ELECTRON MICROSCOPIC OBSERVATIONS OF THE OLFACTORY MUCOSA AND OLFACTORY NERVE*

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Plates 265 to 271

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The olfactory epithelium of mammals is simple in appearance when fixed and stained with conventional techniques and viewed with the light microscope. In it, there are three types of cells, the olfactory receptors, the supporting, and the basal cells, all of which rest upon a thin basement membrane, demonstrable only with difficulty (1–5). In spite of its apparently simple organization and single type of receptor element, the olfactory epithelium is capable of remarkably fine sensory discriminations. Olfactory receptors respond to stimulating substances in extraordinarily small concentration. Moreover, the receptors are sensitive to an enormous range of odoriferous substances.

Electrophysiological investigations (6–9) have led several investigators to suggest recently that discrimination depends upon the existence of different types of olfactory receptors with selective sensitivities to basic odors, and although the spatial distribution of receptors may account for coarse discriminations of odors, fine differentiation seems to depend upon specific sensitivity of individual receptors to particular molecular configurations (9).

These findings pose the question of whether or not the olfactory receptors exhibit morphological differences corresponding to their functional heterogeneity. By way of answering this, the studies of Le Gros Clark (10–12) have demonstrated several histological differences among receptor cells. For example, the receptors vary in their affinity for silver stains, in the length and diameter of the rod processes, in the size of their terminal swellings, and in the number of olfactory hairs. They also differ markedly in their degree of degeneration after destruction of the olfactory bulb (12).

It must be admitted, however, that the limited resolution of the light microscope does not permit a sufficiently detailed analysis of the olfactory receptors and their relationships to the other cells of the olfactory epithelium. For example, the receptor processes are difficult to demonstrate reliably even in the best histological preparations. In addition, many of the central processes of the

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receptors, which consist of the axons of the olfactory nerve, are extremely small and beyond the resolution of the light microscope. An investigation of the olfactory mucosa with the electron microscope was undertaken with these limitations and problems in mind. Preliminary results have been reported elsewhere (24). The observations of this investigation confirm and extend the essential findings of Bloom (23) and Gasser (17).

Materials and Methods

Materials for this study consisted of olfactory epithelium and olfactory bulbs obtained from 12 rabbits, 2 months old. Rabbits of this age were selected in order to avoid the chronic atrophic rhinitis which commonly occurs in adult animals. The tissues were removed from anesthetized animals and fixed at 4°C. in Dalton's (15) osmium tetroxide-bichromate mixture at pH 7.6 and in a $KMnO_4$ solution as recommended by Luft (16). The tissue was then washed briefly in distilled water, dehydrated in increasing concentrations of ethanol (20, 30, 40, 50 60, 70, 80, 95, and 100 per cent), and infiltrated for 3 hours with three changes of *n*-butyl methacrylate monomer containing benzoyl peroxide as a catalyst. Polymerization was carried out at 60°C. for 12 to 24 hours. Hardness of the plastic was controlled by occasionally adding small amounts of *n*-methyl methacrylate to the imbedding medium. Sections were cut on a Porter-Blum (Servall) microtome and examined without removal of the plastic. Electron micrographs were taken with an RCA electron microscope model EMU-2E, with a 40 μ objective aperture, at original magnifications of 1,000 to 8,000 diameters, and photographically enlarged as desired.

OBSERVATIONS

The surface of the olfactory mucosa is covered with mucus which seems to hinder good fixation. Adequate fixation, however, was accomplished with OsO_4 mixture chilled to 4°C. Fixation with permanganate has recently been shown to preserve the membranes of many cells but not certain granular components of the cytoplasm (16). These observations suggested that the use of permanganate might prove advantageous in the case of the olfactory mucosa, since in this tissue membranous components are conspicuous. The results of $KMnO_4$ fixation of the olfactory mucosa were satisfactory (Fig. 5). The general preservation of the tissue compared well with that of OsO_4 fixation, although the mitochondria of the sustentacular cells appeared regularly swollen, regardless of temperature, pH, or osmolarity of the fixing solutions. Its other advantages, however, (increased contrast and membrane specificity) made it particularly useful.

The Olfactory Receptor Cells:

General Appearance.—The nuclei of the receptor cells are contained in a limited area of the olfactory epithelium, the nuclear band (2), which facilitates their identification (Fig. 1). The nuclei are characterized by a dense karyoplasm in which a nucleolus is occasionally seen. The karyoplasm is bounded by a double nuclear membrane. The cytoplasm of the cell body, although scanty, contains the usual complement of formed elements, mitochondria, golgi bodies, small vesicles, the endoplasmic reticulum, and small granules (Fig. 2). Most of the cytoplasm of the receptor cell is contained in the distal process (the dendrite) which extends to the free surface of the epithelium. The dendrite projects beyond the free surface as a swelling, called the olfactory rod, which bears numerous cilia. In OsO_4- and $KMnO_4$-fixed tissues, the olfactory receptors are always less dense than the neighborhood sustentacular cells (Figs. 4 and 5). The proximal processes of the receptors are the axons of the fila olfactoria. These axons are extremely tenuous and follow a tortuous course, and these factors make it extremely unlikely that the plane of section will pass through both the cell body and its axon.

The Dendrite.—The dendritic portion extends from the cell body to the epithelial surface of the nasal passage. The cytoplasm of the dendrite, whether fixed in OsO_4 or $KMnO_4$, is light in appearance (Figs. 4 and 5). A few membranes, identified as elements of the endoplasmic reticulum, are seen in the region of the nucleus. In the remainder of the dendrite, the endoplasmic reticulum is extremely tenuous and slight in over-all amount. Its appearance is similar to that seen in axons and dendritic processes elsewhere (25). This observation differs from that of Gasser who states, "a series of elongated profiles of the endoplasmic reticulum near the edge of the cell is the most useful guide to identification" (17). Gasser has apparently described mainly the proximal region of the dendrite near the nucleus, rather than the major portion of the dendrite which extends into the epithelium. Our observations are in agreement with those of Porter (26). Numerous small granules and vesicles are also present, but the most numerous structures encountered are the mitochondria concentrated in fairly large numbers at the apical end of the dendrite (Fig. 4). As found by Bloom (23), the mitochondria are similar in internal structure to those seen in other tissues. Occasionally, mitochondria are encountered in the olfactory rod. The plasma membrane of the receptor cell is about 150 A thick and pursues a continuous course enclosing the dendrite and the olfactory rod. Interdigitations of the plasma membrane of the dendrite with the cell membrane of the sustentacular cell are occasionally seen. Granules of the ergastoplasm as well as numerous small vesicles are disposed along the inner surface of the plasma membrane. The plasma membranes of adjacent sustentacular cells are apposed in intimate association with the dendritic process of the receptor. In many regions the relationship is similar to that of the Schwann cell to unmyelinated fibers shown by Gasser (17). Further observations of this region are reported below in the discussion of the supporting cell.

The Olfactory Rod.—The olfactory rod is a projection of the dendrite beyond the free surface of the mucosa (Figs. 4 and 5). The membrane limiting the olfactory rod is a continuation of the cell membrane. The cytoplasm of the olfactory rod is similar to that of the dendrite and contains a large number of small vesicles and a few larger vacuoles approaching 0.1 μ in diameter. No granules of the ergastoplasm have been seen near the membranes of these vesicles. The present study has failed to demonstrate any specialized structure in the cytoplasm comparable to the cup-shaped "olfactory vesicle" of van der Stricht (2) or the marginal ring of Le Gros Clark (10–12). Occasionally, mitochondria are seen in the cytoplasm (Fig. 4). The plasma membrane of the olfactory rod follows an irregular course, and invaginations, seemingly continuous with the cytoplasmic vesicles, are often encountered, but, it has not been seen to form any specialized structure compatible with the observations of a marginal ring (12). The membrane, though irregular in its course, is continuous in locations where cilia extend from the surface (Figs. 3 to 5).

