

A CONTRIBUTION TO THE KNOWLEDGE OF THE OLFACTORY APPARATUS IN DOG, CAT AND MAN.¹

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WITH 17 PLATES AND 1 FIGURE.

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STATEMENT OF THE PROBLEM.

1. Position, extent and character of the olfactory epithelium in (a) dog; (b) cat; (c) man.
2. The position and nature of the olfactory cells.

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3. The olfactory nerve fibers as central prolongations of the olfactory cells and the character of their termination in the olfactory bulb.
4. The relations of the olfactory nerve fibers in their passage from the sensory epithelium to the olfactory bulb.
5. The position of the vomeronasal or Jacobson's organ and its sensory epithelium and nerves.
6. The relations and terminations of the branches of the trigeminus in the nasal mucosa.

As will be more fully stated in the body of the paper, I have employed in this work the methods necessary for showing clearly the gross anatomy, and for the fine anatomy the three standard histological methods: (1) Gold chloride; (2) chrome silver or Golgi method, and (3) the methylene blue method.

Except where otherwise stated, the results given depend upon repeated gross dissections and upon clear demonstrations by each of the histological methods. That is, no statement has been made which has not been abundantly verified.

Naturally the quality of the human material available did not make all the histological demonstrations and verifications so extensive as for the dog and cat.

1-3. I have demonstrated in the clearest possible manner that the olfactory sensory cells are present in the slightly pigmented mucosa on the conchæ and septum usually designated as olfactory, and that the sensory cells are true nerve cells and their central prolongations are the olfactory nerves, which extend to the olfactory glomeruli in the olfactory bulb. This work is confirmatory of the published results briefly summarized in the historical part of this paper.

My results as to the extent of the Olfactory Region in man differ considerably from those of von Brunn, the latest and most quoted authority upon this point. He shows only a small area upon the septum and superior concha as olfactory (Figs. 28, 29). My dissection shows that the olfactory nerves extend over a much larger area, about one-third of the septum and nearly the whole of the superior concha (Figs. 30, 31).

4. With regard to the relation of the olfactory nerves in their passage from the olfactory cells to the olfactory bulb, the results of my work are strikingly different from the published statements of human and comparative anatomists from the time of Scarpa to the present.

Naturally the conditions are more completely described for man than for the lower animals. The figures of Leveillé have been and still are

frequently copied into text-books (E. G. Barker's Laboratory Manual of Anatomy, 1904; Quain's Organs of the Senses, 1906) and represent pictorially the opinion of anatomists as to the true relation.

Instead of a plexus of the olfactory nerves I have found that the nerves extend in non-anastomosing bundles to the olfactory bulb. All appearance of anastomosis being due (*a*) to a crossing of the bundle of nerves or (*b*) to a net-like arrangement of the connective tissue or blood vessels.

5-6. The position of the vomeronasal organ and its innervation by the olfactory and 5th nerves have been shown in gross preparations of dog and cat. In histological preparations the sensory cells of this organ with their nerves have been demonstrated in the cat and mouse. Branches of the anterior ethmoidal nerve have been traced among the olfactory nerves of the conchæ in dog and cat; their terminations among the folds were not found in gross specimens.

The naso-palatine nerve was found on the septum in all gross preparations. Nerves with free terminations were seen in histological specimens, both on the nasal septum and in the conchæ; it is thought that these are the endings of the 5th nerve.

These facts are in agreement with the results of other workers.

HISTORICAL SUMMARY.

The olfactory region has been a subject of special investigation for many years. Various opinions concerning the endings of the olfactory nerves have been published. Some views have been disproven, but as early as 1856 Max Schultze had established with considerable certainty the true conditions of the endings of the olfactory nerves in the nasal mucosa. A review of the literature will give the present standpoint.

Eckhard, 1855, found that the olfactory epithelium of the frog was formed of two kinds of cells, a cylindrical cell and a fusiform cell. These were morphologically and physiologically distinct. The cylindrical cell, an epithelial cell, had a central bifurcating end which terminated in the subjacent layer. The fusiform cell was entirely different from the epithelial cell. He suspected a difference in function, and thought, without doubt, that one was the true termination of a nerve fibril; but he did not say which one.

Ecker, 1855, published his observations on the olfactory mucosa of man and some mammals. He saw two kinds of cells, a cylindrical cell

and a fusiform cell. The cylindrical cells reached the free surface and were connected, according to Ecker, by the central prolongations with the olfactory fibrils. These he called the true olfactory cells. The fusiform cells, replacement cells, situated at the base of the epithelium never reached the free surface. These replacement cells were simply stages in the development of the olfactory cells. Thus there was, according to Ecker, only one kind of cell, but in different developmental stages.

Schultze, 1856, worked on man, mammals, birds and amphibia. He found three kinds of cells, olfactory cells, epithelial cells and stellate cells. The epithelial cell was long, with a prismatic peripheral end. The central end was a short process and was connected with neighboring epithelial cells through side processes. These cells were pigmented but not ciliated. Between the epithelial cells he found cells of a peculiar chemical reaction. The cell bodies were round and had two processes, one reaching the free surface of the epithelial cells and the other passing to the connective tissue. This central process was the finer and could be recognized by the enlargements. The peripheral process was wide, at first, but tapered quickly and was then the same width to the surface. It bore at the end six to ten long brush-like hairs which were free in the air current of the nose. He describes each epithelial cell as surrounded by at least four to six of these hair cells.

In a comparison of these peculiar fiber cells of the olfactory region with other known cell forms, he first emphasizes the fact that in no other epithelial layer, either in the nose outward from the olfactory region, or back in the air tubes, is a trace of such varicose fiber cell found. The stellate cells, which lie under and between the surface cells, do not have the form, length or nature of the other cells of the olfactory region.

He believes the nerve cells of the retina to be the most favorable for comparison with these cells. By a comparison of these with the bipolar cells and by a comparison of the chemical reaction of the two cells, it is highly probable, according to *Schultze*, that these cells are also ganglion cells. He adds that comparative researches have made it as good as certain that the varicose fiber cells of the olfactory region are nerve cells. It, however, lacks proof of a direct connection with the fiber of the olfactory nerve. He concludes by saying that it is highly probable that the varicose fiber cells are the peripheral ends of the olfactory nerves. It is to these cells, and not to the epithelial cells, as *Ecker* thought, that the name olfactory cell should be given. These cilia-

bearing cells serve both to collect the molecules of odorous substance and to serve directly in their perception.

In 1862 he still had never seen the olfactory fibers connected with the bipolar cells, but believed there was no ground to doubt this, and says: "The future will prove this view through observation."

Exner, 1872, alone disagreed. In his work on amphibia, birds and mammals, he could find all intermediate stages between epithelial and olfactory cells; the epithelial cells had all the characters attributed to olfactory cells. He believed that the olfactory nerve fibers reached the superficial connective tissue and terminated in a special greatly reticulated layer, the subepithelial network. From this network pass two kinds of fibers, one of epithelial cells, one of olfactory cells. This network forms, with the two kinds of cells, the terminal apparatus of the olfactory nerve. Exner says: "It would be difficult to say whether all parts of this apparatus serve in the same degree in the olfactory perception."

Cisoff, 1874. By use of isolation methods, Cisoff claims to have seen the nerve cell with a long central varicose process, and also to have seen the connection of these cells with nerve bundles. His work, however, seems not to be credited.

von Brunn, 1875, worked on cat, dog, rabbit and sheep. He found the epithelial cells and the olfactory cells. The olfactory cells were pear-shaped with a round nucleus. Beneath the epithelium the central process joined with other processes to form a network in which stellate cells were found. The olfactory nerves were broken up in the same manner in the upper part of the mucous membrane. He did not see the direct connection of these fibers with the central processes of the olfactory cells, and says, "I can only declare such a connection as possible." Both these and the retinal cells are, according to von Brunn, bipolar sense cells with similar function. For mammals, he describes a *membrana limitans olfactoria*, which covers the epithelial cells as a whole. The peripheral processes of the olfactory cells project through pore-like openings in the membrane.

In 1880 von Brunn modifies his views concerning this *membrana limitans*, and thinks it lies underneath the "rudimentary cilia" of the epithelial cells.

Ehrlich, 1886, by methylene blue established with certainty the direct connection of the olfactory fibers and the bipolar cells of the mucosa. This stain is very transitory and lasts only a short time, so the work was not credited until confirmed by the Golgi method.

Arnstein, 1887, confirms Ehrlich's work. He saw the olfactory cells with the central thread-like processes passing into the nerve bundle of the submucosa. He claims also to have seen the same thing in the gold chloride preparations of Cisoﬀ and in the isolated osmium preparations of Dogiel. He, like Ehrlich, used methylene blue.

Ranvier, 1889, found three kinds of cells in batrachians. His general descriptions of these do not differ from those of other investigators. In the frog, salamander, triton, dog and rabbit, Ranvier found a plexus formed from the olfactory fibrils. The central prolongations of the olfactory cells appeared to connect with this plexus. Ranvier claims that the subepithelial plexus described by Exner was above the basal membrane, while the one he found was beyond the basal membrane and hence in the connective tissue. Ranvier does not believe that the fibrils of the olfactory nerve continue directly with the central prolongations of the olfactory cells. He adds that all histologists who pretend to have seen this are victims of a delusion.

Grassi and Castronovo, 1889, worked on dogs from two to six years old. They demonstrated by the Golgi method an olfactory cell with the peripheral process and with the central end connected with a varicose nerve fiber. This fiber is shown as dividing and subdividing in the connective tissue. In one figure two neighboring cells joined. They were undecided whether the supporting cells were such or whether they were also connected with the nerve, but they state "the connection of these cells with the nerve fiber has never been seen," nor have they seen a connection between this supporting cell and the olfactory cell. In the "limiting zone," at the boundary between the respiratory and olfactory epithelium, they find many varicose nerve fibers which are described as ramifying in the deeper and middle layers of the epithelium. From the many horizontal branches there are some which pass up close to the surface of the epithelium and some which end in the cylindrical olfactory cells. The former may end free, but "this is still not determined." They consider it probable that these fibers are olfactory fibers, but they cannot prove it.

They also describe for the cylindrical cells of this zone a varicose central process which appears like the nerve fiber. In some cases these have unmistakable signs of nerve fibers, and one figure shows cylindrical cells joined by these branching processes.

Van Gehuchten, 1890, by his work on the rabbit, has confirmed Cajal's work, and says that Cajal's figures are an almost exact representation

of his preparations. The olfactory fibers unite into thick bundles, but, according to Van Gehuchten, the individual fibers do not vary in size during their entire length.

They are rarely varicose; the varicosity is probably due to an incomplete reduction of the stain. At the base of the epithelium the fibers may turn abruptly or may pass to the olfactory cell directly in a more or less undulating course. The olfactory cell is bipolar, its peripheral end is the longer and reaches the free surface, in some cases where there is no deposit of silver, ending by a cilia-like projection as described by Ranvier for the frog. The central process may be followed for some distance in the connective tissue. Van Gehuchten concludes thus: by methylene blue and by the Golgi method it has been proven that there is a direct continuity of the olfactory fiber and the bipolar cell. There is no plexus, as thought by Exner and Ranvier, no free intraepithelial terminations, nor a connection of the nerve fibers with the cylindrical cells in the limiting zone, as described by Grassi and Castronovo.

von Brunn, 1892, finds the *membrana limitans* and the olfactory hairs; these are on a bud-like swelling of the olfactory cell. He is not certain whether or not the enlargements are due to reagents. The olfactory hairs come out of holes in the *membrana limitans*; this *limitans* is comparable to the homogeneous border which is penetrated by cilia or ciliated cells, and he considers it comparable to a cuticular border.

He has seen the nerves join the olfactory cells and seen them join with other threads, but has never seen free endings which were olfactory fibers. He has seen fibers on the border of the olfactory and ciliated epithelium which pass up into the epithelium, but these did not join with any cell and were therefore free ending fibers.

Retzius, 1892, worked on mouse, cat, dog and rabbit, using the rapid Golgi method. He found two kinds of cells: the supporting cells and the olfactory cells. The supporting cells had a nucleus in the outer third of the cell body. The inner part of the cells had two, three or more wing-like processes which reached to the inner surface of the epithelium. These did not form a fiber. Between these supporting cells were found the olfactory cells. They were bipolar; the cell body was oval or spindle shape with two processes. The outer, thicker process passed to the surface between the supporting cells and bore cilia-like hairs. The inner one was much finer and often varicose. There were several layers of cells, so that the processes were of varying

lengths. The central process had a straight or undulating course. It often passed just under the epithelial layer for some distance and then entered the mucosa to join the olfactory bundle which passed through the foramina of the cribriform plate to the olfactory bulb. The fiber remained often the same width from the olfactory cell to the olfactory bulb; it did not anastomose or divide, at least not before its entrance into the olfactory bulb.

In *mouse* at the transition point between respiratory and olfactory epithelium, Retzius has seen free nerve endings reaching nearly to the surface of the epithelium. He describes them as very fine and varicose, only here and there were small end knots seen, and these did not differ from the varicosities found on the nerve fiber and were not true end knots. He suspects that they are the endings of the 5th nerve, but is not willing to give this verdict.

Cajal, 1894, speaks of his results thus: Our observations prove not only the continuation of a fiber of the olfactory nerves with a bipolar cell of the mucosa, but also the unity and independence of this fiber in all its course as far as the bulb, where it ends by means of a free arborization. The network and the ramification described in the intra or extra epithelial course of these nerves he has not confirmed by the new methods of coloration.

Morrill, 1898, investigated the olfactory organ of dog-fish, using Ehrlich's method. He found continuity of the nerve fiber and cell, and also found free nerve endings. He describes three types of olfactory cells, cylindrical, spindle-shaped and conical; whether the difference in shape is due to function or to mechanical causes has not been determined.

With Reference to the Gross Anatomy of the Olfactory Nerves.—Up to a comparatively short period the olfactory tracts were called olfactory nerves; and further, in speaking of the filaments in the nasal mucosa it was always assumed that they extended *from* the olfactory bulb. In the newer literature, the nerves are described as extending from the olfactory epithelium *to* the olfactory bulb. They are so considered in this paper.

Relation of the Olfactory Fibers and Bundles to the Olfactory Mucosa.—In the newest and most reliable works on anatomy of the present time the authors describe, in their explanations of the olfactory regions of man both for the nasal septum and lateral wall of the nose, a plexus of the large nerve bundles before they pass through the cribriform plate of the ethmoid bone. In many cases the figures of Leveillé

have been used to represent this condition. In cases where the figures used are original, they lack distinctness, which is, no doubt, due to the uncertainty of knowledge of this region.

The idea of a plexus of the nerve bundles is of earlier origin than the work of Leveillé, as will be shown by Figs. 10 and 12. These are copies of the figures of Scarpa, 1785. The ideas of Leveillé did not differ essentially from those of Scarpa, and were, no doubt, strongly influenced by them. Our knowledge at the present day concerning the plexiform arrangement of the olfactory nerve bundles is practically that of Scarpa. Much credit is due Scarpa for his excellent work, the facts of which have formed a basis for the knowledge of that region to the present time, as will be seen by the following résumé of a part of the second book of his *Anatomicarum Annotationum*.

