J. Anat. (1981), **132**, 2, pp. 167–185
With 29 figures
Printed in Great Britain

The vomeronasal organ of the rat

OSCAR L. VACCAREZZA, LILIANA N. SEPICH AND JUAN H. TRAMEZZANI

Instituto de Neurobiología, Serrano 661, 1414 *Buenos Aires, Argentina*

(*Accepted* 13 *June* 1980)

INTRODUCTION

The vomeronasal complex (vomeronasal or Jacobson's organ, cartilage, vessels, glands and nerves) is the most outstanding of the peripheral sensory structures found in the nasal septum of mammals. Although recent findings suggest it could be involved in pheromone-mediated behaviour, much research is still needed fully to understand its function.

Numerous comparative anatomical studies have been performed on the vomeronasal complex using dissection techniques and light microscopy. A precise knowledge of the structure of this complex, as well as of the topographical relationships between its constituent parts, has been provided by the works of Broom (1897), Zuckerkandl (1910), Pearlman (1934) and Negus (1956), among many others.

The most conspicuous and relevant component of the complex is the vomeronasal organ described in man for the first time by Ruysch (1724) who reported and illustrated it in his *Thesaurus Anatomicus*. About one hundred years later Jacobson (1811) presented his studies on the vomeronasal organ of several mammals where he detailed clearly its principal anatomical features. During the fifty years that followed only a few studies were made on this organ, namely the thesis of Gratiolet (1845) and the work of Balogh (1860) in sheep. The morphology of the vomeronasal organ was accurately described between 1875 and 1910, through numerous comparative studies; the great interest in it was revealed by Zuckerkandl (1910), who quoted 118 publications in a review of the subject.

From 1910 until 1970, morphological studies were sparse. The work of Broom (1915) and Addison & Rademacker (1927) and, more recently, Negus (1958) and Schilling (1970) complemented the anatomical knowledge of the vomeronasal organ while the studies of Kallius (1905) and Kolmer (1927) revealed the basic characteristics of its microscopical anatomy.

The last epoch of morphological studies on the vomeronasal organ of mammals began around the 70s when the work of Luckhaus (1969) with rabbits provided the first ultrastructural studies that were later extended by Seiffert (1971), Kolnberger (1971) and Kratzing (1971*a*, *b*) to the cat, *Tupaia*, sheep and suckling rat.

The concept that sexual pheromones play an important role in mammalian reproduction (Estes, 1972) aroused an increasing interest in the vomeronasal organ as a sensor for these substances. Since Tucker (1963) and Müller (1971) demonstrated its sensitivity to odorous stimuli, the old hypothesis of Gratiolet (1845) relating the function of the vomeronasal organ to sexual odours flourished and several experiments were reported claiming its participation in some neuroendocrine and behavioural reproductive effects (Planel, 1953; Winans & Powers, 1977; Johns,

0021-8782/81/2828-8770 $02.00

Feder, Komisaruk & Mayer, 1978). Such a possible function led us to study the anatomy of the well developed vomeronasal organ of the rat, because in this species the neuroendocrine and behavioural mechanisms involved in reproduction are best known.

MATERIALS AND METHODS

Adult male and female Holtzman rats anaesthetized either with ether or with sodium pentobarbital (40 mg/kg) were used. Five animals were decapitated, the jaws removed and the nasal region separated from the remaining skull. The nasal pieces were fixed in 10/% formaldehyde or 6·5% glutaraldehyde in phosphate buffer. They were then decalcified in 5% nitric acid, embedded in celloidin, serially sectioned and stained with gallocyanin. The sections were photographed with a Leitz Aristophot set or with a Zeiss RS III microscope. Another ten animals were fixed in a similar way, but the lateral walls of the nasal cavities were then removed and the vomeronasal organs dissected under a Zeiss stereoscopic surgical microscope.

Light microscopy

Five animals were perfused with 30 ml of 5·4% glucose solution and then with 50 ml of 6·5% glutaraldehyde in phosphate buffer; the vomeronasal organs were removed and cut into four pieces perpendicularly to their longitudinal axis. The pieces were then fixed in 2% osmium tetroxide, dehydrated and embedded in Epon. Serial ultrathin transverse sections, 3 μm thick, were stained with methylene blue and photographed.

Transmission electron microscopy

The vomeronasal organs of ten animals were processed in a similar way as for light microscopy and ultrathin sections were cut in order to select the area to be studied. Sections were then cut with an LKB Ultratome, stained with 2% uranyl acetate and lead citrate (Reynolds, 1963) and observed with a JEOL 100 C electron microscope.

Scanning electron microscopy

This technique has been used with two aims: (*a*) observation of details of the vomeronasal organ *in situ* and (*b*) studies on the lateral and medial walls of the lumen of the organ. The nasal septum was dissected and separated from the rest of the skull. In order to study its internal surface, the vomeronasal organ was removed and cut into four pieces perpendicularly to its longitudinal axis. Each of these pieces was then divided longitudinally, separating the medial from the lateral wall. All the material was then fixed in 1% osmium tetroxide, critical-point dried in acetone, shadowed with carbon, coated with gold-palladium (total thickness 15–20 nm) and observed with a JEOL SMU 3 electron microscope.

RESULTS

Vomeronasal complex

The vomeronasal complex of the rat is a bilateral formation integrated by the vomeronasal organ, cartilage, glands and blood vessels. It is located along the inferior part of the nasal septum, just above the floor of the nasal cavity, forming a horizontal prominence which protrudes into the nasal fossa. Its medial side

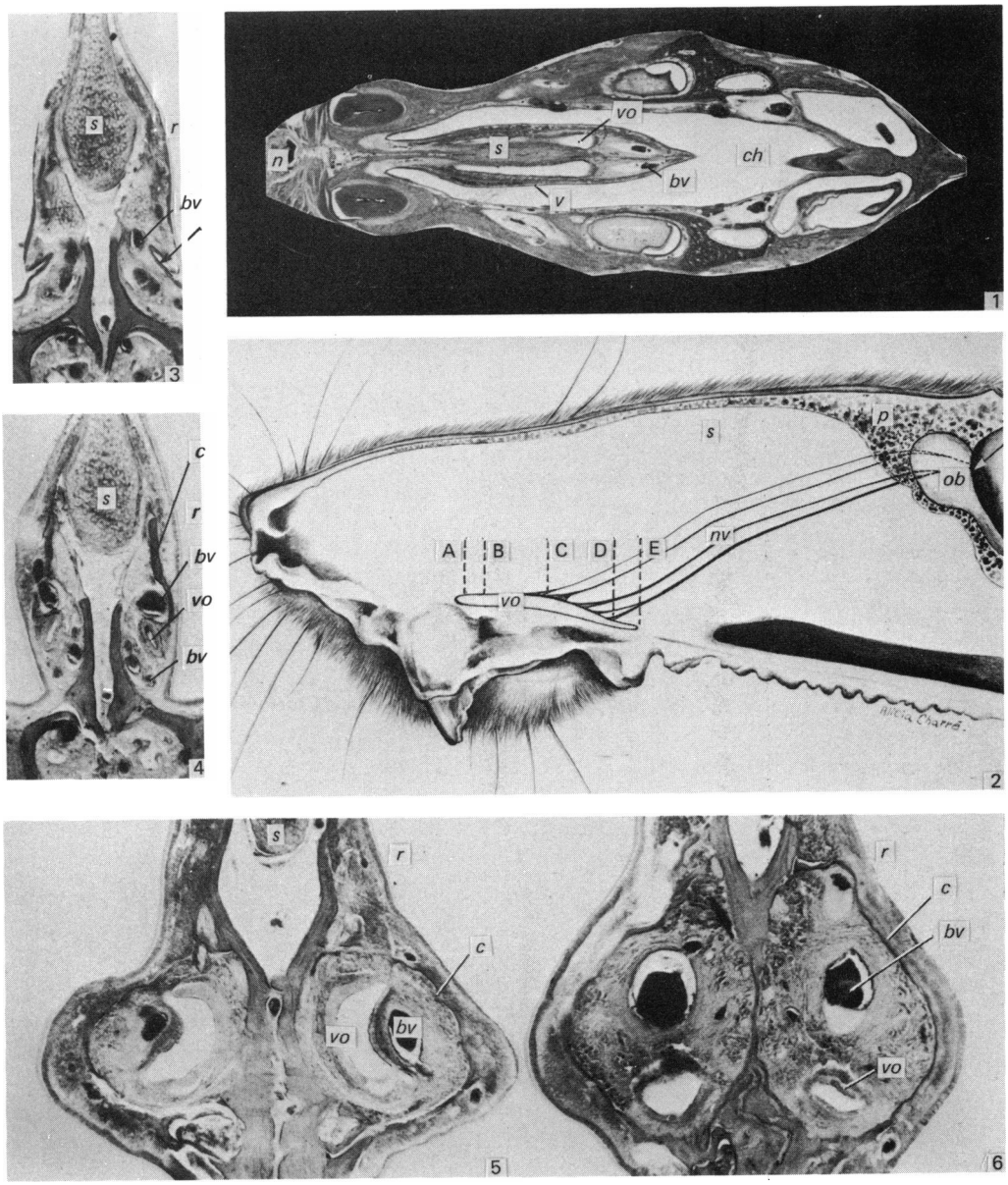


Fig. 1. Horizontal section of decalcified nasal fossae of the rat made at the level at the choanae (*ch*). The vomeronasal complex (*v*) forms a longitudinal protuberance. Its rostral extreme is about 10 mm from the nostrils (*n*); and its caudal end is rostral to the choanae. Note the presence of the vomeronasal organs (*vo*) placed at both sides of the nasal septum (*s*). The lumen of the organ and the related blood vessel (*bv*) can be seen. ×4.

