THE VOMERO-NASAL APPARATUS IN CHRYSEMYS PUNCTATA AND RANA CATESBIANA

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SEVENTEEN FIGURES

In a previous communication the writer ('12) described the vomero-nasal apparatus in the opossum and other mammals. It was shown that the vomero-nasal organ, the vomero-nasal nerves and the accessory olfactory bulb are parts of a special olfactory mechanism the specific function of which still remains doubtful. It is with the idea that a careful comparative study of this apparatus in the different animals may lead to a more definite understanding of its function that this study was undertaken.

The observations about to be reported were based in part on serial sections of the heads of turtles and frogs and in part on dissections of prepared specimens of the same species. Wax plate reconstructions of the olfactory apparatus were made to show, so far as possible, the form and comparative size of its component parts. Figures 7, 8, 15 and 16 represent drawings of these reconstructions.

CHELONIA

Two views have been advanced as to the structure that should be designated the vomero-nasal organ in these forms. One group of observers believe that the vomero-nasal organ exists in a very simple condition, and that in some species it forms a shallow fossa covered by neuro-epithelium situated on the medial wall of the nasal cavity, while in others the neuro-epithelial

area has extended on to the anterior and lateral walls of the nasal fossa. Another group of workers claim that the vomero-nasal organ is a rudimentary structure and consists of a small duct that extends from the surface of the septal mucosa caudalward in the submucosa and ends blindly.

According to Seydel's ('96) communication the nasal cavity in Chelonia may be subdivided into a cranially situated pars olfactoria and a more caudally situated pars respiratoria. The vomero-nasal organ belongs to the last named subdivision. In testudo graeca one can observe the vomero-nasal organ occupying a shallow fossa on the medial wall. The separation of its epithelium from the neuro-epithelium of the olfactory region is completed through a narrow intervening zone of indifferent epithelium. The ventral and lateral portions of the pars respiratoria exhibits no neuro-epithelium. He states that in emys europaea the pars respiratoria is more complicated than in testudo. Here the neuro-epithelium that comprises the vomero-nasal organ is found in four fossae which occupy the medial, the two side walls and the floor of the pars respiratoria. It is separated from the neuro-epithelium of the pars olfactoria by a low ridge that is covered by indifferent epithelium. Seydel accepts the view that the neuro-epithelium in emys has extended from the medial walls onto the floor and side walls of the pars respiratoria. For an explanation of this view he refers to the course of the nerve fibers of the pars respiratoria. The olfactory fibers extend from the medial wall downward and curve lateralward beneath the floor and upward on the lateral wall where they subdivide into branches. These relations have resulted from a condition where the neuro-epithelium occupied a small area on the medial wall and has extended to the anterior and lateral walls.

In one embryo of Chrysemys punctata Seydel observed that the neuro-epithelium of the vomero-nasal organ occupied a small area on the medial wall while on the floor indifferent epithelium was found. In another the neuro-epithelium had extended from the medial wall onto the floor of the pars respiratoria.

Mihalkovics researches on emys europaea has lead him to differ as to the position, form and structure of the vomero-nasal organ. He believes that the vomero-nasal organ is a rudimentary structure in these forms. He describes this organ as a small, blind, tubular structure extending from the surface of the septal mucosa caudalward in the submucosa. It receives at its distal extremity the ducts of the medial nasal glands.

Zuckerkandl ('10) observed a specimen of emys europaea and corroborates Seydel's important anatomical observations. In regard to the structure that Mihalkovics has designated the vomero-nasal organ he is of the opinion that it is the duct of the medial nasal glands. Zuckerkandl further observed that the olfactory nerves arise from two areas of nasal mucosa. A dorsal branch arises from the mucosa of the pars olfactoria and a ventral branch receives filaments from the vomero-nasal area. The dorsal and ventral branches unite to form a common olfactory nerve that passes through a large opening in the cranium together with the nerve of the opposite side. As these nerves approach the olfactory bulb in their course caudalward the nerve bundles become separated, the dorsal branch forms a large lateral bundle that distributes filaments to the apex and the ventral surface of the olfactory bulb and extends dorsalwards over the medial and lateral surfaces. The ventral branch becomes the more slender medial ramus that sends filaments to the upper half of the medial surface and to the dorsal surface of the olfactory bulb.