A series of nerve bundles varying in number with the subject come from the apex of the bulb. These, covered by the meninges, pass through the foramina of the cribriform plate and are spread out as nerves of olfaction within the nose. The principal branches are arranged in an internal and an external series. The internal send out filaments to the nasal septum. When the nasal membrane is turned back from the septum it is found to be filled with filaments of nerves running down in series. They differ in length, some often so long as to reach the lowest base of the septum and almost touch the floor of the nasal cavity. Others descend only half way. Some pass perpendicularly, while others are arched, as the posterior ones (Fig. 10).

The external series is distributed far and wide through the upper turbinal bones. The longest branches reach from the upper nares to the lowest edge of the middle turbinated bones. These are perpendicular at first and then recurved to the posterior. The posterior ones are arched (Fig. 12). These nerves in their course from the cribriform plate to the pituitary membrane form anastomosing plexiform connections. The plexiform nerve bundles are found in canals of the turbinated bones of the nose, as is admirably shown in the figures of Scarpa (Figs. 11, 12). Not many olfactory filaments go to the lower turbinals, and he questions whether they are of much importance.

There are no olfactory nerves to the membranes of the pituitary sinuses, and hence these are not olfactory in function.

His descriptions of the 5th nerve to the nose are practically those of to-day.

The following are Scarpa's own words concerning the olfactory nerves:

"Rami porro isti copiosiora mox emittunt filamenta, quorum magna pars nudo oculo conspicua, inter membranam pituitariam, & periosteum septi narium a summo ad imum septum decurrunt. . . . Maiores vero rami non intermisso per cribriformem laminam itinere continuos canaliculos superiorum turbinatorum ingrediuntur, intra quos iterum, ac saepe divisi, & ramosi porro pergunt late per turbinata ossa superiora distribuendi. Quo in itinere, utpote canaliculorum quamplures communicationem inter se alunt, crebrisque orificiis ad narium cavitatem hiant; ita nervorum, de quibus loquimur, rami intra hos canaliculos adhuc reconditi anastomosim, & plexuosas copulationes (t) inter descendendum in vicem constituunt, frequentesque propagines extus per patula canaliculorum orificia membranae pituitariae turbinata ossa superiora vestienti largiuntur. . . . Medio modo se habent, qui per mediam turbinatorum superiorum regionem feruntur: nempe quo ad numerum, crassitiem, & incessus rationem; in eo autem discrepant, quod omnium huius provinciae longissimi sunt (x) quippe a summis naribus ad imam usque oram turbinati medii pertingunt. . . . Sed neque ad turbinatum inferius paris primi filamenta deduci plura sunt, quae sin minus suadent, saltem dubitationi locum praebent vehementer. . . . Neque enim ad organi olfactus sedem adscribendi sunt finis pituitarii, quoniam olfactilis nervus membranae eas caveas vestienti filamenta nullatenus tribuit."

For Comparative Anatomy the statements of Milne-Edwards, Cheveau and Owen agree very closely with those in the works on human anatomy.

The following is a generalized statement by Owen:

"The nerves are grouped in all Mammals into a set for the septum and a second for the upper or ethmo-turbinals, a third or middle short set being, in some, distinguished for the labyrinth or roof of the nasal chamber. The branches of the second set, after expanding on the ethmo-turbinals, usually converge to become connected with the lateral nasal branch of the 'fifth.' Their mode of distribution is best seen on the ethmo-turbinal: here they divide, subdivide, expand and anastomose with each other, forming a reticular nervous expanse, with long and narrow meshes, and becoming impacted in the central, or inner, layer of the olfactory membrane."

For the true relation of these nerve bundles see the body of this paper, page 33 and Figs. 24-27.

METHODS FOR GROSS DISSECTION.

The nitric acid method was used for gross dissection. The head was placed in 20 per cent nitric acid for 6-12 hours, depending upon the size; the decalcification had then proceeded so far that the bone could be easily cut.

The bones were removed from the nose and orbit, thus exposing the olfactory bulb, the nasal mucosa and the lining of the maxillary, frontal and sphenoidal sinuses.

As the bone was removed from the mucosa the deepest or attached surface of mucosa was exposed (Figs. 5, 6). It is this surface which must be exposed to view them.

In dog and cat the ethmo-turbinal bones were easily removed, as they are not perforated by the nerve bundles. In man, however, this is not so easily accomplished. The turbinated bones are filled with small canals through which the nerve bundles pass (Fig. 11). There is, therefore, an interweaving of bone and nerve. Much care is necessary to free these bundles without injury. If the specimen is favorable there is a marked contrast between the white nerves and the darker mucosa. This differentiation is destroyed if the material is left too long in nitric acid. The olfactory nerves are very prominent and are spread out in a fan-shaped manner upon the olfactory folds. They stand out with remarkable sharpness as white cords against the darker background of the nasal mucosa (Figs. 5, 6). This is also true of the branches of the 5th nerve which innervate the nose. It is this differentiation and the fact that the nerves lie in the deeper layers of the mucosa next to the bone which made this dissection of the fine terminal branches of the 5th nerve possible. Even under these favorable circumstances it was necessary to dissect under water and in brilliant light (sunlight or electric light) with a magnifier giving 8-12 diameters.

Material prepared by the nitric acid method may be preserved during the dissection in 2 per cent formalin without markedly changing color. This does not hinder the dissection and material will not deteriorate in it. Five per cent formalin is recommended for permanent preservation.

If material preserved in formalin is used, further decalcification may not be necessary. There will, however, be no differentiation in color between the mucosa and the nerves, and the material, therefore, does not give as satisfactory results.

HISTOLOGICAL METHODS.

Four methods have been used: the rapid Golgi, the mixed Golgi, gold chloride, methylene blue and dissociation methods.

The Rapid Golgi Method.—Fresh tissue was put into osmium-bichromate mixture for 3-4 days and kept in the dark.

3 per cent potassium bichromate.....2 parts.

1 per cent osmic acid1 part.

This was changed at least once. The material was then placed in $\frac{3}{4}$ per cent silver nitrate for 3 to 4 days, being changed several times in the first half hour until no precipitate formed. Dehydration was as rapid as possible, $1\frac{1}{2}$ per cent, 3 per cent and 8 per cent collodion was used for infiltration. Tissue was left in 8 per cent collodion $\frac{1}{2}$ day without harm and was imbedded in 8 per cent collodion. It was hardened in chloroform vapor for 2 to 12 hours. The knife and block were flooded with 95 per cent alcohol during the cutting; sections were 60 to 80 microns.

The results were very good both in the dog and in the cat. Olfactory cells, with their axones, peripheral processes and the olfactory hairs, could be seen. Sensory cells were found in the vomeronasal organ of the cat. In man the results were less satisfactory, due to the lack of fresh material, but positive verification was obtained.

The Mixed Golgi Method.—Good results were obtained in the dog and the mouse from the mixed Golgi method. (The tissue was treated as for the rapid method, except that it had been previously fixed in Müller's fluid.) The nasal conchæ and the septum of this dog were still cartilaginous, so it was possible to make sections through the entire nose and olfactory bulb. Nerves could be traced for a long distance even through the cribriform plate to the olfactory bulb. Olfactory cells were obtained and also sensory cells in the vomeronasal organ of the mouse.

The Gold Chloride Method.—Both Ranvier's formic acid method and Hardesty's modification of the gold chloride method were used. The difficulty in the use of the former method is due to the fact that the epithelium is very easily exfoliated in fresh material. Good results, however, were obtained from human material by this method. Hardesty's modification of the method² gave good results with dog and cat. The dog material had been in 10 per cent formalin for eight years, the cat only a few weeks. Sections were made from 1 to 20 microns. The sustentacular cells were stained as well as the olfactory cells; in fact, the

²Hardesty, Neurological Technique.

whole mucosa was stained. The thicker sections proved valueless for the olfactory cell. Sections 1 to 3 microns showed the olfactory cells and in some cases a very small part of the axone. Its course is undulating and can be followed only in thick sections. The peripheral process was easily found.

The Methylene Blue Method.—Huber's modification method was used.³ Olfactory cells with their two processes were found in dog and cat. The same difficulty was encountered here as with the gold chloride material, much of the epithelium had been exfoliated.

Dissociation Method.—The gold chloride material and fresh tissue were placed in formaldehyde dissociator (2 cc. formaldehyde and 1 liter of normal salt solution) for forty minutes. Olfactory cells with their two processes were obtained in dog and cat.

GROSS ANATOMY OF THE NOSE.⁴

The cavity of the nose (cavum nasi) is divided into two lateral halves by the nasal septum (septum nasi) (Figs. 15-23). This septum is formed of two parts, the septum cartilagineum or cephalic part and the septum nasi osseum which joins the cribriform plate (Lamina cribrosa). In the dog and cat the septum is extended dorsally by the median parts of the os frontale and os nasale.

In this paper the term septum does not include this area. When referred to, it is designated as the turbinated part of the septum.

The lateral halves of the nose consist of the turbinated bones (conchæ nasales) (Figs. 15-23). In the dog and cat these conchæ may be divided into two parts. The ethmo-turbinals (Figs. 16, 17, 19, 20) and the maxillo-turbinals or concha nasalis inferior (Figs. 15, 18). The ethmo-turbinals are thin plicated bones which are attached to the cribriform plate. In the dog these extend about $\frac{1}{3}$ and in the cat about $\frac{1}{2}$ the length of the nose. Figs. 1 and 3 show the mucosa of the ethmo-turbinals (mucosa nasi), but the bones have been removed.

The maxillo-turbinal is also a plicated bone situated cephalad of the ethmo-turbinals. This is a larger bone and much more plicated in dog than in cat.

In man the condition is much different. There are three turbinal bones (conchæ nasales), concha nasalis superior, media and inferior

³*Journal of Applied Microscopy*, April, 1898, p. 64. The Methylene Blue Method for staining Nerve Tissue, G. Carl Huber.

⁴The B. N. A. terms are introduced as far as possible.

(Fig. 23). These are plate-like bones and are roughened and perforated (Fig. 11), but not plicated, as in dog and cat (Figs. 17, 20).

The superior turbinated bone is attached to the cribriform plate and is more or less united to the median one which lies ventrad to it (Figs. 11, 23). The inferior is just dorsad of the palate (Figs. 11, 23). The extent of the turbinated bones is relatively much less in man.

The nasal cavity is divided into three regions according to the nature of the epithelial lining.

The vestibule or cephalic part of the nose is lined with stratified epithelium which is continuous with the epidermis. In the respiratory region (*regio respiratoria*) the epithelium is replaced by the columnar ciliated type (Fig. 43).

The olfactory region (*regio olfactoria*), with which this paper deals, is adjacent to the cribriform plate. In fresh material the mucosa is slightly yellow, due to the pigment in the sustentacular cells. The extent of this area is relatively much greater in dog and cat than in man. In dog and cat it comprises about $\frac{1}{2}$ of the numerous ethmo-turbinals (Figs. 1, 3, 5), and from $\frac{1}{3}$ to $\frac{1}{2}$ of the nasal septum (Figs. 2, 4, 7, 8). With reference to the three sinuses opening into the nasal cavity, viz., the sphenoidal, the maxillary and the frontal, only branches of the 5th nerve could be traced to the mucosa of the sphenoidal and maxillary. This is in agreement with previous workers. In works on human anatomy (Quain, Piersol) only the 5th is given as innervating the mucosa of the frontal sinus.

In the dog and cat there is one scroll (Jayne) of the ethmo-turbinal extending for a short distance into the funnel-like opening of the frontal sinus. This may be in the form of a somewhat curved leaf, the free margin dividing the funnel-like outlet in part or the scroll may be rolled up more completely so that the free end in the frontal sinus is curved and looks like the open mouth of a snail shell. Olfactory nerves ramify in this scroll. In the dog they extend also for some distance into the mesal mucosa covering the bony wall of the sinus opposite the cribriform plate. In the cat the scroll-like projection is more lateral and the mucosa lining the sinus opposite the orbit has the greater number of olfactory nerves. That is, in the dog the olfactory nerves of the mouth of the frontal sinus are toward the middle line, while those in the cat are lateral in position. The brown coloration of the epithelium in the olfactory part of the sinus is marked. From the position of the olfactory nerves in the cephalic part of the sinus and its

opening into the nose, any movement of the air back and forth through the narrow outlet would be likely to bring the odorous particles in contact with the olfactory epithelium. There is a variation of opinion concerning the extent of the olfactory area in man. According to Scarpa, this is very extended. It includes the entire area of the upper turbinated zones (a few filaments going to the inferior turbinal). Some of the nerves of the septum are pictured as reaching the floor of the nasal cavity (Fig. 10). Sappey's pictures show a less extended distribution of these nerves a little less than $\frac{1}{2}$ of the septum; the superior $\frac{1}{2}$ of the middle turbinated bones. According to von Brunn only a small portion of the superior turbinals and a corresponding area of the septum are olfactory in function (Figs. 28, 29). My results are midway between those of Sappey and von Brunn. Figs. 30, 31 were made from dissections and show that the olfactory nerves reach nearly to the free edge of the superior turbinated bone and about $\frac{3}{4}$ the width of the lateral wall and occupy about $\frac{1}{3}$ of the septum.

THE HISTOLOGICAL STRUCTURE OF THE OLFACTORY EPITHELIUM.

The epithelium of the olfactory region consists of three kinds of cells: the supporting or sustentacular cells, the olfactory cells and the small stellate basal cells (Figs. 39, 42). In the submucosa serous glands are found; these are known as Bowman's glands and are well pictured in all the books. The ducts of these glands are stained by the Golgi method and pictured in Fig. 41.

The supporting cells are elongated and cylindrical; they have an oval nucleus and a thin cuticular border (Figs. 40, 42). The central end has wing-like processes, often irregular in outline, which project toward the basement membrane between the olfactory cells. This cell was distinguished from the olfactory cell by Eckhard in 1855; but he and other early writers were doubtful as to its true nature. These cells occupy the superficial border of the epithelium and contain pigment. Stellate cells lie near the basement membrane among the processes of the epithelial cells.

The olfactory cells have been studied by four different methods: the Golgi, gold chloride, methylene blue, and dissociation (Figs. 32-38). In all, their position appeared the same. They lie in the middle and deeper layers of the epithelium and send their process between the supporting cells. They are fusiform in shape, with a spherical nucleus

in the central end. The peripheral process is often irregular and reaches the surface of the epithelium. Its outer edge is bulbous and has numerous cilia-like appendages, the olfactory hairs (Fig. 34). These extend beyond the outer border of the epithelium, free in the nasal cavity. The central process is the axone or olfactory nerve fiber. It is very fine and extends in an undulating course into the underlying connective tissue. Only in thick sections could this be followed. These were best seen in the Golgi preparations and in methylene blue material (Figs. 32-34). The sections of gold chloride material showed the axone for a slight distance (Figs. 35, 36). In the dissociated material the axone was generally broken off, but in some preparations axones were found (Figs. 37, 38).

My work agrees with the results of Van Gehuchten as to the shape of these olfactory cells. He believes the varicosities are due to imperfect impregnation. I found both varicose fibers and those which were uniform in outline.