Fig. 2. The diagram shows a lateral view of the nasal septum (*s*) and the medial side of the right olfactory bulb (*ob*) (the left olfactory bulb is not represented). Note the location of the vomeronasal organ (*vo*) and the course of the vomeronasal nerves (*nv*) passing through the cribiform plate (*p*) and ending in the accessory olfactory bulb (arrow). (A) indicates the level for Figs. 3, 11; (B) for Figs. 4, 12; (C) for Figs. 5, 13; (D) for Figs. 6, 14; (E) for Fig. 15.

Fig. 3–6. Coronal sections of decalcified nasal cavities of the rat. Four rostrocaudal levels are shown. ×9. In Fig. 3 the vomeronasal organ opens into the nasal cavity (arrow). In Fig. 4 the rostral flattened segment of the vomeronasal tube is seen (*vo*) with a blood vessel on its superior side and another near its inferior side (*bv*). The vomeronasal organ is just beneath the nasal epithelium (*r*). In Figs. 5, 6, the vomeronasal cartilage (*c*) surrounds the vomeronasal organ. *s*, nasal septum.

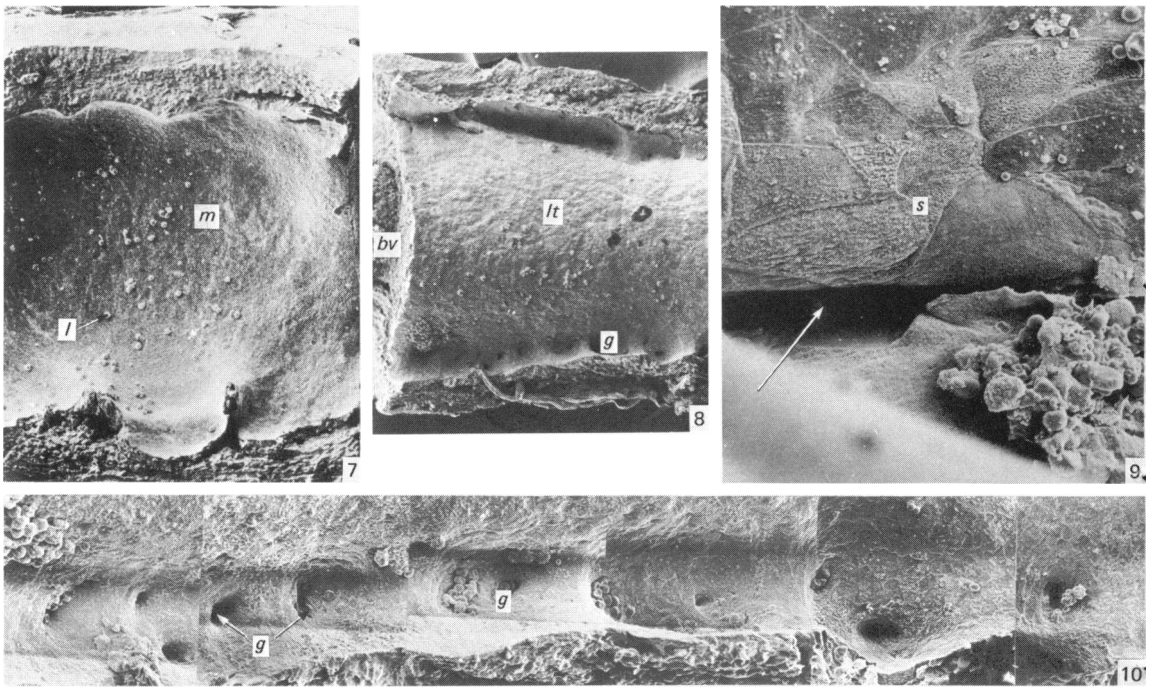


Fig. 7. SEM picture of the inner medial wall (*m*) of the vomeronasal organ. Note the concave shape of the wall and the presence of blood cells (*l*) on its surface. × 75.

Fig. 8. Inner lateral wall (*lt*) of the vomeronasal organ. Note its convex aspect and the blood vessel (*bv*) located on its external side. Gland orifices (*g*) are observed at the edges of the wall. × 75.

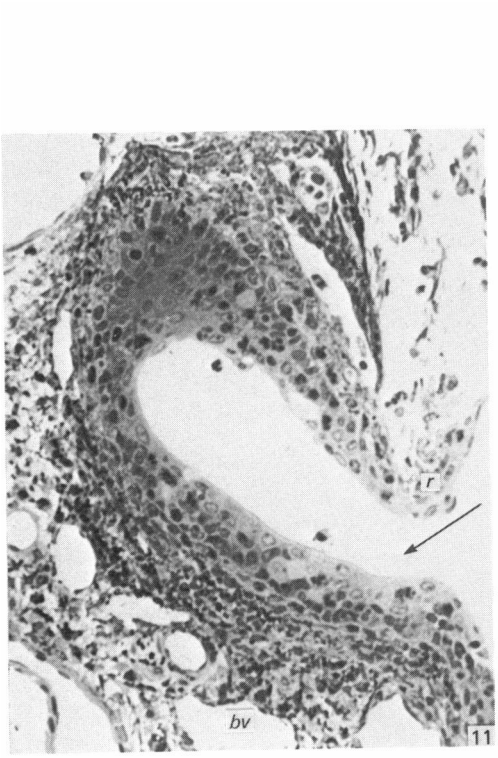
Fig. 9. Lateral view of the rostral inferior portion of the nasal septum (*s*). The opening (arrow) of the vomeronasal organ in the nasal cavity is seen. × 750.

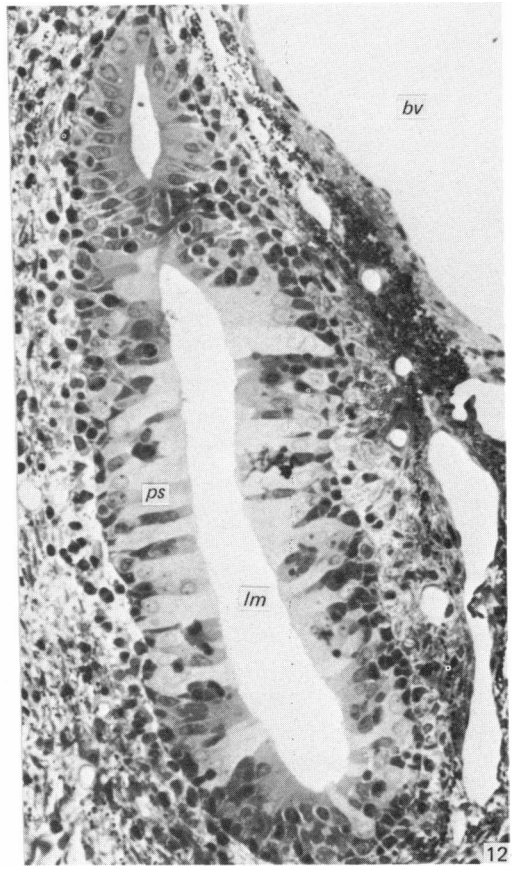
Fig. 10. Vomeronasal glands (*g*) opening in the lumen of the vomeronasal organ. × 300.

contacts the nasal septum while its lateral side is covered by the nasal mucosa. The rostral extremity of this complex is situated about 10 mm from the nostrils and its caudal end is just rostral to the choanae (Figs. 1, 2).

The vomeronasal organ occupies the most medial region of the complex, contacting the nasal septum (Figs. 1, 3–6). In its rostral portion, the vomeronasal organ is related to two blood vessels: one is on its inferior side and the other one on its superior wall (Figs. 3, 4). This latter vessel turns laterally and occupies a concavity in the outer lateral wall of the vomeronasal organ (Fig. 5); caudally, it lies again on the superior side of the organ (Fig. 6).

In the rostral extremity of the complex, the vomeronasal cartilage covers only the inferior and medial aspects of the vomeronasal organ. Thus, in this portion, the outer lateral wall of the organ lies immediately beneath the nasal mucosa (Figs. 3, 4). More caudally the cartilage surrounds the organ and related vessels forming, together with the nasal septum, a channel where these structures are placed (Figs. 5, 6).





Figs. 11–12. Coronal sections of the rostral segment of the vomeronasal organ of the rat. The communication of the vomeronasal tube with the nasal cavity is shown in Fig. 11 (arrow). Caudal to it (Fig. 12), the organ has a flattened shape, presenting a pseudostratified epithelium (*ps*) and blood vessels (*bv*) located on its contour. *lm*, lumen. r, nasal epithelium. × 95.

