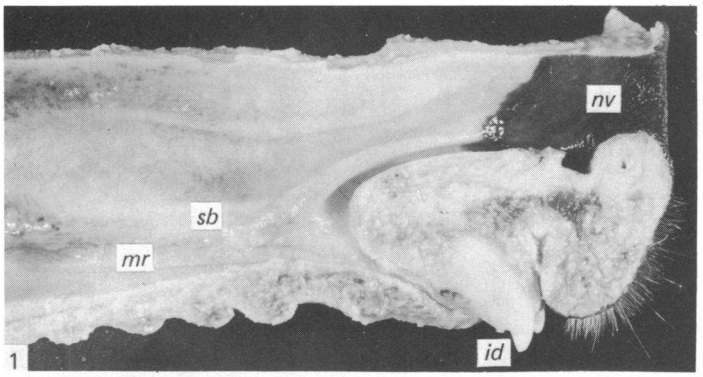
Fig. 2. Transverse section through the mid-portion of the vomeronasal organ. The epithelial tube of the vomeronasal organ (*v*) is positioned between veins of the dorsolateral mucosa (*vl*) and those of the medial vomeronasal mucosa (*vm*). The J-shaped vomeronasal cartilage (*vc*) partially divides the vomeronasal organ from the medial mucosa of the ventral nasal meatus (*nm*). × 28.

Fig. 3. Scanning electron micrograph of the transverse face of tissue taken adjacent to that illustrated in Fig. 2. Labelled structures are as in Fig. 2. × 33.

Fig. 4. Transverse section through the caudal portion of the vomeronasal organ. Labelled structures as in Fig. 2. × 22.

Fig. 5. Transverse section through the dorsal epithelial commissure of the vomeronasal organ at mid-length. Vomeronasal nerves (*vn*) are present deep to the medial epithelium (*me*). Vomeronasal glands (*vg*) and nerves (*n*) containing both myelinated and unmyelinated fibres are present deep to the lateral epithelium (*le*). *l*, vomeronasal lumen. × 157.

Fig. 6. Transverse section through the caudal portion of the vomeronasal organ. Ducts of vomeronasal glands (*vg*) open into the vomeronasal lumen (*l*) through the epithelial commissures, the lateral epithelium (*le*), and occasionally through the medial epithelium (*me*). × 380.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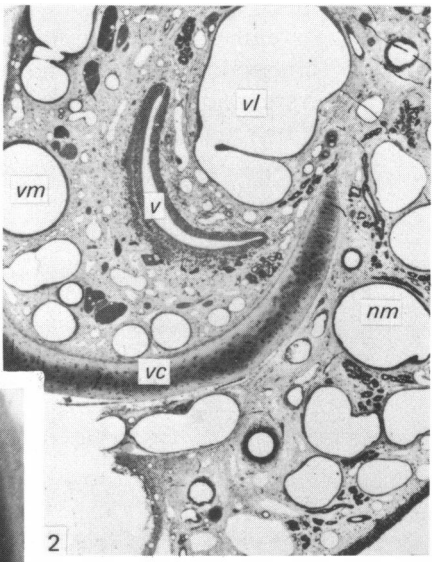
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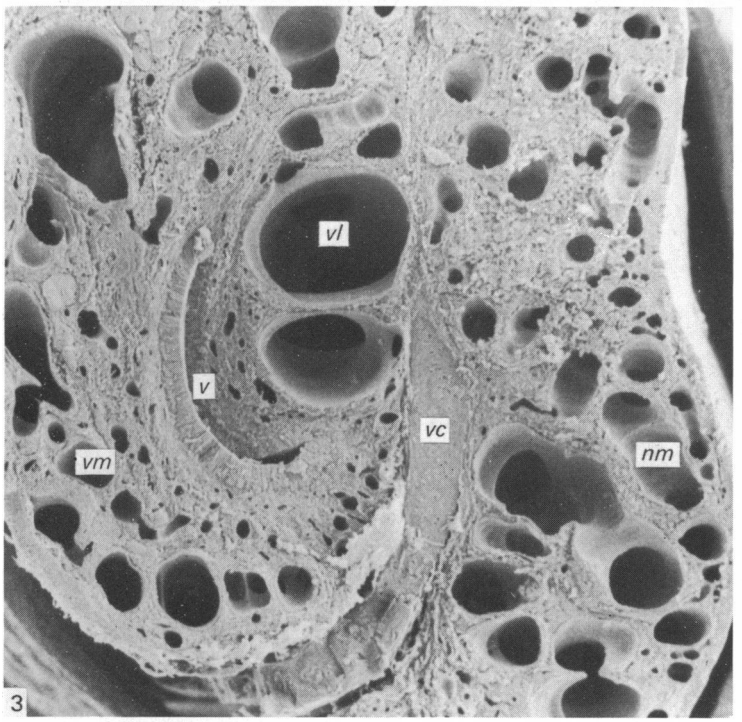
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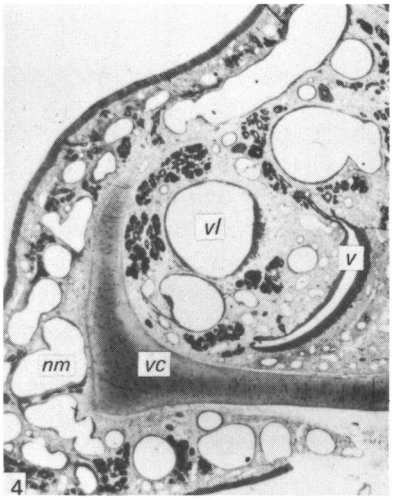
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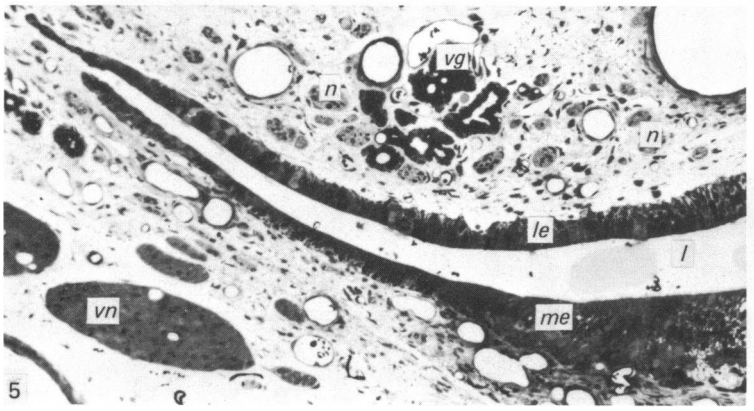
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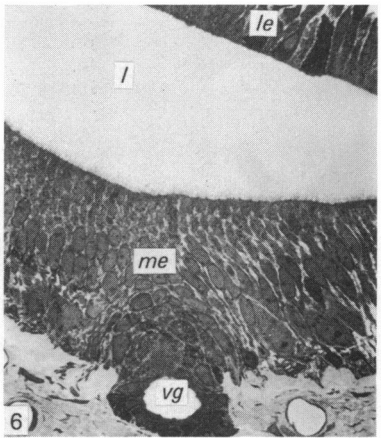
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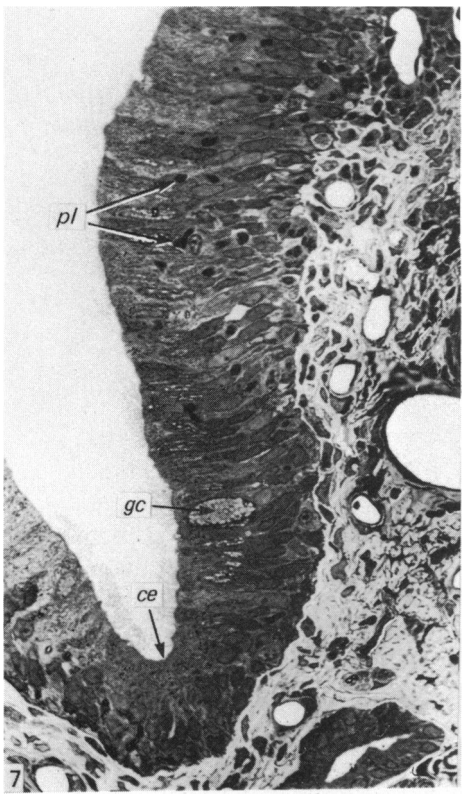
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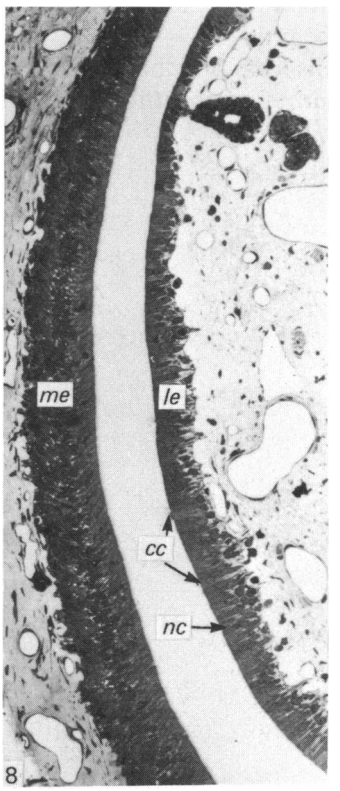
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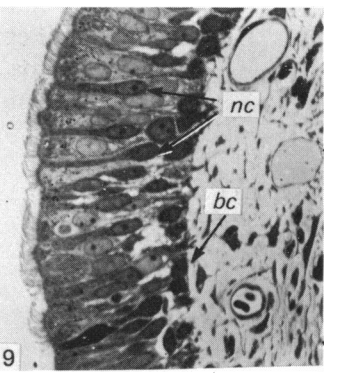
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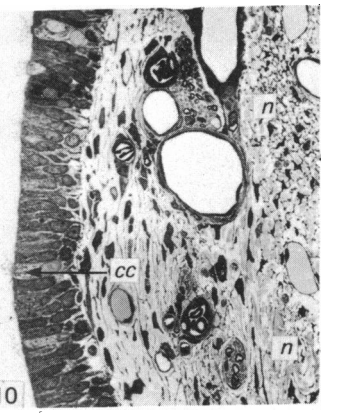
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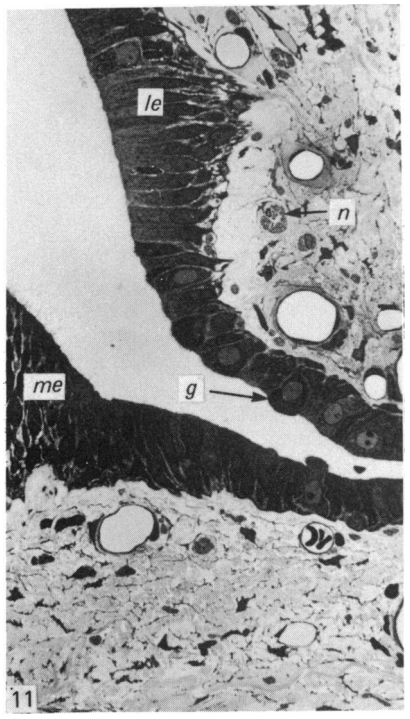
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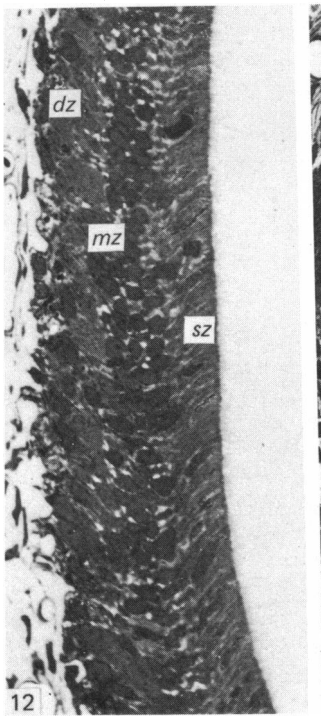
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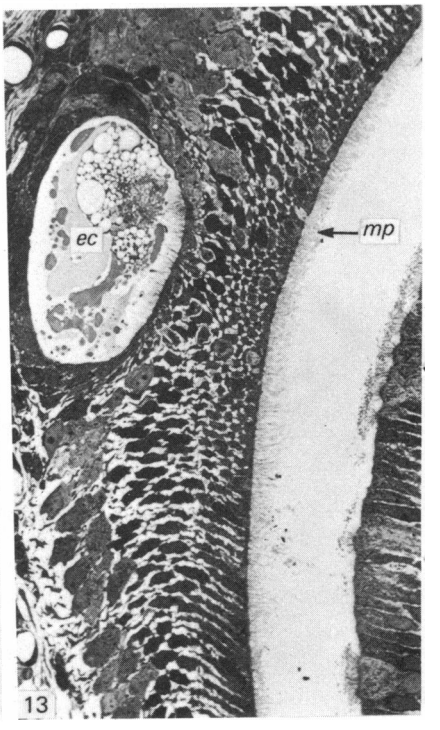
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the vomeronasal epithelium were more abundant in the lamina propria of the medial than of the lateral epithelium.