The number of cilia deriving from an olfactory rod has not been ascertained. Even in the most favorably oriented section, the number in any single rod process rarely exceeds three. The cilia protrude from different parts of the olfactory rod and are oriented at right angles to the surface, which accounts in part for the fact that only a few are seen in any particular section.

The cilia observed in OsO_4-treated tissues are structurally similar to those described by Fawcett and Porter (18) in the oviduct of the human and of the mouse. The cilia contain eighteen longitudinally oriented filaments arranged as nine pairs which are evenly spaced around the margin and two others which are centrally placed. The basal bodies are continuous with the central filaments of the cilium and extend into the cytoplasm of the apical portion of the olfactory rod. Occasional cross-striations are seen in the fibrils of the basal bodies and clusters of small vesicles appear in the nearby cytoplasm. It is of interest that, unlike ciliated regions seen elsewhere (18), the cytoplasm adjacent to the basal body is relatively devoid of mitochondria. Neither the marginal fibrils nor the transverse striations are seen following $KMnO_4$ fixation. No explanation for this interesting difference is available at present.

The Sustentacular Cell:

The supporting cell of the mucosa contains a larger nucleus than that of the receptor cell, and it lies nearer the apical pole than is the case in the latter cell. Since the supporting cell constitutes the most numerous cell type in the epithelium, in most tissue sections the supporting cell nuclei are clearly distinguishable from the deeper, less numerous receptor cell nuclei. It is possible to follow the distal process of the supporting cell from its cell body to its termination on the free surface of the mucosa. The most distinguishing characteristic, however, is the difference in cytoplasmic density as depicted in Figs. 4 and 5, which show sections through the apical portion of the mucosa.

The cytoplasmic organelles of the supporting cell have an unusual concentration. Most of them are located in the distal and in the proximal portions of the cell. In Fig. 6, which represents the region of the nucleus, relatively few formed elements occur. The tissue in this section was fixed with $KMnO_4$ and the cytoplasmic granular component is absent and only the membranous components remain. The cytoplasm of both the apical and basal parts of the cell is filled with a large number of elongated profiles of the endoplasmic reticulum oriented parallel with the long axis of the cell (Fig. 4). Situated along the outer edges of the endoplasmic reticulum are small dense granules as described by Palade (19). In Figs. 4 and 5 numerous mitochondria are seen in the dense cytoplasm of the apical portion of the cell. Their general shape varies from round to ovoid. Their fine structure is similar to that described for other cells. However, the cristae formed by folding of the inner lamina are less numerous and the mitochondrial matrix is more dense than that seen in mitochondria from other tissues. The cytoplasm of the apical portion of the cell contains a vast number of small vesicles and larger vacuoles. A Golgi apparatus is occasionally seen in the cell body lying apically with respect to the nucleus. Secretion granules have not been seen in the cytoplasm.

Comparison of Figs. 4 and 5 illustrates an interesting observation concerning the fixation of the mitochondria of the sustentacular cell. In these cells it can be seen that the mitochondria are regularly swollen (Fig. 5), whereas in the same section the mitochondria of adjacent receptor cells are reasonably preserved. This has been a consistent observation when $KMnO_4$ has been used as the fixative as contrasted with the excellent fixation of all mitochondria when OsO_4 has been employed (Fig. 4). It was originally suspected that the osmolarity of the $KMnO_4$ solution was responsible for this distortion, but variations in the concentration, temperature, pH, and tonicity of the solution gave invariably the same results.

The plasma membrane exhibits no outstanding feature at the proximal end of the sustentacular cell; it lies on a thin and delicate basement membrane. The apical tip of the cell shows a large number of microvilli which extend beyond the free margin of the mucosa (Fig. 3). Enmeshed in the microvilli numerous cilia are recognizable by their fine structure, and are derived from the receptor cells. The microvilli are devoid of the formed elements of the cytoplasm except for small vesicles which occur near their basal ends. The most distal portions of each microvillus contains an amorphous appearing cytoplasm.

Terminal bars, similar to those described in other epithelia (20), are seen as dense thickened regions on the plasma membranes of both the olfactory neuron and an adjacent sustentacular cell (Fig. 4). In such regions accumulations of mitochondria regularly occur, as well as aggregates of small cytoplasmic vesicles distributed in rows and clusters.

It has frequently been observed that a receptor dendrite, quite near the surface of the epithelium, appears surrounded by cytoplasm of the supporting cell (Fig. 8). In Fig. 9, the plasma membrane of the sustentacular cell may be seen to reflect around the dendrite in a fashion entirely analogous to the mesaxon arrangement of the Schwann cell and the unmyelinated fiber described recently by Gasser (17). The olfactory bipolar receptor cell is ensheathed, therefore, through its entire distal course, until it reaches the free epithelial surface as the olfactory rod.

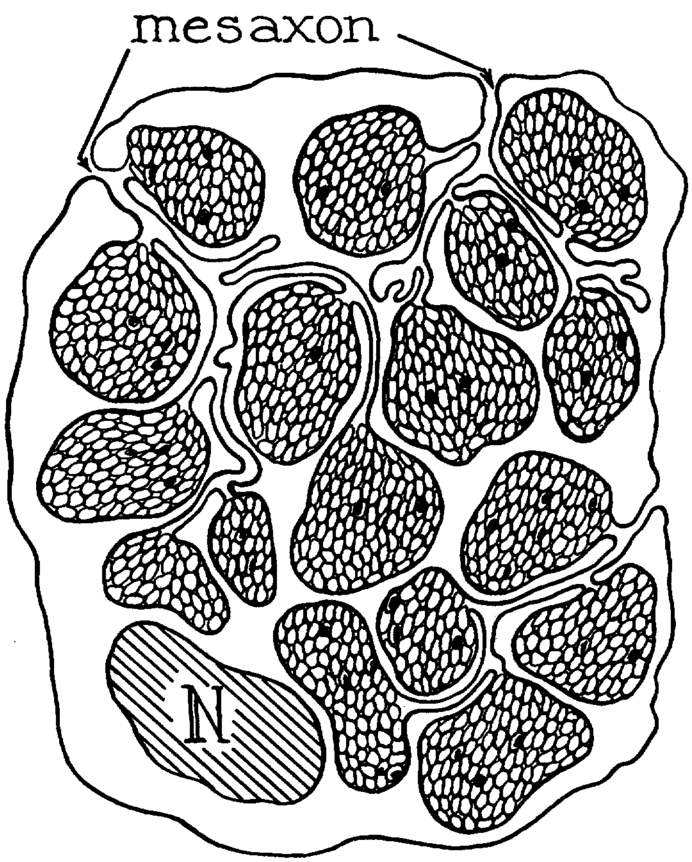
The Basal Cell:

The basal cell has essentially the same characteristics as the sustentacular cell and is characterized chiefly by its location near the thin basement membrane. It is smaller than the supporting cell, but its fine structure is much the same. It has a dense cytoplasm, containing endoplasmic reticulum, cytoplasmic granules, mitochondria, and large dense granules (Fig. 7). The mitochondrial matrix is less dense and contains more numerous cristae than mitochondria of the supporting cell. The mitochondria of the basal cell remain remarkably well preserved with $KMnO_4$ fixation, in contrast to the swollen appearance of those in the sustentacular cell. Gasser (17) has recently shown that the basal cell also exhibits a "mesaxon" investing the central processes of the olfactory receptors. However, in the present preparations this relationship was infrequently seen.