With Max Schultze, I consider these the true olfactory cells. The peripheral process bears the olfactory hairs. The central process is the axone. Early writers described a network for these olfactory axones directly beneath the epithelium as they enter the connective tissue. Recent work has disproven this, and it is now believed that the axone or olfactory fiber "keeps its unity and independence from the olfactory cell to the olfactory bulb," branching only when it reaches the glomerulus of the bulb. In none of my work was the branching or anastomosis of an olfactory fiber seen except at this place. Upon reaching the deepest layers of the connective tissue next to the bone these axones or fibers collect into bundles of various sizes and as olfactory nerve bundles extend to and pass through the cribriform plate to the olfactory bulb.

As has been stated in an earlier part of this paper, almost all authors describe a nerve plexus for these olfactory bundles. This has nothing to do with the network just mentioned, as it concerns only the large nerve trunks and not the individual axones. From the time of Scarpa, 1785, to that of Barker, 1904, and Quain, 1906, the olfactory bundles are pictured and described as forming a plexus on the septum and lateral wall of the nose of man.

If the bone is removed from the orbit and side of the nose (Figs. 13, 14), there is certainly a plexiform appearance of the tissue in which the nerve bundles extend. With a consideration of the gross specimen

only, Scarpa and subsequent authors were justified in their conclusions that the nerve bundles form a plexus in this region. But upon a microscopical examination after differential staining, it is found that the nerve bundles do not anastomose.

This plexiform appearance is due, not to a joining of nerve bundles, but rather to the ramification of the blood vessels and to the arrangement and abundance of the connective tissue which surrounds these vessels and nerves (Figs. 24, 27). The nerves have been traced in these cords of connective tissue. As shown in the drawing and photograph, they pass almost vertically through this to the foramina of the cribriform plate without anastomosis or the formation of a plexus (Figs. 24, 27).

There is but little appearance of a plexus upon the nasal septum (Figs. 25, 26), and the picture of Scarpa (Fig. 10) is much more accurate than are those of Leveillé. Figs. 13, 14, 24 to 27 show strikingly that there is a marked difference in the plexiform appearance of the lateral wall and septum. In both cases, especially upon the septum, there is a crossing and recrossing of nerves, but focusing shows that these do not join. There is, however, some slight joining of the smaller nerve bundles near their origin (Figs. 25, 26).

All authorities on comparative anatomy, wherever the subject is discussed, speak of a plexus of the olfactory bundles. But there is no such marked appearance of this in dog and cat as that found in man. It looks as if the conditions in man had been interpreted for mammals without adequate investigation. Whenever there is an appearance of a plexus, it has been found to be merely a crossing of nerve bundles.

THE OLFACTORY BULB.

The olfactory bulb has been described by various workers as consisting of from two to seven layers, according to the subdivisions made by these investigators.

Golgi, 1875, describes three layers, olfactory fibers, mitral cells and nerve bundles of the olfactory tract. *Van Gehuchten and Martin, 1891*, also describe three main layers. In this paper we are concerned only with the olfactory fibers, the glomeruli and mitral cells; we will not enter into the discussion beyond this.

Van Gehuchten and Martin, 1891, worked on the dog and the cat, both adult and young animals, also the rabbit, rat, and mouse. The

rapid Golgi method was used, with results as follows: The olfactory fibrils collect into bundles which go to the glomeruli; these fibers form the outermost layer of the bulb.

Retzius, 1892, says that the nerve fibers divide either at a short distance from the glomerulus or oftener near it. After a repeated and profuse dichotomous branching the fibers weave through the glomerulus, but do not form a network.

Van Gehuchten and Martin, 1891, have seen these fibers bifurcate in the cat and form fibrils of equal thickness, which pass to a single glomerulus, or each may pass to a different glomerulus. Some fibers bifurcate more than once. Thus a single olfactory cell would be connected with two or more glomeruli. "This bifurcation cannot be said to be constant but it is frequent."

The olfactory glomerulus is formed by an interlacing of the terminations of the olfactory cells and the dendrites of the mitral cells. These are independent of each other, that is, there is no anastomosis as was thought by Golgi, 1875. Olfactory fibrils were free in the glomerulus of the cat, the dog, the rabbit, the rat and the mouse, and a number of olfactory fibrils go to each glomerulus.

In the dog they believe the glomeruli to receive dendrites from a great number of mitral cells. In all mammals studied, each mitral cell is connected with a great number of bipolar cells, but each olfactory cell of the mucosa is connected with one, rarely two, mitral cells; at the glomerulus each olfactory fibril terminates generally with only one mitral cell.

In all animals where the olfactory sense is greatest, each bipolar cell may be in contact with several mitral cells, not because the fiber bifurcates and goes to different cells, but because in the same glomerulus may be found the dendrites of several mitral cells.

Personal Observations.

The following are the results which were obtained from the olfactory bulb of the dog and cat. The olfactory bulb was studied in gross preparations and in sections; in the gross dissection the olfactory nerves were traced from the mucosa through the foramina of the cribriform plate to the olfactory bulb. They could be plainly seen lying irregularly upon the bulb (Fig. 4). This was also seen in the transections and sagittal sections of the olfactory bulb and mucosa. Individual

fibers could be traced for a considerable distance, and in some cases fibers were traced nearly through the cribriform plate. The nerves were not seen to bifurcate in the layer as described by Van Gehuchten and Martin, but remained as individual fibers until near the glomerulus. At their entrance into the glomerulus they divide and subdivide to form many branches which interlace but do not anastomose with the other fibers found there. In some cases four or five of these axones were traced into the same glomerulus (Fig. 47).

The glomerulus of the olfactory bulb is formed by the interlacing of branches from the axones of olfactory cells and the dendrites of the mitral cells of the olfactory bulb (Figs. 48-53). (For clearness these have been shown in separate drawings, that is, axones of nerve cells and dendrites of mitral cells are not shown in the same figure.) A glomerulus may be formed by the interlacing fibers from one axone (Fig. 46), and from one dendrite (Fig. 50), or from several axones (Fig. 47), and several dendrites (Fig. 52). While each axone comes from an individual olfactory cell, the dendrites may come from a single or several mitral cells.

In the cat three dendrites from different mitral cells were found in one glomerulus (Fig. 52). Fig. 51 shows three dendrites from at least two different cells. Fig. 53, two dendrites from the same mitral cell. The branching of a single dendrite to different glomeruli was not seen.

In the dog, dendrites from several different mitral cells were traced to a glomerulus (Fig. 49), and a single dendrite was seen to branch to three different glomeruli (Fig. 48).

In man the olfactory bulb has been studied only in gross preparations. The olfactory nerves were traced through the cribriform plate to the outer layer of the bulb. The histology of the olfactory bulb was not studied, but is given by all authors. The glomeruli are formed by an interlacing of the axones of the olfactory cells and the dendrites of the mitral cells, as in lower animals.

DISTRIBUTION OF THE 5TH NERVE TO THE NOSE.

The nose is innervated by branches of two divisions of the 5th nerve. The anterior ethmoidal (*nervus ethmoidalis*) of the ophthalmic and the sphenopalatine (*nervii sphenopalatini*) of the maxillary division.

In the orbit the anterior ethmoidal nerve passes between the muscles of the eye and enters the cranial cavity through the anterior ethmoidal

foramen (foramen ethmoidale) into the cranial cavity. It passes along the olfactory bulb (bulbus olfactorius) (Fig. 3) cephalad through an opening on the cribriform plate and passes along the upper part of the nasal septum (septum nasi) (Figs. 2, 4, 7, 13, 14), where it divides into the external nasal nerve (nervus nasalis externus) and the internal nasal nerves (nervii nasales interni). The external nasal nerve passes along the sulcus ethmoidalis of the nasal bone (os nasale) and passes out to innervate the skin of the nose (Figs. 13, 14). The internal nasal nerve divides into the median nasal (ramus nasalis medialis), which supplies the septum, and the lateral nasal nerve (ramus nasalis lateralis), which innervates the mucosa of the lateral wall.

The remaining part of the mucosa is innervated by the sphenopalatine nerves (Figs. 1, 3). The naso-palatine branch of this nerve (n. palatinus) was traced along the septum to the canal of the incisors (canalis incisivus). It sends several branches into the middle of the septum (Figs. 2, 4). In dog and cat this was traced into the vomero-nasal organ (Figs. 2, 4). This nerve was also dissected in man and was traced almost into the organ. The terminal branches were so fine that their complete dissection was not successful.

FREE TERMINATIONS OF THE 5TH NERVE WITHIN THE NASAL MUCOSA.

von Brunn, 1892, saw free nerve terminations within the nasal epithelium at the border of the respiratory region. According to him these fibers could not be the olfactory axones, as they were much thicker than those. He, therefore, concludes that they are the endings of the Trigeminus. He quotes Cajal as supporting his decision.

von Lenhossek, 1892, has seen the fibers described by von Brunn, but instead of being thick, as described by that author, those seen by him are finer than the olfactory fibers, varicose and with terminal endings; these did not always reach the free surface of the epithelium. The nerves which are pictured and described by von Lenhossek are like those pictured by Cajal and not of the ordinary much branched appearance of a sensory nerve in epithelium. von Lenhossek did not commit himself as to the origin of these fibers.

Retzius, 1892, pictures in the nasal epithelium of the mouse and cat, both in the respiratory and olfactory regions, fine, much-branched nerve fibers, which end free in the epithelium like other sensory nerves. These are varicose, but not always with an end knot. Retzius wishes to confirm

the appearance of these nerve fibers within the nasal epithelium, but does not wish to give his verdict as to their origin, he adds that it is plausible that these are of a sensory nature. In his work on Fishes he does not find any structures comparable with the "Geruchsknospen" of Blaue. Retzius considers as false the theory of Blaue that there are such structures which have sense cells in direct connection with the olfactory nerve.

Cajal, 1894, in his *Système Nerveux* denies having committed himself upon the character of these nerves, but ascribes their discovery to von Brunn. According to his work, the endings of the 5th nerve are found only in the submucosa and do not extend into the epithelium. He finds in man fibers which end free at the surface of the epithelium, but these are nearly vertical and end in a conical projection at the top, as is shown by von Lenhossek. He withholds his verdict as to the origin of the fibers thus ending until work then in progress was complete. He has seen them only in the embryo, but never in new-born animals or those several days old.

Disse, 1896, found in the nasal mucosa of some mammals "Epithelknospen" which resemble the taste buds in appearance. These buds are of two kinds, the large buds in the olfactory epithelium and the small buds in the respiratory epithelium. These consist of supporting cells and sense cells, (the sense cells are not ganglion cells). By the Golgi method he traced nerve fibers into the large buds. He considers these fibers as belonging to the 5th nerve. Disse does not credit Blaue's theory that these buds are in connection with the olfactory nerves, but thinks that they have to do especially with the sweet and sour sense of taste in the nose.

Kallius, 1905, has seen the free endings of the 5th nerve in the respiratory and olfactory epithelium of calf. He finds nothing in his preparations, except possibly nests of mucous cells, which in any way resemble the "Epithelknospen" of Disse, nor have any such structures been found in the nasal epithelium of man.

Personal Observations.

I have seen in the nasal epithelium of the kitten a few days old, both in the respiratory and olfactory regions, many much-branched nerve fibers. These were varicose and often ended with a varicosity (Figs. 44, 45). From the gross dissection, fibers from the 5th nerve

pass to the olfactory folds (Fig. 3), and to the lateral wall and septum (Figs. 1-4). It would, therefore, seem probable that the nerves described above are the free terminations of the 5th nerve. My preparations agree very closely in appearance with those of Retzius for the mouse and cat. I find no structure in the nasal epithelium of dog, cat or man which resembles the "Geruchsknospen" of Blaué or the "Epithelknospen" described by Disse.

ORGANON VOMERONASALE.

This organ has been the subject of various investigations; a detailed account is given by Kölliker, 1877, 1883, and Harvey, 1882; von Brunn, 1892; von Lenhossek, 1892; Merkel, 1892; Mihalkovics, 1898. Klein worked on the guinea pig, the rabbit and the dog; von Lenhossek on the rabbit; Harvey on the mouse and the cat; von Brunn on the sheep; Kölliker, Merkel and Mihalkovics on man.

The gross structure, briefly stated, is as follows:

The vomeronasal organ of the dog and the cat is a bilateral tubular organ situated in the ventral part of the septum in the region of the pre-maxillary and maxillary bones. It is either entirely or partially surrounded by a capsule of hyaline cartilage (Figs. 15, 18, 54, 55). At the cephalic end of the nose there are two prominent folds on each side of the nasal septum. The dorsal one is due to a solid fold of the mucosa and to the presence of glands. This is the smaller and passes dorsad of the incisors. The cartilaginous capsule is complete in the cephalic part of the vomeronasal organ of the cat. In the remaining portion in the cat and through its entire extent in the dog this capsule is only partial. As stated above, the vomeronasal organ is tubular and is flattened laterally. It is blind at the caudal end, but opens at the cephalic end into the ductus nasopalatinus. In man the vomeronasal organ is much less developed than in dog and cat. It is a bilateral organ situated in the mucous membrane of the ventral part of the nasal septum (Fig. 21). It is a short blind tube only a few millimeters in length which opens anteriorly into the nasal cavity by a small pore-like opening just above the incisors. This opening was seen both in child and adult. The cartilage of this organ is much reduced and lies entirely below the organ (Fig. 21). The shape of the tube in the dog and the cat varies in the different regions; near the cephalic opening it is circular in transection and lined with stratified epithelium; in the

median and caudal parts it is kidney-shaped and the epithelium is columnar. The median and lateral epithelia differ in thickness; the median is sometimes two or three times thicker than the lateral. In the human which were examined the vomeronasal organ of a 6-7 weeks embryo was flattened as described for the dog and the cat and man, and the epithelium of the median wall was the thicker. In a four months human fetus it seemed to be circular in outline for its entire length, with a uniform thickness of epithelium.

The epithelium, like that of the nasal cavity, consists of sustentacular cells and are longer and narrower than those of the nasal mucosa; the sensory cells found in cat had a process which passed to the surface of the epithelium (Figs. 54A, 55A). These cells have not been found in man, according to Mihalkovics, 1898, and Quain, 1906. According to Klein, the sensory cells are found only in the thick median epithelium. von Lenhossek found olfactory cells in the median and lateral epithelium of an embryo kitten. The central process undivided and unbranched passes into the submucosa as a fine varicose nerve fiber. No olfactory hairs were found by von Lenhossek, 1882, as a precipitate was present. He saw in the deeper layers of the epithelium of the vomeronasal organ free nerve endings. An end knot was always present, but a little rod often projected beyond this; according to him, these were either free endings of the 5th nerve or of olfactory nerves whose cells were somewhere in the olfactory course.

von Brunn in Golgi preparations of the vomeronasal organ of the sheep saw the connection of the olfactory cell and nerve. He also found olfactory hairs.

Personal Observations.

Gross Anatomy.