Vomeronasal organ

Morphology

The vomeronasal organ of the rat is a tubular structure measuring 6–7 mm in length and 1·2–1·5 mm in width (Figs. 1, 3–6). The size and the internal contour of the vomeronasal tube vary along its longitudinal axis. Most rostrally the lumen is limited by two flat walls. Caudally, as the organ increases in diameter, the lateral wall of the tube becomes convex and the medial wall becomes concave (Figs. 7, 8). In cross section the organ thus shows a typical crescent-shaped lumen. More caudally, the tube rotates about 90° and shows a superior flat and an inferior concave wall (Fig. 6). The organ is narrowest in its most caudal portion and ends blindly. The lumen of the vomeronasal organ communicates with the nasal fossa through a foramen placed at the rostral end of the organ (Fig. 3). This orifice measures 300–400 × 150 μm (Fig. 9). Numerous glandular ducts open at the junction of the lateral and medial walls (Fig. 10).

Three to four nerves arise from the vomeronasal organ. These vomeronasal nerves lie in the submucosa of the nasal septum, pass through the cribriform plate

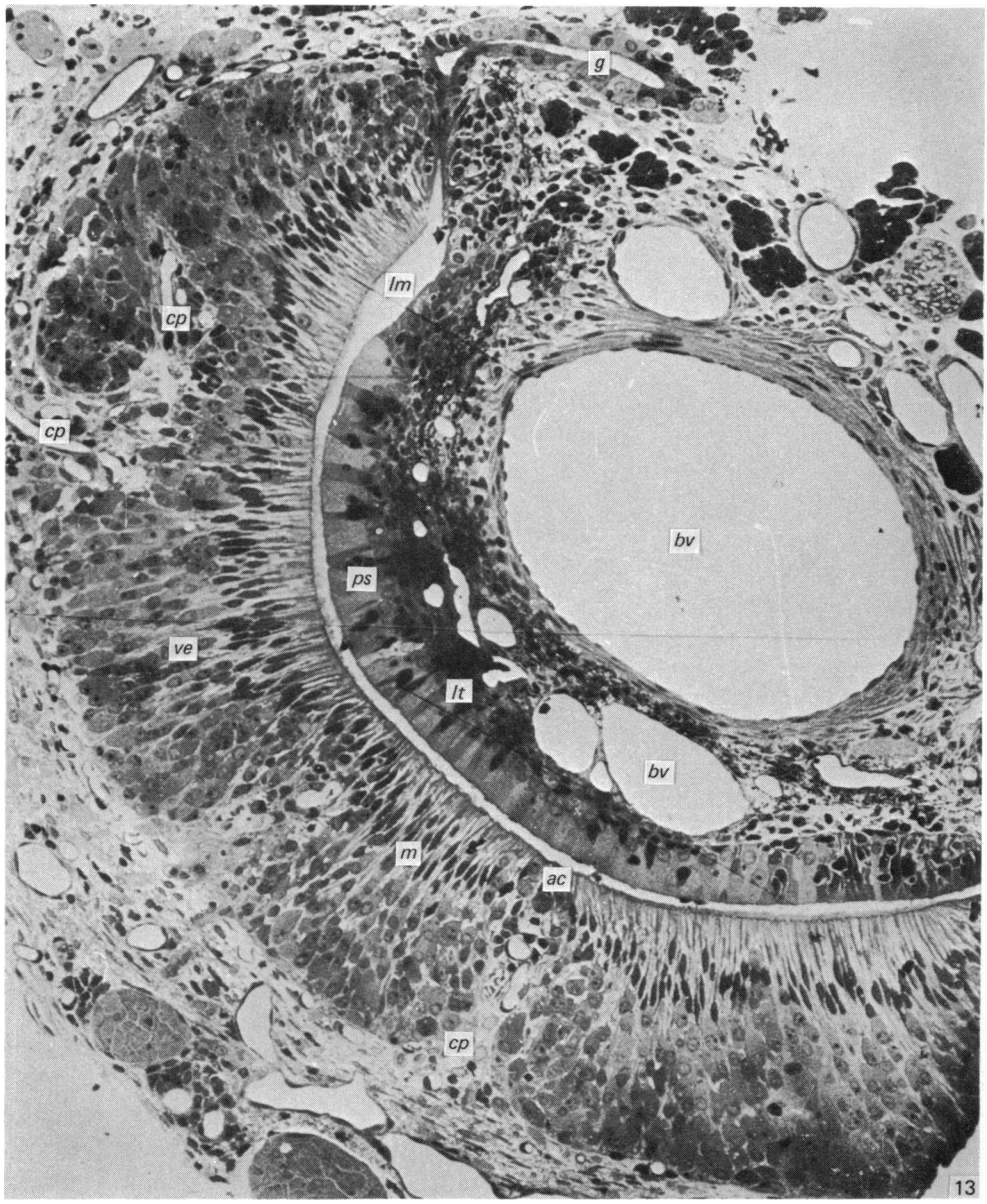
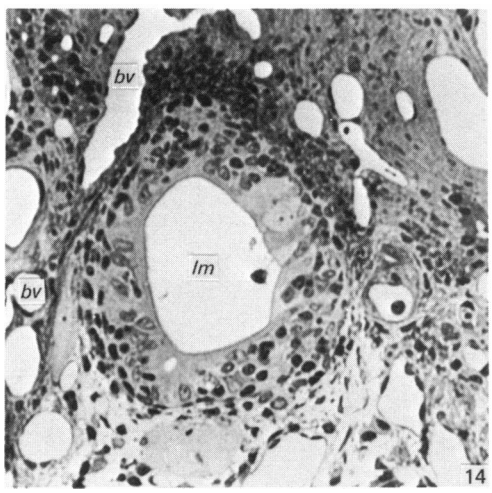
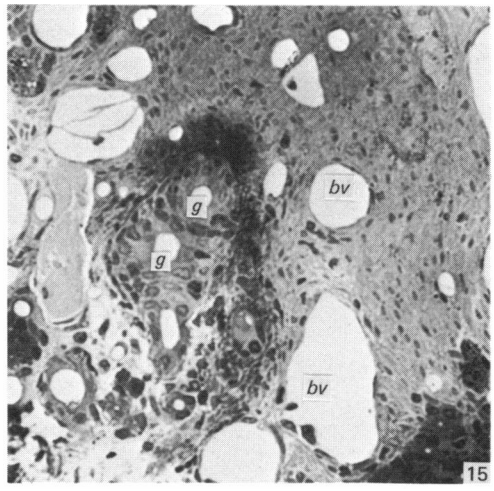


Fig. 13. Coronal section of the vomeronasal organ at the central part of its middle segment. The vomeronasal epithelium (*ve*) covers all the medial wall (*m*) of the tube and a pseudostratified epithelium (*ps*) the lateral wall (*lt*). The organ shows its typical crescent shape. Blood vessels (*bv*) are located in the groove of the lateral external wall of the organ. A vomeronasal gland (*g*) opens at the superior edge of the lumen (*lm*). An area devoid of cellular processes (*ac*) overlying an intraepithelial (*cp*) capillary is seen. ×90.





Figs. 14–15. Caudal segment of the vomeronasal organ. The tube lacks vomeronasal epithelium (Fig. 14) and ends in glandular branches (*g*) (Fig. 15). *bv*, blood vessels; *lm*, lumen. ×95.

and, after running along the medial side of the principal olfactory bulb, end in the accessory olfactory bulb (Fig. 2).

Microscopical anatomy and ultrastructure

Three segments which had different histological structure have been recognized between the rostral and caudal ends of the vomeronasal organ. The rostral segment showed the orifice through which the organ opened into the nasal cavity (Fig. 11). This region was covered by stratified squamous epithelium and continued with a laterally flattened tube, about 1 mm long, the cavity of which was bordered by a columnar pseudostratified epithelium (Fig. 12).

The middle segment (about 5 mm long) began with a flattened shape similar to that of the rostral segment, but continued into a crescent shape towards its caudal end where the crescent shape had rotated about a 90° angle (Fig. 13). The middle segment presented different epithelia in each of its walls. A pseudostratified epithelium, about 30 μm thick (Fig. 16), covered the lateral wall in the rostral part of the segment. In its caudal part, it covered the superior wall (Fig. 13). This epithelium was the continuation of that of the first segment. The typical vomeronasal epithelium, about 140 μm thick, appeared as a rostral patch expanding towards the caudal end to cover all the medial wall (Fig 13), while in the caudal portion of the segment, it covered the inferior wall. The vomeronasal epithelium disappeared at the caudal end of the middle segment and the pseudostratified epithelium gradually changed to a simple columnar cell sheet.

The caudal segment of the vomeronasal organ, 0·5 mm long, ended in two or three glandular branches and showed a simple columnar epithelium all around its lumen (Figs. 14, 15).

Ciliated and basal cells characterized the pseudostratified epithelium (Fig. 18). Two types of ciliated cells could be recognized: dark and light cells, which had microvilli and short cilia. These processes formed a low epithelial border about 1 μm thick. Near the basal bodies, which were connected to the cilia, was an accumulation of mitochondria. The cytoplasm was rich in granular endoplasmic reticulum, showing many ribosomes (Fig. 19).