The Olfactory Nerves:

The central (proximal) processes of the olfactory receptor cells are the unmyelinated axons which comprise the fila olfactoria. Fig. 6 shows one such axon with its ensheathing sustentacular cell. These axons penetrate the basement membrane of the epithelium and reach the Schwann cell in the submucosa. It has been mentioned above that the central processes of the receptor cells are extremely tenuous and follow a tortuous course to the basement membrane. In addition, the cytoplasm of the sustentacular cell is extremely dense in the regions where its processes rest upon the basement membrane. These factors make it extremely difficult to identify accurately a locus in which the axon crosses the level of the basement membrane and reaches the Schwann cell. This region has been described by Gasser (17) who states that "at the delivery point the Schwann membrane becomes continuous with the plasma membrane of the basal cell." This statement implies that the Schwann cell and basal cell constitute a syncytium. Despite the difficulty of visualization, this seems unlikely. In any event, the individual axons become grouped and form small fascicles in the submucosa (Fig. 10) and then enter the cribriform plate of the ethmoid bone. These fascicles then group with others to form the fila olfactoria (Fig. 11) which enters the olfactory bulb and synapses in the olfactory glomerulus.

The axons comprising the olfactory nerve are extremely small as can be seen in Fig. 13, which shows a typical section through a fascicle of olfactory nerve fibers. The mean diameter of these fibers is about 0.2 μ. Indeed, many of the fibers have diameters less than 0.1 μ. Each of the fibers possesses an axolemma about 100 A thick which encloses a rather light axoplasm. The axoplasm contains occasional small mitochondria and a number of small vesicles (Fig. 13). A



TEXT-FIG. 1. Schematic representation of the relationship of the olfactory nerve to the Schwann cell. Several nerve fascicles share a common mesaxon, which is formed by the plasma membrane of the Schwann cell whose nucleus (*N*) is located at the lower left. Since each fascicle contains numerous fibers, only those located at the margin are near the Schwann cell membrane. The axons occupying a central position in the fascicle are flanked on all sides by other fibers. Thus a mesaxon is provided for each fascicle rather than for each individual axon.

small space of about 100 to 150 A separates the individual axons from each other and from the plasma membrane of the Schwann cell.

The relationship of the Schwann cell membrane to the nerve fibers is unlike that seen in other non-myelinated axons. The Schwann plasma membrane forms a mesaxon for small groups of fibers (fascicles). Text-fig. 1 is a schematic representation of this relationship. In Fig. 10 the cell membrane of a Schwann cell in the submucosa is seen forming mesaxons for fascicles which are separated from each other by relatively large areas of Schwann cell cytoplasm. In contrast, Fig. 11 represents a section in the region of the olfactory bulb. In this location the Schwann cell cytoplasm is scant, most of the space being occupied by the attachment to numerous nerve fascicles. Fig. 12 represents a higher magnification of a restricted portion of the previous figure demonstrating several mesaxons (see arrows).

The olfactory glomerulus presents a complex array of fine olfactory nerve terminations, mitral cell dendrites, and neuroglial processes. Only a small percentage of these elements can be identified at the present time. Degeneration experiments are in progress which may help in elucidating this region (14).

DISCUSSION

The observations of this study are in agreement with the essential findings of Bloom and Gasser (17). However, some differences are evident. For example, it has been demonstrated that the receptor cell is light in appearance and contains endoplasmic reticulum which is extremely tenuous in form and concentrated only in slight amounts. The sustentacular cell is characterized by a complex reticulum, highly concentrated and arranged in rows. These observations are in agreement with those of Porter (26) for the main part, but are somewhat at odds with those of Gasser (17). The formed elements of both the receptor and the supporting cell cytoplasm are concentrated at the proximal and distal ends with a paucity of elements in the region of the nucleus. Precise orientation of a section parallel to the long axes of the cells in the epithelium is therefore imperative. Oblique or tangential sections through the epithelium can give an erroneous impression of the distribution of the cytoplasm in the various cell processes.

Electrophysiological experiments (6–9) and morphological investigations (10–13) suggest differences in the olfactory receptors. However, the receptors seen in the electron microscope reveal no significant structural differences. Whether the number of cilia per receptor cell constitutes a significant difference has not been established and only a very complete series of serial sections will be able to answer this question.

Recently, Adrian (21) reported that oscillations in potential were obtained from the olfactory epithelium in the rabbit. The electrical waves indicated an intermittent synchronous activity in certain groups of receptors. Although this suggests possible nervous connections between the receptors, no such contiguity was seen in the electron microscope. The morphological evidence suggests that the olfactory fascicles may be the locus of such activity. In the fascicle the olfactory fibers are grouped closely, with only small spaces (100 to 150 A) separating each fiber from its neighboring axon. Stimulation and subsequent depolarization of one or more such axons within a fascicle would seem likely to depolarize the membranes of adjacent fibers. An alternative explanation might be derived from the arrangement of the olfactory glomerulus (22) where oscillations might be generated as dendritic potentials in the extensive glomerular regions.

Examination of the sustentacular cell of the mucosa suggests a much more active function for this cell than its name implies. In degeneration experiments it has been observed that the sustentacular cell undergoes rapid changes in response to injury of the adjacent receptor cells (14). This cell, according to Le Gros Clark (12), is also capable of active phagocytosis of degenerating debris. The many vesicles and vacuoles seen, particularly near the apical surface of the cell, suggest an active role in pinocytosis. The invariable swelling of the mitochondria which results following $KMnO_4$ fixation cannot be adequately explained at the present time.

The supporting cell forms, moreover, the primary sheath for the olfactory neuron. The receptor cell is sheathed throughout its course in the epithelium. Its dendritic process is ensheathed with the mesaxons of the sustentacular cell and is central process is invested by the plasma membranes of the sustentacular and the basal cells (17). Only the olfactory rod remains bare. When the axon reaches the Schwann cell in the submucosa, several fibers collect to form fascicles sharing a Schwann membrane. The number of fibers in the fascicles raises the question of whether each fiber seen is a direct continuation of the central process of a single olfactory receptor. Counts by Gasser (17) and Le Gros Clark (12) demonstrate nearly a one-to-one ratio between receptors and olfactory nerve fibers.

Identification of the various elements in the olfactory glomerulus has proved to be a difficult problem. Studies of this region during degeneration of the olfactory receptors may help to elucidate the various elements and the accessibility of the olfactory apparatus makes it a particularly useful region for the study of nerve degeneration. Such studies are currently underway.

SUMMARY

The olfactory receptor cell is characterized by a distal process (the dendrite) which terminates in the olfactory passage as the olfactory rod. The olfactory rod is provided with numerous cilia which are similar in structure to those seen in other tissues. The central processes of the bipolar cell constitute the fila olfactoria.

The cytoplasmic organelles of the sustentacular cell are concentrated at the apical and basal ends of the cell with a paucity of cytoplasmic elements in the region of the nucleus.