The gross anatomy of the organon vomeronasale, or Jacobson's organ, has been carefully worked out. As has been previously stated, the large nerves of the nose lie in the deepest layers of the mucosa next to the bone. In order to see these, it is necessary to remove the bone and thus to expose the back or deepest parts of this mucosa. The nitric acid method described above made this possible. The mucosa was freed from the cartilaginous septum, being careful not to tear the nerves which lie almost on the bone. Figs. 2, 4, 8, 9 show such a dissection. In the dog and the cat the vomeronasal organ was also intimately con-

nected with the palate, and this was divided in the median suture. The most successful dissection of this organ in those cases was obtained by sawing the entire head in two from front to back, including both the nose and the brain; the entire septum being on one side. The cartilage and the bone were then removed from the mucosa. The vomeronasal organ was found as an elongated flattened fold at the cephalic end of the nose, just above the palate (Figs. 2, 4, 8, 9). Its small cephalic end passes ventrad to the incisors and opens into the ductus naso-palatinus, which leads from the oral to the nasal cavity. In man the position of this organ is somewhat different (Fig. 21). It is found some distance above the palate and not in intimate relation with it as in the dog and the cat. It opens directly into the nasal cavity. The vomeronasal cartilage is represented by only a small piece of cartilage which lies some distance ventrad of the organ and not enclosing it as in the lower animals (Fig. 21).

I wish to emphasize what has been stated before. It is the deepest layers of the mucosa next to the bone and not the nasal side with which we are at present concerned. There are many nerves in this septal mucosa. These nerves are from two distinct sources: the olfactory nerves, which are connected with the olfactory cells and which can be seen to pass through the foramina of the cribriform plate, and the anterior ethmoidal and sphenopalatine branch of the 5th nerve. The olfactory nerves are found near the cribriform plate (Figs. 2, 4, 7, 9); the branches of the 5th nerve innervate the middle and cephalic parts of the nose (Figs. 2, 4, 7).

There are still several prominent nerves which we have not described (Figs. 2, 4, 8, 9). These are olfactory nerves. They were traced from the olfactory bulb obliquely across the septal mucosa into the vomeronasal organ. In the dog, the cat and man they branch many times just before their distribution in this organ. The vomeronasal organ in dog and cat is also innervated by several branches from the naso-palatine nerve; thus we see that this organ contains nerves from two distinct sources. In man, according to von K  lliker, these olfactory nerves are present only up to the third month of development and atrophy directly after that. Mihalkovics did not find them at all in a three months human fetus. Long olfactory nerves resembling in every way those of the dog and the cat were seen on the septum of a child. These were traced to the vomeronasal organ. The naso-palatine branches were traced nearly to this organ, but the nerve was so fine that further dissection was not successful.

Histology of the Organon Vomeronasale.

Fig. 18 is a transection of the head of an embryo kitten in the region of Jacobson's organ. This shows the position of the organ, the cartilaginous capsule and the thickness of the epithelium. Figs. 54 and 55 will show the complete and partial capsule in the kitten. The fine structure is described by several investigators. I have been chiefly concerned with the sensory cells. In the kitten (Figs. 54A, 55A) sense cells were found. These agreed in every way with the olfactory cells of the nasal mucosa. There are two processes: the thicker, peripheral one, and the fine, somewhat varicose, central fiber. The axone was followed for a considerable distance in the submucosa. No olfactory hairs were found, but in Fig. 54A indications of these are seen in the spike-like process.

I have no hesitation in calling these sense cells nerve cells, apparently identical with those of the olfactory mucosa. Free terminations mentioned by von Lenhossek, 1892, and Cajal, 1894, were not found, but we should consider those, from the gross dissection, to be the endings of the 5th nerve, as several branches of this nerve were traced into the organ. I believe, then, with others, that the vomeronasal organ is intimately connected with the olfactory sense.

RESULTS.

DOG AND CAT.

1. The olfactory nerves are large and numerous in the dog and the cat, relatively less in the cat.
2. About one-half of the ethmo-turbinal folds are olfactory. This is a large distribution as compared with man.
3. All the folds of mucosa adjoining the cribriform plate are olfactory.
4. The mucosa is thick in the olfactory region; thin beyond this; the transition is sharply marked.
5. The mucosa of the septum is in two parts. The upper part is lined by the dorsal turbinated folds; the lower part is lined by a continuation of the mucosa of the cephalic part of the nose. About one-third to one-half is olfactory.
6. The anterior ethmoidal nerve innervates the olfactory folds and septum; its branches extend from the cribriform plate to the tip of the nose; it also innervates the roof and upper lateral wall of the nose. Small branches pass among the olfactory folds.

7. The sphenopalatine nerve innervates the mucosa, cephalad of the ethmo-turbinal folds, the maxillary sinus, the lateral wall of the nose and the maxillo-turbinal folds, also the vomeronasal organ.

8. The vomeronasal organ is a tubular organ found on either side of the septum. It is innervated by olfactory and nasopalatine nerves.

9. The outer layer of the olfactory bulb is formed from the axones of the olfactory cells.

10. The glomeruli of the olfactory bulb are formed by the interlacing of the axones of the olfactory cells and the dendrites of the mitral cells. The number of mitral cells represented in a glomerulus varies in different animals.

MAN.

11. The olfactory nerves are relatively less in number in man than in the dog and cat.

12. They are distributed to the upper third of the septum and to nearly the whole of the superior concha (Figs. 30, 31).

13. The nose is innervated by two divisions of the 5th nerve, the anterior ethmoidal which innervates the anterior part of the septum and lateral wall, and a branch is also sent to the skin of the tip of the nose.

14. The sphenopalatine nerve innervates the lateral wall, the conchæ and the ventral part of the septum.

15. The vomeronasal organ is much less developed in man than in the lower animals. A branch of the olfactory nerve passes to it, at least at the time of birth.

16. The axones of the olfactory cells form the outer layer of the olfactory bulb.

CONCLUSIONS.

DOG, CAT AND MAN.

1. The fusiform cells of the olfactory mucosa are true olfactory cells and true nerve cells. They lie in the deeper parts of the epithelium of the olfactory region.

2. The peripheral process is long and cylindrical and reaches the free surface of the epithelium, passing between the sustentacular cells. It bears the olfactory hairs.

3. The olfactory fiber is the axone of the olfactory cell; these collect to form olfactory nerve bundles and pass through the cribriform plate to end in the glomeruli of the olfactory bulb. These nerve bundles do not anastomose to form a plexus.

4. The supporting cells are cylindrical and the inner process is often divided. Stellate cells are found at the base of the supporting cells.

5. The development of the sense of smell in the dog and the cat may be due to the large number of the olfactory nerves and to the extent of their distribution, and, according to Van Gehuchten, to the number of mitral cells with which each olfactory cell is associated.

6. The vomeronasal organ is intimately connected with the sense of smell. It contains, at least in the cat, sensory cells apparently identical with those of the olfactory mucosa.

7. There are free nerve terminations in the olfactory epithelium. These are the endings of the 5th nerve.

In the position of the olfactory nerve cell we apparently have a primitive condition. This is the only case in vertebrates where the nerve cells are within the epithelium, as are those for the tactile sense in many invertebrate forms. In the other organs of sense there is a gradual recession of the ganglion cell until, in the ganglion of the dorsal root of the spinal cord, the central nervous system is approximated. The branches for the tactile sense end freely either in special organs (tactile corpuscles) or in the free end-knots within the epithelium, but do not reach to the surface of it; while the branches of the nerves of other sense organs end freely *among* special cells, but do not reach the free surface of the epithelium. In the olfactory region the olfactory hairs are above the free surface of the epithelium and in direct contact with the air.

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TERMS AND THEIR ABBREVIATIONS IN THE EXPLANATION OF
FIGURES IN PLATES I-XVII.

- Ax., axone.
- Bo., bulbus oculi.
- B. olf., bulbus olfactorius.
- Crt. v-n., cartilago vomeronasalis.
- Cv. n., cavum nasi.
- Cc. eth., cellulae ethmoidales.
- Cbl., cerebellum.
- Cbrm., cerebrum.
- Ch. n. i., concha nasalis inferior.
- Ch. n. m., concha nasalis media.
- Ch. n. s., concha nasalis superior.
- Ch. n., conchae nasales.
- Cranium, cranium.
- D. i., dens inferior.
- D. s., dens superior.
- Os., developing bone.
- Det. n-l., ductus nasolacrimalis.
- F. l. cr., foramen laminae cribrosae.
- L. cr., lamina cribrosa ossis ethmoidalis.
- Lingua, lingua.
- Mnd., mandibula.
- Mt. n. i., meatus nasi inferior.
- Mt. n. m., meatus nasi medius.
- Mt. n. s., meatus nasi superior.
- Md. sp., medulla spinalis.
- M. n., mucosa nasi.
- M. s. n., mucosa septi nasi.
- M. sn. f., mucosa sini frontalis.
- M. sn. mx., mucosa sini maxillaris.
- M. c., Meckel's cartilage.
- Nn. olf., nervii olfactorii.
- Nn. org. v-n., nervii organi vomeronasalis.

N. eth. a., nervus ethmoidalis anterior.
 N. mnd., nervus mandibularis.
 N. mx., nervus maxillaris.
 N. nph., nervus nasopalatinus.
 N. sph., nervus sphenopalatinus.
 N. org. v-n., nervus organi vomeronasalis.
 Orbita, orbita.
 Olf. c., olfactory cell.
 Olf. h., olfactory hairs.
 Org. v-n., organon vomeronasale.
 Zyg., os zygomaticum.
 Palatinum, palatinum.
 R. n. ext., ramus nasalis externus.
 R. n. lat., ramus nasalis lateralis.
 Rg. olf., regio olfactoria.
 Sen. c., sensory cells of the vomeronasal organ.
 S. n., septum nasi.
 Sn. f., sinus frontalis.
 Sn. mx., sinus maxillaris.
 Sn. sph., sinus sphenoidalis.
 St. c., stellate cell.
 Sust. c., sustentacular cell.

PLATE IA ($\times 1.14$).

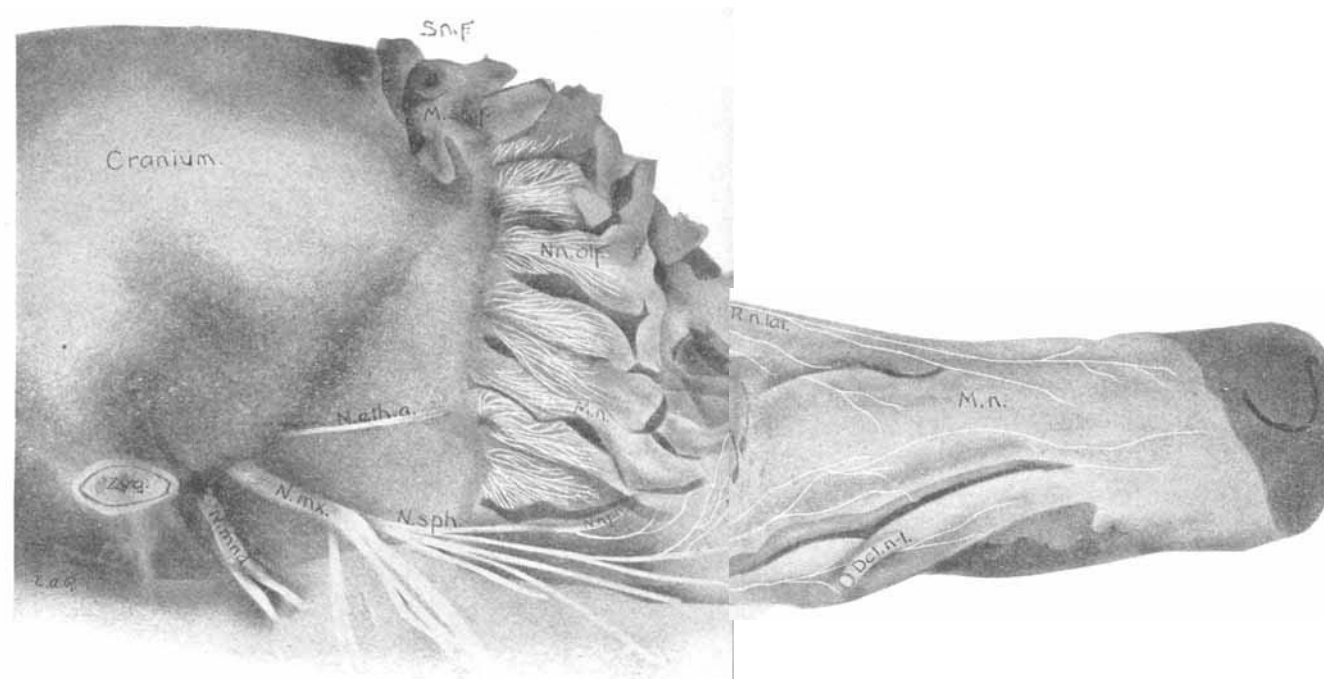
Same as Plate I. To show the lining of the maxillary sinus and its innervation by the 5th nerve.

PLATE I.

FIG. 1 (\times 1.14).

Head of a dog, the bone has been removed from the lateral aspect of the nose and part of the orbit, exposing the deeper layers of the mucosa in which lie the olfactory nerve bundles and their branches.

Note the divisions of the 5th nerve and their distribution to the mucosa of the lateral wall of the nose and to the maxillary sinus.



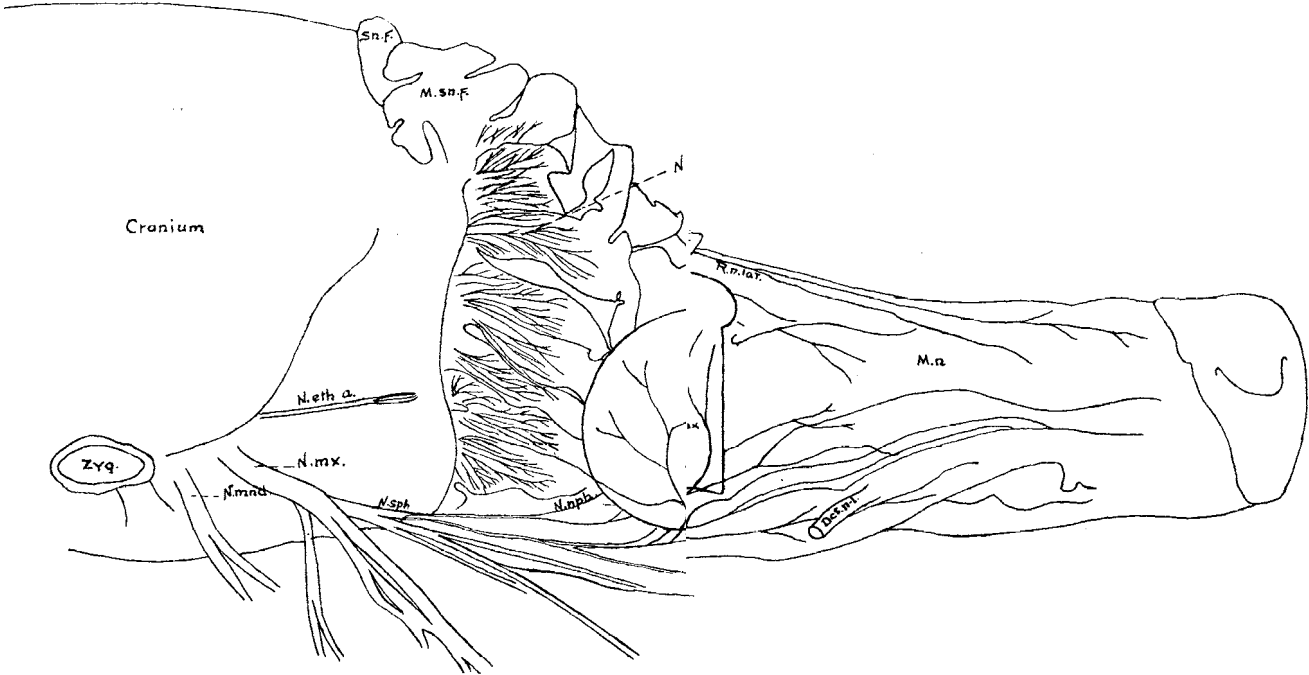


PLATE II.