Numerous plasma cells were present in the lamina propria of the convex mucosa. Small nerves were numerous adjacent to the deep surface of both lateral and medial epithelia; nerves deep to the medial epithelium were unmyelinated while those deep to the lateral epithelium usually contained some myelinated fibres (Fig. 5).

Glandular acini present lay primarily dorsal and lateral to the vomeronasal organ. Ducts of the glands opened into both commissures of the crescentic organ, occasionally through the lateral epithelium, and less frequently through the medial epithelium (Fig. 6).

Vomeronasal epithelium

Light microscopy

Epithelium of the convex mucosa. The lateral epithelium was pseudostratified, 34–72 μm thick, and contained basal, non-ciliated columnar, ciliated columnar, and goblet cells (Figs. 7–10). The basal cells rested along the irregularly serrated basal surface of the epithelium. Typical goblet cells were infrequent.

Ciliated cells occurred singly, in clumps, or as a dense population of cells. They were not stained with Azure II, and had a dome-shaped apex, numerous cilia 6–8 μm long and prominent basal bodies. The non-ciliated cells, which constituted much of the epithelium, had a surface border of microvilli 3 μm long; individual non-ciliated cells exhibited varying degrees of basophilia. Another cell type present in the lateral epithelium was a globular cell, which stained densely and protruded into the lumen (Fig. 11); globular cells occurred adjacent to the commissures in the caudal portion of the organ.

Polymorphonuclear leucocytes were observed frequently in the lateral epithelium and occasionally in the vomeronasal lumen.

Epithelium of the concave mucosa. The medial epithelium was pseudostratified, 55–124 μm thick, and three zones could be distinguished in it (Fig. 12): a deep zone

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Fig. 7. Transverse section through the mid-portion of the vomeronasal organ. The lateral epithelium and lamina propria are densely infiltrated with polymorphonuclear leucocytes (*pl*). Goblet cells (*gc*) are more frequently observed near the commissures (*ce*) than in the mid-portion of the epithelium. × 365.

Fig. 8. Transverse section through the caudal portion of the vomeronasal organ. The lateral epithelium (*le*) may contain few ciliated columnar cells (*cc*) as shown here, consisting primarily of basal cells and non-ciliated columnar cells (*nc*). *me*, medial epithelium. × 153.