CHRYSEMYS PUNCTATA

The nasal fossa in chrysemys punctata consists of a principal nasal chamber that communicates anteriorly with a circular naris by means of a small cylindrical nasal passage and posteriorly with the choana through a larger posterior nasal canal.

By referring to figure 3 it will be seen that the principal nasal chamber is oval in transverse section with the greatest diameter in the perpendicular direction and its shortest diameter in a horizontal plane. The anterior nasal passage communi-

cates with it on the anterior wall about half the distance between the roof and the floor. The posterior nasal canal extends horizontally caudalward on a level with the floor. The otherwise smooth interior is interrupted by many low ridges which course generally in an antero-posterior direction and subdivide the cavity into numerous fossae of varying sizes and depths.

Beginning just above the communication between the principal nasal chamber and the anterior nasal passage are two ridges, one of which extends caudalward over the medial wall, the other in the same direction over the lateral wall and become less pronounced as they approach the posterior wall. These ridges which are covered by respiratory epithelium separate completely a large fossa in the roof of the principal nasal chamber. This fossa is covered by olfactory neuro-epithelium and gives origin to the olfactory nerves. Below the two ridges mentioned above is an extensive fossa that occupies the lower half of the anterior wall, the anterior portion of the floor and adjacent portions of the medial and lateral walls. This area which has a very irregular outline is covered by the vomero-nasal neuro-epithelium and gives origin to the vomero-nasal nerves. By referring to figure 2, which is a transverse section through the anterior portion of the principal nasal chamber, it will be seen that the vomero-nasal organ occupies a single and extensive fossa situated on the lateral, medial and anterior walls of the nasal chamber. By following this fossa caudalward in serial section it will be found that it becomes subdivided into four areas (fig. 3) by the apparent invasion from the caudal direction of three low ridges capped by respiratory epithelium and thereby giving to the vomero-nasal organ the appearance of occupying four separate fossae.

The olfactory neuro-epithelium (figs. 7 and 8) occupies the roof and adjacent portions of the medial, anterior and lateral walls of the nasal chamber. It extends lowest on the anterior wall where it covers one-third the distance from roof to floor. From this point the border gradually recedes dorsally until the caudal wall is reached. The vomero-nasal neuro-epithelium

occupies the lower portion of the anterior, medial and lateral walls and floor of the nasal chamber. It occupies a single irregular fossa and is separated from the olfactory neuro-epithelium by low ridges covered by respiratory epithelium. The remaining portion of the wall of the nasal chamber is covered by respiratory epithelium.

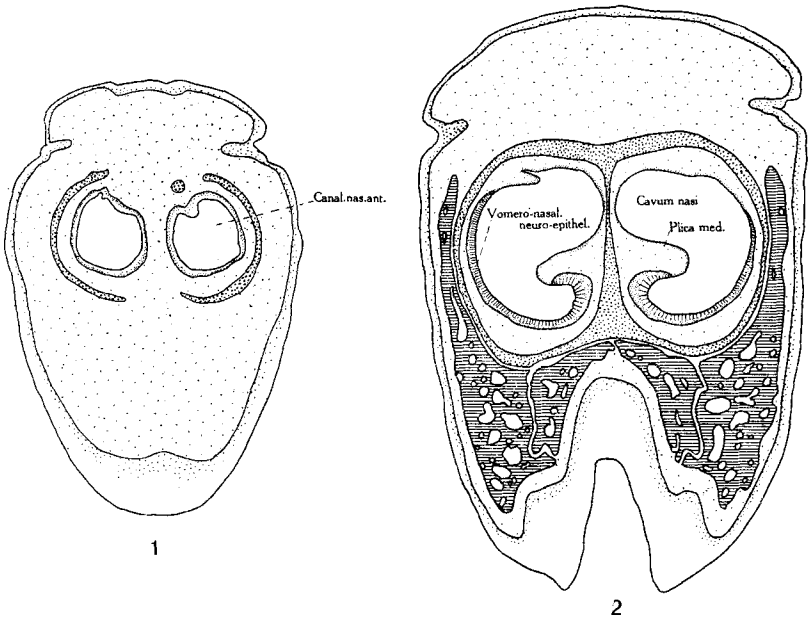


Fig. 1 A transverse section of the head of a turtle at about the middle of the anterior nasal canal. It shows the form of this portion of the nasal fossa. × 10.