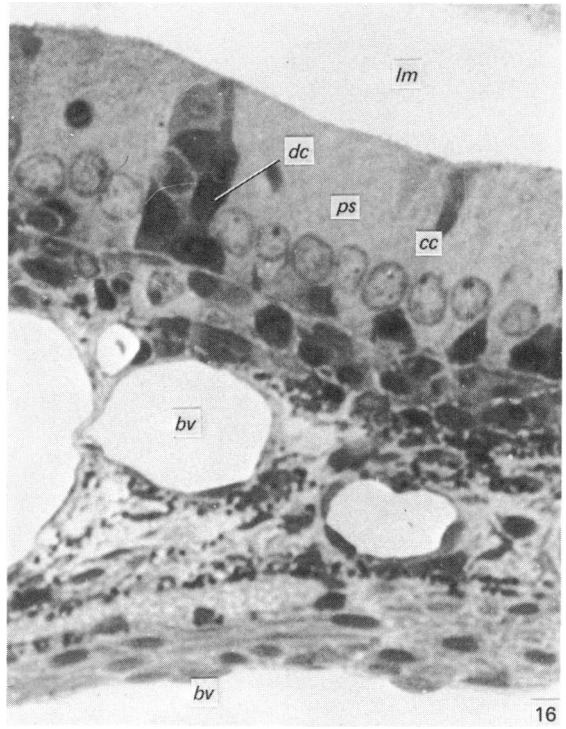


Fig. 16. Pseudostratified epithelium (*ps*) of the vomeronasal organ. Note the presence of clear (*cc*) and dark (*dc*) cells. A rich vascular tissue (*bv*) underlying the epithelium is observed. *lm*, lumen. × 240.

The vomeronasal epithelium consisted of: (*a*) a superficial layer formed by the prolongations of underlying cells; (*b*) a layer of elongated supporting cells with dark oval nuclei; (*c*) several layers of bipolar cells with clear rounded nuclei and (*d*) scarce basal cells dispersed among the deepest bipolar cells, without forming a distinct layer (Fig. 17). Blood capillaries could be seen in the thickness of the epithelium, reaching its most superficial layer. When this happened the bipolar and supporting cells were absent (Fig. 13).

The bipolar cells had a clear round nucleus; their cytoplasm was rich in granular endoplasmic reticulum. Golgi complexes could be seen in the perinuclear zone and some dense bodies were observed (Fig. 20). A dendrite extended from the supranuclear portion of the cell up to the lumen of the organ, coursing between the bodies of the overlying supporting cells. These dendrites showed a narrowing near the apex and distally to it an expansion from whence originated numerous microvilli which projected into the lumen of the vomeronasal organ. Near the narrower part a variable number of centrioles and dense bodies and many mitochondria appeared. Vesicles and microtubules were seen more centrally. Desmosome-like junctions were observed between bipolar and supporting cells (Fig. 22).

The supporting cells showed a dark cytoplasm and an oval nucleus containing peripheral chromatin (Fig. 21). Each cell showed a narrow distal prolongation which lay between the dendrites of the bipolar cells and contained mitochondria, vesicles, microtubules and, only exceptionally, some centrioles. Microvilli different

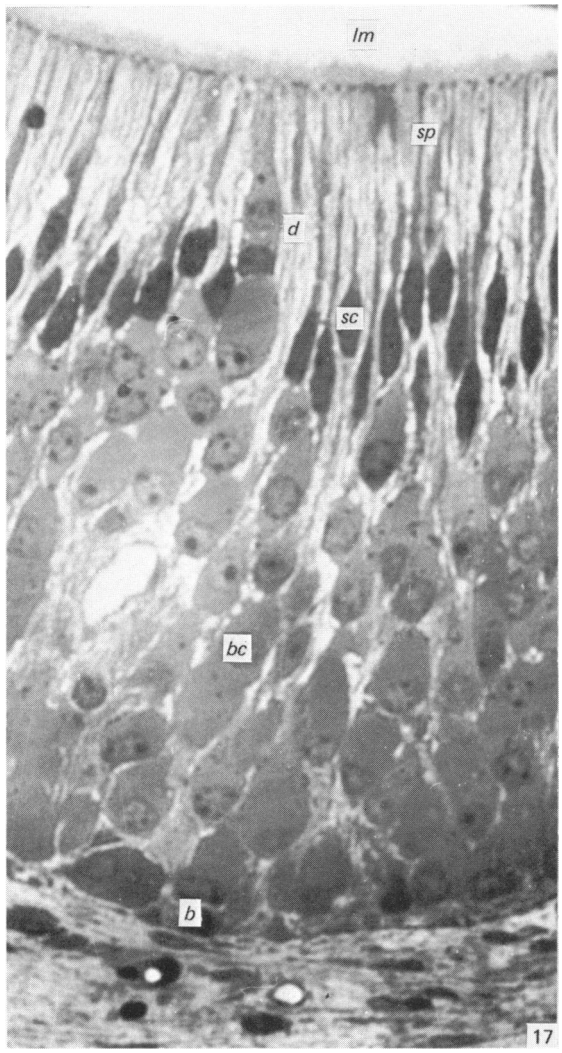


Fig. 17. Vomeronasal epithelium. Note the layer formed by the elongated dark nucleus of the supporting cells (*sc*) and the bodies of bipolar cells with clear round nucleus (*bc*). Scarce dark basal cells (*b*) are observed. The dark apical prolongations (*sp*) of the supporting cells and the clear dendrites (*d*) of the bipolar cells reach up to the vomeronasal lumen (*lm*). × 240.

from those of the bipolar cells, arose from the apex of these prolongations (Fig. 22).

In most animals a variable number of leucocytes was seen in the vomeronasal lumen spreading over the surface of the vomeronasal epithelium (Figs. 7, 23).

Superficial structures in the vomeronasal organ

The surface of the pseudostratified epithelium showed a uniform aspect in all its extent (Fig. 24).

The apical processes of the cells of the medial wall formed a superficial layer 4 μm thick. The scanning electron microscope revealed that this surface of the organ was not uniform; some areas had only one type of microvillus without any

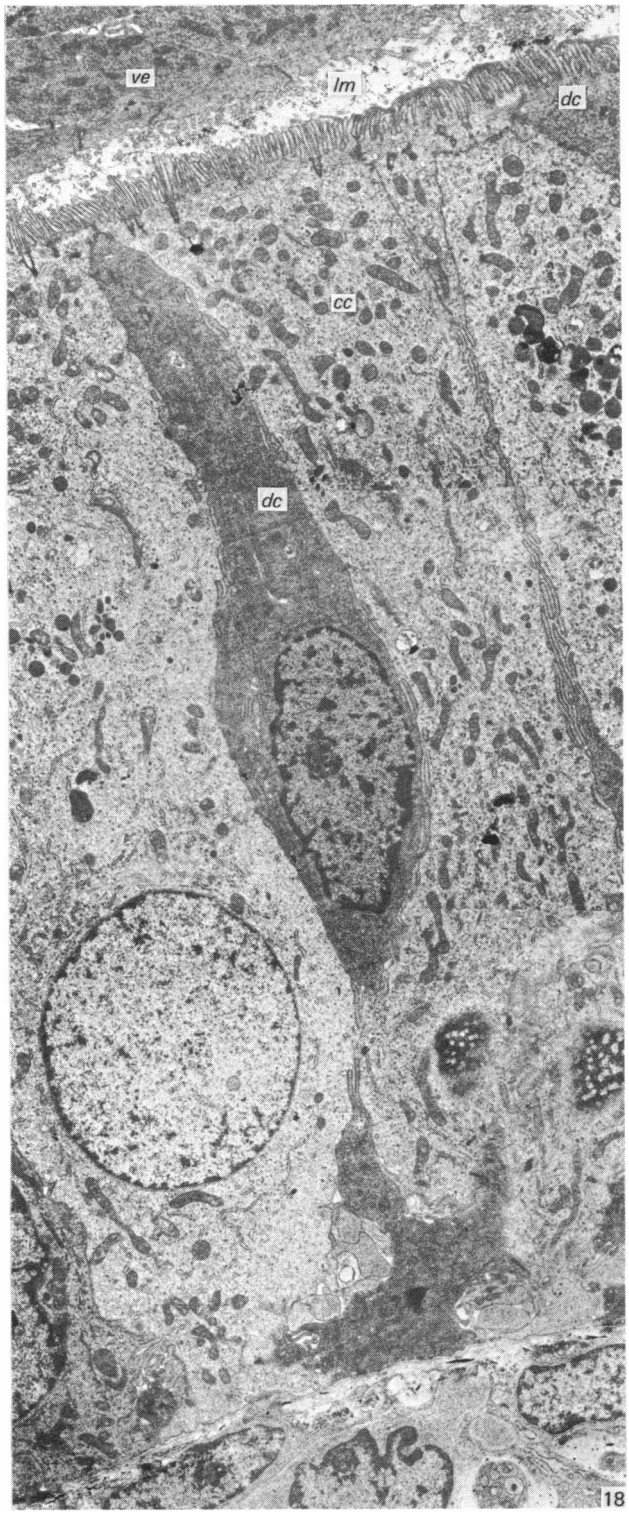


Fig. 18. Ciliated pseudostratified epithelium of the vomeronasal organ showing dark (*dc*) and clear (*cc*) ciliated cells. A narrow lumen (*lm*) separated this wall from the opposite vomeronasal epithelium (*ve*). ×3250.