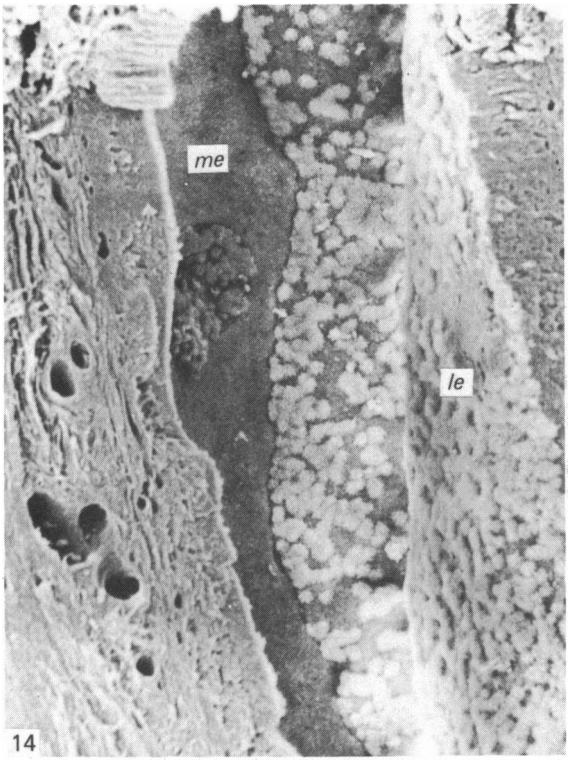
Fig. 9. Transverse section through the lateral epithelium at mid-vomeronasal length. Depending upon the area examined the epithelium may consist of primarily ciliated cells and basal cells (*bc*) with relatively few non-ciliated cells (*nc*). × 390.

Fig. 10. Transverse section through the lateral epithelium near that illustrated in Fig. 9. Only scattered ciliated cells (*cc*) are present in this section. Nerves (*n*), containing both unmyelinated and myelinated fibres, are present adjacent to this 'non-receptor' epithelium. × 207.

Fig. 11. Transverse section through the dorsal commissure in the caudal portion of the vomeronasal organ. Globular cells (*g*), near the ostia of vomeronasal glands, are more commonly present in the lateral epithelium (*le*) than in the medial epithelium (*me*). *n*, nerve. × 387.

Fig. 12. Transverse section through the medial epithelium demonstrating the deep zone (*dz*) of basal cells and nuclei of receptor cells, the middle zone (*mz*) of nuclei of sustentacular cells, and the superficial anuclear zone (*sz*). × 392.

Fig. 13. Intraepithelial cyst (*ec*) in the medial epithelium. Long microprocesses (*mp*) are present on the luminal surface of this receptor epithelium. × 411.



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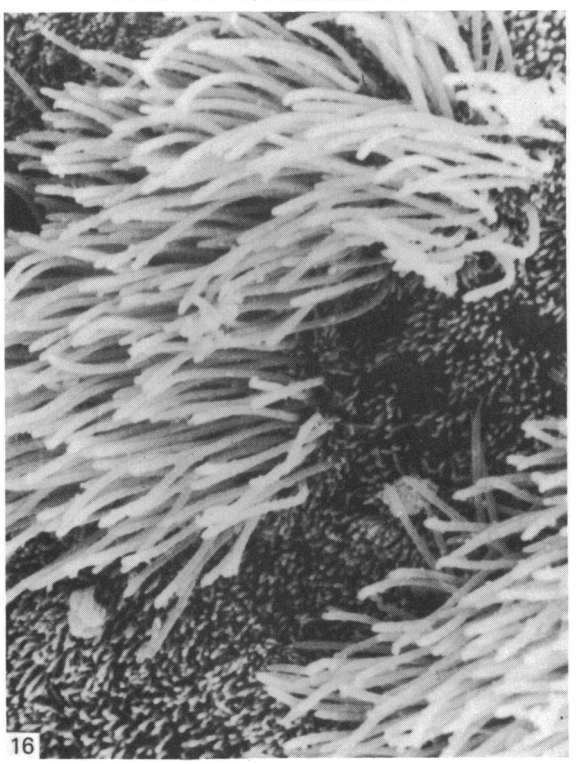
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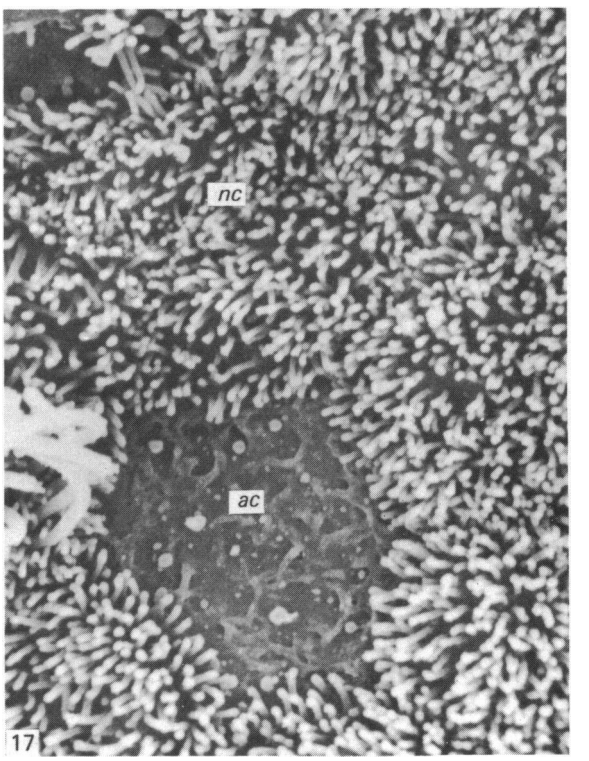

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containing basal cells and receptor cell nuclei which were large, spherical, and lightly staining; a middle zone containing sustentacular cell nuclei which were elliptical, and darkly staining; and a superficial zone containing the supranuclear portions of receptor and sustentacular cells. The medial epithelium was thinnest at each end of the organ towards the commissures. The luminal surface of this medial epithelium presented a dense mass of cell processes which appeared to be of three types: short dense microvilli, about 3·0 μm long; taller, less dense processes approximately 12 μm long; and relatively sparse processes 18–24 μm long. Intraepithelial cysts (Fig. 13), sometimes with goblet cells, were occasionally present.

Ultrastructure

Epithelium of the convex mucosa. The surface of the lateral epithelium was composed of the apices of ciliated and/or non-ciliated cells, depending on the area observed (Figs. 14–17). The electron-lucent cytoplasm of the ciliated cells (Fig. 18) contained an apical profusion of elongated mitochondria with transverse cristae, some apical pinocytic invaginations, vesicles, multivesicular bodies, profiles of both smooth and granular endoplasmic reticulum, Golgi apparatus, and polyribosomes. They had numerous cilia and microvilli on their luminal surface. The cilia, approximately 8 μm long and 0·3–0·4 μm in diameter, had the typical $9+2$ arrangement of microtubules (Fig. 19); microvilli, 3·0 μm long and 0·16 μm in diameter, were frequently branched near their origin.

The non-ciliated columnar cells (Figs. 20, 21) were more electron-dense than ciliated cells and contained elongated mitochondria with transverse cristae, abundant granular endoplasmic reticulum and free ribosomes, a well developed Golgi apparatus, and numerous supranuclear membrane-bounded vacuoles. Microvilli similar to those of the ciliated cells were present at the luminal surface. Two types of non-ciliated cells were observed: mitochondria were larger and more electron-lucent in one type and were smaller and more electron-dense in the other. A number of the non-ciliated cells with the larger mitochondria contained moderately electron-dense vacuoles, which appeared to be mucous granules (Fig. 22). Goblet cells, packed with mucous granules, had granular endoplasmic reticulum with cisternae which were more distended than those in non-ciliated columnar cells.