FIG. 2 ($\times 1$).

Median section of the head of a dog, with the mandible and bony septum removed, to show the septal mucosa and its olfactory nerves; the turbinated part of the septum and its olfactory nerves; the vomeronasal organ and its innervation by the olfactory and naso-palatine nerves.

Note the anterior ethmoidal branch of the 5th nerve along the dorsal wall of the septum and its distribution to the septal mucosa.

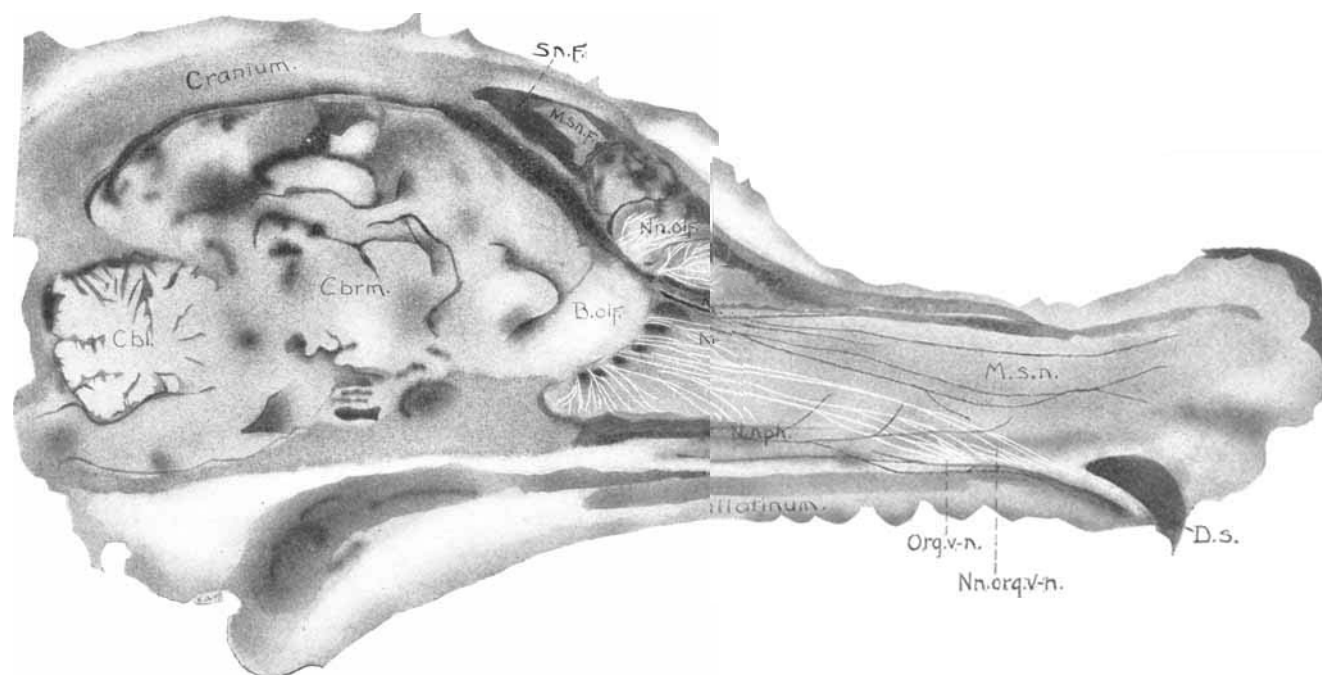


PLATE III.

FIG. 3 ($\times 1.4$).

Head of a cat, except the mandible.

The bone has been removed from the nose, orbit, and a part of the cerebrum, exposing the attached surface of the nasal mucosa. This shows especially the olfactory folds with their nerves, the divisions of the 5th nerve, and their distribution to the lateral wall and mucosa of the maxillary sinus.

Note the small branches of the anterior ethmoidal nerve to the olfactory folds.

FIG. 4 ($\times 1.4$).

Median section of the head of a cat, without the mandible; the bony septum has been removed to show the deep or attached surface of the mucosa. This is to illustrate the mucosa of the septum and its olfactory nerves; the turbinated part of the septum and its olfactory nerves; the vomeronasal organ and its innervation by the olfactory and naso-palatine nerves.

The anterior ethmoidal branch of the 5th nerve passes along the dorsal part of the septum and is distributed to the septal mucosa.



PLATE IV.

FIG. 5 ($\times 1.28$).

The ethmo-turbinals of a dog, showing olfactory nerves in the deeper layers of the mucosa and the branching of the nerves which lie upon each other. The lining of the maxillary sinus is turned forward to show the thinner part of the folds; these are thick in the region supplied by the olfactory nerves; the thin part is not olfactory. The anterior ethmoidal nerve is shown entering the skull through the ethmoidal foramen.

FIG. 6 ($\times 1.8$).

Same animal as shown in Fig. 5. Dorsal view of the ethmo-turbinals to show the olfactory nerves. Note the anterior ethmoidal branch of the 5th nerve to the septal mucosa.

FIG. 7 ($\times 1.2$).

Median section of the head of a dog with the bony septum removed to show the turbinal part of the septum and its olfactory nerves; the septum and its olfactory nerves, the anterior ethmoidal and the naso-palatine nerves.

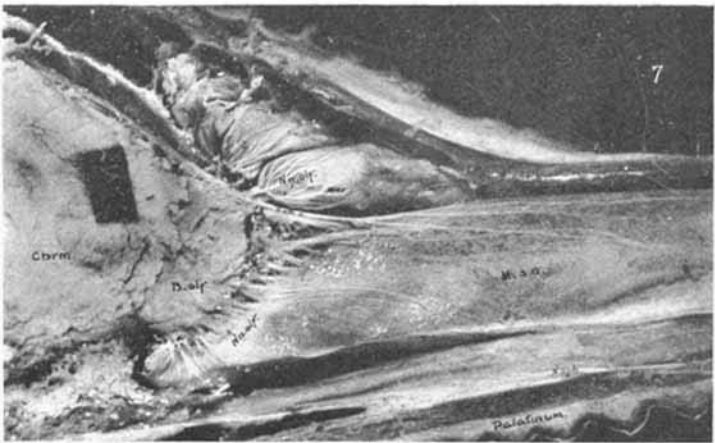
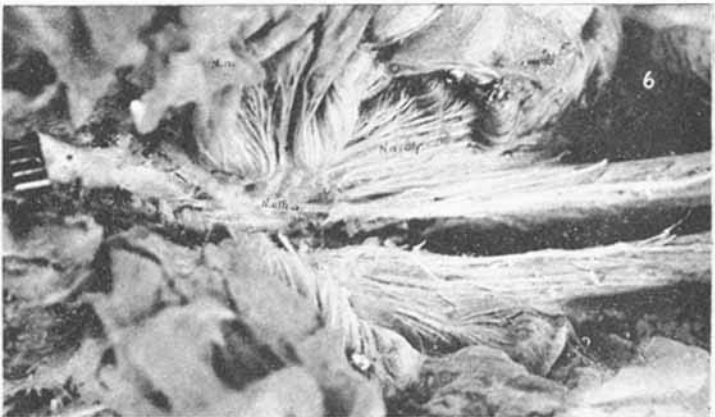
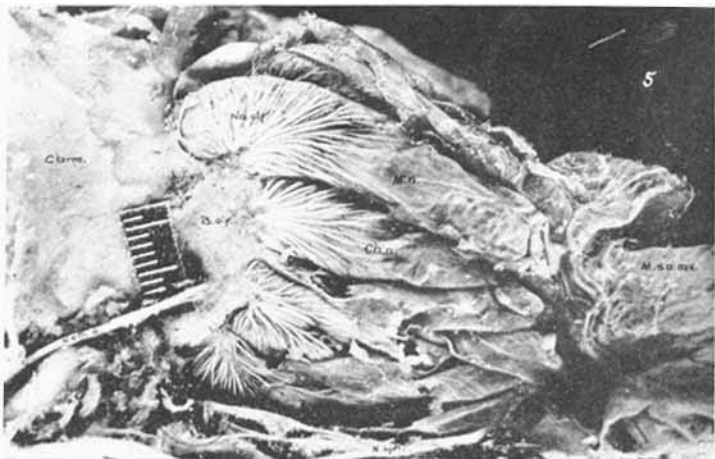


PLATE V.

FIG. 8 ($\times 1.07$).

Median section of the head of a cat with the bony septum removed, to show especially the olfactory nerves to the septal mucosa and the vomeronasal organ. Note the arterial plexus.

FIG. 9 ($\times 3.6$).

The septal mucosa of a cat, with the blood vessels injected. To show especially the vomeronasal organ and its olfactory nerves, and the olfactory nerves of the septum. Note the numerous blood vessels. The thicker part of the mucosa is light, the thinner dark.

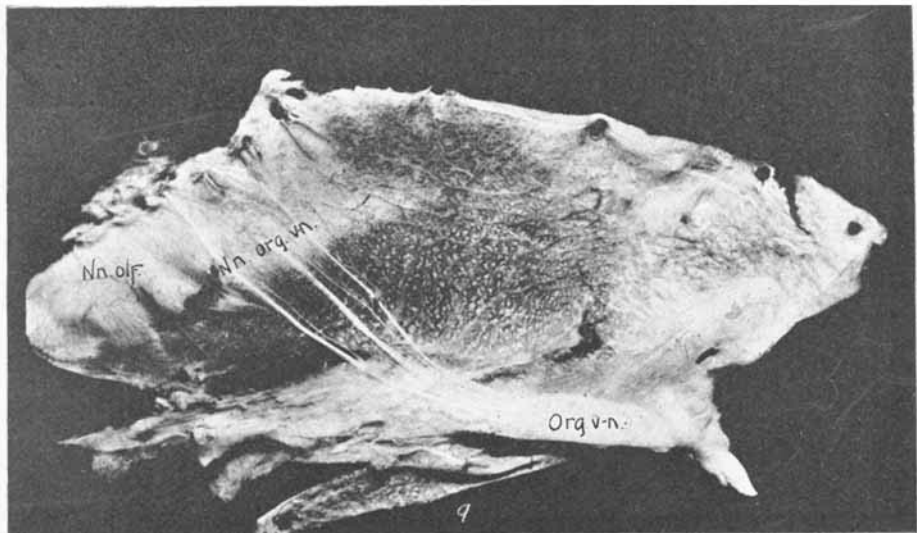
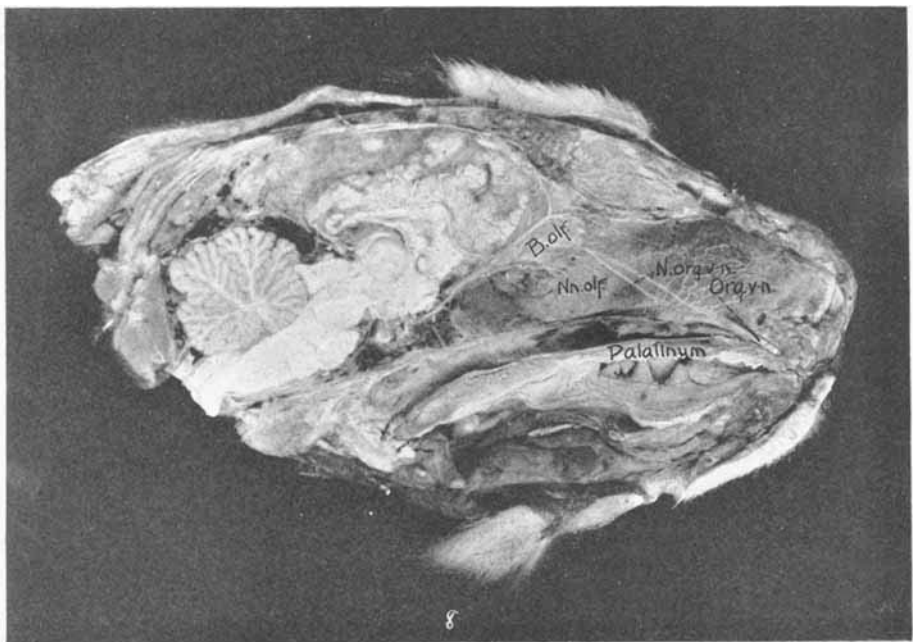


PLATE VI.

FIGS. 10-12.

Photographs of the drawings by Antonio Scarpa of the nose of man.

FIG. 10.

Median section of the nose of man with the bony septum removed to show the septal mucosa. Note the very large distribution of olfactory nerves. The naso-palatine nerve is also shown.

FIG. 11.

A median section through the skull, septum removed, to show the superior, median and inferior conchæ of the nose. Note the perforated appearance of these bones. The olfactory nerve bundles pass through these canals and within them form an apparent anastomosis. To demonstrate the nerves the bony walls of these canals must be removed piece by piece.

FIG. 12.

Septal mucosa removed to show the superior, median and inferior conchæ. Note the apparent anastomosis of the olfactory nerves and their extent; also the distribution of the 5th nerve.