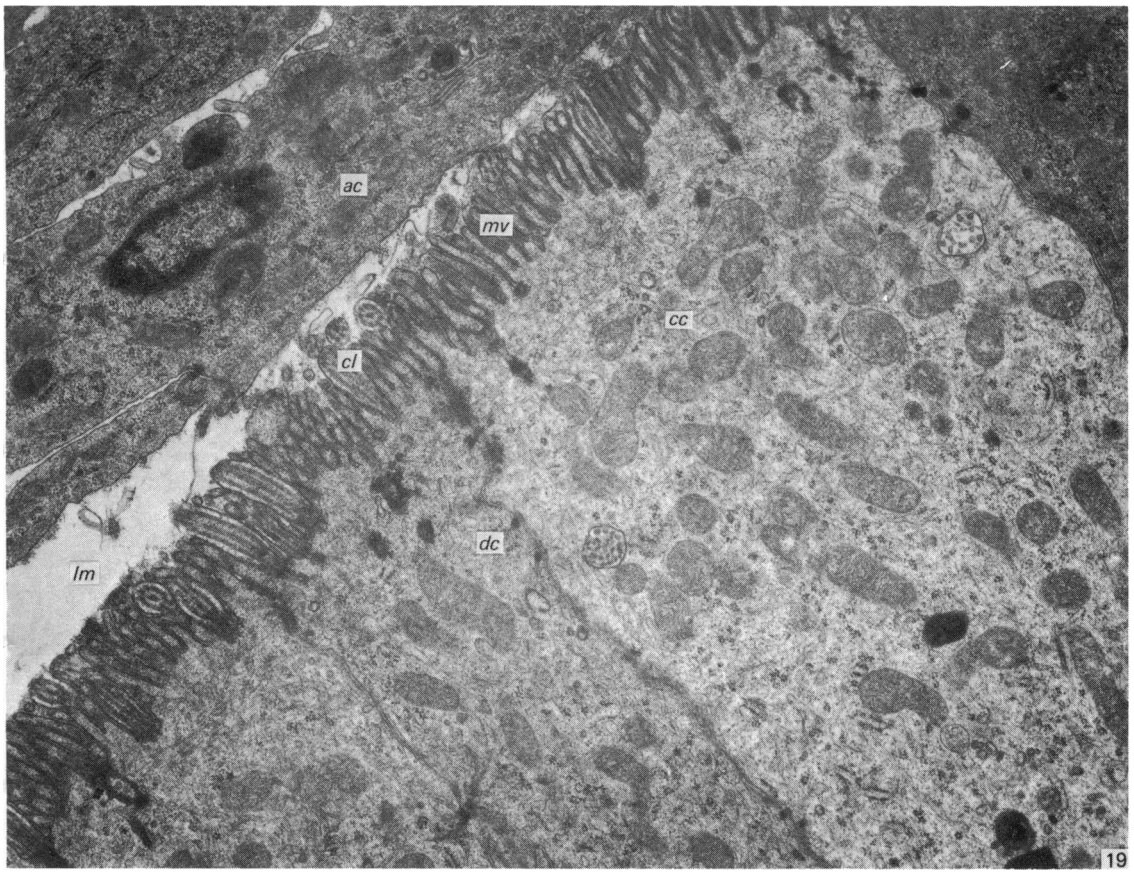
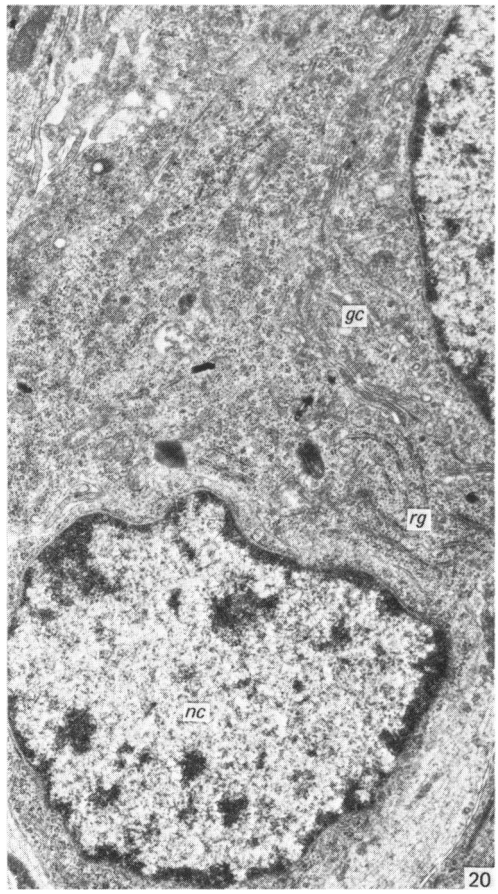


Fig. 19. Detail of the clear (*cc*) and dark (*dc*) ciliated cells of the pseudostratified epithelium. Microvilli (*mv*) and ciliary processes (*cl*) are observed in both types of cells. In the opposite wall, the area overlying an intraepithelial capillary of the vomeronasal epithelium is seen (*ac*). *lm*, vomeronasal lumen. × 7500.

visible orientation (Fig. 25), while others had several types of processes; the largest were few and isolated, the shortest and thinnest were gathered together forming bundles, and those of intermediate size also bunched up like the small microvilli. Some areas appeared to be devoid of microvilli (Figs. 26, 27).

These observations correlated well with the information provided by transmission electron microscopy: three different kinds of processes which intermingled and showed longitudinal, transverse and oblique sections could be recognized in the TEM pictures. The microvilli of the bipolar cells were the thinnest and appeared in the layer adjacent to the cell body. They extended up to 3–4 μm from the cell border and showed a peripheral double membrane, filaments and microtubules. Microvilli were scarcer and slightly wider in the supporting than in the bipolar cells. The internal structure of these microvilli did not show differences from those belonging to the bipolar cells. Larger processes, whose origin was impossible to determine, were found in the epithelial border, mainly in its most superficial layer. These processes had a dense core and dark cytoplasm surrounded by two membranes separated by a clear area (Figs. 28, 29).



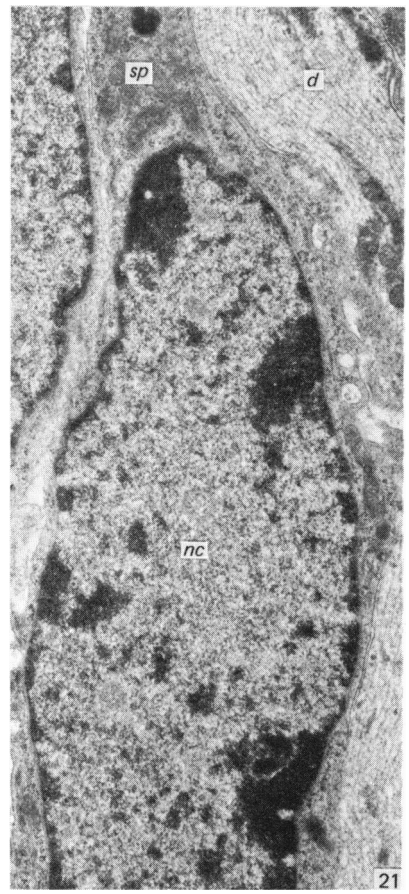


Fig. 20. Bipolar cell of the vomeronasal epithelium. A Golgi complex (*gc*) and a rich granular endoplasmic reticulum (*rg*) is observed in the supranuclear region. Note the round clear nucleus with peripheral chromatin (*nc*). × 5000.

Fig. 21. Supporting cell of the vomeronasal epithelium. Note the elongated nucleus (*nc*), the scarce cytoplasm and the origin of the apical prolongation (*sp*) ascending together with the dendrite of a bipolar cell (*d*). × 5000

DISCUSSION

Our observations confirm the morphological characteristics of the vomeronasal organ of the rat described by Hertzfeld (1888) and Addison & Rademaker (1927), with regard to the topographical relationships between the organ and the adjacent glands, vessels and cartilage. On the grounds of the relationships between the vessels and the organ, Hamlin (1929) postulated a pumping mechanism which would make possible the entrance and exit of mucus. Meredith (1977) confirmed his hypothesis in hamsters and claimed that the pumping mechanism is under the control of sympathetic fibres.