Several brush cells (Figs. 23, 24) observed in this epithelium had microvilli, 0·8 μm long and 0·17 μm in diameter, projecting into the vomeronasal lumen. Bundles of filaments, 0·11 μm in diameter, extended from the microvilli down into the cytoplasm. The contiguous cell membranes of the brush cells and of adjacent epithelial cells were difficult to distinguish deep to the juxtaluminal junctional complexes.

The relatively low epithelium near the commissures of the organ contained at least two types of non-ciliated cell. One of the cell types was similar to that containing the electron-dense mitochondria described above; the other cell type contained a

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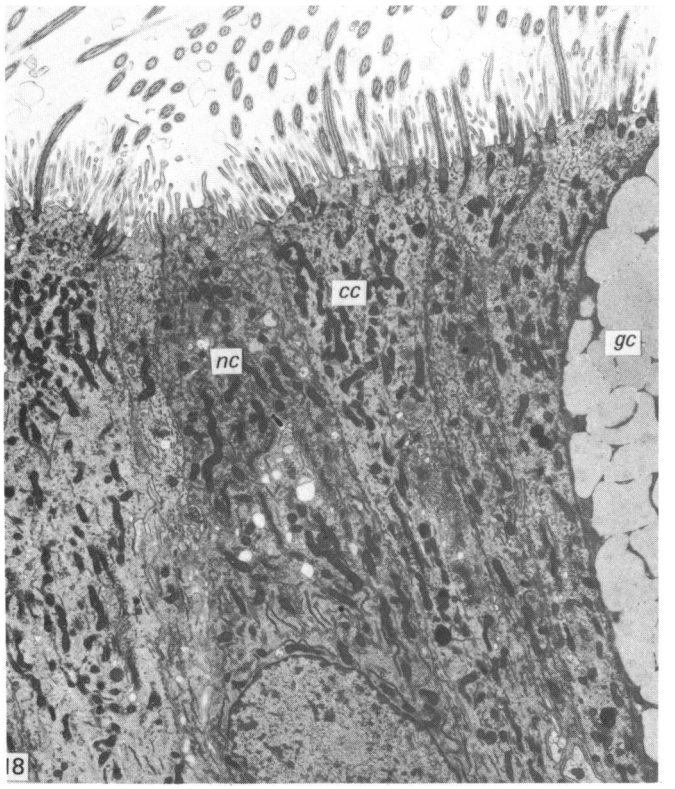
Fig. 14. Scanning electron micrograph of a portion of the vomeronasal organ fractured longitudinally to reveal scattered ciliated cells in the lateral epithelium (*le*). Ciliated cells are present also adjacent to the commissures in the medial epithelium (*me*). ×171.

Fig. 15. Ciliated (*cc*) and non-ciliated (*nc*) cells in the lateral epithelium shown in Fig. 14. ×2165.

Fig. 16. Ciliated and non-ciliated cells in the lateral epithelium. ×4310.

Fig. 17. The luminal surfaces of non-ciliated cells with few microvili (*ac*) are scattered amongst the more numerous non-ciliated cells having many microvilli (*nc*). ×7200.



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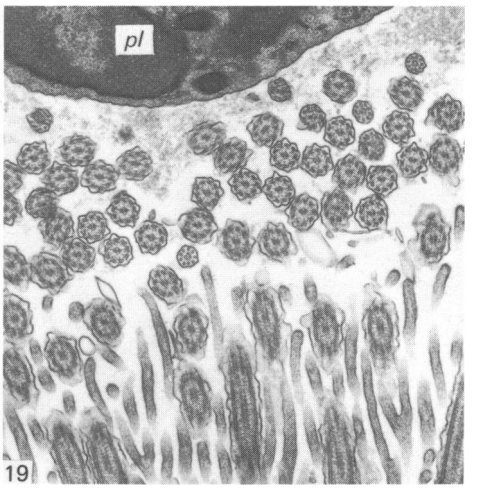

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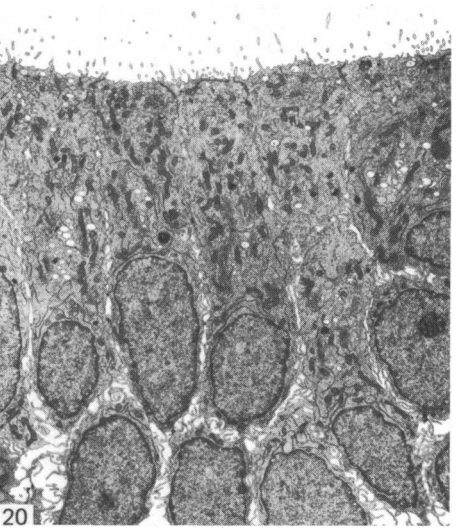

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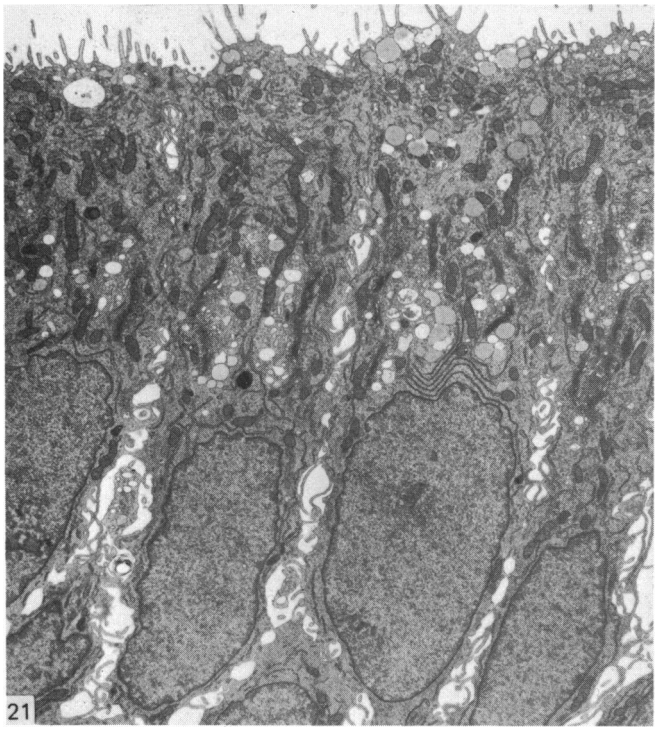

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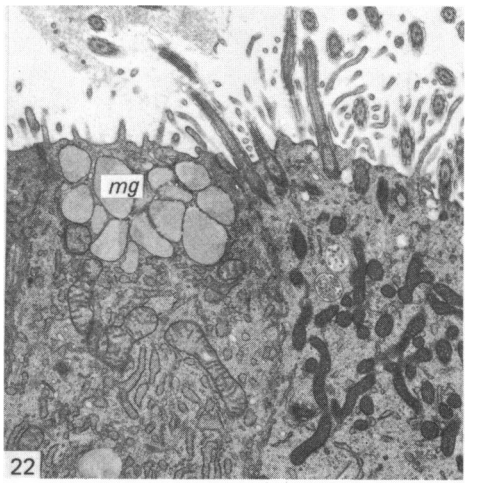

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dense mass of elongated mitochondria and a relatively electron-lucent nucleus. Some of the cells which were rich in mitochondria had a globular shape and bulged into the vomeronasal lumen, held to adjacent deeper cells by desmosomes (Figs. 25, 26). These globular cells had some surface microvilli and contained ribosomes, granular endoplasmic reticulum, Golgi, and small apical clear vesicles (Fig. 27).

Plasma cells occurred on both sides of the basal lamina; if intraepithelial (Fig. 28) they were usually present in the basal region of the epithelium. Polymorphonuclear leucocytes also occurred on both sides of the basal lamina, frequently within the epithelium and on its luminal surface (Fig. 29).