Fig. 2 A transverse section of the head of a turtle passing through the anterior portion of the principal nasal chamber to show the form of the nasal fossa and the position and distribution of the vomero-nasal mucosa. × 10.

The anterior nasal passage extends nearly horizontally caudalward from the naris and communicates with the principal nasal chamber about midway between the roof and floor. It is nearly cylindrical in outline and presents a low ridge that courses obliquely in a caudo-lateral direction from a mediocephalic origin.

The posterior nasal canal extends nearly horizontally caudalward from the principal nasal chamber. It is semicircular in cross section. Attached to the anterior half of the lateral wall and to the cephalic portion of the roof is a crescentic valve-like fold that separates a dorsally placed blind pouch that opens caudalward.

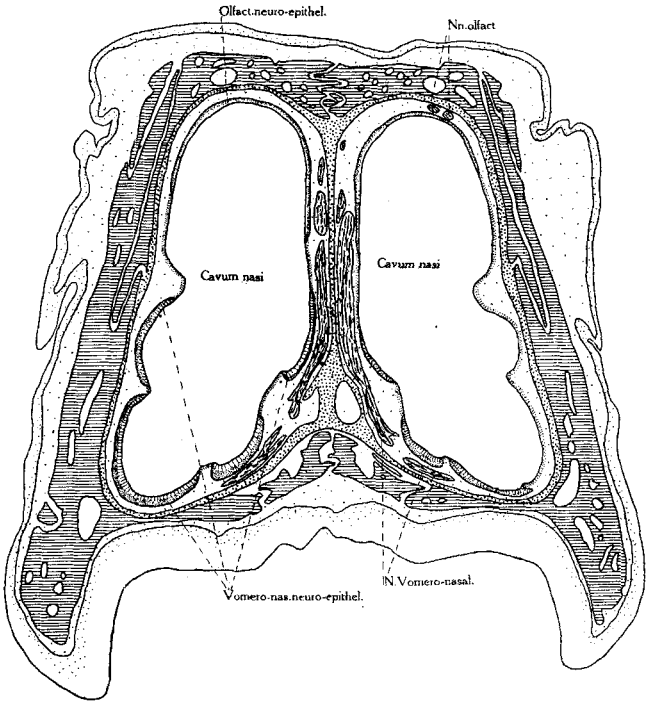


Fig. 3 A transverse section of the head of a turtle passing through the middle of the principal nasal chamber showing its form and size, the distribution of the vomero-nasal and olfactory neuro-epithelium and peripheral course of the vomero-nasal nerves. × 10.

The nerve fibers from that portion of the neuro-epithelium of the vomero-nasal organ situated on the lateral wall collect into two limbs—an anterior and a posterior. The former is the smaller and courses downward in the lateral wall of the nasal fossa. The latter is a broad flat band that passes medially beneath the floor and is joined by the anterior limb.

These combined filaments form a broad sheet of nerve fibers coursing medially beneath the floor to the medial wall and at the same time receiving additional fibers from the neuro-epithelium. In the medial wall the broad flat band of nerve fibers becomes somewhat narrowed and thickened and courses dorsally and somewhat caudally to the roof of the nasal fossa. Here it is joined by the bundle of olfactory nerves of the same side and the