Histological descriptions of the vomeronasal organ frequently show a uniform organization all along the tube: vomeronasal epithelium in the medial wall and respiratory-like epithelium in the lateral wall. However, Schilling (1970) observed in *Microcebus murinus* that the rostral portion of the vomeronasal organ had only

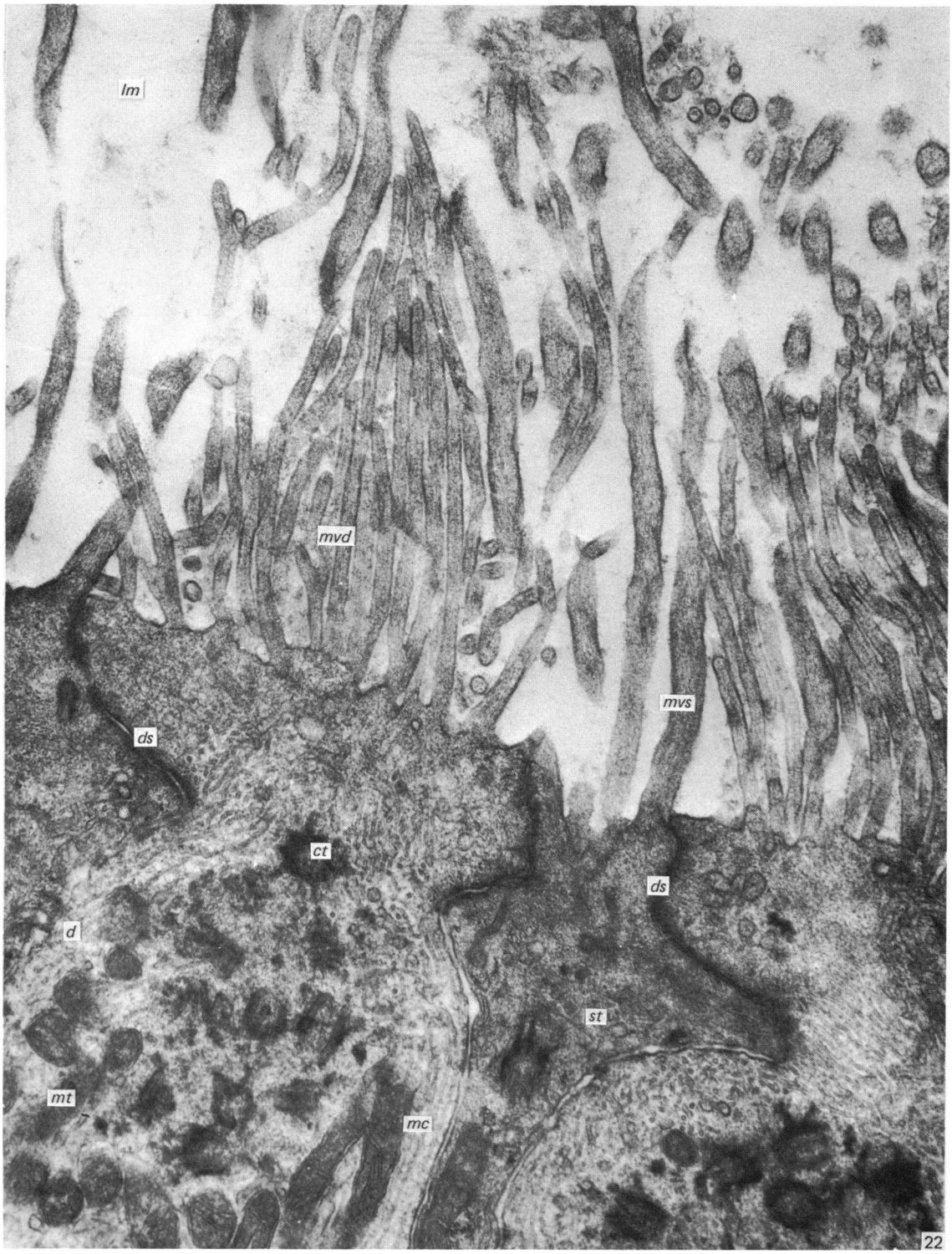


Fig. 22. Detail of the apical processes of the bipolar dendrite (*d*) and supporting cells (*st*). The dendrite shows numerous thin and clear microvilli (*mvd*) while the supporting cells have scarce darker and wider microvilli (*mvs*). Desmosomes (*ds*) are observed. *ct*, centriole; *lm*, lumen; *mc*, microtubules; *mt*, mitochondria. ×25000.

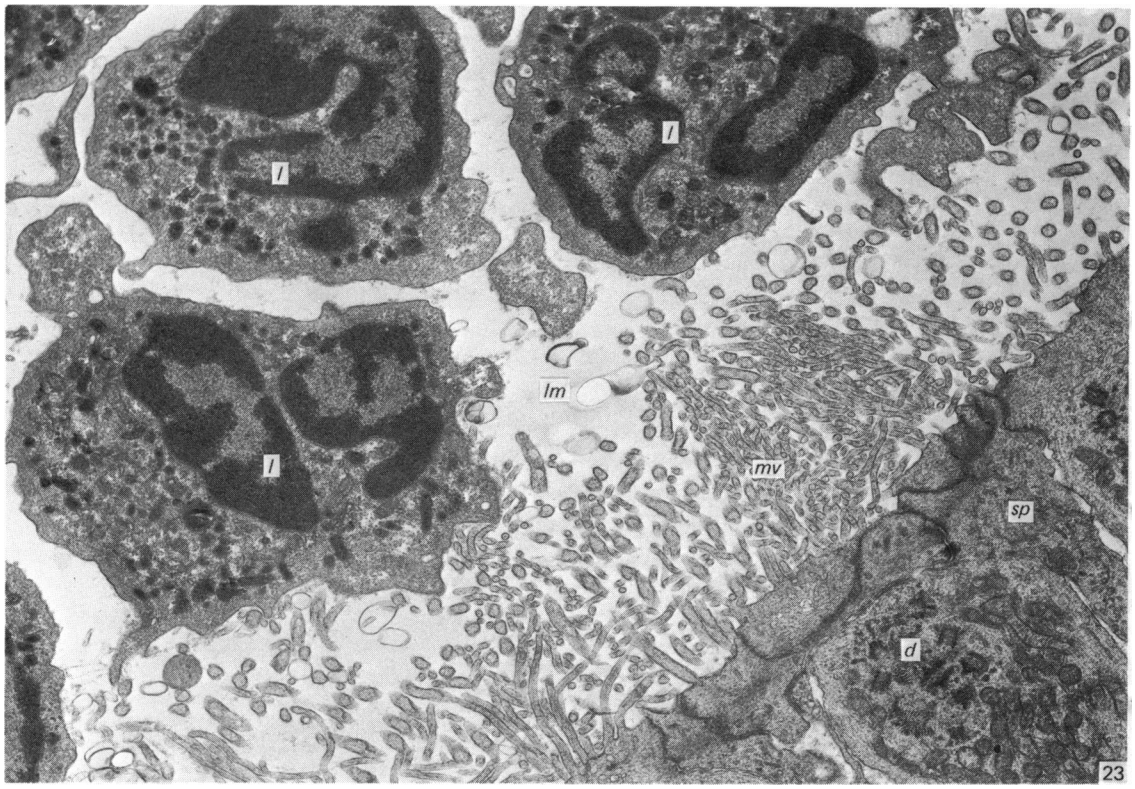


Fig. 23. Leucocytes (*l*) are observed in the vomeronasal lumen (*lm*), spreading over the microvilli (*mv*) of the dendrites of the bipolar cells (*d*) and supporting cells (*sp*). × 7000.

one type of epithelium around its lumen. Our study in the rat confirms the observations of Addison & Rademaker (1927) that, although the vomeronasal and pseudostratified epithelia are present in most of the length of the tube, only the pseudostratified epithelium can be found at its cranial end.

The cell types described in the lateral wall of the vomeronasal organ of the adult rat are similar not only to those of the very young rat (Kratzing, 1971*b*), but also to those of sheep (Kratzing, 1971*a*) and rabbits (Luckhaus, 1969). In the rat, as in other animals, only a few secretory cells are found in this epithelium. Our observations agree with those of Luckhaus (1969) regarding the nature of this ciliated epithelium, which seems to be a modification of that of the vomeronasal glands. The functional integration between the vomeronasal epithelium and the ciliated one is a possibility that deserves further study.

The cells of the vomeronasal epithelium of the rat, particularly in their apical processes and the way they are arranged to form the epithelial border, show some differences from those described in other animals which may have important functional implications. The bipolar cells of the rat and of the rabbit show a significant difference: the absence of cilia in the bipolar cells of the rat and their presence in the bipolar cells of the rabbit (Luckhaus, 1969). The microvilli of the bipolar cells of the rat are slightly different from those of the supporting cells but this is not the case in either sheep or cats (Kratzing, 1971*a*; Seiffert, 1971).