Numerous profiles of nerve fibres were observed between epithelial cells; these cell processes were electron-lucent and contained microtubules, approximately 200 nm in diameter, and spherical mitochondria (Figs. 30, 31). Ribosomes were not found in these fibres. Similar profiles of neural tissue lying immediately deep to the juxtaluminal junctional complexes of adjacent epithelial cells contained both small electron-lucent vesicles and larger vesicles with electron-dense cores (Figs. 31–33); the dense-cored vesicles were spherical and 0·1 μm in diameter. Some of these nerve fibres, in turn, were contained within other profiles of similar nerve fibres. Although most frequent between adjacent non-ciliated cells, these nerve processes also occurred between ciliated cells. Small nerves containing unmyelinated nerve fibres were found in the basal portion of the epithelium.

Epithelium of the concave mucosa. The medial epithelium contained two main cell types which differed strikingly: (*a*) receptor cells with electron-lucent cytoplasm and markedly electron-dense mitochondria; (*b*) sustentacular cells with electron-dense cytoplasm (Fig. 34).

Microvilli, approximately 0·17–0·20 μm in diameter, were present on the luminal surface of both sustentacular and receptor cells (Figs. 34–36). Some microvilli branched near the surface in both cell types. Bundles of microfilaments passed from the cytoplasm of receptor cells into the microvilli.

Cilia, 0·25 μm in diameter, frequently occurred on the surface of receptor cells, each cell possessing one to four cilia in most sectional profiles (Figs. 37, 38). Profiles of cilia containing an internal substructure of microtubules were seldom observed in the vomeronasal lumen and never at a distance of more than 1·5 μm from the cell surface. In the relatively few cross sections of cilia, seven or eight peripheral pairs and one axial pair of microtubules were observed instead of the typical 9 + 2 internal structure (Fig. 39); dynein arms and radial spokes were not found. Radiating microtubules were present on the basal bodies. Centrioles, electron-dense precursor bodies of cilia, and small (250 nm) and large (750 nm) electron-lucent vesicles lay in the adluminal portion of the receptor cell. A constriction present in the dendrite,

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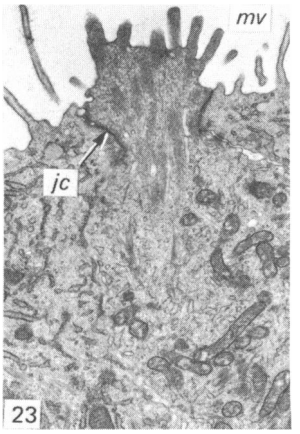
Fig. 18. Transmission electron micrograph of the lateral epithelium of the vomeronasal organ at mid-length. Ciliated columnar (*cc*), non-ciliated (*nc*), and goblet cells (*gc*) are present × 3580.

Fig. 19. Cilia and a polymorphonuclear leucocyte (*pl*) on the luminal surface of the lateral epithelium from tissue adjacent to that illustrated in Figs. 2 and 9. × 11484.

Fig. 20. Non-ciliated cells of the lateral epithelium from the caudal portion of the vomeronasal organ. × 1960.

Fig. 21. Non-ciliated cells of the lateral epithelium adjacent to the section illustrated in Fig. 8. × 3520.

Fig. 22. The apical portion of a ciliated cell and a non-ciliated cell from the lateral epithelium of the vomeronasal organ. This type of non-ciliated cell has relatively abundant granular endoplasmic reticulum, large electron-lucent mitochondria, and apical mucous granules (*mg*). × 5775.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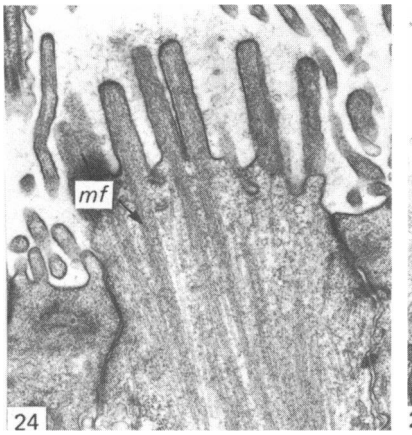
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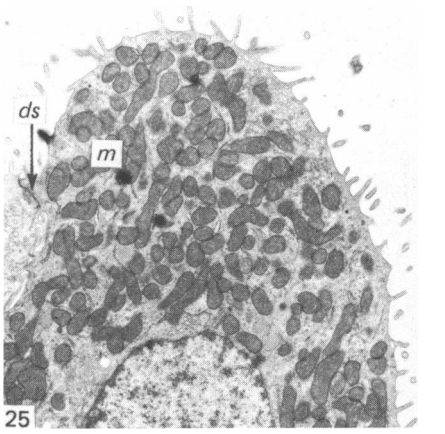
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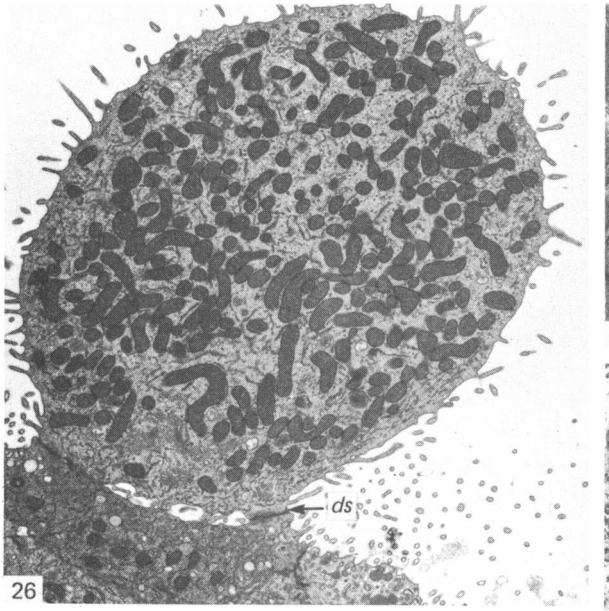
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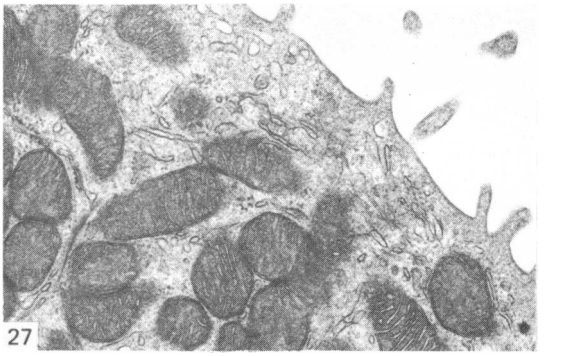
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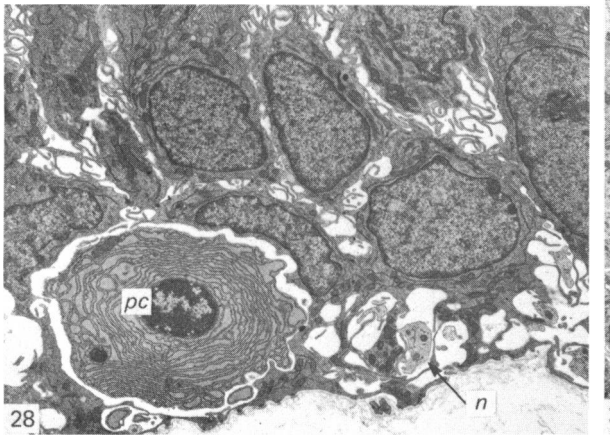
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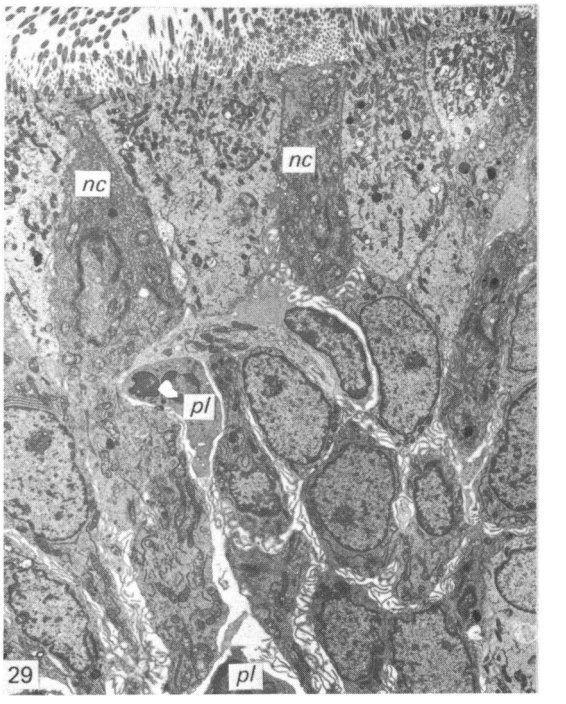
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immediately deep to the juxtaluminal junctional complex, was occupied by cytoplasm of adjacent sustentacular cells. A thick cluster of elongated mitochondria, each containing a longitudinal crista, was present in that portion of the dendrite deep to the neck. Microtubules, about 250 nm in diameter, did not lie parallel in the dendritic apex but were arranged linearly in the deeper portion of the dendrite. The supranuclear portion of the dendrite contained polyribosomes, granular endoplasmic reticulum, Golgi membranes, vesicles, and mitochondria.