The plasma membrane of the supporting cell forms a mesaxon for both the dendrite and axon of the bipolar cell. Terminal bars are present in the epithelial cells.

The axons constituting the fila olfactoria form fascicles which are ensheathed

by mesaxons of adjacent Schwann cells. Thus the olfactory neurons are ensheathed throughout their course by the membranes of sustentacular and Schwann cells.

Observations of the olfactory mucosa with the electron microscope are discussed with respect to recent electrophysiological studies.

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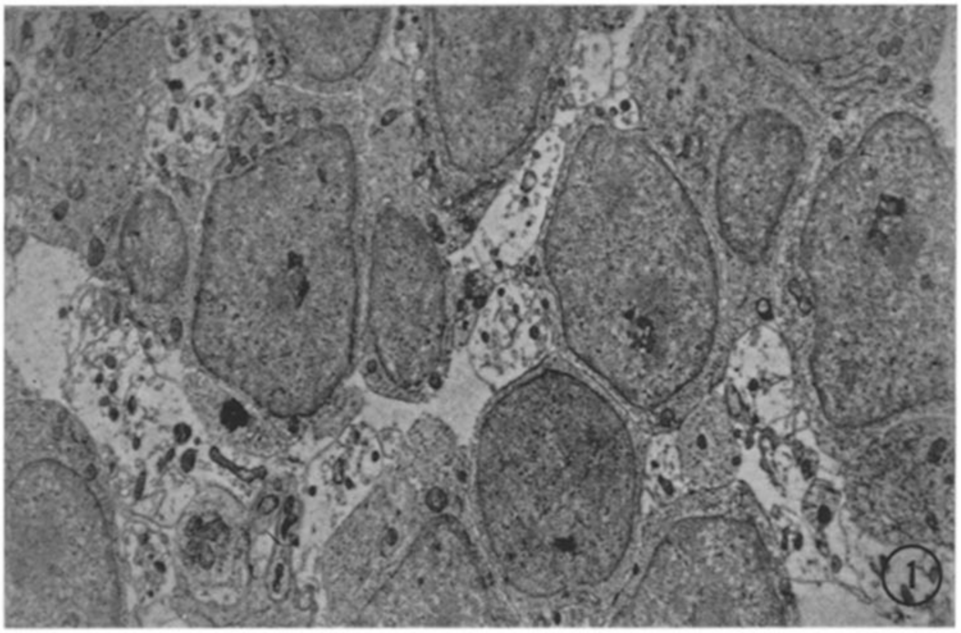
EXPLANATION OF PLATES

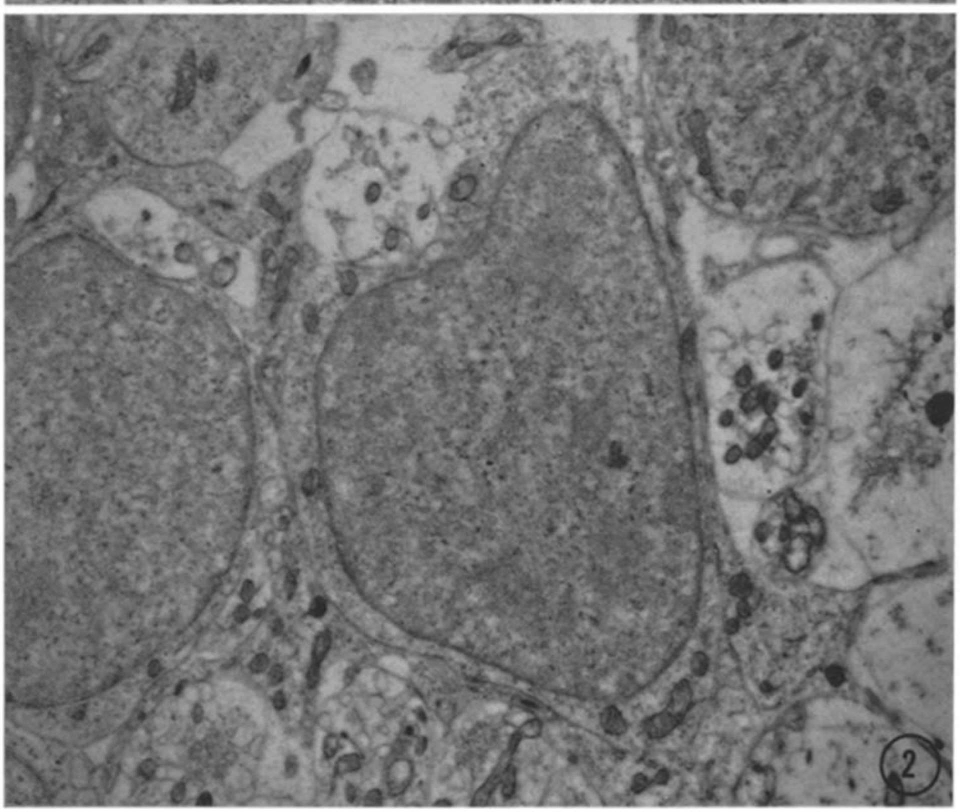
PLATE 265

FIG. 1. Region of the olfactory epithelium in which the receptor cell nuclei predominate. Note the scanty cytoplasm which contains the usual formed elements. Elongated profiles of the endoplasmic reticulum, however, are not conspicuous. × 4500.

FIG. 2. Higher magnification of the perikaryon of a receptor cell illustrating the paucity of cytoplasmic membranes in this region. In the upper right hand corner the section passes tangentially through the perikaryon of another receptor missing the nucleus. The endoplasmic reticulum is tenuous and slight in over-all amount. However, small cytoplasmic granules and vesicles are evident.

OsO_4 fixation. × 8500.





(de Lorenzo: Olfactory mucosa and nerve)

Plate 266

Fig. 3. Electron micrograph of the olfactory epithelium fixed with $KMnO_4$. Two light processes can be seen as the dendrites (*D*) of the olfactory bipolar cells. The peripheral processes of these dendrites are seen to extend beyond the free surface of the epithelium. The adjacent darker cells are the sustentaculars. The apical end of these cells terminate in numerous microvilli (*V*) which project into the nasal passage. Note that although the mitochondria of the dendrite (*D*) located at the extreme right are preserved in a satisfactory manner, the mitochondria of the neighboring supporting cells are uniformly swollen. × 12,500.

Fig. 4. Section through the olfactory epithelium following OsO_4 fixation. Two light processes are identified as the dendrites (*D*) of the receptor cells. The distal process of olfactory rod (*OR*) can clearly be seen extending beyond the free surface. Two cilia extend from the olfactory rod located at the left. The mitochondria (*M*) of the dendrite are preferentially located at the apical end of the dendrite and only rarely are any mitochondria seen in the olfactory rod such as is the case in the olfactory rod at the right. Vesicles of various sizes are seen in the cytoplasm of the dendrite and rod.

The sustentacular cells (*S*) are readily identified as the much denser cell type, located on either side of the receptors. Their cytoplasm contains a dense concentration of elements of the endoplasmic reticulum (*E*) and numerous cytoplasmic granules. Mitochondria are seen at the apical portions of the cells. It is to be noted that these mitochondria are not distorted in any way comparable to those of similar type following $KMnO_4$ fixation (see Fig. 1). Microvilli and terminal bars (arrow) are noted. × 17,100.

