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I.

MORPHOLOGY AND EMBRYOLOGY OF THE NASAL
FOSSAE OF VERTEBRATES.*

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INTRODUCTION.

The nasal fossæ are hollow cavities in the facial bones, of varying importance, depending upon whether the animal is water-breathing or air-breathing; in the first group they serve exclusively as organs of olfaction, in the second they constitute, in addition, special canals through which the inspired air passes in order to reach the pharynx and the bronchial tubes.

*This translation is made with the approval of Professor Dieulafé, and with the kind consent of M. Félix Alcan, publisher of the *Journal de l'Anatomie et de la Physiologie Normales et Pathologiques de l'Homme et des Animaux*. The translator feels that the high merit of Prof. Dieulafé's monograph and the absence of a similar work in English justify the effort here made to extend its sphere of usefulness.

The nasal organ is constant in all species of vertebrates; single in *Amphioxus* and cyclostomes, double in all other classes. Its development is in proportion to the acuteness of the sense of smell in the lower, water-breathing vertebrates; it is independent of this in air-breathing vertebrates, and in them it is very complex and greatly extended by reason of the influence of the respiratory area. The Amphibia constitute an intermediate form between these two groups, which is of great interest.

The necessity for active respiratory combustion entails a greater amplitude of the nasal fossæ in warm-blooded animals, while their extension is proportionately less in cold-blooded animals. A single anatomic characteristic is sufficient to show this difference: the posterior nares of amphibians and reptiles open into the buccal cavity, but into the pharyngeal cavity in birds and mammals. In the latter, the air passes more directly into the respiratory tract and its renewal is therefore easier of accomplishment. In measure as we advance in the scale of vertebrates, we may observe complexities of structure designed to purify and to warm the air (promoted by the ciliated mucosa and the rich vascularity). Two factors are responsible for this action, the turbinates and the sinuses. The venous plexuses produce the great vascularity. In the course of these transformations, the olfactory region is more deeply placed, where it is protected against the grosser impressions and reserved for the more specific.

Olfaction is the perception of odorous particles carried by the atmosphere which surrounds us, these particles being held in suspension in the air which comes in contact with the olfactory surface. The sense of olfaction, such as we know it, conveys to our minds an idea of the penetration of gas or vapor; but a mechanical action, a current of air, is necessary in order to bring it in contact with the nasal mucosa. Bernstein remarks that olfaction is the sense which has the greatest acuity. Toulouse and Vaschide (1899) measured the olfactory power with camphor water, testing their subjects with a series of solutions of 1 to 10,000, 1 to 100,000, and 1 to 10,000,000. The subject's eyes were bandaged and the solutions were presented to him successively, beginning with the weakest. The writers determined that olfaction was more acute in women than in men, and in girls than in boys. They also made a study of olfactory fatigue and demonstrated the great

resistance of this sense, which was explained mainly by the simplicity of the perceptive apparatus.

The transportation of odorous particles by a gaseous medium is so necessary to our olfactory function, that it is difficult to recognize it in a liquid medium, which accounts for the doubts entertained as to the olfaction of fish. In man it seems probable that olfaction in a liquid medium is impossible. Weber demonstrated this in the following fashion: He filled his nose completely with cologne water (this experiment may be repeated without danger by lying in a horizontal position and allowing the head to hang downward vertically; the palate is thus raised, and water introduced into the nose cannot escape); as long as the water remained in the nasal cavity Weber could not perceive any odor, although he observed it perfectly at the time of the introduction of the water.

In aquatic animals, however, olfactory sensation may be of a different character, otherwise we should be compelled to deny the possibility of olfaction in fish. They have, at the disposal of this sense, a special apparatus, varying in its complexity with the different species, according as the corresponding nervous system (olfactory nerve and lobe) is developed. Geoffroy Saint-Hilaire speaks of the olfactory branchiæ, and we may foresee in this single term the explanation which this author gives: The olfactory branchiæ, like the respiratory branchiæ, extract the air from the water and this air disengages the odorous particles dissolved in it. Carus, on the contrary, does not accord to fish any great olfactory power. The strongest gas, such as ammonia or chlorin, makes no impression on the olfaction of fish, while frogs are greatly affected by this same gas. According to this writer, the sense which guides fish towards prey should be called scent. Bernstein compares the olfaction of aquatic animals to the phenomena of gustation. Blaue bases this same opinion upon his histologic researches, and demonstrates olfactory buds analogous to taste buds in a large number of fish. Duméril bases his opinion on the testimony of sailors and upon the results given in fishing with certain kinds of bait, and reports the arguments made by Cloquet to show the olfactory sense of fish: "Sailors state that when the blacks and whites bathe together in places frequented by sharks, the blacks, whose odorous emanations are more powerful than those of the whites, are more exposed than the whites to the attacks of these terrors of the seas."

Lacépède admits a most delicate olfactory susceptibility in fish.

It is, above all, in air-breathing animals that we find the olfactory sense least developed (birds, dolphins). The ancients were unanimous in claiming that birds had a very remarkable acuity and certainty of olfaction. They even cited the fable of the crows and vultures flying from Africa and Asia to Europe after the battle of Pharsalia. In modern times it is claimed, on the contrary, that birds are poorly endowed with this power. Buffon and Cuvier report that hawks seize upon their prey when it is struck and before it exhales any odor, while a few leaves thrown over it are sufficient to protect it from their attack. Milne Edwards has made some experiments in the Museum of Natural History. He placed, in a cage of vultures, a box covered by a curtain. This was torn at different times, until the birds became accustomed to the object and paid no attention to it. He then introduced into this box, covered in this simple way, some food with a strong nauseous odor, without the birds noticing it. When they were deprived of their customary nourishment they were bewildered, but made no attempt to attack the box. It is sight that plays the chief role in all birds of prey.

Toussenel (1873) says that the birds have no smell, just as they have no taste. It is not necessary, in animals which are to eat many things and to like everything they eat, that there should be a watchful sentinel before the stomach which would bring difficulty in the way of acquiring nourishment.

Raspail (1899) made, very recently, a series of observations concerning the sense of olfaction in birds. He noticed pheasants, partridges and wood pigeons leaving their usual bait when the wind carried towards them odorous effluvia betraying a concealed enemy. These birds discovered, by means of olfaction, an invisible vessel of water, the situation of which was often changed. The odor of a piece of Swiss cheese makes it possible to capture a titmouse. The titmouse, the crow and the magpie descend from great heights in search of worms buried in the ground.

The opinions of observers differ, but none is of any absolute value. In reality, the olfactory power of birds exists, but it is very feeble.

In cetaceans, the nasal fossæ are without any olfactory region and moreover the olfactory nerve is very much reduced or absent. However, Cuvier has observed an organ of olfac-

tion in the dolphin and in the porpoise. Whales have olfactory sensations. In fact, Lacépède reports that Pleville le Peley has seen whales leave a boat which contained decaying codfish. The property of secreting spermaceti has been attributed to these nasal fossae without sensorial role, or to the sinuses. Pouchet and Beauregard have observed that, in the cachelot, this substance is deposited in the recesses independent of the nasal cavities and their adnexa.

Besides these animals with a more rudimentary olfactory sense, mammals present varying degrees of olfactory power. They are divided into osmatics and anosmatics, depending upon the acuity of this faculty.

Distinct anatomic differences do not exist between these groups, carnivorous animals (macrosmatic) and the ruminants (microsmatic); there exists, however, some variation in structure.

The olfactory region occupies a greater or less extent of the nasal cavity and its relation to the respiratory region is very variable. My aim is to establish the respective value of the nasal organ upon anatomic and embryologic observations, and it is only by a study made upon the entire series of vertebrates that we can arrive at conclusive results. The anatomic literature abounds in works relative to the nasal fossae and this has furnished me numerous references.

In my study I have been occupied only with the nasal cavity and its adnexa, leaving out entirely the description of the corresponding nervous system. I have divided this into three chapters: I, Morphology, II, Embryology, III, General Considerations. In the final résumé, I report only the facts which have a value from the standpoint of comparative study.

I have carried on the greater part of my investigations in the Laboratory of Zoology of the Faculty of Science at Toulouse, where I have found extensive material for study.

In so far as embryology is concerned, I have been enabled to make numerous observations upon the rich and priceless collection in the laboratory of histology of the Faculty of Medicine at Toulouse. In the course of my work I have received numerous favors from Profs. Charpy, Moquin-Tandon, Tourneux and Dr. Jammes, Head of the Conference of Zoology, and Dr. Soulie, Professor Agrégé of Anatomy. I thank them for their advice and for their invaluable suggestions, for their generous hospitality, and I assure them of my gratitude and devotion.

Prof. Giard, Member of the Institute, has had the kindness to furnish me with suggestions and I express to him my deepest gratitude.

My friend, Dr. Mandoul, Préparateur of Zoology, has facilitated my task by procuring for me a large amount of material; I thank him sincerely.

I am very grateful to Messieurs Roques and Durand and to Dr. Soule for kindnesses which they have shown in the execution of the figures which accompany the text.

MATERIALS FOR STUDY.

For the anatomic portion, I have had recourse to dissections and microscopic sections imbedded in paraffin. I have followed, several times, the procedure of Retterer (1903) (imbedding in vacuum at 40 degrees). For embryologic study I have used serial sections after fixation in Kleinenberg's fluid.

The adult specimens were decalcified by the procedure of Morel and Soulié (formic acid 1-5), stained en masse with alum carmine.

My studies have been carried on with the following animals:

I. MORPHOLOGY—*Cyclostomes*: Petromyzon, Ammocetes. *Selachians*: Scyllium, Acanthias, Raja. *Teleosts*: Barbel, Gurnard, Trout, Eel, Cod. *Ganoids*: Sturgeon. *Amphibians*: Toad, Frog, Triton, Axolotl. *Reptiles*: Adder, Viper, Blindworm, Python, Boa, Galeote, Crocodile. *Birds*: Pigeon, Duck, Turkey, Vulture. *Mammals*: Complete series of bone specimens; Guinea Pig, Mouse, Rat, Badger, Sheep, Cat, Dog, Monkey, Man.

II. EMBRYOLOGY—*Cyclostomes*: Petromyzon planeri of 4 and 6 mm. *Selachians*: Pristiurus melanostomus of 3 to 22 mm. and Scyllium canicula, 30 millimeters. *Teleosts*: Salmon Trout 22nd day of development and 30 days after hatching, and Rainbow Trout, 30 and 60 days after hatching. *Amphibians*: Toad and Frog, larva of 4 mm. *Reptiles*: Adder of 4 cm., Blindworm, 25 mm. to 7 cm., Viper 4 cm. *Birds*: Undulated Parrot of 5 to 23 mm., Duck 4th to 12th day of incubation. *Mammals*: Guinea pig 5 to 14 mm., Sheep 8 to 25 mm., Mole 4 to 17 mm., Human Embryos 8 to 16 mm., 23.5 cm. The first stages of the undulated parrot and of the sheep, the complete series of the mole and human embryos have been studied in Prof. Tourneux' collection.)

CHAPTER I.

MORPHOLOGY.

AMPHIOXUS.

Koelliker described, in 1843, the olfactory organ of *Amphioxus*. This very rudimentary organ is formed by a single involution which is attached to the nervous system by its sharp inferior extremity.

This shallow, cupuliform depression is situated on the left side of the head, in front of the left eye, and is separated from it by the most anterior nerve trunk.

This organ is not united to the buccal cavity. It consists of an external cartilaginous envelope and a mucosa with a ciliated epithelium. The presence of cilia is the most characteristic sign that causes us to think that the fossa is really the olfactory organ.

De Quatrefages (1845) described the same fossa with all the characteristics noted by Koelliker.

Paul Langerhans (1876) found in the epithelium, which lined the fossa, two kinds of cells, one tall, narrow and cylindrical, each one provided with a long cilium. The others also have cilia, but are distinguished from the first by the smallness of their bodies and the largeness of their nuclei. These elements are easily separable into small groups and may be regarded as true olfactory cells, and their cilia as sensory cilia.

FISH.

I. CYCLOSTOMES.

The cyclostomes belong to the *Monorrhina*. They have a single olfactory organ placed in the median line, which opens on the dorsal surface of the head.