Sustentacular cells contained numerous profiles of granular endoplasmic reticulum, some apical pinocytic vesicles, and elongated mitochondria with transverse cristae (Fig. 40). Many of the cisternae of the endoplasmic reticulum were dilated.

DISCUSSION

The structure of the canine vomeronasal organ is highly developed and unique amongst that of adult mammals. The thorough description by Klein (1881) is incorrect in stating that cavernous tissue is altogether absent from the lateral wall of the dog vomeronasal organ. Not only is the venous plexus well developed in the lateral wall, but it is also present though less extensive in the medial wall of the canine vomeronasal organ. The apparent lack of vascularity observed in the early work may be due to the methods used. Constriction of these vessels results in dilation of the vomeronasal lumen; an enlarging vomeronasal lumen may draw fluid from the incisive duct into the vomeronasal organ, as reported for the cat (Eccles 1982). Although the dog does not utilise the typical Flehman response (Ewer, 1973), soluble substances may enter the vomeronasal organ via the incisive duct through either the nasal vestibule or the oral cavity. Unlike the rat (Vaccarezza, Sepich & Tramezzani, 1981) and hamster (Taniguchi & Mochizuki, 1982) where the 'receptor' epithelium does not cover the caudal portion of the vomeronasal tube, that of the dog extends quite far caudally.

Generally only one cilium at the most is present on the surface of mammalian vomeronasal receptors (Bhatnagar, Matulionis & Breipohl, 1982; Ciges *et al.* 1977; Kolnberger & Altner, 1971; Kratzing, 1971; Loo & Kanagusuntheram, 1972; Taniguchi & Mochizuki, 1982; Vaccarezza *et al.* 1981). Therefore, it is usually accepted that cilia are not necessary for olfactory receptivity in the vomeronasal organ. Receptors of the canine vomeronasal organ are exceptional in that they do possess cilia. Structurally the cilia do not appear to be of the motile type. Cilia with the

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Fig. 23. Apical portion of a brush cell with short microvilli (*mv*), separated from adjacent non-ciliated cells of the lateral epithelium by juxtaluminal junctional complexes (*jc*). × 5965.

Fig. 24. Apical portion of a brush cell with bundles of microfilaments (*mf*) extending from the cytoplasm up into the core of the microvilli. × 16365.

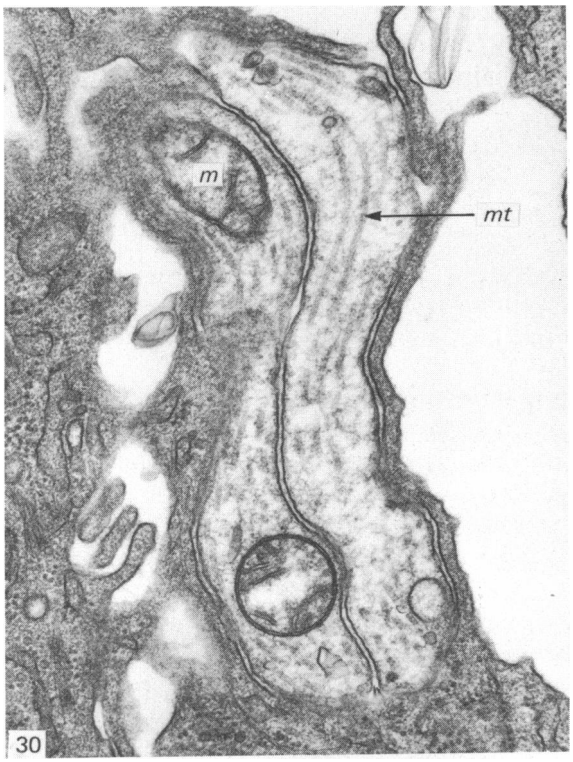
Fig. 25. A surface cell of the lateral epithelium containing numerous mitochondria (*m*) is attached to adjacent cells by desmosomes (*ds*). This globular cell type occurs near duct openings of vomeronasal glands in the caudal portion of the vomeronasal organ. × 5400.

Fig. 26. A globular cell similar to that illustrated in Fig. 25. *ds*, desmosome × 4100.

Fig. 27. Apical portion of cell illustrated in Fig. 25 demonstrating granular endoplasmic reticulum, lucent vesicles, and mitochondria. × 18330.

Fig. 28. Basal region of the lateral epithelium from the caudal portion of the vomeronasal organ illustrating the intraepithelial location of plasma cells (*pc*) and nerves (*n*). × 2455.