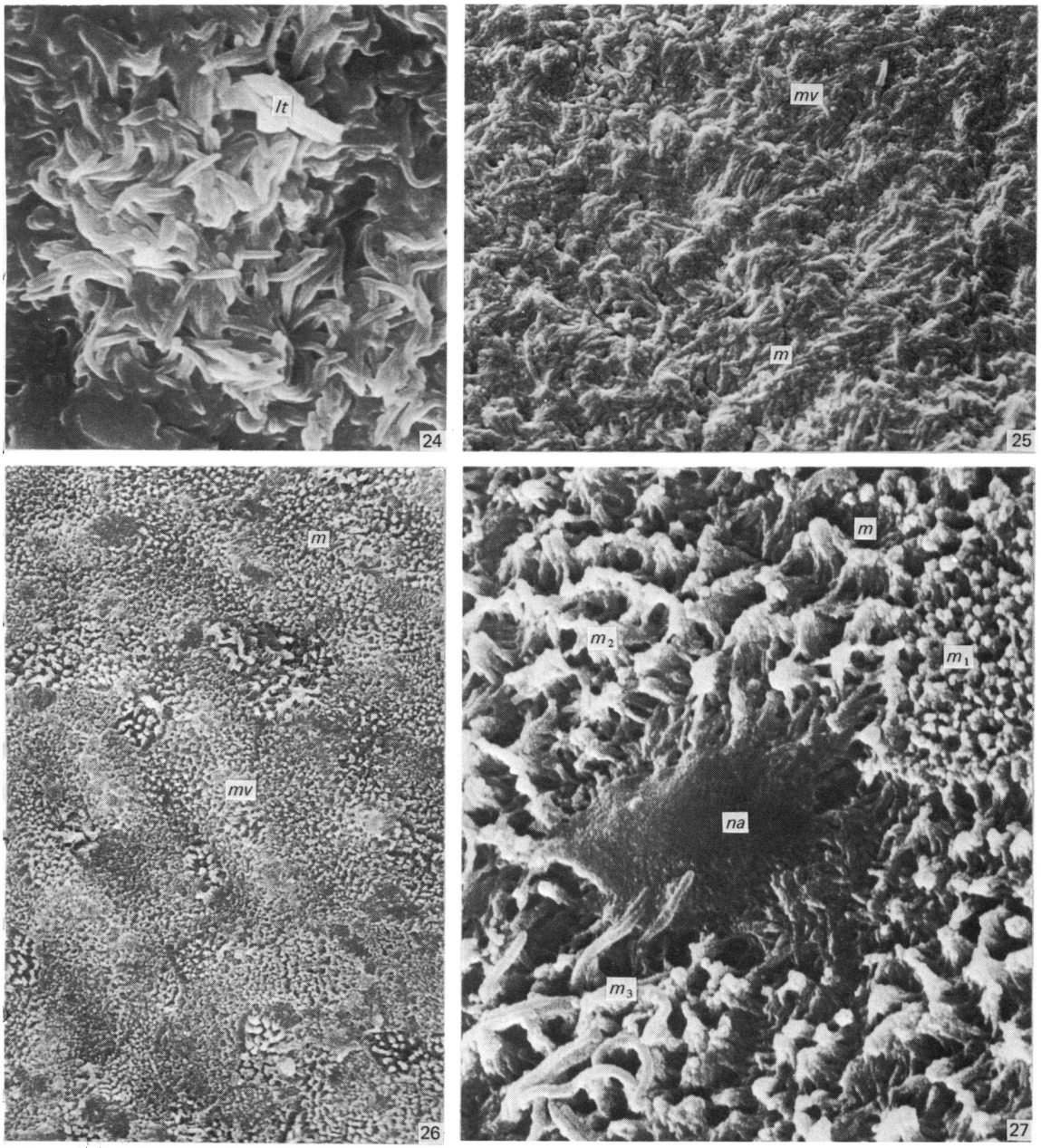
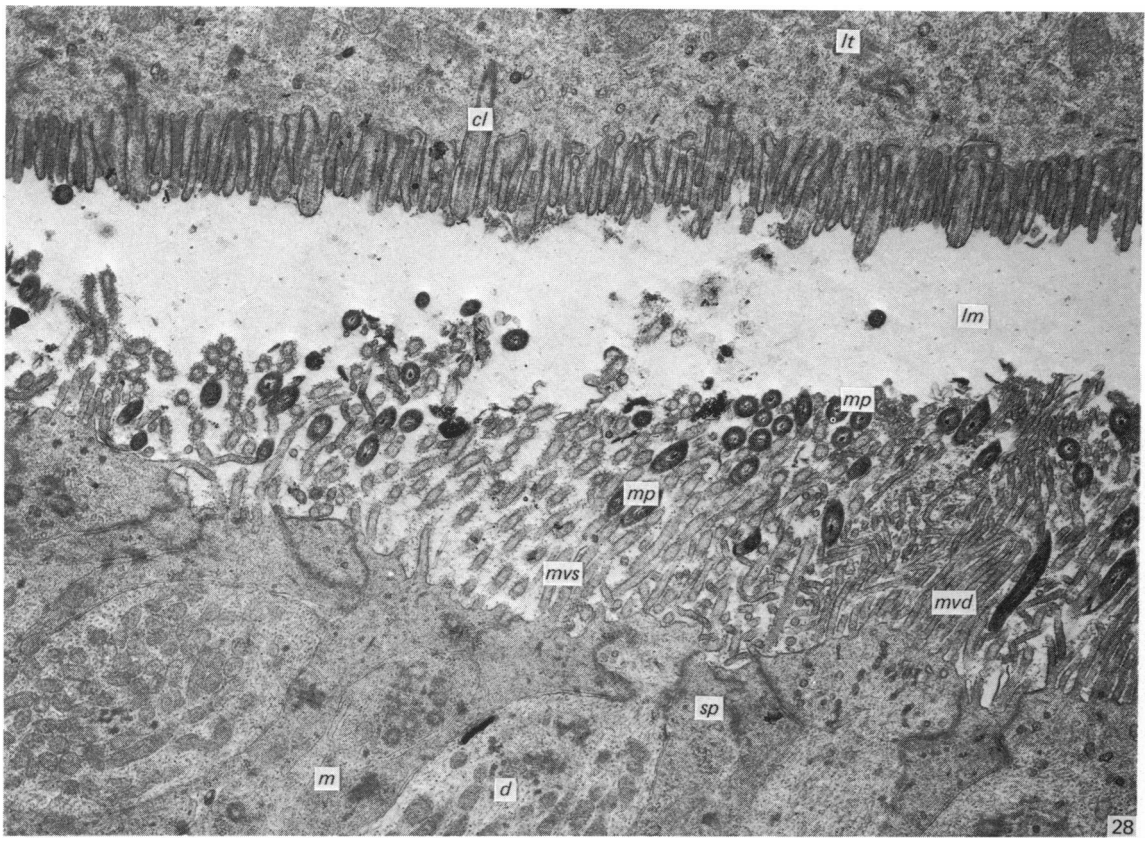


Fig. 24. SEM picture of the inner lateral wall (*lt*) of the vomeronasal organ. × 5000.

Figs. 25–27. SEM photographs of the inner medial wall (*m*) of the vomeronasal tube. The arrangement of microvilli (*mv*) is variable. In Fig. 25 only one type is observed covering the surface without any clear orientation. × 5000. In Figs. 26, 27 a different pattern and three kinds of processes are seen (*m*1, *m*2, *m*3). Areas devoid of microvilli are observed (*na*). Fig. 26. × 1000. Fig. 27. × 7500.

The other type of process found in the epithelial border of the adult rat is similar to the 'Microzoten' described by Seiffert (1971) in the supporting cells of the cat and to sensorial microprocesses of the sheep (Kratzing, 1971*a*). Although the size



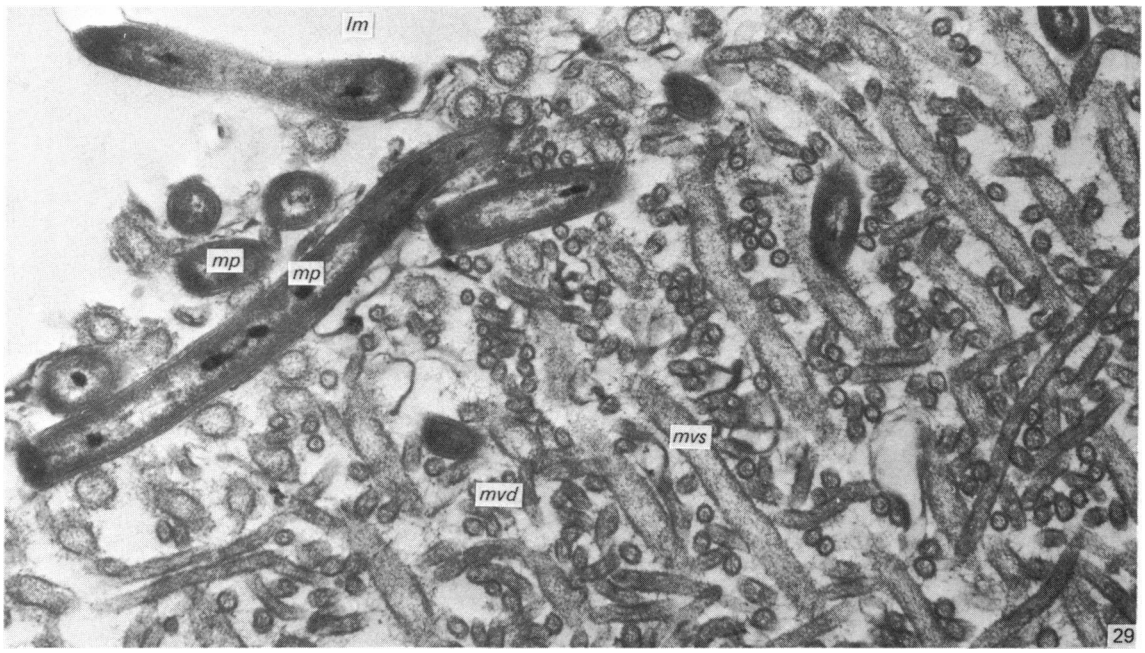


Fig. 28. The epithelial borders surrounding the vomeronasal lumen (*lm*) are shown. The border of the lateral wall (*lt*) is formed by microvilli and cilia (*cl*). The border of the medial wall (*m*) is formed by the microvilli (*mvd*) originating in the dendrites of the bipolar cells (*d*), the microvilli (*mvs*) of the supporting cells (*sp*) and microprocesses of undetermined origin (*mp*). × 5000.