ORIFICE.—The orifice is round, narrow, usually terminating in a small tube which projects 1 to 2 mm. above the integument. Its situation corresponds to the blow-hole of the dolphins, so one must admit that there exist *Monorrhina*

among the Mammalia. But here the Monorrhina is characterized not only by a single nasal opening, but also by a single nasal sac.

Vogt and Yung (1894) described, in these folds, a fibrous thickening of the subcutaneous tissue, and in the interior of the tube, close to where the entrance opens into the sac, a very peculiar valvular apparatus analogous to those of the cardiac arteries. This tube, or more correctly the folds that enclose it, is detached from the rest of the integument at the bottom of a depression, in such a way that the tube projects above the dorsal surface less than its entire height, and is surrounded by a circular, uninterrupted groove. While in *Petromyzon*, the tube is narrower at its extremity than at its base, in *Ammocoetes* it widens exteriorly into a funnel.

It extends from above downwards and from before backwards, and leads into the nasal sac, its base being lost in the walls of the latter.

NASAL CAVITY.—The dimensions of the nasal cavity are not great. It is situated at a considerable distance behind the tip of the snout, immediately in front of the brain, above the digestive tube, from which it is separated by a very thick mass of muscle in *Ammocoetes*, while in *Petromyzon* there is only a cartilaginous septum between the two organs. Its position is well shown by a sagittal section of *Petromyzon* (Fig. 1).

The interior of the nasal cavity is occupied by lamellae which cause folds of the mucosa. In *Petromyzon*, the lamellae are arranged around all the walls in such a way that they converge towards the center. They are thick and very slightly elevated. Langerhans, Vogt and Yung observed a median, vertical lamella which divided the cavity into two symmetrical halves, and these correspond to the nasal fossae of more highly organized animals. We have never found anything similar in *Petromyzon*, and Pogojeff never observed any trace of this relation. It was different, however, in *Ammocoetes*. In a transverse section passing through the middle of the nasal cavity (Fig. 2), a long thick lamella can be seen running vertically downward from the dorsal wall nearly to the floor, and in the exact median line.

On each side is found a fold of the ventral wall forming an ascending lamella which is almost vertical and concave on its internal aspect.

Between the lamellae, in *Petromyzon*, is a star-shaped cavity, of considerable size in comparison with the nasal sac. In *Ammonoetes*, there are only stellate fissures.

An axis of connective tissue extends into the interior of each lamella. This is condensed at the periphery and forms a layer separating the mucosa from the cartilaginous sac. In the connective tissue, in *Petromyzon*, there are numerous pigment cells, which give a dark color to the nasal organ.

CAPSULE.—The cartilaginous capsule completely surrounds the olfactory apparatus. It is open at its anterior pole to communicate with the entrance tube. Behind, it is perforated to give passage to the olfactory nerves. Furthermore it is in relation with the naso-palatine tube, a kind of diverticulum from

Fig. 1. Half natural size. *Petromyzon planeri* (Sagittal section).
1. Nasal cavity; 2. Central nervous system; 3. Digestive tube;
4. Naso-palatine canal terminating in an ampullar cul-de-sac.

the ventral wall, which is directed downwards towards the digestive tube but does not reach it. As our sagittal section (Fig. 1) shows, this canal arises at the anterior part of the nasal sac, and runs obliquely backwards and downwards, and ends in a large cul-de-sac, which lies below the cranial cartilaginous capsule and above the digestive tube. Its posterior wall is in relation with the branchial laminae. In *Myxine*, the writers describe the communication of this canal with the buccal cavity, which brings the cyclostomes close to the vertebrates in aerial respiration, and this finding is favorable to the hypothesis that the cyclostomes are vertebrates that have degenerated under the influence of a parasitic life.

The extent of the cartilaginous capsule can be easily seen in sections or upon dissection.

While completely isolated in *Ammocoetes* and separated from the neighboring organs by connective or muscular tissue, in *Petromyzon* it is in intimate relationship with the cranial capsule and fuses with its anterior wall; at this level a simple partition separates the olfactory organs from the brain. The filaments of the olfactory nerve are very short as the result of the topographic relations of these two organs. In the interesting horizontal sections of the nasal cavity and nervous

Fig. 2—X 70. *Ammocoetes* (transverse section passing through the nasal cavity). 1. Median dorsal lamella; 2. Ventral lamella; 3. Cartilaginous capsule; 4. Muscular portion.

system, two series of olfactory filaments (Fig. 3) are to be seen, between these two structures. They arise from the anterior wall of the brain, on each side, from the interhemispheric fissure and meet at the bottom of the nasal cavity; the different branches are distributed to the two symmetrical regions, posteriorly convex, which are placed on either side of a median lamella. On the ventral side, a layer of connective tissue

separates the capsule from the cartilaginous roof of the digestive tube.

GLANDS.—The olfactory apparatus of the cyclostomes is distinguished from that of other animals with aquatic respiration by the presence of glands. They are situated, according to Pogojeff (1888), Vogt and Yung, at the bottom of the organ, in the segment which is limited to the olfactory bulb; they penetrate into the cartilaginous tissue and are surrounded by nerve fibres. The cellular elements of these glands described by Pogojeff are formed of two kinds of goblet cells;

Fig. 3—X 70. *Ammocoetes* (transverse section showing the nasal cavity and two olfactory nerves). 1. Nasal cavity; 2. Cartilaginous capsule; 3 and 4. Olfactory nerves; 5. Brain.

one is very long, very contracted and provided at its lower extremity with a long, very thick prolongation: towards the superior extremity there is a striated area, while the nucleus lies in the middle of the cell. The other cells are larger with a round base containing the nucleus. We have not found this glandular apparatus in *Ammocoetes*.

Scott found in a larva of *Petromyzon*, $12\frac{1}{2}$ mm. long, in the posterior part of the nasal cavity, a diverticulum whose place in the adult is taken by the gland we have just described.

He considers this formation to represent the organ of Jacobson, in which opinion Bujour concurs.

There can be no question of such an organ in these animals. The independence of the nasal apparatus and the buccal cavity is sufficient to explain its uselessness and its existence only adds to the regressive characters which connect the cyclostomes with air-breathing vertebrates.

MUCOSA.—Retzius (1880), in *Myxine*, found a cylindrical epithelium without nervous terminations at the free, anterior border of the folds and at the posterior fixed border, as well as in the furrows between them. On the surfaces of the folds, turned towards each other, the epithelium which is, on the contrary, much taller, is the olfactory epithelium.

In *Petromyzon*, a similar distribution is found in the topography of the nasal epithelium. The true olfactory epithelium shows two fundamental cellular forms. The first consists of long processes which extend the entire height of the olfactory epithelium, in the middle third of which the nucleus is found. The protoplasm is entirely clear with hardly a granule. The superior extremity is covered with a finely granular border from which delicate, wavy cilia extend. The inferior extremity of the cells is very often enlarged. In the other cellular form, the body is shorter, pea-shaped and the nucleus is very much higher. The superior extremity is thin and the inferior extremity does not reach the deepest layer of epithelial cells, and encloses the nucleus. The substance is clear, but distinctly granular. The delicate inferior prolongation extends to the connective tissue, but Retzius was not able to find its communication with the nerve fibres.

Pogojeff (1888) found in *Petromyzon* a flattened epithelium at the edge of the free border of the folds, as well as in the depressions which limited them. These cells are large and slightly elevated and are provided with cilia.

Upon the lateral surfaces two series of cells are found, which are made manifest by two series of nuclei placed at different heights. Some are cylindrical, in the form of goblet cells; others are conical, with an enlarged superior extremity and an inferior extremity pointed and bent inward. These are the supporting cells. The second variety of cells merits the name of neuro-epithelium. They are round and fusiform, terminating inferiorly in a varicose prolongation, and their superior extremity forms a sort of cap. Furthermore, they are

as small as the first, are almost cylindrical and are narrowed towards the extremity, from which a nerve prolongation arises.

In *Ammocoetes*, we have found in the whole extent of the nasal cavity, as well as in their intervening folds, delicate, greatly elongated, cylindrical cells, which present a clear and homogenous central portion and a peripheral portion containing the nucleus and highly colored protoplasm. Between the peripheral prolongations of the cells, there are found irregular elements, some rounded and some slightly elongated. The epithelium upon the dorsal lamella measures 36 mikra in thickness; upon the ventral lamella, 26. The cells throughout the mucosa have an average height of 14 mikra (Fig. 2).

Fig. 4. Half natural size.—*Scyllium catulus* (ventral surface of the head, showing the valve of the anterior border of the nasal orifice). 1. External part of nasal orifice; 2. Valve of the anterior border; 3. Buccal orifice.

II. SELACHIANS.

We will commence the series of *Amphirhina* with the selachians; they are distinguished from the other animals of this large group by the ventral position of the nasal orifices.

ORIFICE.—For each nasal cavity there is only one orifice. In *Scyllium catulus* the nasal cavities are very far from one another. This peculiarity distinguishes it from *Scyllium canicula*, where they are contiguous in the median line. Each

nasal orifice or naris is a very wide, transverse cleft placed in front of the buccal orifice. A large, high valve, a prolongation of the anterior or superior border, covers the greater portion of this slit (Fig. 4), only the external region being free; it has the form of a circular opening. This region is accessible to the current only from the front. On lifting the valve, the entire extent of the opening is visible, but it is divided into two regions by a tubular prolongation, which extends forward from the posterior or inferior border.

On examining the naris from its internal instead of its external face, after the nasal cavity has been opened wide, it is seen that the prolongation from the posterior border represents a kind of a valve which masks the external part of the orifice (Fig. 5). Seen from this side, the latter is freely opened in its inner two-thirds and has the form of a funnel. This internal part of the orifice favors the exit of the current of water.

To sum up, two incomplete valves are opposed to one another. The portion of the orifice which is not covered by the anterior valve is open outward. This is the orifice of entrance. The part which the posterior valve leaves free has a wide opening internally which is the orifice of exit. This valvular apparatus forms a double orifice, from a functional standpoint.

In *Raja batis*, the anterior valve is arranged as in *Scyllium*, while the posterior valve does not exist.

Lacépède (1867) ascribes to these animals the power of completely closing their nasal orifices by means of the valve, and of being able to close the olfactory apparatus, under certain circumstances, to useless or very intense sensations. He compares this valve to an eyelid.

CAVITY.—The cavity has an almost elliptical form and is occupied by lamellae arranged in two long rows with a transverse axis, and inserted in the roof of the nose in such a way that they run vertically downward. The inferior border is free, the external border is bound to the wall by a little, delicate, non-resistant tract. Their height is from 18 to 20 mm. and their transverse extent from 5 to 6 mm.

The nasal cavity is bounded by a connective tissue partition which contains numerous pigment cells. Surrounding it is a cartilaginous capsule analogous to those which surround the eye, ear and brain.

This very simple capsule moulds itself around the nasal sac. Behind, it is in relation with the olfactory bulb, the filaments of which penetrate it in order to enter the nasal sac.

Within the cavity, the mucosa presents numerous folds inserted at the level of the roof and lateral walls; the highest are situated at the middle of the dorsal wall. They are composed of a connective tissue axis containing blood vessels,

Fig. 5. Five-eighths natural size. *Scyllium catulus* (both nasal cavities and the cranial cavity are opened on their dorsal surface. On the right, the olfactory sac; on the left, nasal cavity with contents, showing on the floor the internal part of the nasal orifice and the valve inserted on the posterior border of that orifice). 1. Valve of the posterior border; 2. Internal portion of the nasal orifice; 3. Cavity containing mucous tissue; 4. Olfactory sac; 5. Cartilaginous capsule; 6. Olfactory bulb.

covered with an epithelium which is uniform in structure and formed of cylindrical cells.

Blaue (1884) did not find among the plagiostomes the olfactory buds which he describes in a large number of teleosts. As Leydig and Max Schultze have already shown,

there is no particular region for the olfactory epithelium; it is spread out over the folds of the mucosa, but does not reach their free border and is especially abundant in the intermediate grooves.