Fig. 29. Ciliated pseudostratified columnar epithelium adjacent to that illustrated in Figs. 2, 9, 19. Non-ciliated epithelial cells (*nc*) and polymorphonuclear leucocytes (*pl*) are indicated. × 1775.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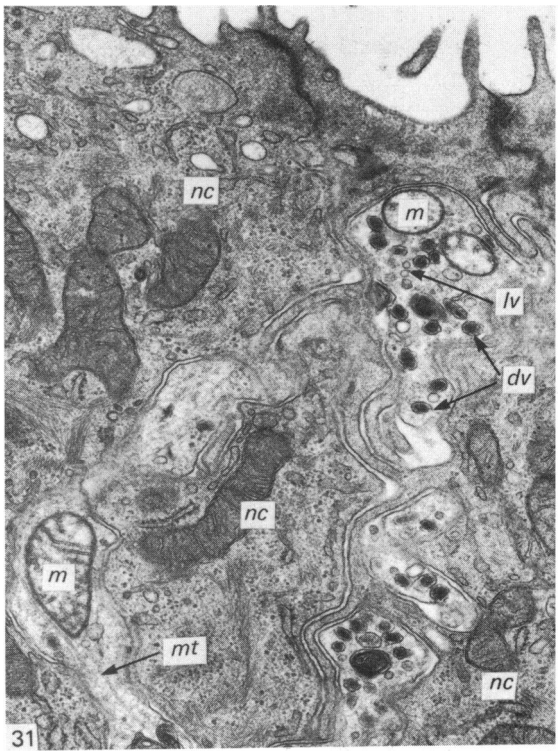
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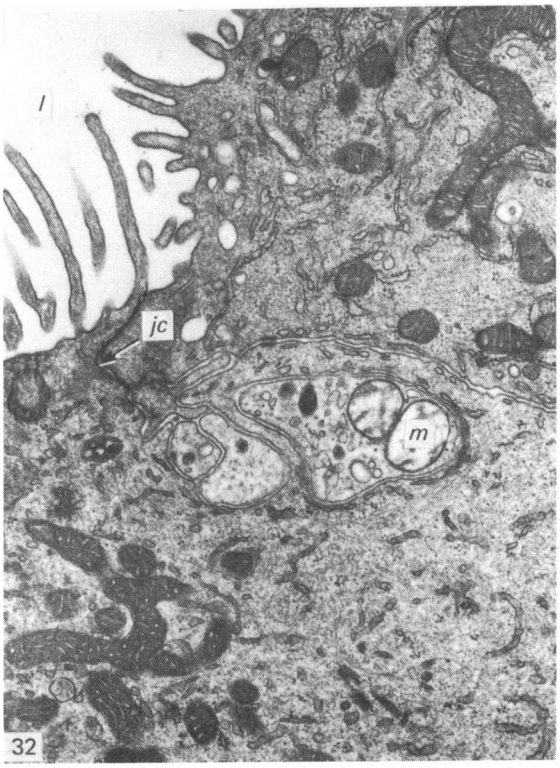
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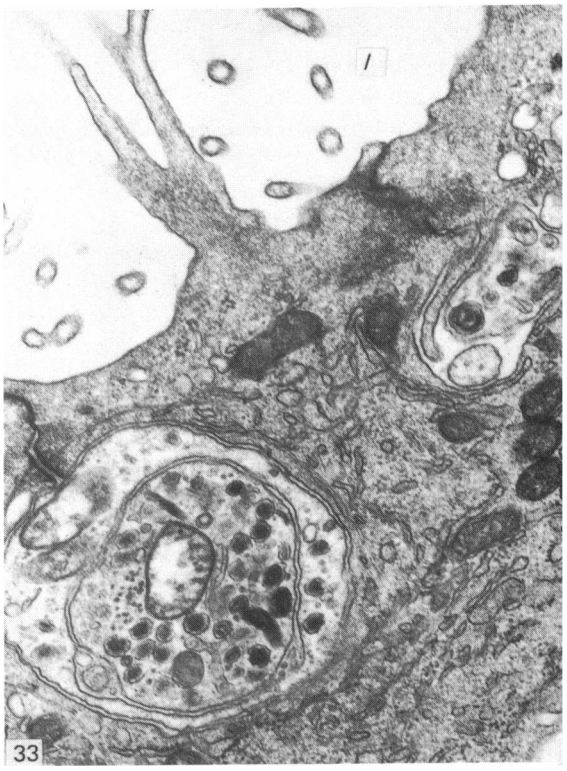
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typical internal 9+2 microtubular structure have only been reported in the rabbit receptor cell (Luckhaus, 1969). Seifert (1971) describes the receptor cell of the feline vomeronasal organ as having about 200 sensory 'hairs', each about 4 μm long and containing bundles of fine filaments. Sensory hairs in illustrations of the vomeronasal organ of the cat (Seifert, 1971) do not resemble the cilia of the dog. Other cilia associated structures such as basal bodies, ciliary precursor bodies, and an apical profusion of mitochondria are also present in the receptor cells of the dog.

The expansion of the dendritic apex into the luminal surface, found in typical olfactory epithelium, has also been described in the vomeronasal organ of *Artibeus* (Bhatnagar *et al.* 1982), guinea-pig (Ciges *et al.* 1977), sheep (Kolnberger, 1971), cat (Seifert, 1971), tree shrew and slow loris (Loo & Kanagasuntheram, 1972). The dendrites of the canine vomeronasal receptors have an apical neck but do not generally bulge into the lumen.

The occurrence of several cell types in the lateral or 'non-receptor' part of the epithelium has also been reported in a number of mammals. Basal cells and non-ciliated columnar cells are generally present in the lateral epithelium. Ciliated cells, absent in *Nycticebus* (Hedewig, 1980) and slow loris (Loo & Kanagasuntheram, 1972), are abundant in the hamster (Adams & McFarland, 1972; Taniguchi & Mochizuki, 1982), *Tupaia* (Loo & Kanagasuntheram, 1972), and guinea-pig (Ciges *et al.* 1977). As cilia are irregularly distributed in the convex epithelium of the dog vomeronasal organ, it is difficult to believe that their function is to propel secretions along the vomeronasal organ. They may serve a purpose in mixing the fluid contents of the vomeronasal lumen so that contact between molecules and receptor cells is enhanced. Both light and dark cells with small numbers of cilia, 1 μm long, are present in the 'non-receptor' epithelium of the rat (Breipohl, Bhatnagar & Mendoza, 1979). Here also the relatively few, short cilia would be ineffective in moving secretions unidirectionally.

The occurrence of globular, densely-stained cells near the commissures of the caudal portion of the organ has not been reported previously. These cells, which bulge into the lumen, are densely packed with mitochondria and have unspecialised surface membranes. It is difficult to surmise how a capacity for an elevated level of oxidative phosphorylation or cation concentration by these cells might aid the vomeronasal organ in its function. As the globular cells occur near the openings of gland ducts they may have a role in secondary modification of secretions.

The presence of numerous profiles of nerve fibres within the lateral epithelium is both unique and interesting. Although vesicles 100 nm in diameter and with dense cores are observed frequently in various types of nerve cell (Jones & Cowan, 1983), the concentration of such intraneural vesicles together with smaller lucent vesicles in a superficial epithelial position is unusual. Similar structures also occur in both the

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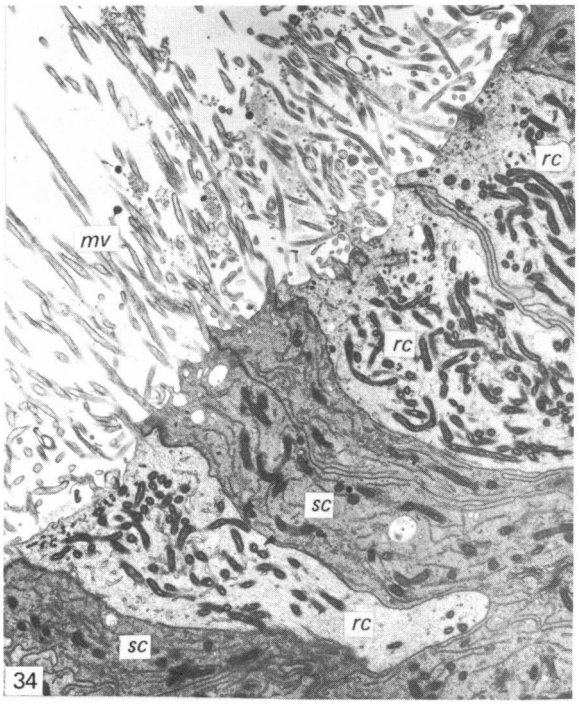
Fig. 30. Nerve fibres, in a mid-intraepithelial position in the lateral epithelium of the vomeronasal organ, contain spherical mitochondria (*m*) and microtubules (*mt*). ×25845.

Fig. 31. Nerve fibres and nerve endings between non-ciliated cells (*nc*) within the lateral epithelium. Microtubules (*mt*), spherical mitochondria (*m*), dense-cored vesicles (*dv*), and lucent vesicles (*lv*) are evident. ×16400.

Fig. 32. Nerve endings containing spherical mitochondria (*m*), dense-cored vesicles, and moderately dense to lucent vesicles are separated from the vomeronasal lumen (*l*) by juxtaluminal junctional complexes (*jc*). ×15830.