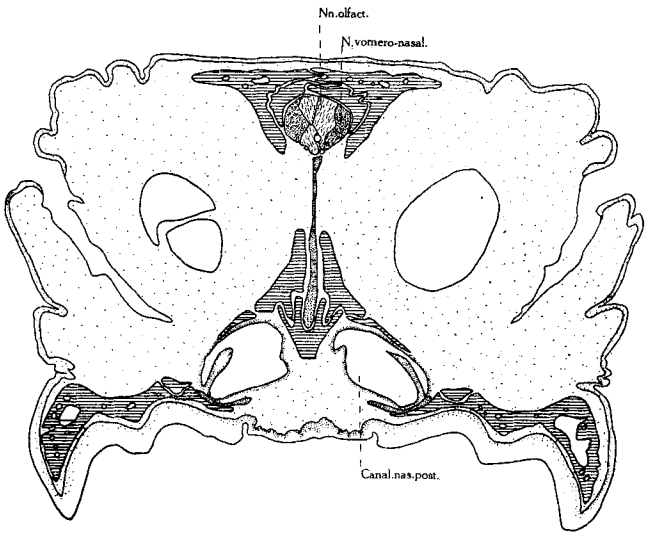


Fig. 4 A transverse section of the head of a turtle passing through the middle of the posterior nasal canal. It shows the form of this passage and the relation of vomero-nasal and olfactory nerves in their course through the cranium. × 10.

combined filaments of vomero-nasal and olfactory fibers of the opposite side. The combined filaments form a large round nerve bundle that courses caudalward through a large opening in the cranium to the cranial cavity. Although the right and the left vomero-nasal and olfactory nerves course through the cranium together the nerve fibers of the different bundles do not intermingle. They lie contiguous to one another and may be separated from each other with little effort as will be seen by referring to figure 4.

As they enter the cranial cavity the vomero-nasal and olfactory nerves separate; the former pass dorsal to the olfactory nerves and to the dorsal surface of the olfactory bulb where the filaments spread out over the vomero-nasal area.

The nerve fibers of the olfactory neuro-epithelial area collect into numerous filaments that course dorsalward and converge to form a large oval bundle above the roof of the nasal fossa. The bundle of olfactory nerves lie lateral to the vomero-nasal fibers in its course through the large opening in the cranium.

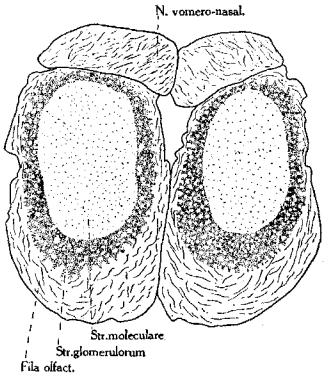


Fig. 5. A transverse section through the anterior portion of the olfactory bulbs of the turtle to show the relation of olfactory and vomero-nasal nerves. × 20.

Upon reaching the cranial cavity olfactory fibers separate from the vomero-nasal fibers and pass ventralward to be distributed to the olfactory area on the apex and ventral surface of the olfactory bulb.

The olfactory bulb is an ovoid mass extending horizontally forward from the forebrain. It is separated from the latter by a well defined oblique groove that defines a very short olfactory peduncle. By referring to figures 5, 6, 7, and 8 it will be seen that the surface of the bulb is sub-divided into two definite and separate areas. An oval area occupying the entire dorsal surface and upper half of the medial surface of the bulb to which the vomero-nasal filaments are distributed is the vomero-nasal

area of the olfactory bulb. This area is homologous to the accessory olfactory bulb of mammals. The olfactory area of the bulb is somewhat more extensive. It occupies the apex, and ventral surface and extends some distance upward on the

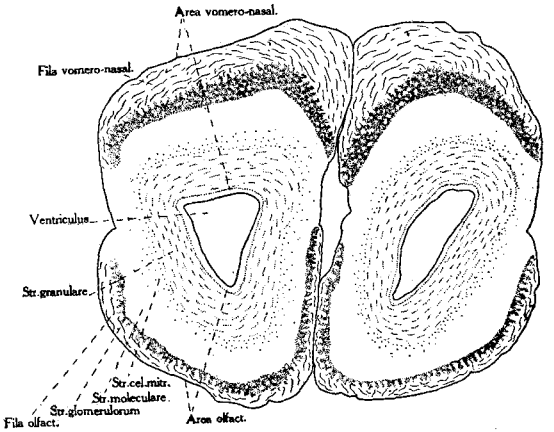
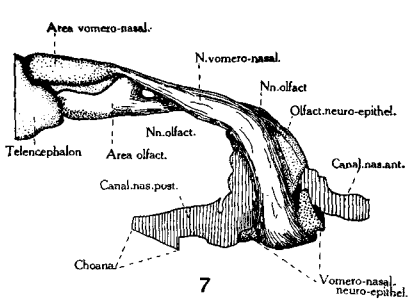


Fig. 6 A transverse section through the middle portion of the olfactory bulb to show the relation of the vomero-nasal and olfactory areas. × 20.

lateral and medial surface. The filaments of the olfactory nerves are distributed to this area. An extension forward of the fore brain cortex separates the vomero-nasal and olfactory areas of the olfactory bulb.