The olfactory epithelium, according to Max Schultze, covers bands which reveal themselves in the mucous folds; it consists of ciliated cylindrical cells which have a long basal prolongation, of fusiform olfactory cells with a basal segment containing the nucleus and provided with two prolongations, and of replacing cells which are attached to the underlying tissue by a series of fine denticulations. Between the flattened feet of these cells lie stellate connective tissue cells, which form the most superficial layer of the membrana propria.

Koelliker assigned a nervous function to this epithelial layer, but Max Schultze does not agree with this; he finds that the finer branches of the olfactory nerve enter into the epithelium.

III. TELEOSTS.

These form the second group of Amphirrhina. Their nasal apparatus shows certain common, primordial characters, with considerable variation in detail. The latter are mentioned in works dealing with their classification.

ORIFICES.—The nasal cavity is entered by one orifice, or by two orifices both of which open externally. An exception is described by Wiedersheim (1890) among the Dipnoa (*Prototereus*) where there are two nasal orifices, one situated near the upper lip, the other much further back. The nasal organ has no direct communication exteriorly, but opens into the buccal cavity. In other fishes, the orifices show certain differences in form and position. The anterior orifice is sometimes pierced at the level of the skin by a posterior lip prolonged as a tentacle (*Gadus*, *Mustelus*), and sometimes it reaches the extremity by a tubular prolongation (conger, gurnard and eel).

• The posterior orifice always opens on the surface of the skin, is usually elliptical, but in the gurnard it is a simple slit. It is joined to the anterior orifice in the barbel; it might be said that a single orifice is converted into two by an antero-posterior bridge. The anterior orifice, which at the same time

is the internal, has a sort of valve covering it formed by simple prolongations of its internal border. This valve prevents the entrance of water into the nasal cavity but allows its exit. The tube or tentacle, which is found in a large number of species, is said to play the same role. The posterior orifice is used for the entrance and the anterior orifice for the exit of the current.

CAVITY.—The nasal cavity is a very simple sac. If the dorsal wall in the barbel or the gurnard is lifted, a large number of folds will be found extending into the cavity and in a measure occupying it. These folds resemble rays disposed around a central lumen. They are inserted at the bottom and periphery of the nasal sac, and all have the same dimensions. Between their free borders, the nasal lumen has the form of a cup, and from its center it radiates between their surfaces.

The olfactory nerve enters the nasal sac from below, about the middle, and from there it is distributed to the lamellae.

In the eel, there is a different disposition of the lamellae; they are placed on each side of a longitudinal axis, parallel to each other, and are inserted into the floor of the cavity (Fig. 6). They have a quadrangular form, narrow in front, prolonged into a cylindrical tentacle towards the anterior orifice, and extend beyond the end of the nose. The large, round, posterior extremity shows the posterior orifice at its external angle.

A transverse section of the head of the eel (Fig. 6) shows the insertion of the lamellae along the floor, and the contour of the nasal sac, formed by a connective tissue sheath. This is usually pigmented, black or brown, which makes the nasal sac easy of recognition in dissection. As they are placed near the dorsal aspect, the nasal organs are completely independent of the buccal cavity, from which they are separated by a bony wall. A vertical bony septum separates them from each other in the median line. The bones are never in direct contact with the nasal sac, being separated from it by a considerable amount of connective tissue.

SKELETON.—The skeleton is formed by a series of facial bones which are arranged not so as to define a bony nasal cavity, but to form an irregular interspace in which the fibrous nasal sac is situated without any adaptation of form. We have studied this nasal skeleton in the cod, where there is a superior wall

formed by the middle ethmoid and the nasal bone, an external wall formed by the anterior frontal, and an inferior wall formed by the vomer and the lateral ethmoid (Fig. 7).

Nasal Bone.—A paired, flattened bone, larger behind than in front, with rectilinear internal and external borders. The posterior extremity shows a groove. Longitudinal undulations of the superior surface form a projection along each border with a groove in the middle. The inferior surface is concave in its external portion, projecting in its internal. It is articulated in front with the maxillary bone and, external to this extremity, with the anterior frontal; behind with the frontal, internally (posterior third) with the median ethmoid.

Fig. 6—X 40. Eel (transverse section of the nasal cavity passing through the posterior orifice). 1. Posterior nasal orifice; 2. Lamellae.

Frontal Bone.—Single bone, large, squamous, bifid anteriorly, each half corresponding to one nasal bone. It is only by this anterior extremity that this bone enters into the formation of the nasal skeleton. At the angle formed by these two points, it articulates with the middle ethmoid and, by lamellae derived from its inferior surface, with the lateral ethmoids.

The Middle Ethmoid.—Single bone, presenting a large anterior part and a thin, tapering posterior part. The anterior part is thick and curved at a right angle, so as to present a horizontal and a vertical segment. Some lamellae derived from

the borders of this bone are directed backwards and outwards, forming together an inverted funnel. The middle part of this bone is prolonged backward to form a posterior part which tapers out, articulating with the lamellae of the frontal bone. The anterior part is united along the median line with the vomer and laterally with the lateral ethmoids.

Lateral Ethmoid.—Paired bone, irregular, with a very thick massive body from which wing-like lamellar prolongations extend on all sides.

Fig. 7. Half natural size. Cod (external view of the head showing the bone surrounding the nasal region). 1. Space for the nasal sac.

Anterior Frontal or Prefrontal Bone.—This is a bone of large size, very long, flat, of triangular form, with its anterior apex joined to the premaxillary bone, with its posterior base united internally with the lateral ethmoid, and externally with the infraorbital. Its internal border is at some distance from the nasal and frontal. There exists between them a large interspace which in the fresh state is filled by a fibrous membrane. This membrane is pierced by the orifices of the nasal sac.

Vomer.—Single bone with an anterior enlarged portion which zoologists call chevron (Moreau) and a long posterior prolongation. The inferior face of the vomer, in the place corresponding to the edge of the chevron, is provided with teeth; behind it is smooth. The vomer is united in front with the two maxillary bones, with the palatal bones by the projections of the chevron; above with the ethmoids; below it is free and forms part of the palatal vault.

The names given above are taken from the nomenclature of Cuvier and Agassiz.

The osseous part of the cranium is subject to variations of one kind or another, and we were not able to make a detailed study. Sagemehl (1885) made an extended study of the crania in the Characinidae. His nomenclature is very similar to that which we have given for the cod. The prefrontal forms the posterior limit of the nasal region and contains two canals, which run from the orbit to the nasal fossa. The inferior orifice gives passage to the olfactory nerves and the superior to a branch of the trigeminus. The middle and inferior boundaries of the nasal apparatus are formed by a part of the primordial cranium which has remained cartilaginous; the inferior part of the septum is formed by the vomer which behind is united with the parasphenoid. The roof of the cavity is formed by the nasal bone. In the work of Swinerton (1902) upon the development of the cranium of the teleosts, we find plates showing *Gasterosteus aculeatus* with the bones of the nasal region similar to those which we have described and designated.

NASAL SAC.—The connective tissue which surrounds the nasal cavities is condensed into a fibrous membrane and forms a complete envelope broken only at the level of the nasal orifices. This wall is delicate, of little resistance and contains a considerable deposit of pigment. The deep layers are formed by a looser connective tissue which deep down is directed toward the cavity and acts as a support for the lamellae of the mucosa. It contains vessels and nerves.

MUCOSA.—Schultze, Grimm, Blaue, Sophie Pereyaslawzeff and Dogiel have studied the structure of the olfactory mucosa. Two kinds of cells have been found; one epithelial (supporting cells), and the other neuroepithelial (olfactory cells). Dogiel (1887) described the supporting cells of the ganoids as very fine membranous formations which seem concave be-

cause they are adjusted to the convexity of the adjacent olfactory cells. Their staining reaction is similar to that of mucous cells. He found three kinds of elements among the olfactory cells: The first is the olfactory cell of Schultze, which is very delicate, with central extremity thickest and peripheral part appearing as a varicose prolongation in direct continuity with the primary fibril of the terminal roots of the olfactory nerve. The second has a cylindrical form, and the third is a thick structure in the form of a cone or cask.

The researches of Blaue (1884) were carried out upon a large number of species of fishes. He has found two kinds of animals. In some, the olfactory cells are grouped to form olfactory buds in every way analogous to the taste buds. These open upon the epithelial surface by pores which open into a small cup. The epithelial elements are long, extending from the basal connective tissue to the level of the tube. They are alternately supporting and sensory cells. Between the pores, the indifferent epithelium is composed of cells arranged in the form of overlapping cells. The most superficial are flattened; deeper down, they are polyhedral, cylindrical and, finally, fasciculated. The olfactory buds show a very variable distribution, sometimes spreading out over the entire lamella and the intermediate spaces (*Belone*), sometimes lying only in the intermediate spaces (*Trigla gurnardus*, *Exocetus volitans*, *Umbra canneri*, etc.). Sophie Pereyaslawzeff (1876) considers the olfactory bulbs to be groups of olfactory cells and does not mention supporting cells.

In another group of fishes (the eel, conger, the carp, tench, etc.) the olfactory epithelium is such as has been described by Leydig and Max Schultze. It extends over the entire lamella and generally, in the intermediate spaces, it is replaced by indifferent epithelium. Huot (1902) found in *Lophobranchia*, by the method of Golgi, that the olfactory cells were composed of a large, oval, basillar portion and a narrow prolongation, which extended toward the free surface of the epithelium. This prolongation slightly projects into the cavity and may be either simple or bifurcated.

In the eel and the trout, a homogenous epithelium extends over the lamellae and their interspaces. The cells are long, cylindrical, with a deep part containing a large oval nucleus and a superficial part containing clear, finely granular protoplasm.

The dorsal and lateral walls of the nasal cavity are clothed

with a stratified epithelium. The deeper cells are rounded, the most superficial are elongated, but their height is irregular.

There are no traces of glands in the nasal mucosa.

Winther described in the salmon a canal which he considered the organ of Jacobson. It runs downward, is situated below the olfactory cavity and terminates in a cul-de-sac. According to Jungersen and Sagemehl, this is simply a mucous canal which extends transversely between the two nasal cavities during embryonic life, persisting through life in *Amia*. Wiedersheim admits the presence of an organ of Jacobson in *Polypterus bichir*, an opinion which is not shared by Waldschmidt (1887).

Garnault did not find the organ of Jacobson in the dipnoans, nor did Seydel in the teleosts. Even during embryologic developments, we have never found any diverticulum which could correspond to it.

IV. GANOIDS.

The sturgeon has two nasal orifices placed just in front of the eyes, one at the internal border of the dorsal aspect of the head and the other on the external. The first, which is the most internal and anterior, is circular. Its borders are rigid and distinct.

The other, which is external and posterior, has an elliptical form with a large vertical axis. Its borders are gradually lost in the neighboring parts. On the anterior border, a movable membrane is placed, which covers a large part of the orifice like a valve. This valve is to close the opening under the influence of an external force, and seems to prevent the entrance of water through the postero-internal opening, while permitting its exit. The antero-internal orifice has a large opening, is accessible to the exterior current and serves for a port of entry.

Between these two orifices is a cartilaginous bridge covered with a dermo-osseous plate running from above downward and from behind forward; it is very narrow (5 mm. in a specimen of 1 metre total length). The valve of the posterior orifice seems to enlarge it.

The walls of the nasal cavity are composed of thick, resistant cartilage; furthermore, the external, dorsal and internal walls are covered with a bony sheath.

After ablation of this bridge, lying between the two nasal cavities, a large recess gives entrance to the nasal cavity. This has the form of a semi-hemispherical capsule. In the center, there is a cylindrical axis from which runs numerous lamellae towards the borders of the cavity. These lamellae are largest near this axis, gradually decreasing as they approach the periphery.

We have not found the secondary lamellae noted by Moreau (1881). A long cartilaginous conduit placed within the orbital cavity extends obliquely from within outwards and from behind forward from the cranial cavity to the floor of the nasal capsule. It contains the olfactory nerve, a large cylindrical cord, which reaches, in this form, the axis of insertion of the lamellae and then divides into branches which are distributed throughout the whole organ.

The nasal cavity, as a whole, is situated in front of the eye, but in the same horizontal plane. It is very far in front of the cranial cavity, and separated from that of the opposite side by a distance of $2\frac{1}{2}$ cm. It is situated on a vertical plane considerably anterior to the buccal orifice.