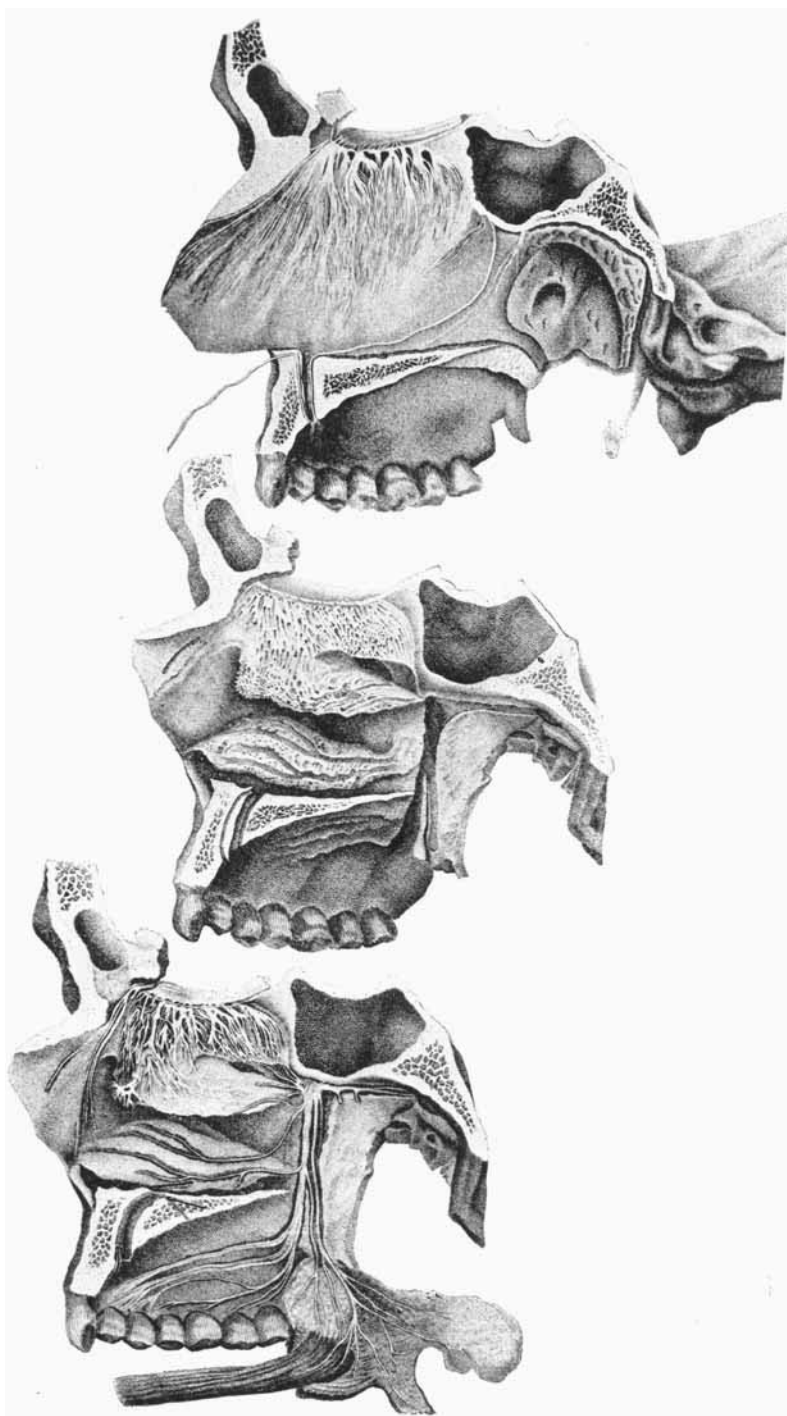


PLATE VII.

FIG. 13 ($\times .64$).

Head of a child, about one year. The lateral wall of the nose and orbit have been removed to show the deeper layers of the mucosa in which lie the nerve bundles. Note the anterior ethmoidal nerve.

FIG. 14 ($\times 3.75$).

Lateral wall of the nose of a child about one year. Same as 13, enlarged. To show especially the plexiform appearance of the olfactory region of the lateral wall of the nose, which has been interpreted by all workers to be a plexus of olfactory nerves. These cords, however, are formed not only of olfactory nerve bundles, but also of blood vessels and connective tissue, as shown by Figs. 24, 26, 27. Note also the anterior ethmoidal nerve.

EFFIE A. READ

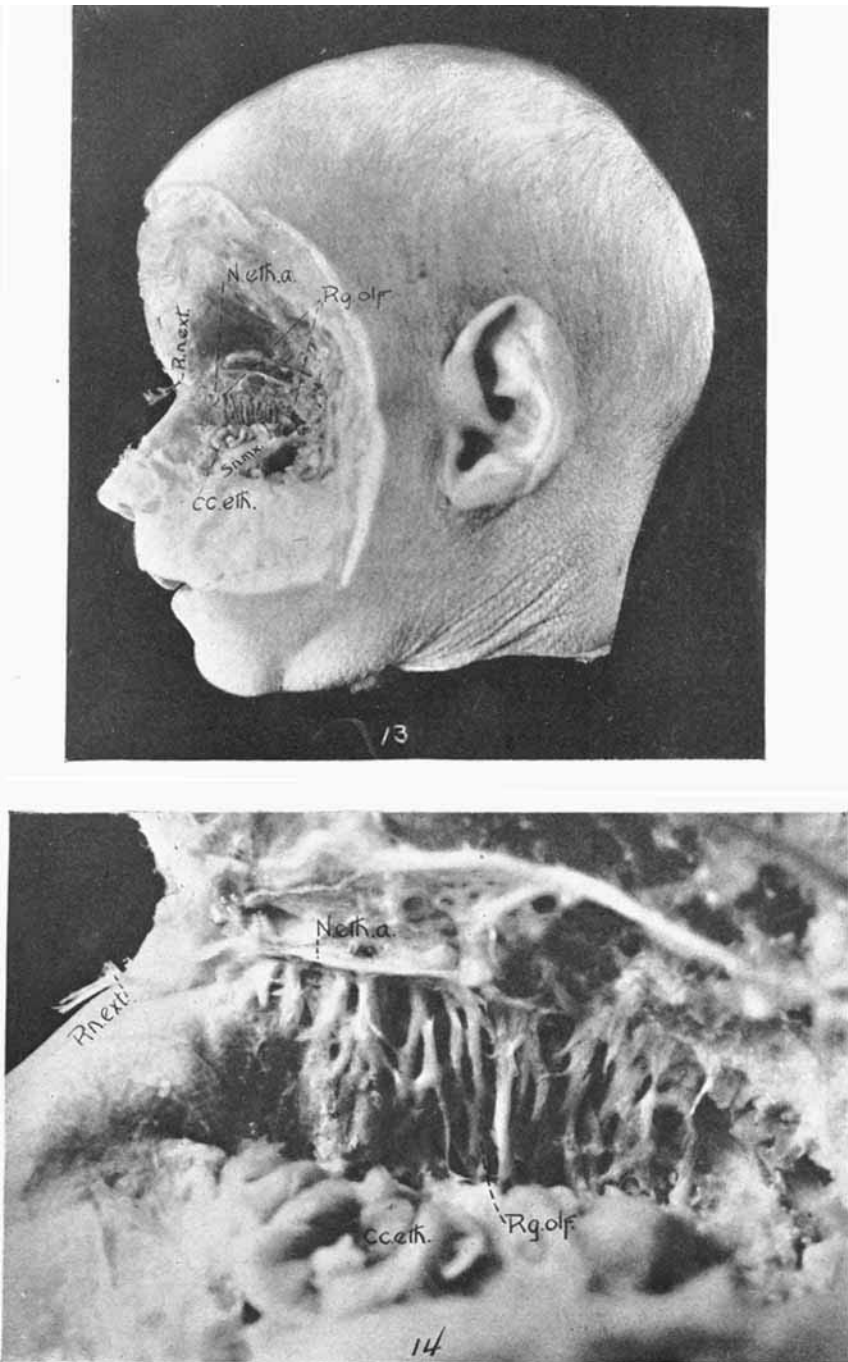


PLATE VIII.

FIGS. 15-17 ($\times 5$).

Transections of the head of an embryo dog.

FIG. 15.

In the region of the vomeronasal organ. Note its relation to the vomeronasal cartilage. Maxillo-turbinals are shown.

FIG. 16.

In the region of the maxillary sinus. Note the number of folds of the ethmo-turbinals.

FIG. 17.

Near the cribriform plate. Note the increased number of folds of the ethmo-turbinals and the maxillary sinus.

FIGS. 18-20 ($\times 5$).

Transections of the head of an embryo cat.

FIG. 18.

In the region of the vomeronasal organ. Note its relation to the vomeronasal cartilage. The inferior turbinal is shown.

FIG. 19.

In the region of the maxillary sinus. Note the number of folds of the ethmo-turbinals.

FIG. 20.

Near the cribriform plate. Note the increased number of folds of the ethmo-turbinals.

FIGS. 21-23 ($\times 5$).

Transections of the nose of a four months human fetus.

FIG. 21.

In the region of the vomeronasal organ. Note its relation to the septum and to the vomeronasal cartilage. Inferior concha is shown.

FIG. 22.

Shows the relation of the inferior and median conchæ.

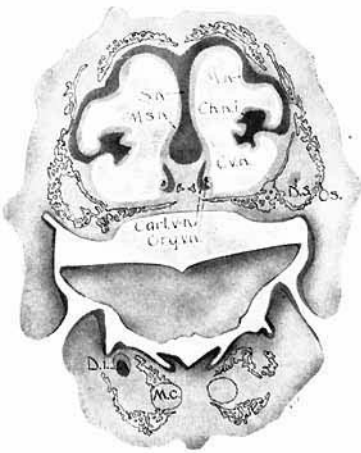
FIG. 23.

Shows the relation of the superior, median and inferior conchæ. Note the olfactory bulb, the cribriform plate and a section of an olfactory bundle.

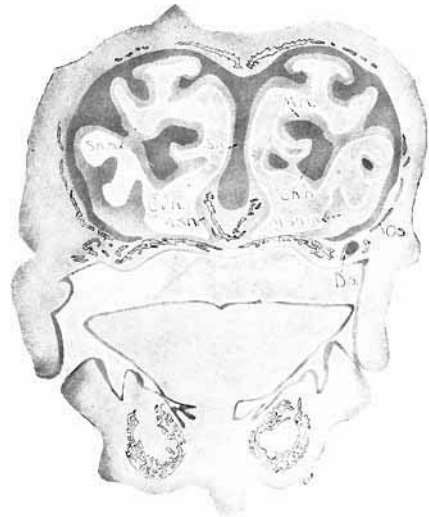
PLATE IX.

FIG. 24 ($\times 17.5$).

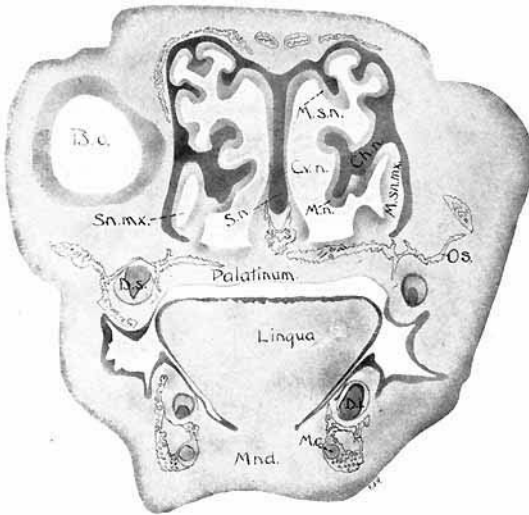
The right lateral wall of the nose of a child about one year. This was stained with a differential stain to demonstrate that the olfactory nerves pass as dark bands within the cords of connective tissue and to show that the plexiform appearance is due, not to these olfactory nerve bundles, as has always been stated, but to the ramification of blood vessels and to the amount and arrangement of the connective tissue.



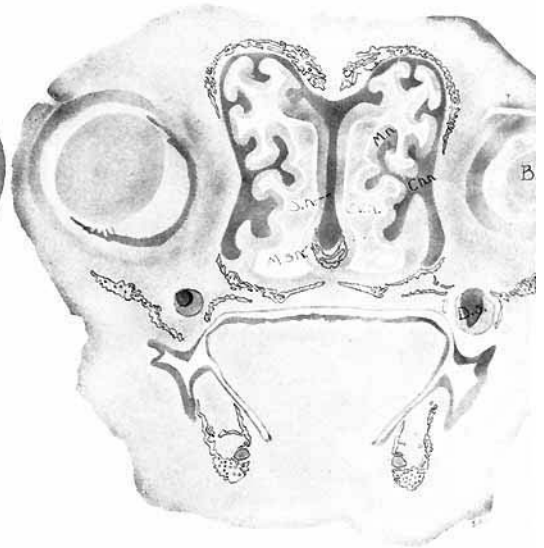
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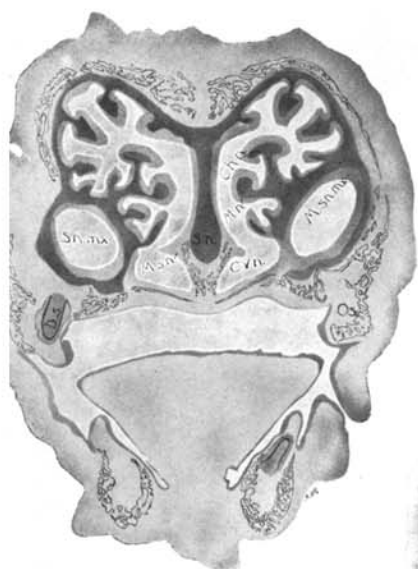
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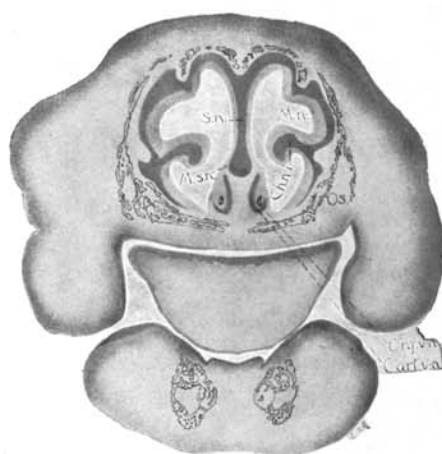
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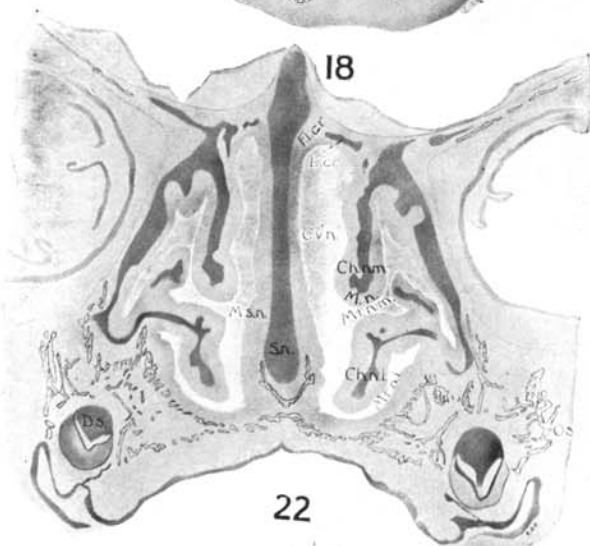
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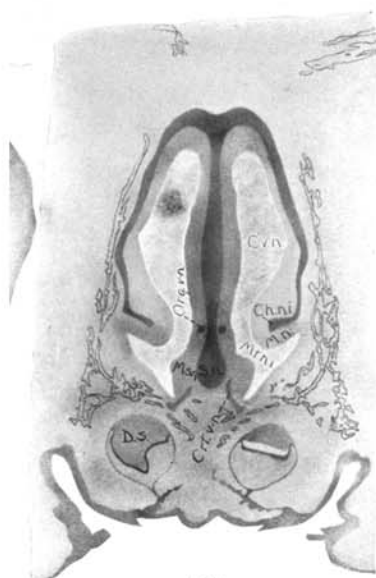
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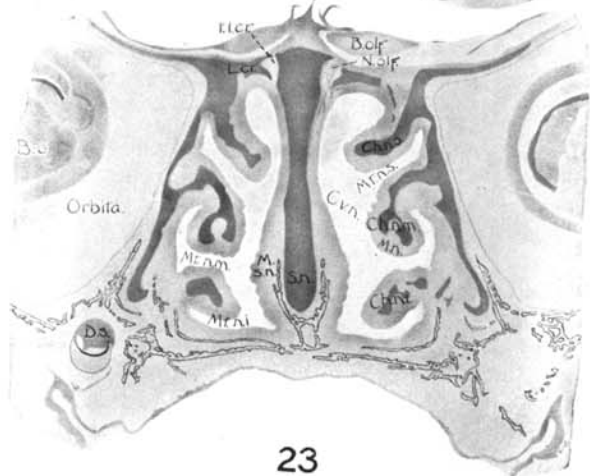
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22



21



23



PLATE X.