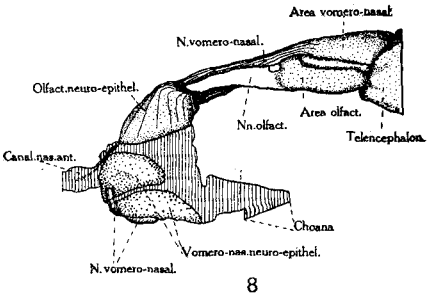


Fig. 7 A medial view of a wax plate reconstruction of the olfactory apparatus of the turtle to show the origin course and distribution of the vomero-nasal and olfactory nerves. × 3.

Fig. 8 A lateral view of a wax plate reconstruction of the olfactory apparatus of the turtle to show the origin, course and distribution of the vomero-nasal and olfactory nerves. × 3.

In transverse section (fig. 6) the olfactory bulb exhibits a large ventricle oval in form. One can distinguish the different concentric layers that have been described for this portion of the brain in other forms. The nerve fiber layer is incomplete and presents a dorsal segment of vomero-nasal fibers and a ventral segment of fila olfactoria. The latter completely encircles the olfactory bulb in the lower mammals. The glomerular layer presents a dorsal and a ventral segment. The former is much thicker than the latter. Then follow the molecular, nerve cell, the granular and ependymal layers in order.

RANA

The excellent description of the nasal fossa in Rana by Ecker and Gaupp has been frequently consulted and, as far as possible, the same terminology has been used in this communication. While he recognized the origin of the olfactory nerves from the olfactory mucosa by two branches—a large dorsal and a small ventral—and that the vomero-nasal nerves join the dorsal ramus, he failed to determine the further course and termination of the vomero-nasal nerves as a separate bundle. He states that the olfactory nerves on entering the cranium separate into two roots, an anterior distributed to the antero-ventral surface of the olfactory bulb, and a posterior root that is distributed to the accessory olfactory bulb.

Zuckerkandl ('10) was the first to recognize a separate vomero-nasal apparatus for the amphibians. He describes the formation of the common olfactory nerves as of fibers formed by the union of the olfactory and vomero-nasal nerves but fails to state the relations of vomero-nasal and olfactory nerves in their passage from the nasal cavity to the brain.

RANA CATESBIANA

Although the nasal cavity of the frog has been very carefully described by Ecker and Gaupp and in text books on comparative anatomy it appears to me advisable, owing to the complexity of the arrangement of its subdivisions, to summarize briefly its more important features.

The nasal cavity of the frog is situated in the anterior part of the cranium. It is very much flattened dorso-ventrally and expands anteriorly and laterally so that in a dorsal view it presents a semicircular outline. The anteriolateral curved

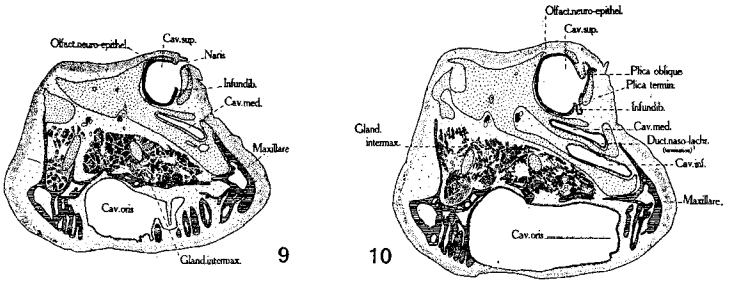


Fig. 9 A transverse section through the head of the frog in the region of the external nasal opening. It shows the form of the principal and middle nasal chambers and the distribution of the olfactory mucosa. × 2.5.