AMPHIBIA.

The nasal cavities begin to assume the aerial type; a portion of the air in passing through them reaches the pulmonary apparatus. From now on, they occupy a double role, olfactory and respiratory, but the latter is still of slight importance.

ORIFICES.—In taking as a type the frog (*Rana esculenta*) or the toad (*Bufo vulgaris*), which presents the same conditions, we find the nasal cavities provided with two openings, one external, the other internal. The external dorsal orifice is situated upon the side of a median antero-posterior projection, and extends from the biocular line to the end of the snout, penetrated at the junction of its anterior and middle thirds by this projection. It is circular and limited by well-marked, rigid borders. These form a slight cushion in the external part of the orifice which, according to certain authors [Vogt and Yung (1894) Chatin (1880)] constitutes a short tentacle which closes the nose when the frog plunges into the water. The border is bony only on its inner side; otherwise it is composed of integument alone. The muscular fibres below the

skin have been studied in the frog, triton and salamander by numerous authors. Zenker, Duges, Klein, Ecker, Gaupp, Volkmann and Collan have described certain bundles, disposed around the external nasal orifice. Moreover, Henry Bruner (1902) published an extensive study of the mechanism of respiration in the Amphibia, with lengthy and minute descriptions of the nasal muscles. There is a dilator muscle and, in some species, one or two constrictor muscles.

The inner orifice, visible at the edge of the palatal vault, a short distance from the lip, is a little posterior to the external orifice. The air passing through the nasal cavity must go through a large part of the buccal cavity before reaching the respiratory passages. The nasal air passageway is still imperfect. The internal orifice is circular, wide open, surmounted within by a small round tubercle visible in the frog and absent in the toad. It is further from the median line than is the external orifice.

In the siren, Vaillant (1863) found that the internal orifice is quite anterior, in the gingivo-labial fold, at the level of the posterior part of the dental laminae. This is the result of the almost exclusively aquatic character of the animal.

CAVITY.—The cavity, possessing these two kinds of orifices, is simple with almost smooth walls. Upon removal of the superior wall, the cavity may be seen, rectangular in form, measuring, in a frog of average size, 5 millimeters in its antero-posterior diameter and 7 mm. in its transverse. At the level of the floor, there are a groove within and an antero-posterior ridge externally. The posterior part of the ridge is especially well marked; external to it is found the internal orifice. Irregular folds of the mucosa are observed at the antero-internal angle of the cavity. At the level of the folds, the color of the mucosa is darker than that of the rest of the nasal cavity, while at the level of the posterior part of the groove it is a spotted dark brown. The cavity is flattened in its dorso-ventral diameter; its vertical diameter is 2 millimeters.

The study of the nasal cavity by dissection is incomplete as the principal cavity, to be described, cannot be seen. It is only by transverse histologic sections that we can see all the details of the olfactory apparatus. We have always used formic acid for decalcification before subjecting the specimens to the various manipulations necessary for paraffin imbedding.

On a transverse section through the middle part of the cav-

ity, the main cavity may be seen communicating, at the external border of the floor, with a large hollow cavity in the facial bones, which has a large transverse diameter and is concave inferiorly. This accessory cavity presents an internal portion adjacent to the main part and an external portion, directed towards the side of the head, whose outlines (Fig. 10) are parallel with those of the head itself.

Transverse sections made anterior to the orifice of communication between these two cavities show the main cavity communicating extensively with an inferior diverticulum, while the accessory cavity is completely closed and diminishing in measure as it approaches the anterior border. Behind the zone of communication, the accessory cavity is modified; the lumen of its internal portion disappears, a large glandular mass taking its place. The external portion forms a diverticulum of the main cavity, extending backward to the level of the choana.

Posterior sections at the choana show only the main cavity with a very regularly elliptical form. We can study the general anatomic construction of the nasal apparatus better by transverse sections than in any other way.

CARTILAGINOUS SHEATH.—In a large part of its extent, the nasal cavity and its diverticula are surrounded by cartilaginous bands. In Fig. 10, we see a mass occupying the median line in the form of a septal partition from which the laminae extend externally. A lamina, prolonging the posterior border of the septum, forms the roof of the nasal cavity, and ends in the vicinity of the supero-external angle of this cavity. A middle lamina extends from the external border, in a slightly oblique direction inferiorly and externally, and then extends horizontally. It separates the nasal cavity from the adjacent diverticulum and borders internally the orifice of communication between the two cavities. Upon the same horizontal plane, another fragment of cartilage borders this orifice externally. An inferior lamina, continuing the inferior border of the septum externally and below, forms the floor of the inferior diverticulum and at the same time the framework of the roof of the mouth. At this place, the external wall and a portion of the roof of the nasal cavity are divested of their cartilaginous envelope, likewise the outer part of the inferior diverticulum. The appearance of this cartilaginous investment depends upon the particular transverse section considered. In the most anterior sections it is complete, and is moulded to the nasal

cavities. The inferior lamina is very large in the anterior portion of the nasal region and the inferior diverticulum is completely ensheathed. At the orifices, there is a sudden interruption in the cartilaginous wall, but the area divested of cartilage is larger in extent than the orifices themselves.

Behind, the cartilaginous sac has a large opening externally and inferiorly, so that the external diverticulum is free of cartilage in its entire periphery and a large portion of the buccal roof is formed of soft parts alone. It is in this zone that the choana opens.

Finally, behind this, the cartilaginous lamina of the buccal roof is once more of great size and the nasal cavity, single at this level, is once more completely encapsulated.

Born gives a lengthy description of the cartilaginous framework of the nasal fossae: "The nasal cavities are separated from one another by a septum of hyalin cartilage and at their anterior and posterior extremities are surrounded by two cartilaginous shells, extending from the septum, which are united to each other by a slight roof along the septum and by a floor complete in front and cut off by the choanae behind."

Ecker describes and depicts the cartilaginous framework of the cranium as constituted by laminae which fill up the interosseous spaces. His figures are views of the surface which show well the importance of this supporting tissue, which is indispensable for enclosing and protecting the cephalic organs contained in bony spaces with very incomplete walls. It is these bony walls which serve to support the cartilaginous skeleton.

BONY SKELETON.—In the nasal region, the bony limits anteriorly are the intermaxillary and the maxillary bones, internally the intermaxillary, behind the *os en ceinture* (fronto-parietal) and the prefrontal and below the palate and vomer.

Intermaxillary.—Single bone, presenting a posterior part, flattened from above downward, situated in a horizontal plane, becoming more attenuated as the posterior end is approached, having a superior surface, with a median groove formed by two longitudinal ridges and an inferior concave surface. The anterior part of the bone is enlarged, is directed obliquely forward and downwards and presents a free border armed with teeth. It articulates behind with the *os en ceinture* and laterally with the superior maxillary bones.

Superior Maxillary.—Bilateral, elongated, flattened laterally,

straight, slender, with smooth surfaces inclined from above downwards and from within outwards, with a posterior extremity prolonged outward as a spur. It articulates anteriorly with the intermaxillary bone, posteriorly with the pterygoid, at the center of its superior border with the prefrontal and at the same level, upon its internal surface, with the palate. The inferior border is provided with teeth.

Os en Ceinture.—As designated by Cuvier, this bone represents the frontals, parietals and ethmoid. Ecker describes separately the fronto-parietals and ethmoid. This bone, which is large, has a groove, in the median line, on the superior surface and is bent around at the level of its anterior extremity so as to change its plane and is directed backwards towards the sphenoid, with the point of which it unites. The anterior extremity, which, alone, takes part in forming the nasal skeleton,

Fig. 8. Natural size. Frog (dorsal surface of skull). 1. *Os en ceinture* (fronto-parietal); 2. Prefrontal.

presents a median ridge separating two very deep grooves which constitute the base of each nasal cavity. In the center of this depression is an orifice for the passage of the olfactory nerve.

Prefrontal (Fig. 8).—(Frontal-nasal of Ecker.)—Bilateral, quadrangular, slender, directed transversely, situated immediately beneath the skin adjacent to the palate, with which it is almost parallel. It passes from about the middle of the superior border of the maxillary to articulate with the antero-external angle of the *os en ceinture*. It forms a simple truss upon the nasal roof.

Palate.—Bilateral, flattened, slender, directed transversely, passing from the middle of the superior border of the maxil-

lary a little in front and below the prefrontal to the inferior surface of the *os en ceinture*. It is more slender in its middle portion than at either end.

Vomer (Fig. 9).—The vomer is a bilateral bone placed on the same plane as the corresponding palate, presenting two surfaces almost smooth, one superior and the other inferior. It has an antero-posterior diameter of three millimeters and a transverse diameter of two. Its anterior border runs obliquely downwards, its posterior border is united with the palate and the adjacent portion of the *os en ceinture*. The antero-external and antero-internal angles present long osseous points, an intermediate point originating on its anterior border. The inferior surface is provided with teeth.

Fig. 9. Natural Size. Frog (inferior surface of cephalic skeleton). 1. Intermaxillary; 2. Vomer; 3. Palatal; 4. Superior maxillary; 5. Sphenoid; 6. Pterygoid.

The maxillary and intermaxillary are united to form the arch of the upper lip. The *os en ceinture* and superimposed pterygoid constitute a thick column upon which the prefrontals, palate and vomers rest. A true osseous nasal cavity does not exist. It is a simple interspace in which the cartilaginous capsule is placed.

Wiedersheim (1877) presents an extensive, well-illustrated study of the skull in the urodeles. In *Menobranchius lateralis*, the nasal capsule is limited anteriorly by the intermaxillary or premaxillary, superiorly by the frontal

and inferiorly by the vomer. The bones are large; they surround nasal fossae which are much more complete. In *Batrachoseps attenuatus*, the large bones of the superior wall are the premaxillary, with a large, long ascending process directed posteriorly, upon each side of which the nasal bones are placed. Between the nasal and maxillary, there is a small bone, the prefrontal. The inferior wall is formed by the vomer. The internal half of the bone is prolonged posteriorly and this portion has teeth upon its posterior edge.

Triton viridiscens has very large nasal bones in contact along their internal border, the ascending process of the premaxillary filling up the defect. On the other hand, the premaxillary is very much spread out upon its inferior surface, which has a quadrangular form. The vomer, which is very large, is hollowed out upon its posterior border in order to permit the choanae to pass; the postero-internal angle is prolonged backward in the form of a long apophysis resting against the inferior surface of the parasphenoid.

The species examined by Wiedersheim are numerous. All possess a nasal skeleton arranged in such a manner as to limit the true nasal cavities.

NASAL MUCOSA.—The cells of the nasal epithelium are arranged by Exner in two groups: epithelial cells and olfactory cells. Max Schultze and Hoffmann do not agree with this author, but admit two very distinct forms of cells. Max Schultze in *Proteus* described olfactory cells and supporting cells. Babuchin found olfactory cilia upon the olfactory cells and established the absence of vibratile cilia on the supporting cells. Blaue (1884) studied the mucosa of the lower Amphibia, and found, particularly in *Proteus*, numerous points of resemblance with that of the plagiostomes. There are folds, of slight height it is true, covered with stratified epithelium with flattened cells. The most superficial cells have a cubical form and their free surface permits the implantation of vibratile cilia.

In the interval of the folds, exist the long cells described by Schultze and Babuchin, disposed in groups forming olfactory buds. Blaue represents them in several plates. The buds have the same appearance as those of fish. In the triton and salamander, the essential details are analogous.