FIG. 25 ($\times 9.2$).

A part of the septal mucosa of the nose of a child about one year. (Same child as shown in Fig. 24.) This is stained with a differential stain to demonstrate that the large olfactory nerve bundles do not form an anastomatic plexus.

FIG. 26 ($\times 9.2$).

A drawing from Fig. 25. The nerves were carefully followed out to show that any plexiform appearance is due to the crossing and recrossing of nerves. Joining was found in a few cases of the smaller nerve bundles.

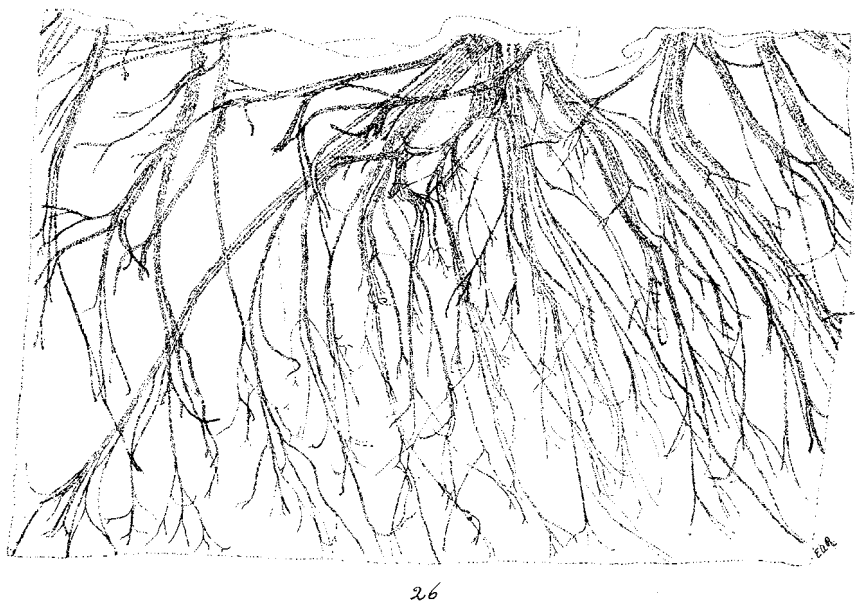
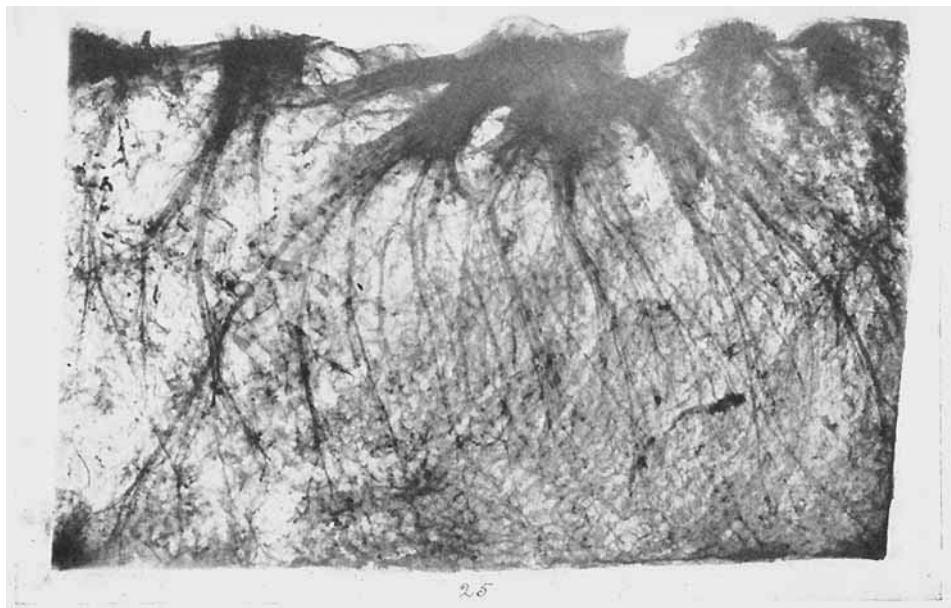


PLATE XI ($\frac{1}{2}$ natural size).

FIGS. 28, 29.

Von Brunn's 1892 diagram of nasal cavity of man to show the area of olfactory nerve distribution (blackened area).

Fig. 28 = man 40 years; Fig. 29 = man 30 years.

FIGS. 30, 31.

Diagram of olfactory nerve distribution made from my dissection.

Fig. 30 = child about 1 year.

Fig. 31 = man 30-40 years.

OLFACTORY APPARATUS IN DOG, CAT AND MAN
EFFIE A. READ

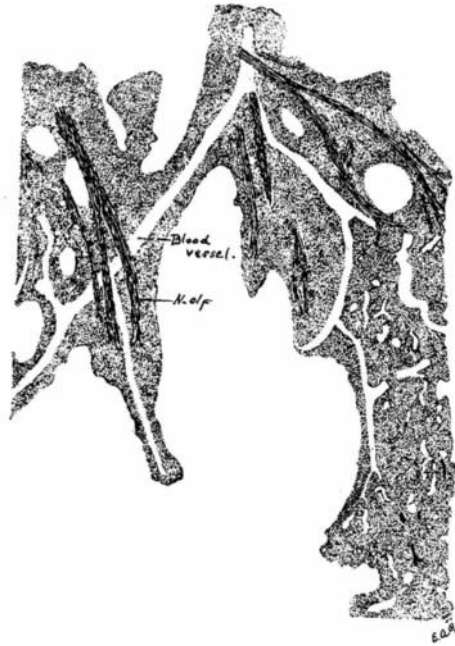


FIG. 27 ($\times 123$).

Longitudinal section of the left lateral wall of the nose of a child about 1 year, same child as shown in Figs. 24 & 26. This figure shows in section what is demonstrated in Fig. 24, that is, that the plexiform appearance of this region is due to blood vessels, and not to nerves.

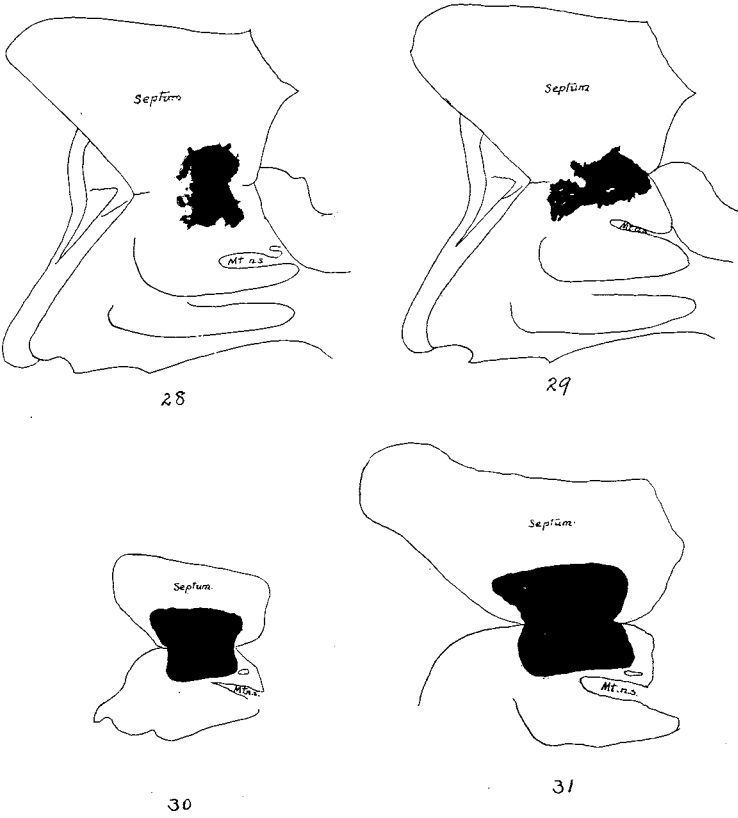


PLATE XII.

FIG. 32 ($\times 585$).

Olfactory cells from the nasal mucosa of the dog (Golgi stain). Note the long axones and the olfactory hair. (Enclosing lines indicate the thickness of the epithelium.)

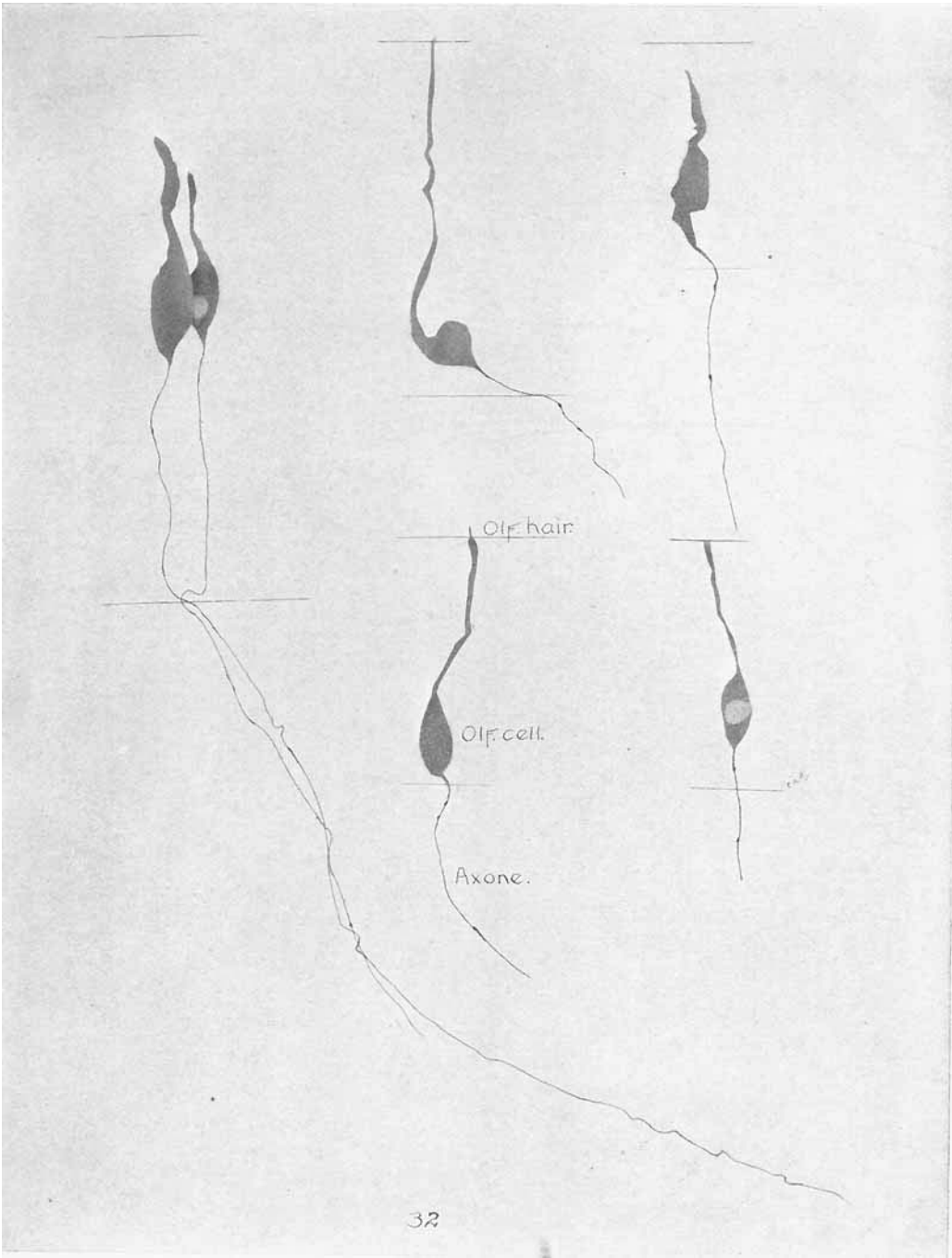


PLATE XIII.

FIGS. 33, 34.

Olfactory cells from the nasal mucosa of the cat. (Enclosing lines indicate the thickness of the epithelium.)

FIG. 33 (\times 833.4).

Cells stained with methylene blue.

FIG. 34 (\times 625).

Cells stained by the Golgi method. Olfactory hairs are very distinct at the free end of several of the cells.

EFFIE A. READ

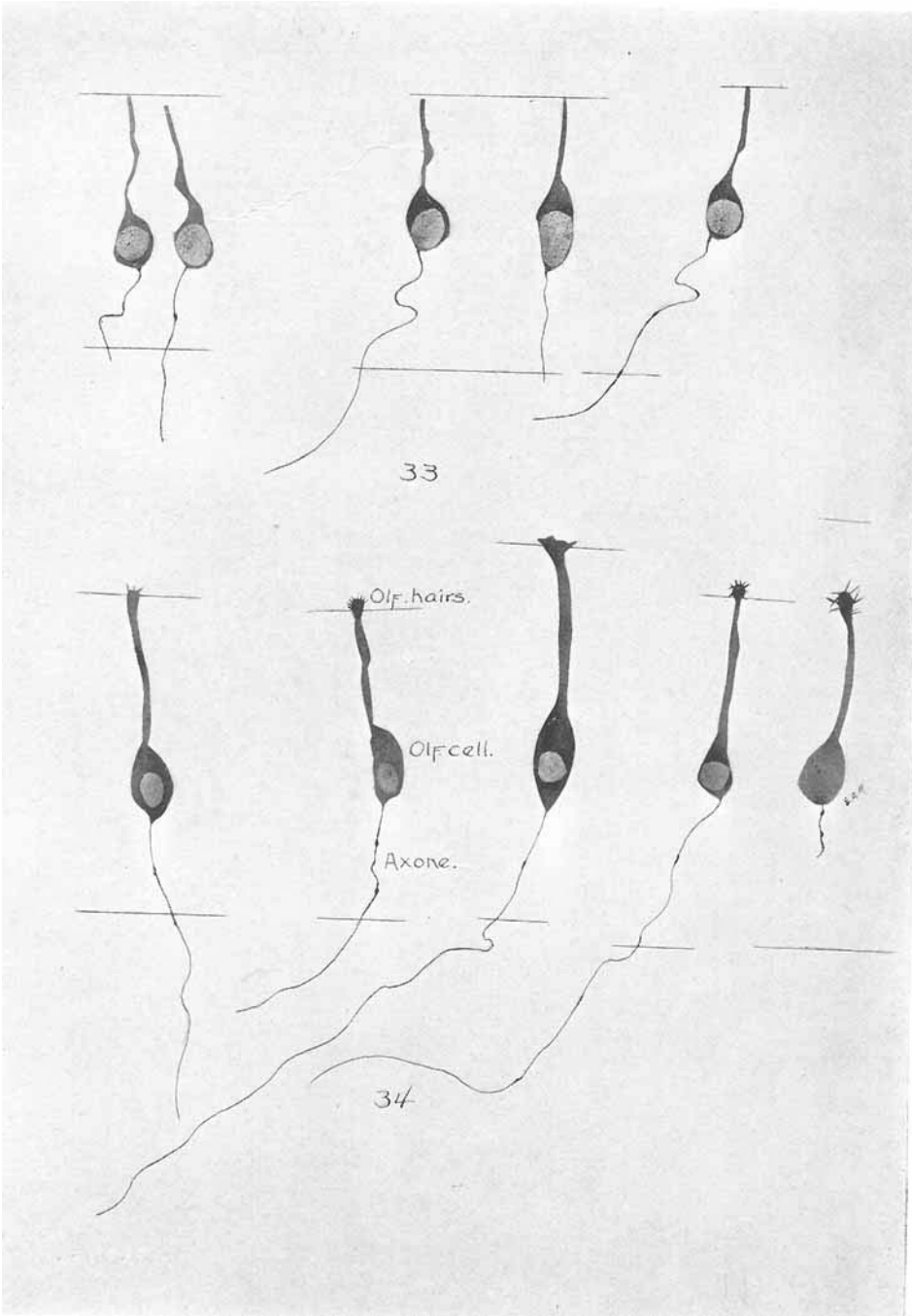


PLATE XIV.