Fig. 29. Detail of the vomeronasal epithelial border. Microvilli of the bipolar cells (*mvd*) and supporting cells (*mvs*) appear to intermingle with microprocesses (*mp*). *lm*, lumen. × 25000.

and structure of these prolongations allows an easy differentiation from microvilli, we were unable to find the cells from where they originate.

In relation to the reception mechanism and the structures involved, it is important to point out the absence of cilia in the vomeronasal epithelium of the rat. In the olfactory epithelium, the cilia of the bipolar cells have been considered necessary for the generation of the negative slow potential in response to odours (Ottoson, 1971). However, the absence of ciliary processes in the vomeronasal epithelium does not interfere with the generation of slow potentials similar to those of the olfactory mucosa (Müller, 1971). On the other hand, the regional differences observed in the vomeronasal epithelium due to the variable density of processes suggest that the receptor area is not uniform all along the tube. This different concentration of cellular processes may be explained through a hypothetical mechanism of cellular degradation and posterior replacement. In fact, Barber & Raisman (1978*a*) have described the formation of new cells in the vomeronasal epithelium of mice, suggesting a mechanism of turnover as opposed to continuous degradation. Intraepithelial capillaries may represent a special anatomical arrangement for the high metabolic activity that the continuous cell formation would require. On the other hand, the phagocytic cells spread over the vomeronasal epithelium might participate in the cellular degradation process.

The presence of leucocytes in the lumen could be a component of an inflammatory response. Kratzing (1971*b*) has mentioned the high frequency of bacterial populations in the upper respiratory tract of mature rats compared to younger animals. Damaged vomeronasal cells could be replaced according to the regenerative capacity of the epithelium (Barber & Raisman, 1978*b*).

Previous anatomical research and our own results strongly suggest that the vomeronasal structures constitute a highly organized sensory system, centrally connected to neural areas involved in the regulation of reproductive mechanism.

SUMMARY

The anatomical organization of the vomeronasal complex of the rat (vomeronasal organ, blood vessels, cartilage and glands) and the structure of the vomeronasal organ were studied. This organ is a tubular formation that shows different characteristics along its longitudinal axis. In its rostral portion it has a lateral flattened shape, but caudally the organ acquires a typical crescent shape and a greater size. The organ is rotated along its longitudinal axis, the medial wall becoming inferior and the lateral one, superior. In its most caudal portion the organ decreases in size and ends in glandular branches.

Three histological segments were recognized in the vomeronasal organ. The rostral one shows a pseudostratified epithelium surrounding all the lumen. The middle segment presents in one of its walls a similar epithelium and, in the other wall, the vomeronasal epithelium. The caudalmost segment shows a simple columnar epithelium that continues with that of glandular ducts.

The vomeronasal epithelial border is formed by three types of cellular processes which intermingle, each one showing particular features: (*a*) microvilli originating from dendrites of bipolar cells; (*b*) microvilli from supporting cells and (*c*) microprocesses of undetermined origin. The surface of the vomeronasal epithelium shows an irregular distribution and arrangement of these processes.

The authors are grateful to Miss Alicia Charré for drawing the diagrams; Miss Paula Fanelli for preparing the material for light and electron microscopy; Mr Marcelo Reguero for his technical assistance; Mr Luis Millara and Mr Angel Fusaro for producing the photographs. This work was supported by the Fundación Instituto de Neurobiología and grants from the Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina.

REFERENCES

ADDISON, W. & RADEMAKER, L. A. (1927). The postnatal growth of the vomeronasal organ of the albino rat. *Journal of Comparative Neurology* **44**, 69–86.

BALOGH, C. (1860). Über das Jacobson'sche Organ des Schafes. *Sitzungsberichte der Akademie der Wissenschaften in Wien* **42**, 449.

BARBER, P. C. & RAISMAN, G. (1978*a*). Cell division in the vomeronasal organ of the adult mouse. *Brain Research* **141**, 57–66.

BARBER, P. C. & RAISMAN, G. (1978*b*). Replacement of receptor neurones after section of the vomeronasal nerves in the adult mouse. *Brain Research* **147**, 297–313.

BROOM, R. (1897). A contribution to the comparative anatomy of the mammalian organ of Jacobson. *Transactions of the Royal Society of Edinburgh* **39**, 231–255.

BROOM, R. (1915). On the organ of Jacobson and its relations in the insectivora. Part I. *Tupaia* and *Gymnura*. *Proceedings of the Zoological Society of London* **13**, 157–162.

ESTES, R. O. (1972). The role of the vomeronasal organ in mammalian reproduction. *Mammalia* **36**, 315–341.

GRATIOLET, H. (1845). Recherches sur l'organe de Jacobson. These Médecine, Paris.

HAMLIN, H. E. (1929). Working mechanisms for the liquid and gaseous intake and output of the Jacobson's organ. *American Journal of Physiology* **91**, 201–205.

HERZFIELD, P. (1888). Ueber das Jacobson'sche Organ des Menschen und der Säugethiere. *Zoologische Jahrbücher* **3**, 551–574.

JACOBSON, L. (1811). Description anatomique d'un organe observé dans les mammiferes. *Annales du Museum D'Histoire Naturelle (Paris)* **18**, 412–424.

JOHNS, M. A., FEDER, H. H., KOMISARUK, B. R. & MAYER, A. D. (1978). Urine induced reflex ovulation in anovulatory rats may be a vomeronasal effect. *Nature* **272**, 446–448.

KALLIUS, E. (1905). Geruchsorgan (organon olfactus). In *Bardeleben's Handbuch der Anatomie des Menschen*, vol. 5, p. 78. Jena: G. Fischer.

KOLMER, W. (1927). Geruchsorgan. In *Möllendorff Handbuch der mikroskopischen Anatomie des Menschen*, vol. 3, part I, pp. 192–249. Berlin: Springer.

KOLNBERGER, I. (1971). Vergleichende Untersuchungen am Riechepithel insbesondere des Jacobsonschen Organs von Amphibien, Reptilien und Säugetieren. *Zeitschrift für Zellforschung und mikroskopische Anatomie* **122**, 53–67.

KRATZING, J. (1971*a*). The structure of the vomeronasal organ in the sheep. *Journal of Anatomy* **108**, 247–260.

KRATZING, J. (1971*b*). The fine structure of the sensory epithelium of the vomeronasal organ in suckling rats. *Australian Journal of Biological Sciences* **24**, 787–796.

LUCKHAUS, G. (1969). Licht-und electronen-mikroskopische Befunde an der Lamina epithelialis des Vomeronasalorgans von Kaninchen. *Anatomischer Anzeiger* **124**, 477–489.

MEREDITH, M. (1977). Vomeronasal accessory olfactory system: stimulus, access and unit responses. *Olfaction and Taste*, vol. VI (ed. J. Le Magnen & P. MacLeod), pp. 200. London: Information Retrieval Ltd.

MÜLLER, W. (1971). A comparative electrophysiological study of sensory epithelia in the nose and vomeronasal organs of Amphibians (*Rana*), Reptiles (*Lacerta*) and Mammals (*Mus*). *Zeitschrift für vergleichende Physiologie* **72**, 370–385.

NEGUS, V. E. (1956). The organ of Jacobson. *Journal of Anatomy* **90**, 515–518.

NEGUS, V. E. (1958). *The Comparative Anatomy and Physiology of the Nose and Paranasal Sinuses*. pp. 1–402. Edinburgh: Livingstone.

OTTOSON, D. (1971). The electroolfactogram. *Handbook of Sensory Physiology*, vol. IV (ed. L. Beidler), pp. 95–131. Berlin: Springer-Verlag.

PEARLMAN, S. J. (1934). Jacobson's organ (organon vomeronasale Jacobsoni): Its anatomy, gross, microscopic and comparative, with some observations as well on its function. *Annals of Otology, Rhinology and Laryngology* **43**, 739–768.

PLANEL, H. (1953). Etudes sur le physiologie de l'organe de Jacobson. *Archives d'anatomie, d'histologie et d'embryologie* **36**, 197–205.

REYNOLDS, E. S. (1963). The use of lead citrate at high pH as an electron-opaque stain in electron microscopy. *Journal of Cell Biology* **17**, 208–212.

RUYSCH, F. (1724). *Thesaurus Anatomicus*, vol. III, p. 26. Amsterdam: Jans Waesberg.

SCHILLING, A. (1970). L'organe de Jacobson du lémurien malgache *Microcebus murinus* (Miller 1777). *Mémoires du Muséum nationale d'histoire naturelle (série A)* **61**, 203–280.

SEIFFERT, K. (1971). Licht-und elektronenmikroskopische Untersuchungen am Jacobsonschen Organ (Organon vomeronasale) der Katze. *Archiv für klinische und experimentelle Ohren-Nasen-und Kehlkopfheilkunde* **200**, 223–251.

TUCKER, D. (1963). Olfactory, vomeronasal and trigeminal receptor response to odorants. *Olfaction and Taste*, vol. I (ed. Y. Zotterman), pp. 45–69. Oxford: Pergamon.

WINANS, S. & POWERS, J. (1977). Olfactory and vomeronasal deafferentiation of male hamster. Histological and behavioral analyses. *Brain Research* **126**, 325–344.

ZUCKERKANDL, E. (1910). Das Jacobsonschen Organ. *Ergebnisse der Anatomie und Entwicklungsgeschichte* **18**, 801–843.