Fig 10 A transverse section through the head of a frog posterior to naris. It shows the relation between the superior, middle and inferior nasal cavities and the distribution of the olfactory mucosa. × 2.5.

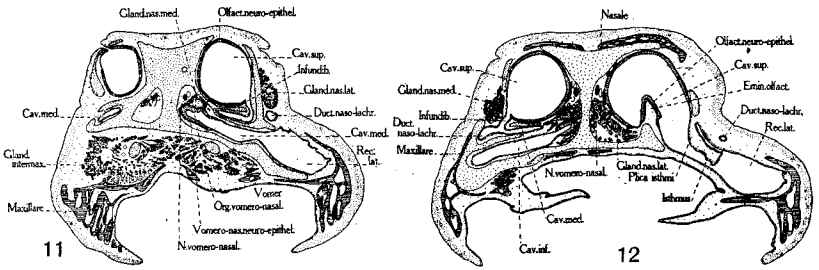


Fig. 11 A transverse section through the vomero-nasal organ of the frog showing the relation of the superior, middle and inferior nasal cavities and the distribution of the vomero-nasal and olfactory mucosa. × 2.5.

Fig. 12 A transverse section through the middle of the principal nasal cavity of the frog showing distribution of olfactory mucosa and the relation of vomero-nasal and olfactory nerves. × 2.5.

margins follow closely the curvature of the maxillae. It consists of two parts, the right and the left nasal fossae. Each fossa communicates with the exterior by an external nasal aperture, the naris, and with the oral cavity by an oval internal nasal aperture—the choana.

The nasal fossa is subdivided into several irregular communicating chambers which have become separated to a greater or less extent during the process of development, by the ingrowth of septa and ridges. It, therefore, presents for description a

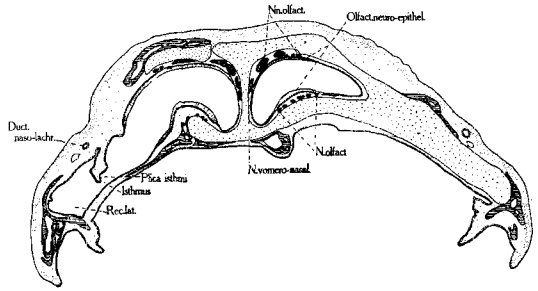


Fig. 13 A transverse section through the choana of the head of a frog. It shows the distribution of the olfactory mucosa and the relation of the vomero-nasal and olfactory nerves. × 2.5.

superior or principal, a middle and an inferior nasal chamber, a lateral recess, the vomero-nasal organ, and two well defined narrow connecting channels, the infundibulum and the isthmus.

The principal nasal chamber occupies a dorso-medial position and comprises about three fourths of the fossa (figs. 15 and 16). By referring to figure 9, it will be seen that a transverse section

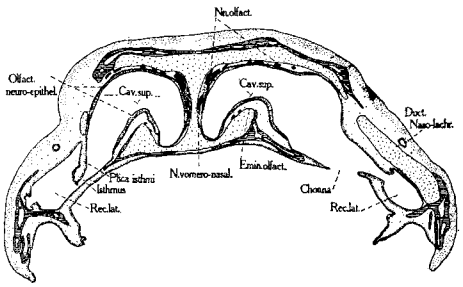


Fig. 14 A transverse section of the head of a frog passing through the posterior part of the superior nasal cavity. It shows the distribution of the olfactory mucosa and the relation of the vomero-nasal and olfactory nerves. × 2.5.

of the cephalic portion of the superior chamber has a circular outline and communicates with the exterior by means of the naris. At the lower part of the lateral wall can be seen the

plica terminalis which marks off a deep groove which is the beginning of the infundibulum. In this region the principal nasal cavity is covered for about three-fourths of its circumference by olfactory neuro-epithelium.