The Anura have two kinds of cells; epithelial cells or supporting cells (Ecker, Vogt and Yung) described by Exner, Max Schultze and Hoffmann. The first are long and slender

with a large nucleus forming an ovoid enlargement from which the cell is prolonged in the form of a long varicose filament, which comes into relation with the filaments of the olfactory nerve. The extremity which is directed towards the nasal lumen appears either as a brush with delicate hairs or as a single stiff hair. The other cells, which are cylindrical, long and unprovided with cilia, are prolonged into the subjacent connective tissue by a long and irregular filament. In the

Fig. 10—X 27. Frog (transverse section showing the nasal cavity opening externally and communicating with the inferior cul-de-sac). 1. External nasal orifice; 2. Principal nasal cavity; 3. External nasal gland; 4. Cartilaginous capsule; 5. Infero-external cul-de-sac; 6. Superior maxillary; 7. Olfactory region; 8. Cartilaginous septum; 9. Infero-internal cul-de-sac (organ of Jacobson).

lower Amphibia, the epithelium is uniform in the nasal cavities. There is no distinction possible between the respiratory and olfactory epithelium. In the urodeles (triton), however, Mihalkovics (1899) found that the epithelium over the greater portion of the lateral fossa has the characteristics of respiratory epithelium, with mucous secretion. There were remains of the rays of olfactory epithelium. The branches of the olfactory nerve, according to this author, extended only

to the roof of the lateral fossa. In the Anura, there is a very distinct demarcation between the respiratory epithelium and the olfactory epithelium in the principal nasal cavity and in the accessory. Seydel considers the epithelium as olfactory in the entire extent of the accessory cavities. Mihalkovics reports the existence of an indifferent epithelium throughout the external region (recessus maxillaris).

According to my observations upon different Amphibia, the nasal epithelium is characterized by cylindrical elements such as those described by the preceding authors. Their topographic distribution presents some differences when comparing one group with another. In the urodeles (axolotl, triton), the nasal cavity and the diverticulum which it sends downwards and outwards are covered uniformly with the same type of cylindrical epithelium with very long cells. In the axolotl, however, the highest points of the nasal mucosa are less prominent.

In the frog, it is necessary to distinguish several regions in the nasal organ (Fig. 10). The principal cavity is entirely covered with thick epithelium of which the superficial elements are cylindrical. These elements, as in the urodeles, and for that matter in all the vertebrates, present a clear, homogenous, pinkish gray central segment.

The thickness of the epithelium upon the internal wall reaches 135 mikra. As it approaches the external nasal orifice, the epithelium is gradually lessened, forming a covering 21 mikra in thickness composed of two or three layers of polyhedral cells with large nuclei. In the infero-internal cul-de-sac, the epithelium, which is very thick (150 mikra), is of a sensory nature. It is here that the cells are highest, reaching 40 mikra. In the middle and infero-external cul-de-sacs, the epithelium, about 35 mikra in thickness, presents a superficial layer of cubical ciliated cells. At the level of the choanae, the thick epithelium of the principal nasal cavity is gradually merged into the buccal epithelium.

GLANDS.—In the vicinity of the buccal and nasal cavities, numerous glands are found in the Amphibia. In the frog and toad, the entire mouth and the region anterior to the nasal sacs are occupied by an enormous number of cul-de-sacs and glandular ducts. Several groups are connected with the nasal mucosa. Born and Ecker have studied these. Two groups correspond to the nasal cavity and two other groups to the

buccal cavity. Upon transverse sections three groups (Fig. 10) are found: an external placed upon the external wall of the nasal cavity, composed of a large number of tubes agglomerated into a mass with quadrangular form, bounded above by the nasal vestibule (a portion of the cavity which is directed towards the depression of the skin which corresponds to the external nasal orifice), externally by the integument, internally by the nasal mucosa, inferiorly by a portion of the cartilaginous capsule. This is the superior gland of Born, whose ducts are situated around the lachrymal canal.

An inferior group is placed above and within the inferior extremity of the infero-external diverticulum. A fibrous band limits this glandular mass and permits it to be in direct connection with the mucosa of the diverticulum, altogether removing it from the buccal cavity. This group, very extensive antero-posteriorly, is in connection posteriorly with the buccal roof. It is the pharyngeal gland of Born which, at its anterior portion, approaches the buccal mucosa and merges with the median mass situated anterior to the cartilaginous capsule. This median mass, which is far anterior, is prolonged posteriorly below the nasal septum and is the intermaxillary gland of Born.

An internal group, placed upon the septum in the cartilaginous capsule of the infero-internal cul-de-sac and represented in Fig. 10 only by some tubes, acquires, in the posterior sections, considerable importance and fills up the entire posterior part of the diverticulum corresponding to the fibrous capsule. This is the inferior gland of Born.

The nasal glands comprise the external or superior gland and the internal or inferior gland. The intermaxillary is a buccal gland, but Born describes it as having numerous openings in the inferior cul-de-sac. The inferior or pharyngeal gland opens into the infero-external cul-de-sac and into the buccal cavity. The groups scattered along the buccal roof, especially in the anterior portion, end in the buccal cavity.

The glands are less abundant in the triton. Two important groups are found: the external gland, the ducts of which form a true diverticulum of the nasal cavity; the intermaxillary gland, well developed and exclusively buccal, except some tubes scattered upon the anterior part of the palatal vault. Their arrangement is almost analogous to that of axolotl.

According to the investigations of Blaue, the lower Amphibia, such as the proteus, do not have any glandular formation.

The glandular cells in all of these groups are cylindrical and have a nucleus situated in the basal part and an extremity, directed towards the lumen, clear and filled with homogenous protoplasm. These are mucous cells. Their existence is a formal indication of the adaptation of the animal to life in the air. According to Bruner, the muscles around the external nasal orifice evacuate the mucus of the external nasal gland into the nasal cavity at the moment when they contract so as to close this orifice when the animal plunges into the water.

NASAL CAVITY.—We have already described in the nasal cavity a principal portion and two diverticula: an inferior diverticulum and a middle diverticulum interposed in the anterior region between the nasal cavity proper and the inferior diverticulum, and branching from the canal of communication between the two cavities. The middle diverticulum, or lateral diverticulum of Born, is at no point entirely covered by cartilage; its external wall is always uncovered; it is in relation with the cul-de-sacs of the external gland and with the lachrymal canal; it is the first step towards perfecting the nasal cavity, and thus increases its respiratory region. According to Seydel, the existence of this cul-de-sac is intimately connected with that of the lachrymal canal; it is absent in the proteus and siren, which have no lachrymal canal, and also in the Gymnophiona, in which the lachrymal canal opens into the organ of Jacobson. This extension is still further manifested by the presence of the inferior cul-de-sac. This begins in front of the anterior extremity of the nasal cavity proper and extends to the choanae. Its transverse extent is considerable; we may observe two portions: an internal between the septum and the canal of union to the nasal cavity, and an external situated external to the canal and extended far externally and inferiorly almost to the maxillary bone. The internal portion is shorter than the nasal cavity and the external portion; it terminates a little in front of the choanae. Therefore, in a posterior section in the neighborhood of this orifice, two cavities are to be seen: a large one, internal and superior, the nasal cavity; another external and inferior, the infero-external diverticulum, which Seydel calls the lateral nasal canal; this is the portion which extends to the posterior limit of the choanae. Born (1876) attributes to the

inferior cul-de-sac the importance of a maxillary cavity homologous to the sinus maxillaris of mammals. The direct relation of this to the buccal cavity at the level of the choanae, according to him, depends upon the shortness of the frog's palate; the length of the palate in the higher vertebrates brings the maxillary cavity into exclusive relation with the nasal cavity.

According to Seydel, the inferior cul-de-sac represents the organ of Jacobson. Goette, Fleischer, Koelliker had already expressed this opinion. The Sarazin brothers considered the middle cul-de-sac homologous with this organ. The investigations of Seydel were made upon the entire series of *Amphibia*: *Perennibranchiata*, *Gymnophiona*, *Urodela*, *Anura*. He showed in all of these the existence of a fossa (diverticulum upon transverse sections) situated in the inferior part of the nasal cavity, beginning forward in a cul-de-sac and terminating posteriorly in the choanae, in which it opens extensively. This fossa, which is simple in the three first groups, is complicated in the *Anura*, in which it forms a true inferior cavity which possesses, as we have seen, external and internal diverticula. But this inferior cul-de-sac, according to Seydel, from its position and connection, is homologous to the fossae of the other groups. These formations covered with sensory epithelium and receiving the branches of the olfactory nerve, constitute an olfactory region placed in the passage for the respiratory air in order to exercise a sensory control. Burckhardt (1891), who described this fossa in the triton, demonstrated its innervation from the olfactory nerve and considered it the organ of Jacobson. Wiedersheim (1902) accords to it the same function.

The absence of a fossa of this sort in *Proteus* and *Menobranchus*, established by Seydel, is a new proof demonstrating their more primitive organization. It is the increasing extension of this fossa which causes the complicated disposition in the higher forms.

In the triton, there is a fossa placed at the infero-external angle of the nasal cavity passing outward into the maxillary region in continuous communication with the nasal cavity and terminating at the level of the choanae. This fossa, as in the inferior cul-de-sac of the *Anura*, has, according to our observation, for its principal role the enlargement of the respiratory region and its constant termination at the level of the choanae seems to us to be in favor of this function. In the lower species, in which the division of the nasal mucosa into olfactory

and respiratory zones is not established, the fossa has the function of participating in the olfactory sense, but it is not organized into a true organ of Jacobson. Mihalkovics (1899) refuses to accord to this fossa, as Seydel does, the value of an organ of Jacobson. The distant position of the septum and the presence of respiratory epithelium in this zone has made him insist that it represents the recessus maxillaris.

In Anura (*Rana esculenta*, *Bufo vulgaris*), a portion of the inferior cul-de-sac is differentiated and one could say that in these animals it appears as a true organ of Jacobson. It is the internal segment (infero-internal diverticulum) of the inferior cul-de-sac which we consider thus. The epithelium at this level has all the character of a sensorial epithelium. It is on the presence of this epithelium localized in the infero-internal diverticulum that Mihalkovics has based his opinion that the organ of Jacobson is confined to that part of the inferior diverticulum. A very important gland, the internal gland, opens into this diverticulum. Seydel observed it in relation to the inferior cul-de-sac and called it the gland of Jacobson. Burckhardt and, later, Seydel found these glandular cul-de-sacs in relation with the fossa in the urodeles, and gave to them the same denomination as in the Anura.

With regard to the exterior portion of the inferior cul-de-sac of the Anura, we consider it as forming a simple extension of the respiratory region. The functional division of this cul-de-sac agrees with the respiratory role of the nasal cavity.

Seydel does not admit the homology of the inferior cul-de-sac with the sinus maxillaris of mammals as Born claims. It is, nevertheless, the first appearance of an exclusively respiratory region, which represents not a true sinus maxillaris, but rather a zone which, in reptiles, birds and mammals, is situated below the inferior turbinate.

The nasal cavity of the axolotl closely resembles that of triton, showing the same external cul-de-sac. The epithelial wall is very thick, averaging 300 mikra. The nasal lumen is effected by the sinking in of the thick portions of this wall in the form of fissures. Between these fissures, the distribution of which is very irregular, are found circumscribed folds with a thick base. At the summit of the projecting portions, the thickness of the epithelium is only 75 mikra. The projections represent the folds of the nasal mucosa of fish, and constitute a morphologic character, permitting the grouping of the water-breathing animals with those of the air-breathing class.

REPTILES.

We have studied especially the saurophidians and the crocodilians; we have made few observations on the chelonians.

I. SAUROPHIDIANS.

The adder, blindworm, viper, python, boa and the galeote form the basis of our description. The nasal organ in these animals has pretty much the same disposition.

ORIFICES.—The external orifice in the adder is pierced in the center by a scale in the neighborhood of the end of the snout, upon the lateral side of the head. This orifice, which is circular, surrounded anteriorly, superiorly and inferiorly by a very distinct border, does not project beyond the plane of the integument, but is in distinct relief, and has no border internally and posteriorly, where the surface of the scale forms the limit of the orifice. In the python, this orifice is placed upon the dorsal surface of the snout.

The galeote presents an external orifice pierced at the center by a scale; it is round, very distinctly limited throughout its periphery, and is placed midway between the anterior border of the orbit and the end of the snout upon the line of separation between the dorsal and external surfaces.

A large number of observers have reported that reptiles which live in the water have nasal orifices placed upon the dorsal surface of the head—they need expose but a small portion of the snout in order to breathe the air. To prevent the water penetrating the nasal cavities when the animal plunges into the water, there is a sort of valve at the edge of the external orifice. According to Cantor, a valve is present; according to Duméril and Bibron, there are movable membranes which take the place of valves. Schmidt, Pagenstecher, Hoffmann, Brehm, Fleischmann and Kathariner (1900) report a valve as present. Furthermore, Kathariner describes an arrangement which constantly and without expenditure of muscular work closes the nasal orifice and accomplishes the necessary work when the air passages need to be opened for the purposes of respiration.