FIG. 35-38 (\times 760).

Olfactory cells. (Enclosing lines indicate the thickness of the epithelium.)

FIG. 35.

Olfactory cells from the dog, stained with gold chloride.

FIG. 36.

Olfactory cells from the dog, stained with gold chloride.

FIG. 37.

Olfactory cells from the cat; isolated by formaldehyde dissociator.

FIG. 38.

Olfactory cells from the nasal mucosa of man, stained with gold chloride and dissociated by formaldehyde. Note the short axones in two of the cells.

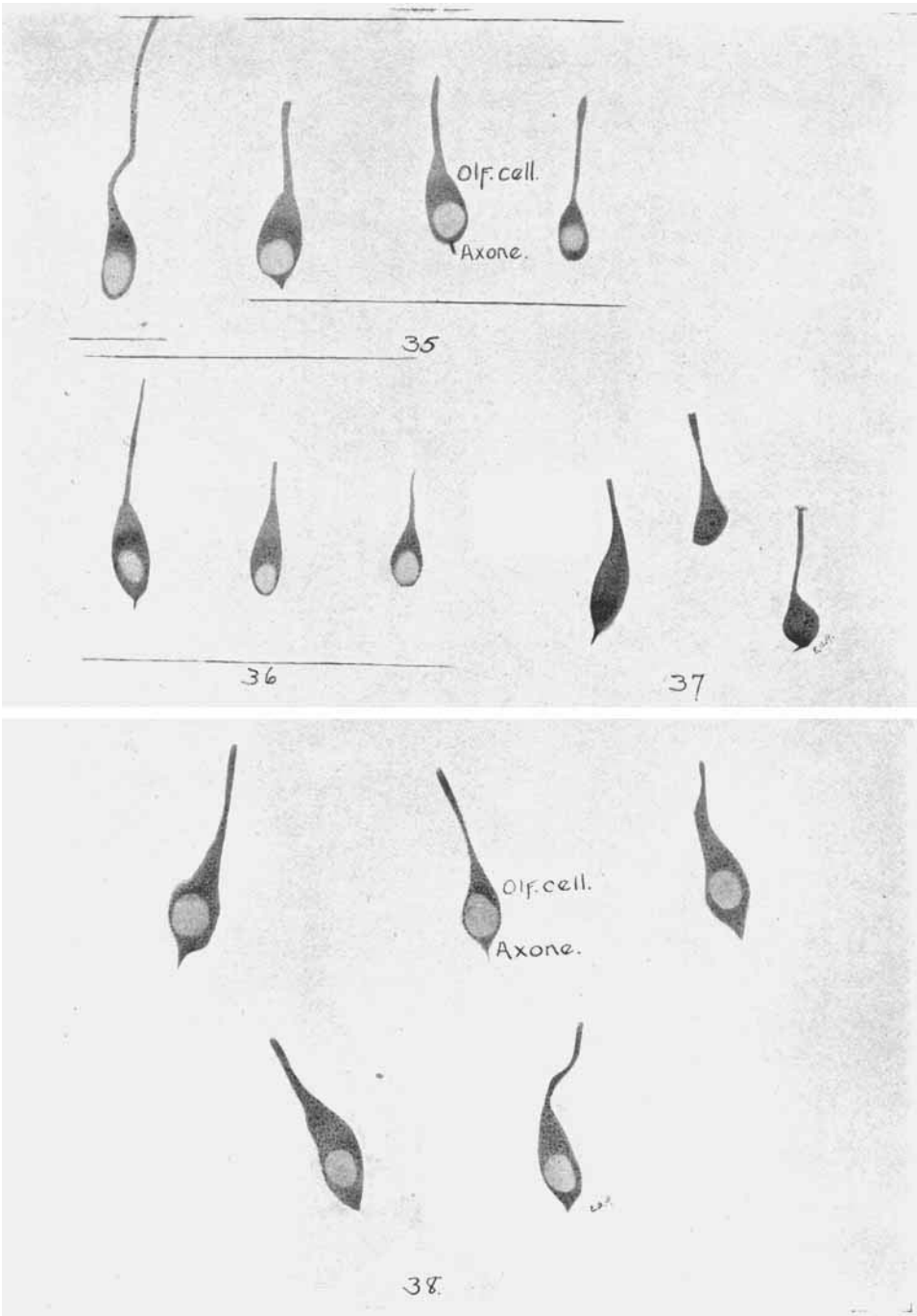


PLATE XV.

FIGS. 39-45.

FIG. 39 ($\times 450$).

Olfactory epithelium of the cat; formaldehyde dissociation.

FIG. 40 ($\times 450$).

Isolated sustentacular cells of the cat.

FIG. 41 ($\times 300$).

Duct of Bowman's gland of the cat. Golgi stain.

FIG. 42 ($\times 450$).

Olfactory epithelium of an embryo dog; gold chloride stain.

FIG. 43 ($\times 450$).

Ciliated cells from the respiratory epithelium of the nose of the cat.

FIGS. 44, 45 ($\times 450$).

Free nerve terminations of the 5th nerve in the nasal mucosa of the cat.

FIG. 44.

In the respiratory region.

FIG. 45.

In olfactory region.

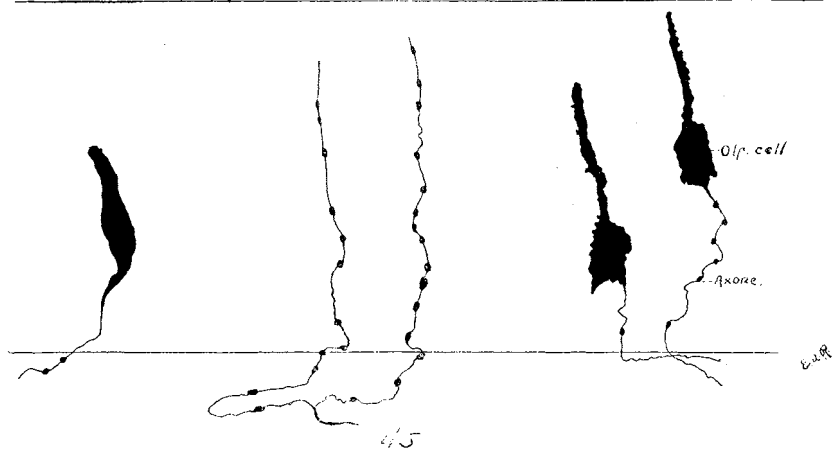
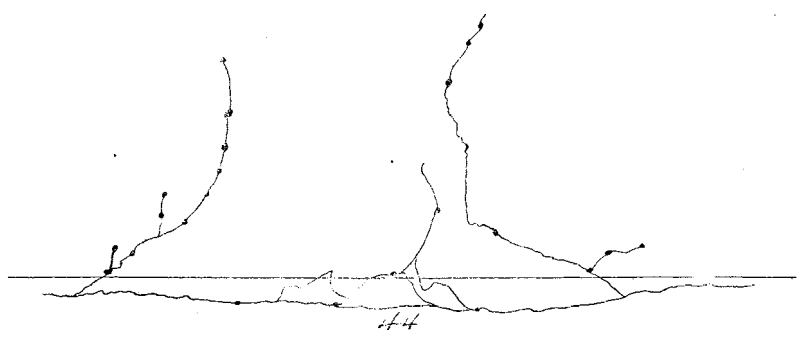
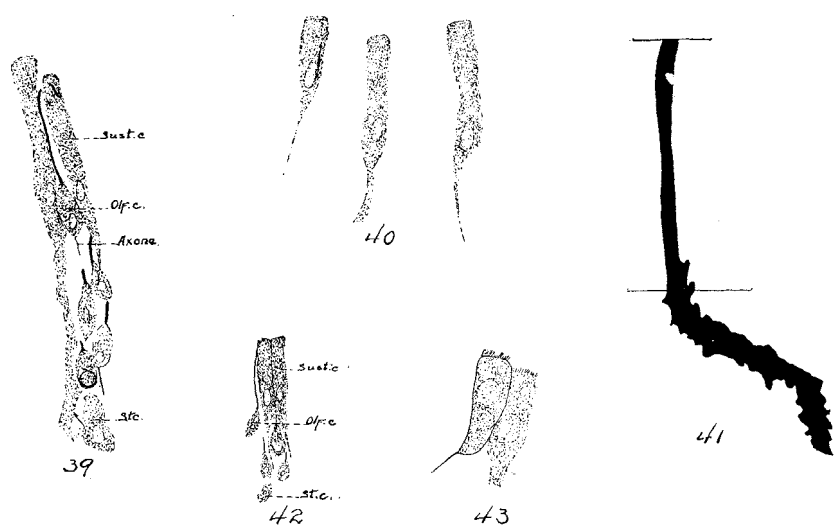


PLATE XVI.

FIGS. 46, 47.

Glomeruli of the olfactory bulb in the dog (Golgi stain), showing the end brushes of the olfactory axones.

FIGS. 48-50.

Glomeruli of the olfactory bulb in the dog (Golgi stain), showing the end brushes of the mitral cell dendrites.

FIG. 48 ($\times 310$).

Three glomeruli formed by the branching of one dendrite.

FIG. 49 ($\times 310$).

Glomerulus formed of dendrites from two different mitral cells.

FIG. 50.

Glomerulus formed by the branching of one dendrite.

FIGS. 51-53.

Glomeruli of the olfactory bulb of the cat. Golgi stain. Mitral cells and dendrites.

FIGS. 51, 52.

Glomeruli formed of three dendrites from at least two mitral cells. Fig. 51 ($\times 310$), Fig. 52 ($\times 475$).

FIG. 53 ($\times 310$).

Glomerulus formed by two dendrites from the same mitral cell.

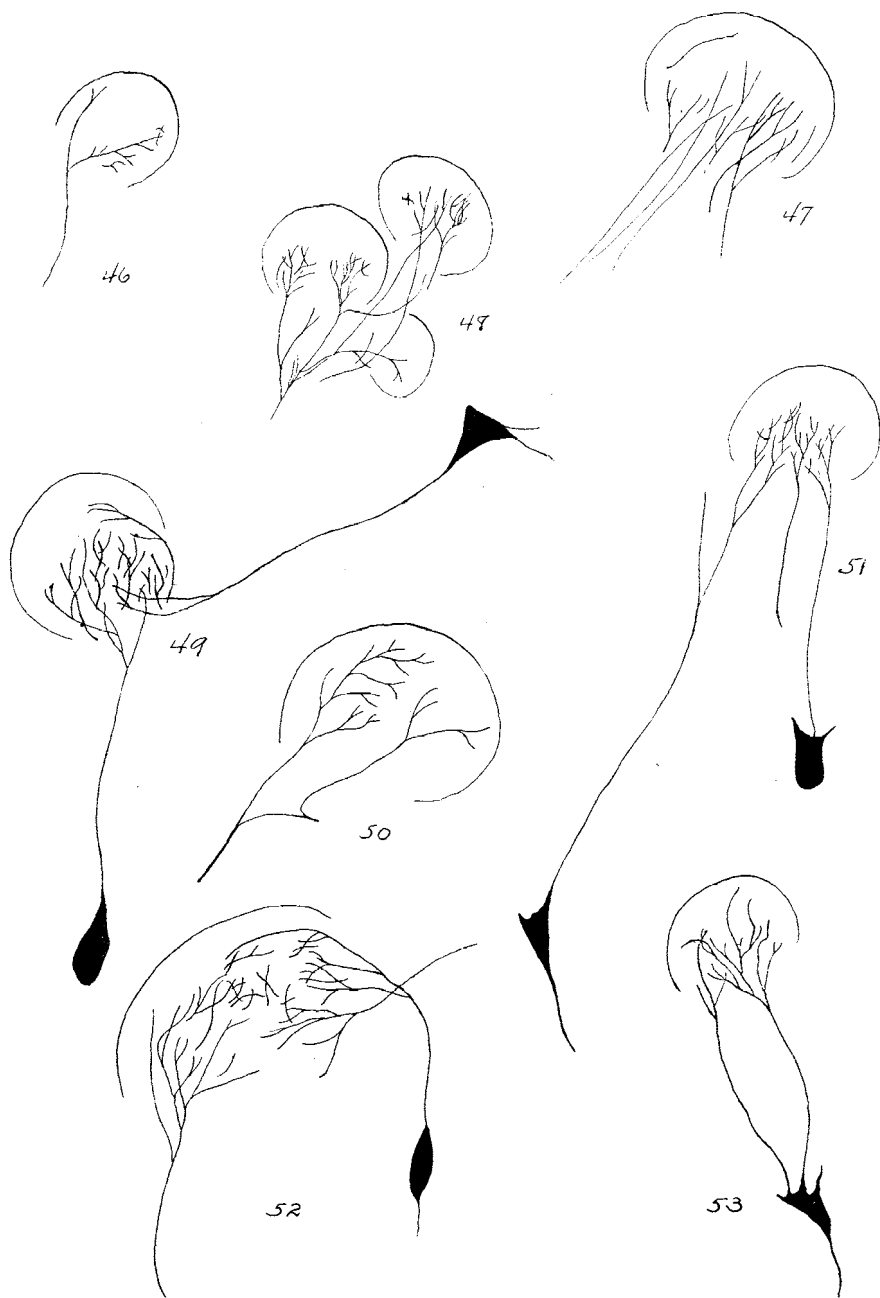


PLATE XVII.

FIGS. 54-55A.

FIG. 54 ($\times 50$).

Vomeronasal organ in an embryo kitten.

Section through the cephalic region of the organ, the cartilaginous capsule entirely enclosing it. Two olfactory cells are shown in the upper part of the lining of the epithelium.

FIGS. 54A, 55A ($\times 488$).

Olfactory cells of the vomeronasal organ, with varicose axones. The cell with the longest axone was drawn from a different region of the same organ (enclosing lines indicate the thickness of the epithelium).

FIG. 55 ($\times 30$).

Section through the middle of the vomeronasal organ; cartilaginous capsule not entire. Note the difference in thickness of the median and lateral epithelium; an olfactory cell is shown in the epithelium of the median wall.

EFFIE A. READ