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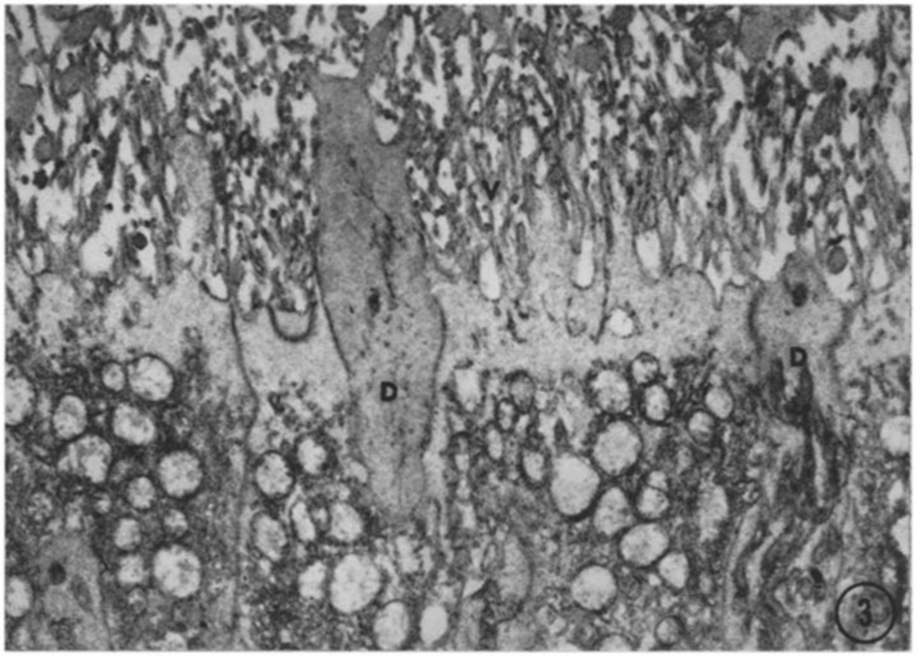
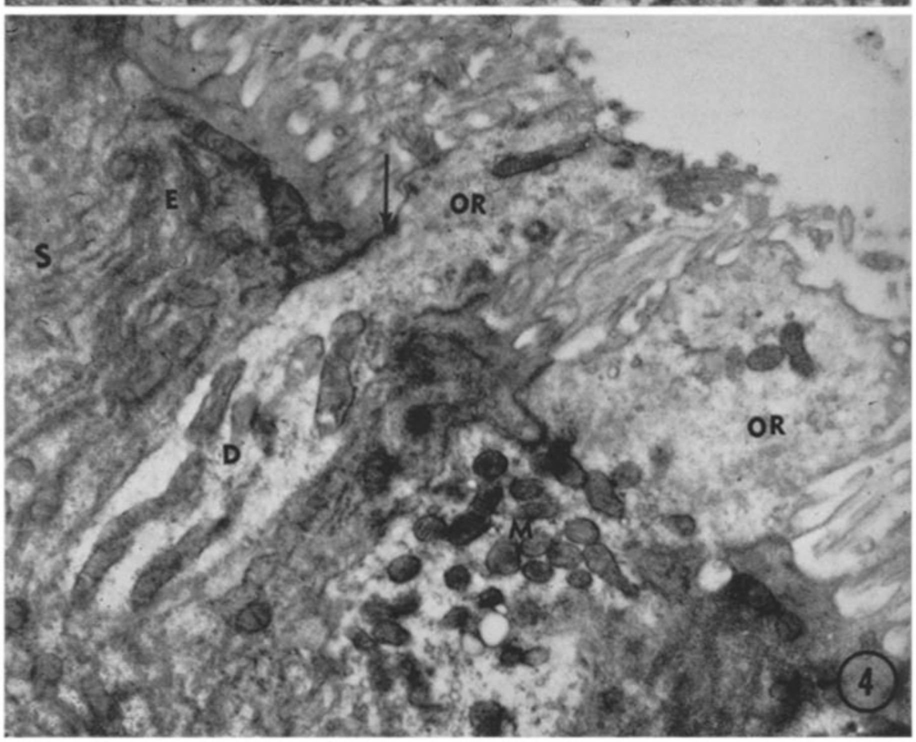
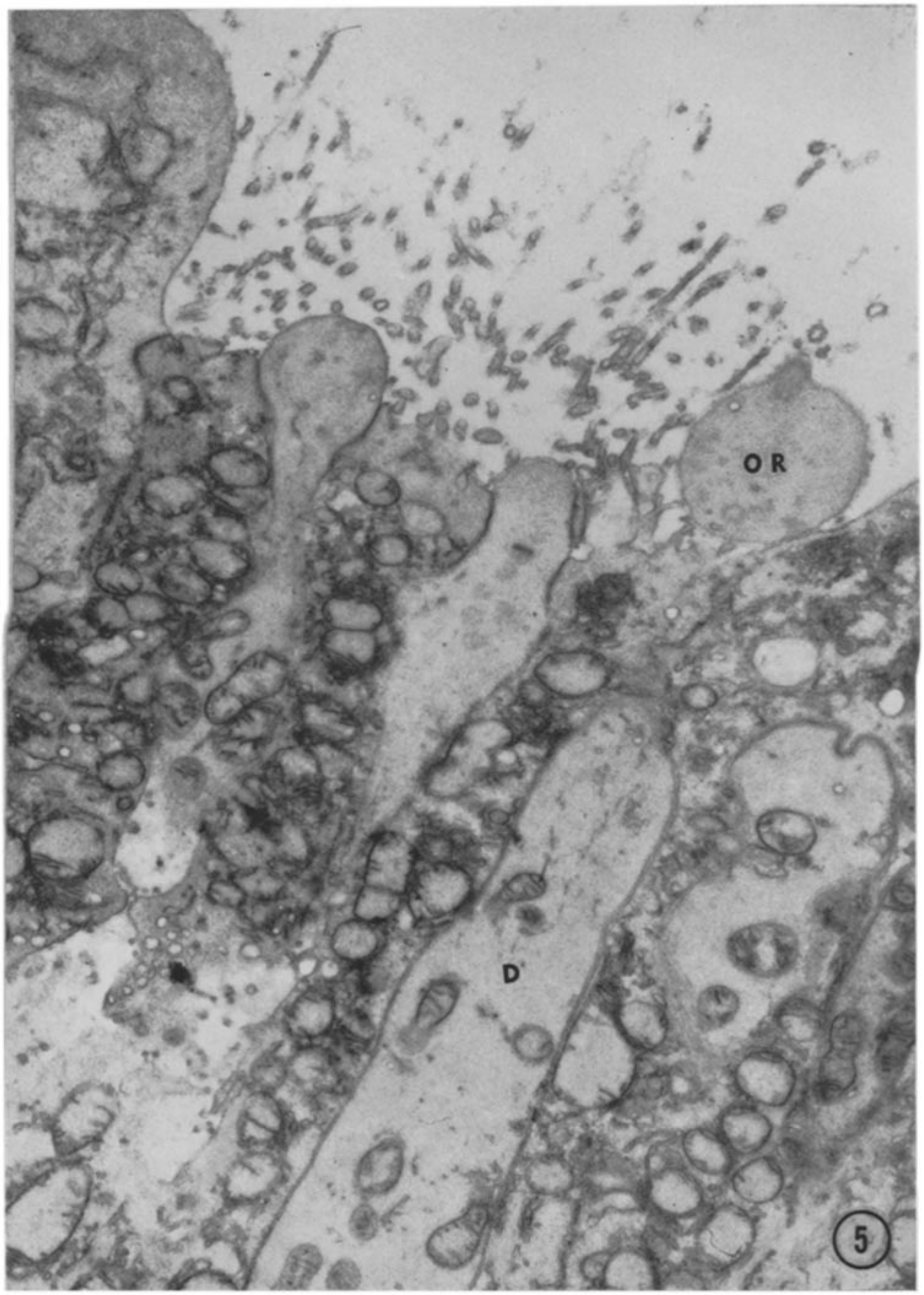




(de Lorenzo: Olfactory mucosa and nerve)

PLATE 267

FIG. 5. Micrograph of a section through the olfactory epithelium after fixation with $KMnO_4$. The receptor cell dendrites (*D*) are clearly recognizable. Several olfactory rods (*OR*) are noted. The cytoplasm of the apical portion of the sustentacular cells is extremely dense, being filled with numerous distorted mitochondria and vesicles of various sizes. This figure is to be compared with Fig. 6, which demonstrates a much less dense cytoplasm in the region of the nucleus of the supporting cell. × 18,000.