The posterior orifice of the ophidians opens at the level of the palatal vault in an antero-posterior fossa, limited above by the

palatal vault, below by a kind of transverse membrane extending from one to the other of the projections which border the fossa laterally. At its anterior extremity, this communicates with each nasal cavity by a large orifice situated in a plane oblique from above downward and from behind forward. This canal, separated from the buccal cavity where the choanae open, is found in all the ophidians. The choanae of the galeote are placed on the anterior third of the palatal vault; they are elliptical orifices with the long axis antero-posteriorly, opening freely into the buccal cavity, and are placed immediately external to a median ridge of the palatal vault, which supports two round tubercles. This is the usual disposition of the choanae of the saurians.

Fig. 11. Natural size. Python (Sagittal section showing the external wall of the nasal cavity with the turbinal). 1. Turbinal; 2. Vestibular orifice; 3. Choana.

NASAL CAVITY.—From the external orifice, we enter an almost cylindrical passage, which opens inferiorly and posteriorly into the nasal cavity proper. This is the vestibule described by Leydig (1872) and Born (1879). In the python, a large, round orifice establishes the communication of the vestibular passage-way with the nasal cavity. The blind-worm has a vestibule less distinctly separated from the nasal cavity. It is simply the anterior portion narrowed. The histologic characteristics permit this distinction between the two spaces, which is also found in the adder. Leydig, in *Lacerta*, describes the vestibule as a passage-way slightly elevated, which connects a fossa with the external nasal orifice.

Solger (1876), in *Lacerta*, *Anguis*, *Leguan*, *Chameleo*,

Hemidactylus, showed that the two nasal spaces communicate by a more or less narrow orifice, which runs in various planes, e. g., parallel to the longitudinal diameter of the head (Laguan), or to the transverse diameter (Lacerta), or even oblique (Chameleo). This author remarks the constant absence of a vestibular turbinal analogous to that which we shall describe in birds.

The principal nasal cavity is quadrilateral in form and, with the vestibule, consists of a long cartilaginous sac. The external wall in the python (Fig. 11) presents a cartilaginous fold, the turbinal, which is free at its superior border, adherent at its inferior border and extremities. We find it in the boa; it is very much reduced in the adder and in the galeote, but it attains a considerable importance in the blind-worm. Stannius, Leydig, Born, Gegenbaur and Solger have described this single turbinal in reptiles. Born studied minutely the turbinal of Lacerta and notes its rectangular deflection. In the blind-worm, the turbinal, by its anterior extremity, forms a simple prominence on the lateral wall, then progressing backwards is elevated, pedunculated and rolled up (Fig. 12). On transverse sections in the middle portion, the turbinal appears as a graceful projection arising from the inferior portion of the external wall directed internally and superiorly, then becoming bent and directed internally and inferiorly. It presents a free border looking downward and considerably enlarged. At the posterior portion of the cavity, the turbinal is prolonged behind by its pedicle in such a way that transverse sections at this level show the turbinal isolated in the center of the nasal cavity.

According to the definition of Gegenbaur, the turbinal should be a projection extending from the nasal wall by a narrow portion. Solger and Mihalkovics did not find this characteristic in that of reptiles, and called it a false turbinal (*pseudoconcha* of Solger), comparable to the superior turbinal of birds. If their observation is correct for a number of types, galeote and adder, it is not the case with the python and still less with the blind-worm. It is only necessary to compare Figs. 12, 18 and 20 to see the resemblance which exists between the turbinal of this animal, the middle turbinal of birds and any turbinal of the mammals. By its position and great development, it appears to correspond to the maxillary turbinal of the mammals.

No hollow cavity is found in the bones or cartilages of the nasal region. There is no homologue of the infero-external diverticulum of amphibians or the sinuses of birds and mammals. In the anterior vestibular region there is found under the cartilaginous floor of the nasal cavity, situated near the septum, a passage-way with thick walls, which anteriorly and posteriorly is represented by a solid mass. The

Fig. 12—X 34.3. Adder (transverse section of the nasal cavity, turbinal and choanal canal). 1. Cartilaginous capsule; 2. Turbinal; 3. External nasal gland; 4. Choanal canal; 5. Intermaxillary gland.

lumen of this passage-way is narrow in comparison to the thickness of its walls. The superior wall is the thickest. The inferior wall in its middle portion is projected into the lumen in the form of a convex pad, resembling a mushroom in transverse section. At this level, the lumen upon transverse section is reduced to a fissure with inferior concavity. This passage-way is the organ of Jacobson. Behind the mushroom-like pad, the floor presents a narrow fissure which establishes

the communication with the buccal cavity. Mihalkovics found this orifice in the lizard upon the side of the palatal papilla. The cartilaginous nasal septum separates the two organs of Jacobson. A cartilaginous box envelopes this organ and separates it from the nasal cavity on one side and from the buccal roof on the other. The posterior extremity of the organ of Jacobson corresponds to the anterior part of the turbinal. The different ophidians and saurians studied by Leydig (1897), Born (1879), Beard (1888) and Mihalkovics (1899) possess a well-developed organ of Jacobson, analogous to that of the blind-worm.

NASAL SKELETON.—The nasal cavity is completely enveloped in a cartilaginous sac which follows all of its contours. Internally the two sacs are fused, forming the septal wall, which is greatly extended vertically, even to the buccal roof. The external wall of the nasal cartilage sends out a lamella which becomes the axis of the turbinal. In the posterior part of the nasal cavity, the cartilage becomes thin near the floor and disappears in such a manner that the nasal mucosa and the buccal mucosa are attached to each other in the neighborhood of the choanae.

The bones of the nasal region lie external to the cartilaginous wall. We studied these bones in a python of large dimensions. The nasal cavity is bounded above by the nasal and prefrontal, internally by the vertical plate of the nasal, the vomer and the intermaxillary, below by the vomer and palate and externally by the prefrontal and maxillary (Fig. 13).

Intermaxillary.—Small, single bone composed of two parts, of which the posterior, flattened and arranged as a vertical lamina, is connected to the other which forms a transverse wall, upon the inferior surface of which the teeth are implanted. Laterally, it is united with the maxillary.

Maxillary.—Double bone, compact, elevated in front, becoming thinned out at its posterior extremity. The external face, which is smooth, is slightly oblique from above downward and from within outward. The internal face is smooth and slightly excavated. The inferior border is supplied with teeth. The round exterior extremity unites loosely with the intermaxillary. The posterior extremity is united with the transverse portion and the middle portion of the superior border with the prefrontal. It unites with the palate by a ridge on the internal surface near the superior border.

Palate.—Double bone, slender, almost cylindrical, with the inferior surface flattened and supplied with teeth. A prolongation from the internal border articulates with the posterior extremity of the vomer and the anterior extremity of the sphenoid. This prolongation is situated in the posterior third of the bone. The anterior extremity is free and the posterior extremity is articulated with the pterygoid. The middle portion of external border is in contact with the maxillary.

Fig. 13. Two-thirds natural size. Python (skull seen from its inferior surface). 1. Intermaxillary; 2. Vomer; 3. Superior maxillary; 4. Palatal; 5. Sphenoid; 6. Pterygoid.

Vomer.—Double bone as in the amphibians, formed of two laminae, the vertical one contributing to form the nasal septum in connection with that of the opposite side, and a lamina directed horizontally outward, with the superior surface concave and limited by a greatly elevated external border. This lamina exists only in the anterior third of the bone, but its border is prolonged backwards under the form of a very slender process. The bone has the shape of a fish hook. The

vomer articulates above with the nasal, externally with the prefrontal and posteriorly with the inferior surface of the sphenoid.

Nasal.—Double bone, large and slender, with the superior surface convex transversely, while its inferior surface is concave in the same direction. The internal border is rectangular, the external border uniform, so that the bone resembles a crescent. A lamina extends from the internal border vertically downward and joins with the vertical lamina of the vomer. The intermaxillary lies between the anterior extremities of the nasal bones.

Prefrontal.—Double bone, triangular, formed of two laminae, an anterior horizontal, the other almost vertical and directed downward, extending from the posterior border of the bone and constituting an orbital process. The anterior angle of the horizontal lamina is inserted between the frontal and maxillary. The external border is in contact with the nasal bone and the posterior part of the external border with the maxillary. The posterior border or base of the triangle is articulated by its internal half with the frontal, and by its external half aids in forming the orbit. Fischer (1900), in the *Amphisboenia*, noted the general plan of the structure of the saurians, and described several points of divergence in the skeleton, particularly the imperfect development of the cartilaginous envelope.

NASAL MUCOSA.—In the vestibular region, the mucosa presents a stratified pavement epithelium. At the posterior limit of the vestibule, a transition is effected between this indifferent epithelium and the respiratory epithelium. In this zone, the inferior wall and a part of the internal wall are covered with stratified pavement epithelium, while the superior wall, the external wall and a part of the internal wall are covered with stratified epithelium, of which the most superficial layer is composed of cylindrical, ciliated cells. In the blind-worm, the respiratory region anterior to the turbinal presents a diverticulum placed at the level of the external border of the floor and directed horizontally outward, the lateral recess of Mihalkovics.

All over the turbinal, the mucosa is of the respiratory type. The corium of the turbinal contains numerous blood vessels and glands. The axis of the turbinal is formed by a

cartilaginous lamina extending from the nasal capsule, which is of slight thickness but is enlarged at the level of its free border.

The epithelium is very thick, the layers of round cells are very numerous, the superficial layer is formed by very high cells with basal nuclei. They are clear and refractive in their remaining portions. At the level of the nasal roof and of the superior border of the turbinal the thickness of the epithelium is 85 mikra and 50 in the portion adjacent to the turbinal.

In the saurians, Mihalkovics described olfactory epithelium in a considerable portion of the cavity; the respiratory epithelium covers only the inferior surface of the turbinal. This author finds many Bowman's glands in the olfactory mucosa.

Max Schultze describes, in the adder, blind-worm and lizard, cylindrical epithelial cells which never have any vibratory cilia, and olfactory cells provided with a bundle of long cilia.

GLANDS.—The mucosa of the blind-worm contains in the corium some few glandular tubes which are found along the external and internal walls. There is only one large gland in relation with the nasal cavity, which is situated externally towards the middle portion of the external wall. This glandular group begins at the level of the posterior portion of the vestibule and acquires a considerable importance at the level of the lateral diverticulum of the respiratory region, and continues as far as the middle of the turbinal.

ORGAN OF JACOBSON.—We have seen the situation and form of the long canal; it is enveloped in a cartilaginous tube which is connected with the septum and the nasal capsule. The vomer and the palate are the bones protecting this cartilaginous envelope inferiorly and internally.

Leydig (1897) describes, at length, the organ of Jacobson in serpents. Two bones are in relation with it, the turbinal and the vomer; its cartilaginous wall is connected above with the nasal cartilage. Mihalkovics (1900), in the adder and *Lacerta agilis*, represents and describes the vomer as forming the roof of the organ of Jacobson, which it separates from the nasal cavity, and the intermaxillary as constituting a part of the floor and of the internal wall.

Internally, the cartilaginous wall presents a mucosa with a very thin corium and very thick epithelium. On the dorsal

wall, the thickness of the epithelium is 257 mikra and on the ventral 42. We find in the blind-worm and viper, at the level of the dorsal wall, a large quantity of round cells, crowded closely together. The superficial layer is composed of very high cells (54 mikra), having a basal nucleus, clear in the remaining portion. At the level of the floor, and especially on the ridge which it forms in the cavity, the epithelium is much thinner than that of the roof; the cells have a superficial clear segment and terminate in a border supporting the cilia; their height is 16 mikra.