Fig. 33. Nerve endings in the lateral epithelium of the vomeronasal organ are within 0·5 μm of the vomeronasal lumen (*l*). ×18340.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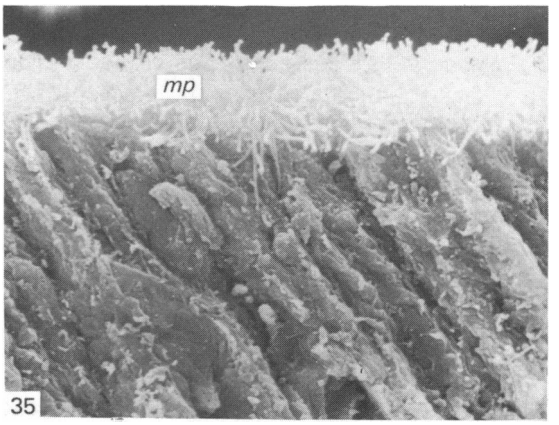
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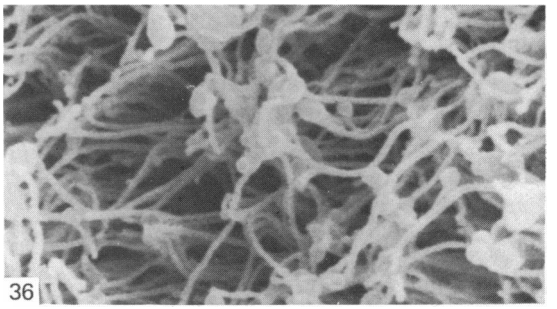
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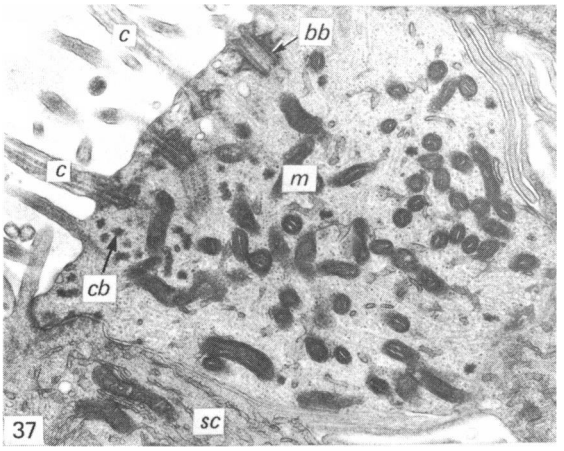
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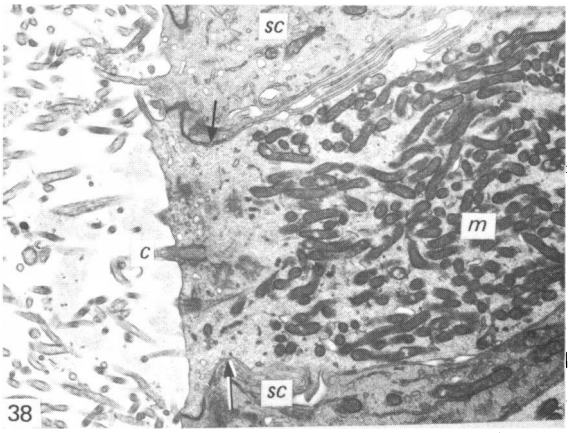
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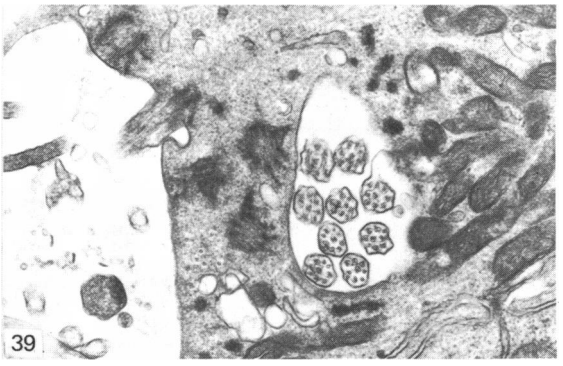
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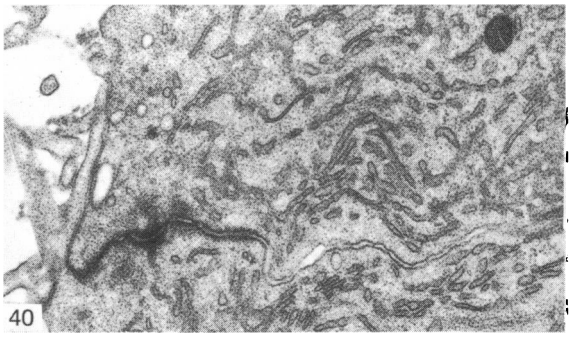
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'receptor' and 'non-receptor' epithelia of the pig (Kratzing, 1979). The nerve processes present in the pig receptor epithelium are situated between adjacent sustentacular cells; nerves with dense-cored profiles in the dog non-receptor epithelium occasionally lie between ciliated and non-ciliated cells but usually between adjacent non-ciliated cells. Kratzing (1979) suggests that these fibres might be branches of the trigeminal nerve or possibly of the nervus terminalis. The intraepithelial nerve processes of the canine vomeronasal tissue appear to be axons since there is no evidence of ribosomal material. If these terminals are adrenergic they may either control secretion by the non-ciliated cells or alter surface membrane permeability; either functional role is a possibility as apical pinocytic vesicles, membrane-bounded lucent vacuoles, and mucous granules are present in non-ciliated cells of the non-receptor epithelium. As the nerve terminals are adjacent to the juxtaluminal junctional complex, modification of either the junctional complex or the adjacent membrane of the cell is more likely.

Brush cells in the lateral epithelium of the dog are not clearly distinguishable deep to the juxtaluminal junctional complexes of adjacent non-ciliated cells. Kratzing (1972) describes similar structures in the bovine vomeronasal organ as separate specialised processes of ciliated cells. However, if these formations in the dog are not separate brush cells then they are processes of non-ciliated cells.

SUMMARY

The vomeronasal organ was studied in mature dogs with the optical, transmission electron, and scanning electron microscopes. The canine vomeronasal complex is structurally well developed. Large blood vessels are present deep to both the lateral, 'non-receptor' and medial, 'receptor' epithelia. In addition to the unmyelinated vomeronasal nerves in the lamina propria deep to the 'receptor' epithelium, numerous nerves containing both myelinated and unmyelinated fibres are present deep to the 'non-receptor' epithelium. The 'non-receptor' epithelium consists of basal cells, ciliated and non-ciliated columnar cells, and globular cells packed with mitochondria. Contained within the 'non-receptor' epithelium are leucocytes, plasma cells, and

Fig. 34. Transmission electron micrograph of the medial epithelium from the mid-portion of the vomeronasal organ. Microvilli (*mv*) of sustentacular (*sc*) and receptor (*rc*) cells are seen. × 5165.

Fig. 35. Scanning electron micrograph of the fractured surface of the medial epithelium. An apical profusion of microprocesses (*mp*) is present. × 2040.

Fig. 36. Scanning electron micrograph of the luminal surface of the microprocesses illustrated in Fig. 35. × 5715.

Fig. 37. Transmission electron micrograph of the apical portion of a receptor cell adjacent to that of a sustentacular cell (*sc*). The receptor cell has cilia (*c*) and contains basal bodies (*bb*), ciliary precursor bodies (*cb*), and elongated mitochondria (*m*) with longitudinal cristae. × 11450.

Fig. 38. The apical portions of receptor cells are frequently constricted by lateral projections of adjacent sustentacular cells (*sc*) forming a dendritic neck (arrows). A cilium (*c*) and a mass of mitochondria (*m*) are seen. × 6225.

Fig. 39. Profiles of sectioned cilia are infrequent in the vomeronasal lumen adjacent to the medial epithelium. When observed, the cilia do not have the 9+2 internal arrangement of microtubules, dynein cross arms, or radial spokes. × 16000.

Fig. 40. Sustentacular cells have microvilli on their luminal surface and contain an abundance of granular endoplasmic reticulum and apical pinocytic vesicles. × 19195

nerve endings. The 'receptor' epithelium consists of basal, sustentacular, and ciliated receptor cells. The microtubules in cilia of the receptor cells do not appear to have dynein arms or radial spokes.

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