(de Lorenzo: Olfactory mucosa and nerve)

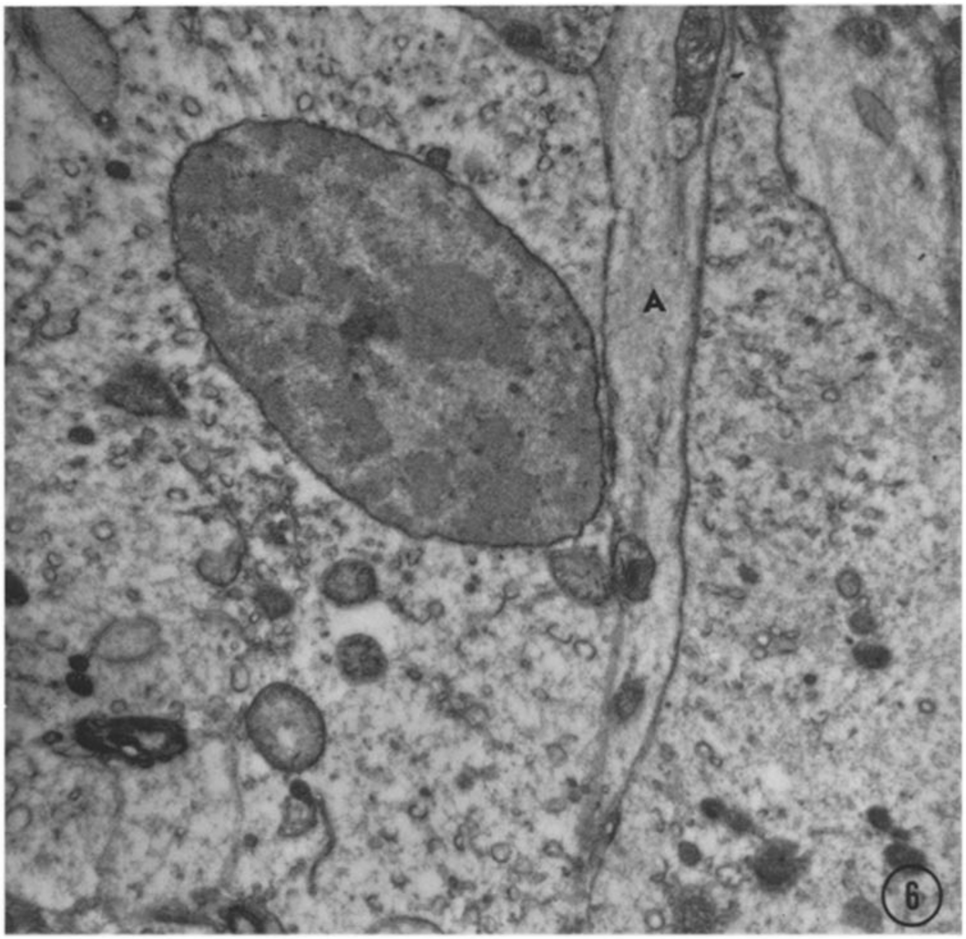
PLATE 268

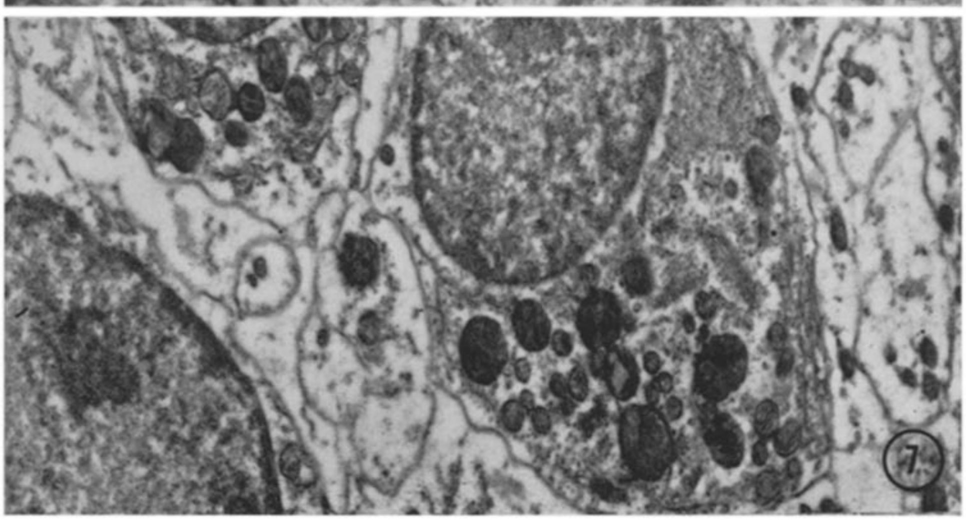
FIG. 6. Electron micrograph demonstrating a basal region of the epithelium. A small central process (*A*), the axon of a receptor cell, passes downward on its way to the basement membrane. Several interesting features are noted. The axon is ensheathed by the sustentacular cell whose nucleus is located in the middle of the section. Mitochondria are seen in the axoplasm of the nerve fiber. The cytoplasm of the supporting cell demonstrates a paucity of formed elements in the region of the nucleus. Numerous small vesicles and a few distorted mitochondria are present, but the cytoplasmic density is notably less in this area as compared with the apical regions of the cell. (See Figs. 4 and 5.)

$KMnO_4$ fixation. $\times$ 28,500.

FIG. 7. Section through the olfactory epithelium near the basement membrane. The section has passed through at least two basal cells. Their cytoplasm is characterized by a dense concentration of granules, a few well preserved mitochondria, endoplasmic reticulum, and chiefly large dense granules. The basement membrane lies below and out of the plane of section.

OsO_4 fixation. $\times$ 9000.





(de Lorenzo: Olfactory mucosa and nerve)

Plate 269

Fig. 8. The apical portion of the olfactory epithelium demonstrating one of several locations where a distal receptor process (*P*) seemingly passes through the cytoplasm of a supporting cell.

$KMnO_4$ fixation. × 13,000.

Fig. 9. A region comparable to that in Fig. 8. In this section the distal processes or dendrites (*D*) of the bipolar cells are ensheathed by the adjacent sustentacular cells. Mesaxons formed by the plasma membranes of the supporting cells are designated by arrows.

$KMnO_4$ fixation. × 13,500.