Wright (1883) describes a well-developed neuroepithelium upon the roof of the canal of Jacobson, while the floor is covered with an epithelium composed of shorter cells provided with cilia. Leydig found cylindrical cells in the epithelium of Jacobson, and described numerous fibres of the olfactory nerve and nerve cells in the corium. Mihalkovics found cells with cilia of various lengths in the epithelium of the floor. In several places, there was a slightly elevated cuticle upon the superior wall. He found, at the external limit of the layers of small cells, a capillary network in which the branches penetrated in a radiate direction into this layer. The olfactory cells showed the limiting membrane of Brunn through which the fine, short olfactory filaments projected.

The organ of Jacobson is greatly developed among the sauropshidians, and Beard accounts for the relative simplicity of the nasal cavity on this ground.

Mihalkovics (1899) notes the narrow communication of the organ of Jacobson with the buccal cavity in serpents, but does not agree as to this organ with the opinion of Seydel, who accorded to it, in the Amphibia, the role of sensory control of the expiratory current. He considers it an organ whose purpose is to perceive genital odors, which are well developed in all crawling animals, being absent in fish and birds, which have recourse to their visual apparatus, and atrophied in man because of the development of the intelligence and the retrogression of the olfactory powers.

II. CROCODILIA.

The nasal fossae of the crocodile are more complex than those of other reptiles. The external nasal orifices are placed upon the dorsal surface of the snout in the vicinity of the

anterior extremity and almost in the median line. They are of small dimensions, of elliptical form and directed obliquely from within outward and from behind forward. The choanae open upon a plane horizontally placed upon the prolongation of the palatal vault; they are situated about 2.5 cm. from the insertion of the palate. They are of quadrangular form and have bony boundaries throughout.

The external orifice begins as a vertical canal about 1 cm. in height and bends so as to become horizontal, making a sort of nasal vestibule. Its dimensions increase from before backwards and it becomes a very large cavity, especially in a vertical direction. This cavity contains a long, large, round ridge inserted in the roof of the nose, free on its inferior

Fig. 14. Half natural size. A. Crocodile (transverse section passing through the anterior region of the nasal cavity). 1. Maxillary; 2. Nasal mucosa; 3. Cartilaginous septum; 4. Nasal lumen; 5. Maxillary cavity.

border. It is a true turbinal. This is of cartilaginous consistency. Another ridge occupies the bottom of the cavity formed at the expense of the external surface, upon the entire vertical extent of which it has its insertion. It is a false turbinal according to the definition of Gegenbaur.

The floor of the vestibule is convex. Posteriorly, at the limit of the principal nasal cavity, it becomes depressed into a fossa and leads to a cylindrical canal which occupies the most internal and inferior portion of the principal nasal cavity. This canal, circumscribed by an osseous wall, opens into an osseous canal of the same form, but much larger, which terminates in the choanae.

The various details may be well seen in a series of trans-

verse sections. Section A (Fig. 14) passes across the vestibule; the section of the cavity is elliptical. It is surrounded by a cartilaginous wall. Internally this forms a septum. The floor is entirely cartilaginous. At the level of the roof and externally, a very thick osseous wall is observed. The very large maxillary cavity is situated external and inferior to the vestibule. Section B (Fig. 15) shows the principal nasal region. The nasal cavity has an irregular form and presents the turbinal which is pedunculated, has an axial cartilaginous skeleton and is inserted on the dorsal region of the nasal capsule. The external wall is markedly convex and cartilaginous, and is constituted by the surface of the false turbinal, which is hollow. Its cavity appears on section. The

Fig. 15. Half natural size. B. Crocodile (transverse section passing through the middle portion of nasal cavity). 1. Skin; 2. Superior maxillary; 3. Cartilaginous capsule; 4. Nasal mucosa; 5. Olfactory region of the nasal cavity; 6. Turbinal; 7. False turbinal; 8. Respiratory region of the nasal cavity.

inferior half of the internal wall is also convex, due to a cylindrical osseous canal placed below the septum and adjoining a similar canal on the opposite side. The posterior portion of the cavity is a simple cylindrical osseous canal covered with a thin mucosa, analogous to periosteum.

As Section B and the antero-posterior sections show, there are two small nasal cavities behind the vestibule. The cavity containing the turbinals terminates in a cul-de-sac and the cylindrical cavity, prolonged posteriorly, which leads the respiratory current directly from the vestibule to the choanae. The olfactory apparatus is distributed only to the principal nasal cavity which contains the olfactory nerve. The superposition and complete separation of the olfactory cavity from

the respiratory cavity is very remarkable and does not exist anywhere else. In the tortoise, this division is well established, but the two canals communicate with one another.

The respiratory canal is bony; the other is cartilaginous and completely surrounded by very large and thick bones.

NASAL SKELETON.—The bones bounding the nasal cavity are superiorly the nasal, prefrontal, a part of the maxillary and the intermaxillary; inferiorly the intermaxillary and the palatal lamina of the maxillary; externally the maxillary, internally the cartilaginous septum. The interior of the cavity thus circumscribed encloses the respiratory region, limited by the ethmoid and the palatal in its anterior half, and hollowed out of the pterygoids in the posterior region (Fig. 16).

Fig. 16. Half natural size. Crocodile (Sagittal section of the skull passing somewhat external to the median line). 1. Intermaxillary; 2. Palatal lamina of the maxillary; 3. Ethmoid; 4. Palatal; 5. Respiratory region of the nose; 6. Pterygoid; 7. Nasal; 8. Prefrontal.

Intermaxillary.—A double bone, of which one wall constitutes the external surface and inferior border, the latter provided with teeth. The external surface is rough, a characteristic found in all the bones immediately subjacent to the skin. The palatal lamina, directed horizontally inward, extends from the lower border of this wall; the free border is thin and hollowed out at the middle portion. The internal surface of the lateral wall is concave vertically. This bone articulates internally with that of the opposite side and posteriorly with the nasal and maxillary.

Nasal.—Double bone, long and flat, trapezoid in form, with a large internal base. The inferior surface is slightly concave

transversely. The internal and external borders are rectangular, the anterior and posterior, squamous and bevelled. It articulates internally with the bone of the opposite side, externally with the maxillary, anteriorly with the intermaxillary and posteriorly with the prefrontal and frontal.

Maxillary.—Double bone, of large dimensions, quadrilateral, with rough external and superior walls and an inferior border supplied with teeth. The palatal lamina is flat, its free border rectangular. The internal surface of the bone is concave and forms a longitudinal fossa by uniting with the palatal lamina. It articulates anteriorly with the intermaxillary, posteriorly with the prefrontal, the lachrymal and the jugal, internally with the nasal by its superior border and by the palatal lamina with that of the opposite side.

Prefrontal.—Double bone, limiting the orbital cavity, the inferior surface of which sends out a process directed vertically downwards, which establishes the solid relations between the vault and the nasal floor by articulating with a process of the palate. This bony interval is the posterior limit of the olfactory region.

Palatal.—Double bone, quadrilateral and thin; the internal portion of its superior surface is hollowed out by a longitudinal groove. A thick process is projected vertically upward from its middle portion to articulate with that of the prefrontal. The inferior surface is flat and thin, the internal border rectangular; the external border oblique from without inwards in the anterior half where it is thin. Behind, it is thick. The anterior and posterior borders are divided into lamellae. Internally, it is united with the bone of the opposite side, anteriorly with the palatal plate of the maxillary, posteriorly with the pterygoid, superiorly by its process with the frontal and by the edges of the groove on its superior surface with the ethmoid and pterygoid. It is thus that the respiratory canal is limited.

Ethmoid.—Double bone, long and lamellated; a vertical lamina constitutes the principal part of the bone; its external surface is hollowed out by a groove. About the inferior border and posterior half of the bone, a lamella projects outward and downwards. It is articulated below with the ethmoid of the opposite side, and also with the vomer (median

prolongation of the pterygoid); anteriorly it is insinuated between the two palatal laminae of the maxillary; by its posterior border it articulates with the process of the prefrontal. The external lamella articulates with the palate, forming a canal between these two bones.

Pterygoid.—Single bone, large in size, presenting a median body directed antero-posteriorly, which posteriorly stretches out in the form of a wing. It is prolonged anteriorly by a long coping, which represents the vomer (hérisséal of Geoffroy Saint-Hilaire).

The posterior border, which is very thick, presents a median tubercle and is bordered by high ridges. The superior surface presents a median fossa which is prolonged with one hollowed out on the vomer. The inferior surface, which is flat, is enlarged by lateral wings. It presents posteriorly two large orifices of almost quadrangular form which are the choanae. Each of these gives access to the canal hollowed out in the pterygoid. This bone is in relation anteriorly with the ethmoid, and the palate bones of the vomer, with the processes of the frontal and the palate by the lateral ridges, with the palate and the transverse by the anterior border of the wing, above with the pre-sphenoid, the basi-sphenoid and the ali-sphenoid.

STRUCTURE.—We cannot give the details of the structure of the mucosa of the nasal cavity of the crocodile. We found neither glands nor organ of Jacobson. Beard (1888) found no trace of the organ of Jacobson in the embryo. Howes (1891) described two cartilaginous sacs which represented the vestiges of this organ. Meek, in young embryos with a head measuring $5\frac{3}{4}$ to 7 mm. in length, considered a small invagination of the inferior part of the nasal cavity as a rudimentary organ of Jacobson.

Sluiter (1892), in young embryos, found an organ of Jacobson well developed, analogous to that of the lizard. There was no trace in old embryos. He concludes from this observation that the ancestors of the crocodile were provided with a perfected organ of Jacobson.

Roose (1893, 1), in a series of embryos having a head from 5 to $12\frac{1}{2}$ mm. in length, describes the organ of Jacobson as an evaginated cul-de-sac of the postero-inferior ex-

trernity of the nasal cavity. This evagination will develop into the posterior nasal canal, which in the adult forms the respiratory passage-way. The anterior extremity of the organ projects from the nasal passage-way in the form of a solid epithelial cone. Later, in an embryo with a head measuring 41 mm., the rudimentary organ appears under the form of a mucous fossa 2 mm. in length, lodged in the concavity of the vomer.

The absence of nasal glands in the crocodile is as universally admitted as that of the organ of Jacobson. However, Stannius, Wiedersheim, Gaupp, Roese (1893, 2) described a large gland opening into the nasal cavity.

Roese finds it between the cartilaginous roof and bony layer (premaxillary and nasal). It opens by one or two excretory ducts on each side of the septum in the posterior extremity of the external nasal orifice. This gland appears in the form of an epithelial bud in embryos with the head $12\frac{1}{2}$ mm. in length.

III. CHELONIANS.

According to the nasal skeleton of *Testudo mydas*, this group of reptiles may be considered as intermediate between the sauropheids and crocodilians.

The choanae open about the middle of the palatal vault and the pterygoid does not participate in the constitution of the hard skeleton as in the crocodile.

The ethmoids are large bones participating in the formation of the nasal fossa. The vomer is enlarged at its posterior extremity and aids in the constitution of the palatal vault. There exists, therefore, in these animals a special respiratory canal, but, according to Wiedersheim, it communicates by several orifices with the remaining portion of the nasal cavity. Seydel, who has studied the nasal cavity of the tortoise with much care, finds an organ of Jacobson well developed in them, in the form of a canal covered with olfactory epithelium. Mihalkovics represents this organ as a diverticulum transformed later into a canal lying against the nasal septum and covered with sensory epithelium.

BIRDS.

The nasal cavities in birds are hollowed out in part in the beak and in part in the facial walls, anterior to the orbital cavity.

ORIFICES.—The external nasal orifice is variable, in form, dimensions and situation, depending on the species.

Ornithologists distinguish basillar nasal cavities (at the root of the nose) median (at the middle of its length) and marginal (at the borders). They may be round, oval or linear. They are masked by hard plates in the crow, and by cartilaginous scales in the Gallinaceae. They are sometimes very small, as in the heron and pelican (Chatin), at other times freely open, of large dimensions and elliptical, as we have found in the duck. In the turkey, they are provided with a sort of valvular apparatus which protects the entrance of the nasal cavity. This animal has an external elliptical nasal orifice, looking outwards, bordered by a thick integument of dark color and scaly appearance. The framework is cartilaginous; no portion of the border is provided with bony support. A cutaneous fold extends diagonally from before backwards and from below upwards, dividing this orifice into two parts, an external part which is a simple cul-de-sac terminating at the posterior level of the orifice, the other internal, which leads into the nasal vestibule. In the external cul-de-sac, small solid particles (especially dirt) are found, which the anatomic disposition has prevented from entering further into the nasal cavity.