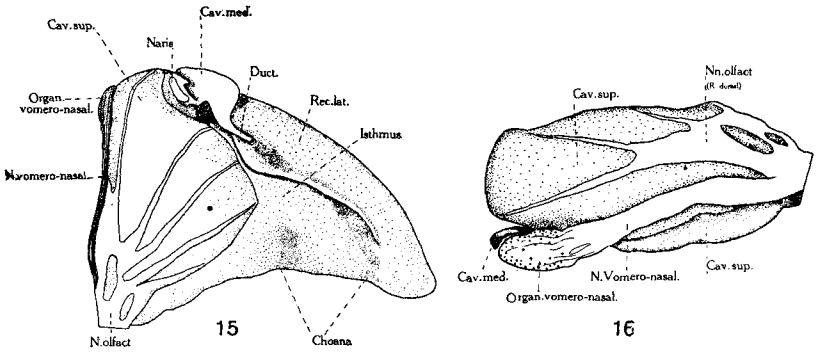


Fig. 15 A medial view of a wax plate reconstruction of the nasal fossa of the frog. It shows the origin and peripheral course of the vomero-nasal and olfactory nerves. About three times natural size.

Fig. 16 A dorsal view of a wax plate reconstruction of the nasal fossa of a frog showing the origin and peripheral course of the vomero-nasal and olfactory nerves. About three times natural size.

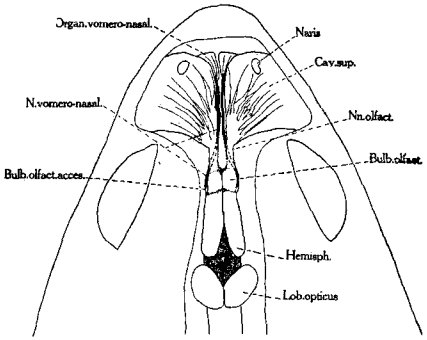


Fig. 17 Represents a dissection of the olfactory apparatus of the frog showing the origin course and distribution of the vomero-nasal and olfactory nerves. Two and one-half times natural size.

Figure 10 represents a cross-section of the principal nasal chambers posterior to the naris. It presents the beginning of the infundibulum separated from the principal nasal chamber by

the broadened plica terminalis. It may be seen that the olfactory neuro-epithelium covers the floor, the medial wall and the greater portion of the roof. The remaining one-third of the circumference is clothed by respiratory mucosa. The principal nasal chamber in figure 11 presents a nearly circular outline and communicates at its ventro-lateral margin with the middle nasal chamber by means of the infundibulum. The olfactory neuro-epithelium covers about three-fourths of its circumference. The lateral wall is covered by simple mucosa. In figure 12 the principal nasal chamber presents the form of an inverted horse shoe. The lateral limb of which communicates through the isthmus with the lateral recess. The olfactory eminence which extends dorsally from the floor aids materially in giving the peculiar form to this portion of the cavity. It will be seen that the olfactory neuro-epithelium has become separated into two areas by a narrow intervening zone of indifferent mucosa. One area covering the olfactory eminence and a more extensive layer lining nearly all of the medial and lateral walls and the roof.

Figure 13 represents a section passing through the choana. The principal nasal chamber has an outline similar to that of figure 12. It communicates directly with the choana. The olfactory eminence has increased in height and breadth. The olfactory neuro-epithelium occupies two areas on the circumference of the chamber. One caps the olfactory eminence, the other covers the upper part of the medial wall and about the medial two-thirds of the roof. The former is more extensive and the latter less extensive, than shown in figure 12. These two areas are separated by a broad intervening zone of respiratory epithelium.

Figure 14 represents a section posterior to the choana. The principal nasal chamber shows marked reduction in size and has a semilunar outline. The olfactory eminence is very much flattened. The olfactory neuro-epithelium caps the olfactory eminence and covers a portion of the medial wall and roof of the nasal chamber; the remaining circumference in this region is covered by respiratory epithelium.

The small middle nasal chamber is situated ventro-lateral to the cephalic extremity of the principal chamber. It is much flattened dorso-ventrally and broad in a transverse direction (figs. 15 and 16). The naso-lachrymal duct communicates with its postero-lateral angle (fig. 10). Posteriorly it communicates with the principal nasal chamber through the anterior part of the infundibulum (fig. 11), and more caudally with the inferior nasal chamber. In fact, the middle chamber appears to be merely an anterior sacculated expansion of the tear duct. It is lined by simple mucosa.