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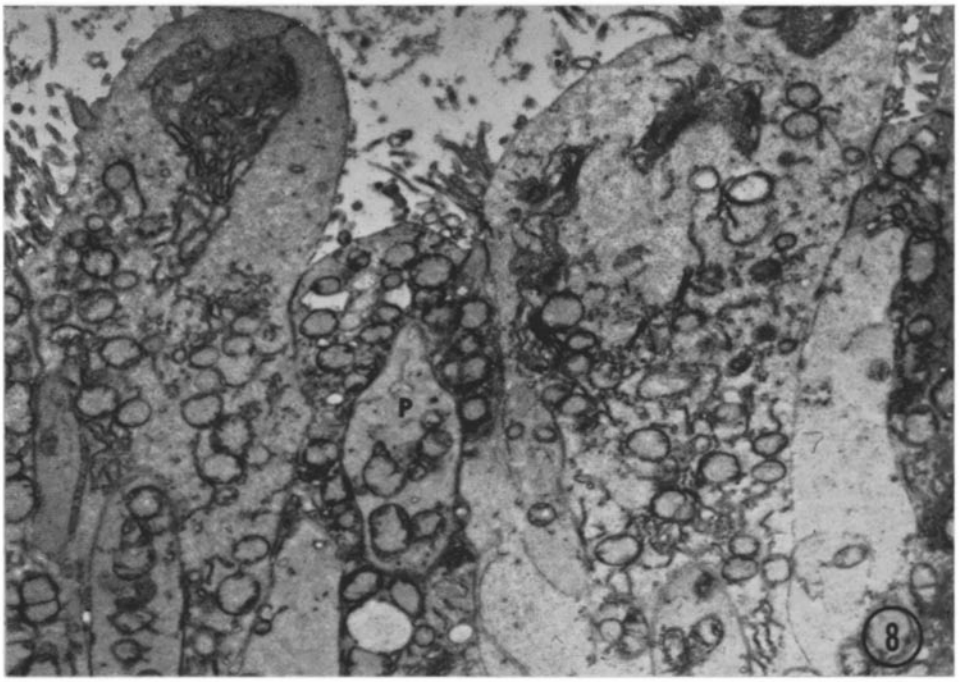
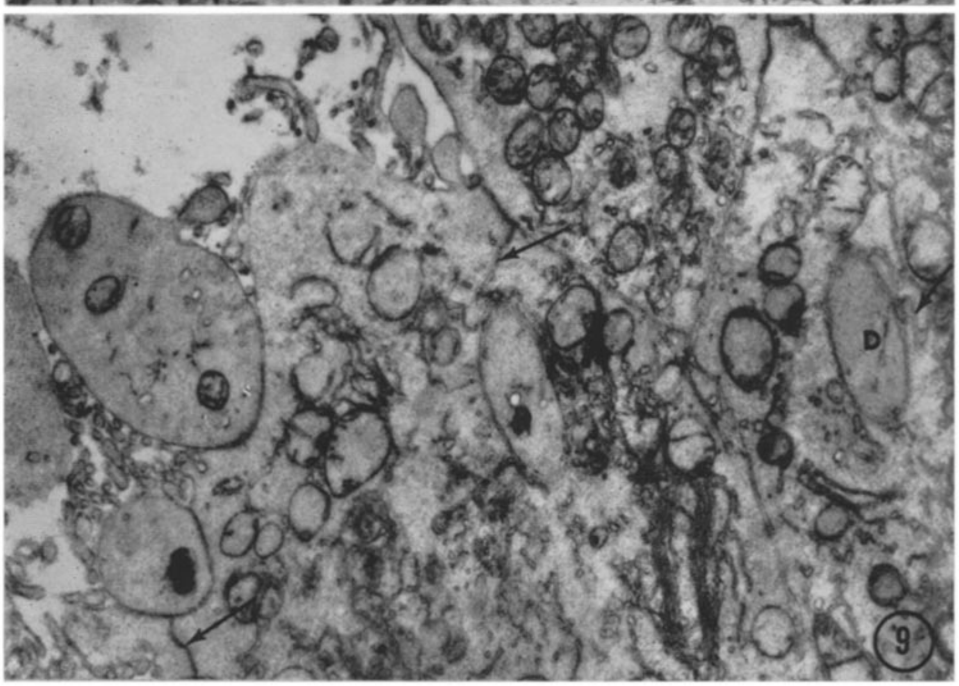




(de Lorenzo: Olfactory mucosa and nerve)

Plate 270

Fig. 10. Micrograph of a section through a group of olfactory axons in the submucosa near a basal cell (*B*). A very tenuous basement membrane is seen between the basal cell and the Schwann cell whose cytoplasm (*SC*) is extremely sparse. The axons are grouped into small fascicles, and the fascicles are in turn ensheathed by mesaxons (arrows) of the Schwann cell membrane. Note that the fascicles are separated from each other by Schwann cell cytoplasm, although the axons within a fascicle are closely packed. In the lower right the connective tissue space (*CT*) contains collagen.

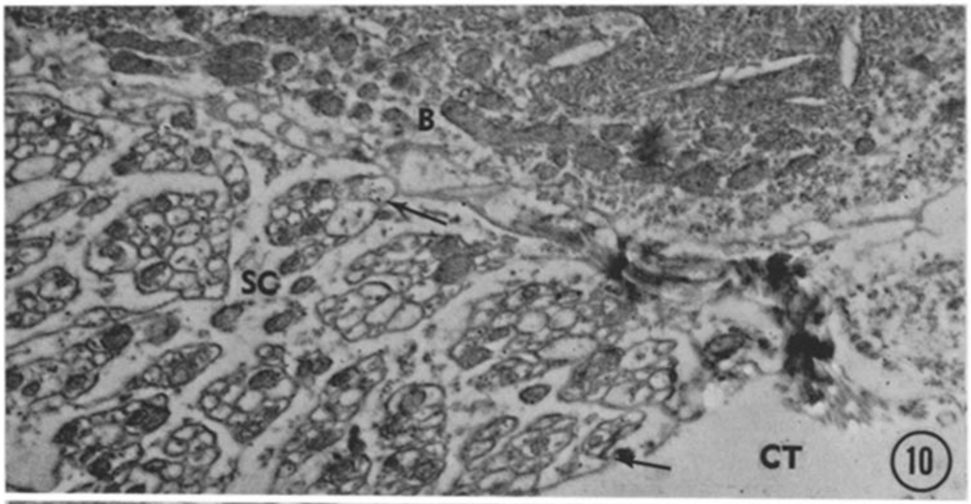
OsO_4 fixation. × 12,500.