The inferior nasal chamber is an elongated, transversely placed cavity lying ventral to the cephalic extremity of the principal nasal chamber. It is directly continuous laterally with the lateral recess and medially with the vomero-nasal organ. The inferior nasal chamber as shown in figure 10 is an obliquely placed cavity, oval in outline, and clothed by ordinary mucosa. In figure 11 this cavity is shown in direct communication laterally with the lateral recess and medially with the medial recess, the vomero-nasal organ. It is everywhere covered by simple mucosa.

The lateral recess is the direct latero-caudal extension and expansion of the inferior nasal chamber. It is oval in outline and follows the curvature of the maxilla. It communicates anteriorly with the inferior nasal chamber (fig. 11), medially with the principal chamber through the isthmus (fig. 12), and more caudally with choana and oral cavity (figs. 13 and 14). It is lined by simple mucosa.

The vomero-nasal organ is a cup shaped structure that lies at the medial extremity of the inferior nasal chamber and communicates directly with it laterally. It is clothed by neuro-epithelium (fig. 11). The infundibulum is a broad flattened channel which permits communication between the anterior portion of the principal nasal chamber and the middle and the inferior nasal chambers.

The isthmus is an obliquely placed slit (fig. 12), broad in a sagittal plane that serves as a means of communication between the principal nasal chamber and the lateral recess.

It will be seen from the foregoing and by referring to figures 9 to 16 inclusive that the neuro-epithelium is found in two separate and distinct regions of the nasal fossa.

The olfactory mucosa consists of a very extensive and irregular area on the wall of the principal nasal chamber. From an extensive area covering the anterior wall and the adjacent portions of the floor, medial wall and roof as shown in figures 9, 10, and 11, the olfactory mucosa extends caudalward in two strips or zones separated by intervening zones of respiratory epithelium, figures 12, 13, and 14. The ventral, caudal prolongation covers the olfactory eminence and gives origin to the small ventral branch of the olfactory nerves. The dorsal, caudal prolongation covers a variable portion of the medial and lateral walls and the roof of the principal nasal chamber. This portion of the olfactory mucosa together with the extension forward on to the anterior wall gives rise to the large dorsal branch of the olfactory nerves.

The vomero-nasal mucosa lines the wall of the cup-shaped vomero-nasal organ and gives rise to the vomero-nasal nerves. All the remaining portion of the nasal cavity is lined by respiratory epithelium.

It will be seen from the foregoing description that the vomero-nasal apparatus in the turtle equals in size and importance that of the ordinary olfactory mechanism. That the olfactory bulb exhibits an olfactory and a vomero-nasal area which share about equally in its formation. In the frog, however, the vomero-nasal apparatus apparently performs a secondary roll in olfaction. It is very small compared to the olfactory mechanism. The accessory olfactory bulb is situated on the lateral surface of the hemisphere caudal to the olfactory bulb and is only about one twenty-fifth the size of the olfactory bulb.

By referring to figures 12, 13, and 14 it will be seen that the olfactory nerves collect into two separate groups. Filaments collecting into nerve bundles on the dorso-medial wall of the superior chamber form the large dorsal ramus of olfactory nerves and filaments collecting into nerve bundles from the mucosa of the olfactory eminence form the small ventral branch

of the olfactory nerves. These branches course caudalward and join to form a single bundle at the caudal extremity of the principal nasal chamber. From this point it courses to the olfactory bulb where it becomes distributed over the antero-ventral surface.

The vomero-nasal nerves formed by filaments from the dorsal, ventral and medial walls of the vomero-nasal organ form a single rounded bundle that courses dorso-caudally in the medial wall of the principal nasal chamber. At the caudal extremity of this chamber it joins the bundle of olfactory nerves. Although there is a slight intermingling of the vomero-nasal and olfactory bundles the majority of the fibers of the former can be followed in their spiral course caudalward where they wind beneath the olfactory nerves to gain the lateral side of this bundle and course over the lateral surface of the olfactory bulb to reach the accessory olfactory bulb, which lies more caudally (fig. 17).

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