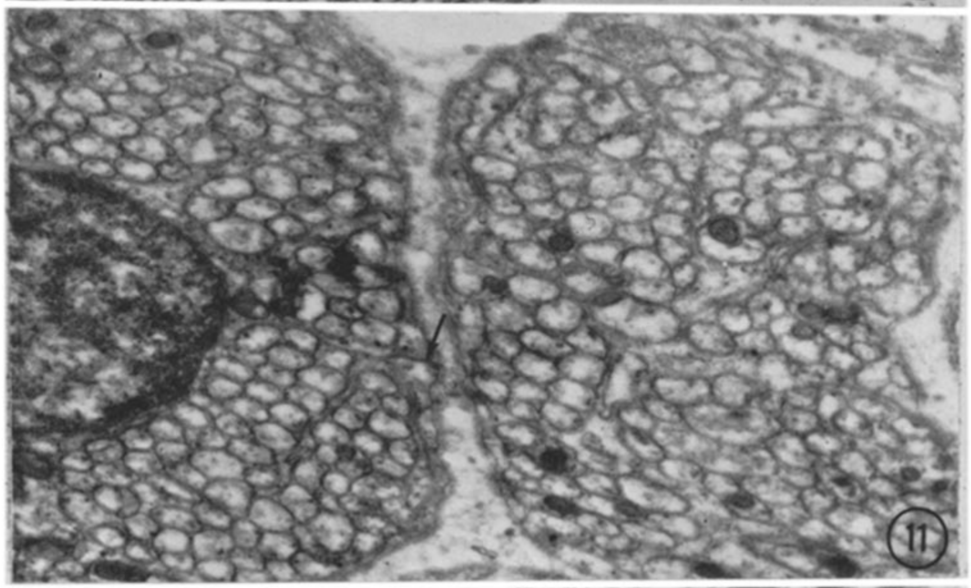
Fig. 11. Section through the fila olfactoria as it enters the olfactory bulb. A Schwann cell nucleus is located at the left. A mesaxon, formed by the Schwann cell membrane, is designated at the arrow. Note that the individual fascicles are much more closely packed and more numerous than in Fig. 10, making the Schwann cytoplasm less evident.

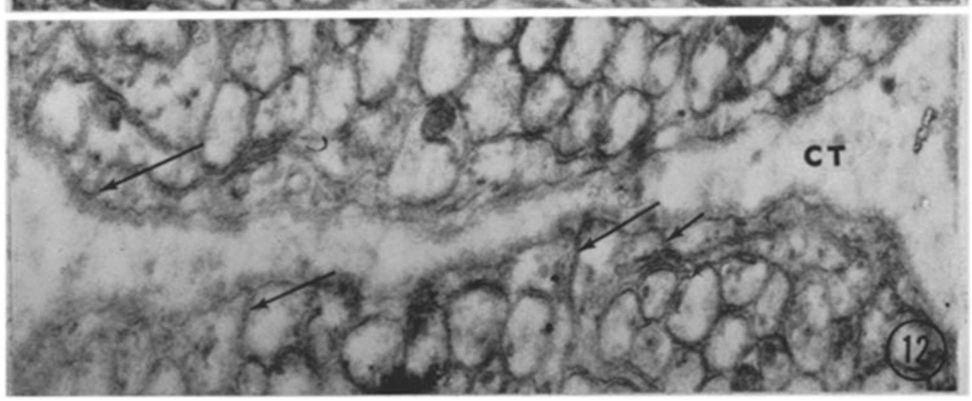
OsO_4 fixation. × 20,000.

Fig. 12. Higher magnification of a restricted region of Fig. 11, showing the plasma membrane of the Schwann cell as it forms mesaxons (arrows) for the fascicles.

OsO_4 fixation. × 33,500.







(de Lorenzo: Olfactory mucosa and nerve)

PLATE 271

FIG. 13. A restricted region of an olfactory nerve fascicle demonstrating the relative sizes of the unmyelinated fibers (*UF*) of the group. The mean diameter of the nerves is about 0.2 μ. Several fibers, however, are 0.1 μ and smaller in diameter. A rather clear axoplasm containing an occasional mitochondrion is bounded by a single axolemma about 100 A thick. Small spaces 100 to 150 A wide separate the fibers from each other. A Schwann cell nucleus (*SN*) is located at the right. The scanty Schwann cytoplasm (*SC*) contains a few membranes and granules.

OsO_4 fixation. $\times$ 28,500.

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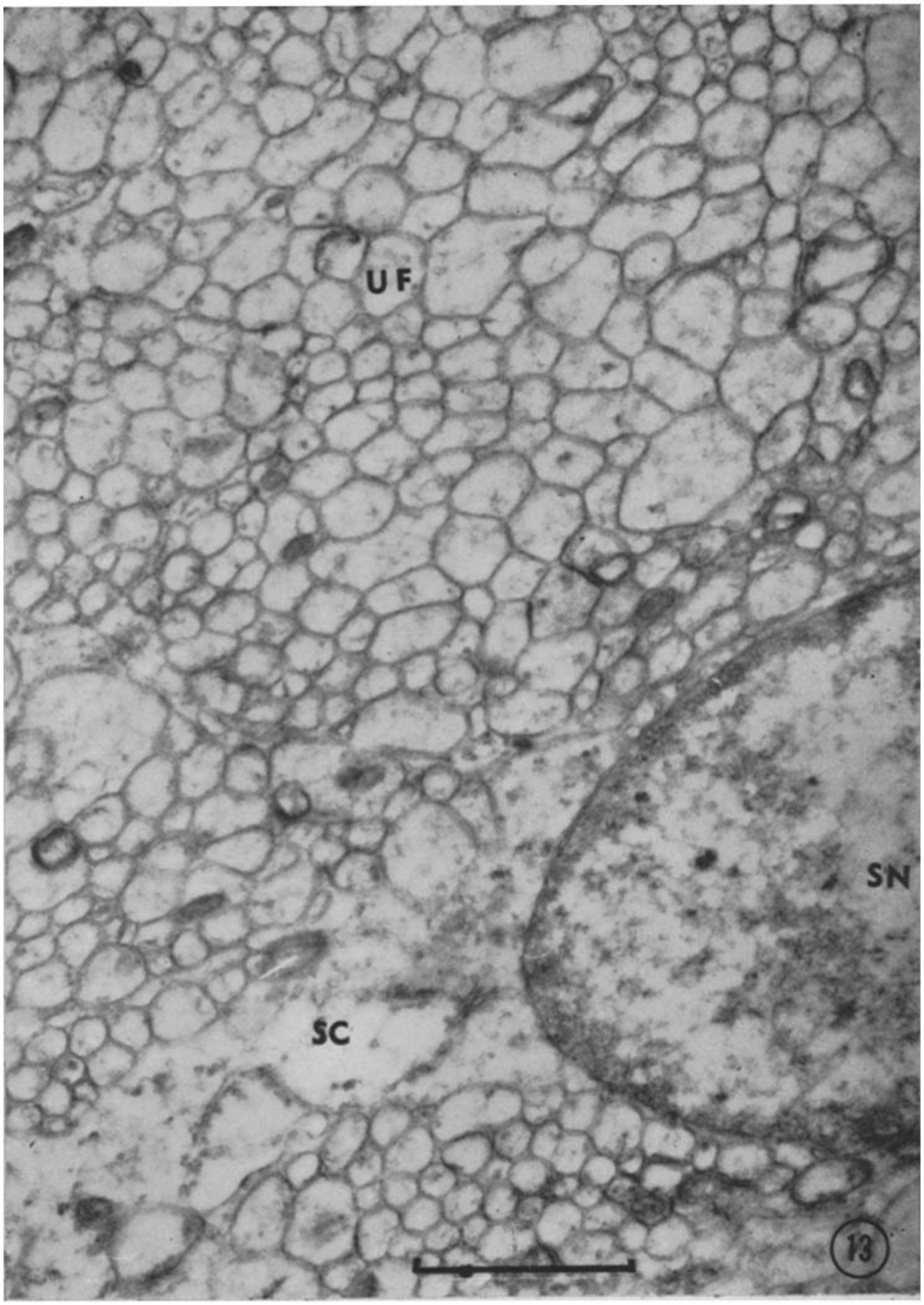

(de Lorenzo: Olfactory mucosa and nerve)