The nasal orifice of the duck, which gets its food at the bottom of muddy ponds, is wide, with no protecting apparatus.

The nasal fossae open together into the buccal cavity by a median fissure of the palatal vault, a simple cleft in the anterior portion, having the appearance of an elliptical buttonhole in the posterior half, in the turkey, duck and pigeon. The border of this orifice is composed of soft parts, of which the free border is provided with very long calcified odontoid papillae. The opening of the larynx in the form of a large elongated cleft is found at the level of the base of the tongue, immediately subjacent to the palatal orifice. The respiratory air passes, therefore, almost directly from the nasal cavity into the larynx. On lifting the borders of the palatal arches, the nasal septum is observed in the median line too short vertically to reach the

palatal vault, and on each side are to be seen the nasal cavities with an open floor.

NASAL CAVITY.—The nasal cavity has no bony wall, but is, as in *Anura*, limited by a cartilaginous sac. It is separated from the integument by a large empty space, larger below than above. If it is examined on longitudinal sections made a little external to the septum, it is seen to be considerably elongated in an antero-posterior direction. Its vertical diameter increases progressively from before backwards. An anterior region may be isolated from the rest of the cavity, the vestibule described by Born. Posterior the nasal cavity proper is found. The external wall is the seat of three very prominent ridges projecting into the cavity, representing the true turbinals. The

Fig. 17. Six-sevenths natural size. Turkey (Sagittal section, showing external wall and three turbinals). 1. Vestibular turbinal; 2. Superior turbinal; 3. Middle turbinal.

anterior turbinal, inserted in vestibular region, has the name of vestibular turbinal [Born (1879), Gegenbaur (1873), Mihalkovics (1879)]; the two others belong to the principal cavity. In the turkey, the vestibule represents about one-third of the whole cavity. It opens externally by the external nasal orifice, and communicates with the principal nasal cavity by a narrow cleft between the external wall and the posterior border of the vestibular turbinal. This turbinal, which is attached to the roof of the vestibule, is a true fold of the cartilaginous capsule, as are all the other turbinals. It descends from the entire length of the vestibule down to the floor, from which it is separated only by a narrow cleft. It is thin anteriorly, rolled up posteriorly, and presents an inferior border of bony consistency. It is a true sagittal septum dividing the vestibule

into two parts, an external which terminates posteriorly in a cul-de-sac, and an internal one which communicates with the nasal cavity proper.

In the duck, the vestibule communicates largely with that of the opposite side and has no turbinal. Its posterior limit is marked by an almost vertical fold of the external wall, which, narrowing the lumen at this level, forms the border of the orifice of communication between the two cavities. In the pigeon, there is a vestibular turbinal which is situated exactly under the supero-internal angle of the vestibule.

The nasal cavity proper in the turkey, duck and pigeon is narrowed by the projection of the two turbinals. They are both inserted on the external wall. The anterior turbinal, which is the middle turbinal in the turkey and in all birds which have a vestibular turbinal, has an elongated form and presents a round contour vertically and extends from before backwards and slightly from above downwards. It has an enlarged anterior extremity, and a slender posterior extremity; its free border is thick and round in the turkey, in which this turbinal has a large base of insertion (Fig. 17). In the pigeon, on the contrary, the middle turbinal is a cartilaginous lamina, slightly curled from above downwards and from within outward, with a thin pedicle and with a free border of slight thickness looking internally and inferiorly (Fig. 18).

The superior turbinal is a globular ridge placed in the neighborhood of the nasal roof and the posterior part of the cavity.

A large space, in the form of a fossa opening internally, is found between the middle turbinal and the nasal floor. A simple groove lies between the superior and the middle turbinals. Only the two turbinals of the nasal cavity proper belong to the olfactory organ. The vestibular turbinal is independent (Gegenbaur), and we have seen that in certain birds it is absent. According to Gegenbaur (1873), there is a special arrangement in the head of the bird which separates the external nasal orifice from the interior. According to what we have seen in the turkey, it has the role of dividing the vestibule into two parts, an external cul-de-sac and a very narrow internal canal; it thus protects the entrance of the nasal cavity.

The middle turbinal is the equivalent of the inferior turbinal or maxillary turbinal of mammals (Gegenbaur). This

opinion is based on the insertion of this turbinal at the level of the superior maxilla and above the opening of the lachrymal canal. Its high insertion upon the external wall does not correspond to the insertion of the maxillary or inferior turbinals of mammals. It has no relation with the maxillary bone, since it is the cartilaginous capsule which supplies it,

Fig. 18—X 34.3. Pigeon (transverse section of the nasal cavity, passing through the middle portion) (left side). 1. Septum; 2. Middle turbinal; 3. Chorionic glands; 4. Palatal fissure (choanal cleft); 5. Pneumatic spaces.

but its base is in relation with the lateral spaces which correspond to the sinus maxillaris. The superior or posterior turbinal corresponds to the first olfactory cushion of mammals. Mihalkovics homologizes it with the single turbinal of the saurians. According to Gegenbaur, there is in birds no

homologue of the ethmo-turbinal, besides, the superior turbinal is not, in his opinion, a true turbinal, and he compares it to the pseudo-turbinal of the crocodile. The superior turbinal of the vulture, through its insertion in the supero-internal angle of the nasal cavity, appears to correspond to the ethmoidal turbinal.

The nasal region is surrounded by numerous, extensive, pneumatic cavities, attaining in this respect a high degree of development. These different spaces may well be studied in transverse sections of the head of a pigeon. They are divided into two groups, an inferior and external group corresponding to the maxillary sinus, and a superior and internal corresponding to the frontal sinus.

Figure 18, representing a transverse section in the middle region of the nasal cavity, shows large lacunae external to this cavity, extending along the whole of the external wall, separated from one another by cartilaginous or fibrous septa.

They are either quadrilateral or round. Internally they are limited by the nasal capsule; externally by the fibrous tissue formed by the condensation of the deepest layers of subcutaneous connective tissue. In more anterior sections there appears a space, prolonged into the palate, limited by cartilaginous walls on all sides. This inferior space represents the palatal sinus, reported by Mihalkovics, the lateral spaces corresponding to a true sinus maxillaris. At the level of the base of the septum, below the intermaxillary and the nasal bones, the cartilaginous septum bounds a triangular space with base posterior, just where it unites with the opposite side.

At a more posterior level, this space is enlarged and is subdivided by cartilaginous lamellae. Extending posteriorly very far between the orbits, is a frontal sinus corresponding to the sinus orbitalis of Mihalkovics. The end of the septum widens into the shape of a playing-card heart, containing hollow cavities in the inferior extremity of the septal cartilage.

The direct relations between the different cavities and the nasal fossae are not visible; it shows, simply, the phenomenon of preumatisation so greatly diffused in the skeletons of birds.

NASAL SKELETON.—The cavity is surrounded above, externally and below by a cartilaginous wall which gives rise to the turbinals. It is thick and resisting, interrupted below by the palatal fissure; within, the cartilaginous capsule forms, in

connection with that of the opposite side, a lamina which becomes the septal cartilage.

This cartilaginous capsule is lodged in a bony space of the facial walls, where the bones are reduced to long pieces and can constitute only an imperfect protective investment.

In the turkey, the nasal skeleton is constituted above by the intermaxillary and nasal, below by the superior maxillary and

Fig. 19. Natural size. Turkey (skull seen from the inferior surface; the dotted lines indicate the position of the choana). 1. Superior maxillary; 2. Palatal process of the superior maxillary; 3. Choana in the fresh state (Schematic representation); 4. Palatal; 5. Jugal.

palate, externally by a part of the nasal and a part of the maxillary; internally by the septal cartilage (Fig. 19).

Intermaxillary.—Single, narrow, long bone which forms the median part of the superior surface and the point of the beak. A slight median groove indicates the division of the bone into two halves. The enlarged anterior extremity articulates with the superior maxillary, while its median part is

pointed. The posterior extremity is placed between the two nasal bones and comes in contact with the anterior border of the two frontals. The inferior surface belongs to the roof of the nasal fossae.

Maxillary.—Double complex bone of quadrilateral form. The external surface, slightly convex and smooth, is oblique from above downwards and from within outwards. The inferior surface is hollowed out by an antero-posterior fossa. The anterior extremity articulates with the intermaxillary. The posterior extremity presents three prolongations, an external portion which is continuous with the external portion of the inferior surface, a middle, very slender, which articulates with the os jugal behind, an internal one, large and flat, directed obliquely backwards and inwards, placed in a horizontal plane—the palatal prolongation.

Nasal.—Double bone, situated on each side of the intermaxillary, anterior to the frontal and internal to the lachrymal. It is large, flat and of quadrangular form; the superior surface is placed almost horizontal and is slightly hollowed out in the middle. Its inferior surface is concave transversely. The internal rectangular border articulates with the intermaxillary. The anterior concave border limits a large space filled with fibrous tissue. The posterior convex border articulates with the frontal, the external border with the lachrymal. The antero-external angle of this bone is prolonged into a long process which descends almost vertically to meet the maxillary. It constitutes the only bony part of the external nasal wall.

Palate.—Double bone, very slender, very long, passing horizontally from the posterior extremity of the maxillary to the pterygoid. The septal cartilage takes the place of the vomer. There is no bony turbinal.

In the vulture, the bones are more extensive. The anterior space between the nasal, intermaxillary and maxillary is partially filled with osseous laminae belonging to the maxillary. The palate is a large bone which forms a large part of the nasal floor. The turbinals are bony; the vestibular turbinal is a simple crochet inserted on the superior surface; the middle turbinal, inserted upon the external surface, is very voluminous, composed of the lamellae which are enlarged, perforated with numerous orifices, giving access to the air cavities; the superior turbinal, which is placed upon the most internal portion of the surface, is composed of a lamella rolled once upon itself.

In birds with a long beak, it is the anterior part of the nasal fossae, the vestibule, which is modified. The intermaxillary and maxillary bones are greatly elongated, and the nasal space which they surround is increased in length; the other bones and the principal nasal cavity do not present any essential modifications.

Parker (1869), in his study of the development of the cranium of the cock, shows the evolution, form and connections of the different bones. They are arranged in the same manner as in the turkey. The numerous figures which accompany this work are of great interest.

NASAL MUCOSA.—Throughout the vestibule and upon the vestibular turbinal, the mucosa presents a connective tissue corium and a stratified pavement epithelium having all the characteristics of epidermis, with the superficial layers strongly flattened and refractive. It is very thick over the turbinal and in the neighborhood of the external nasal orifice. The turbinal contains no cartilaginous lamina; but connective tissue and numerous vessels are present.

In the principal nasal cavity, the mucosa has the respiratory characteristics over the greatest portion of its surface; the olfactory part is limited to the nasal roof and the superior turbinal.

Over the middle turbinal is found an investment of the respiratory type, characterized by a cylindrical, ciliated epithelium and numerous depressions covered with clear cylindrical cells, as well as a great number of glands in the corium. In a section made in the middle portion of the cavity, the entire mucosa, except that of the roof, shows a considerable thickness of the chorionic layer, which contains a large number of glands. It may be said that the corium is formed by glandular tubes. They are held tightly together by one another, and the interspaces, occupied by fine connective tissue septa holding blood vessels, are very narrow. Towards the inferior border of the septum, the thickness of this glandular layer is 178 mikra. Some of these glandular tubes attain great dimensions. There are also numerous crypts, simple depressions of the epithelial surface, opening largely into the nasal cavity. Every portion of the nasal cavity possesses this richness of glands. It is most remarkable in the inferior portion of the septum and throughout the middle turbinate, with the exception of its inferior surface. The epithelial cells, which line the glandular tubes, are cylindrical and elongated. They present a

base larger than the central extremity. The basal portion contains the nucleus and some strongly colored granules; it occupies almost a third of the cell. The other portion is clear, very refractive and without visible granules. In certain cul-de-sacs, the entire height of the cell presents refractive characteristics, due to the mucous glands.

Their presence gives to the mucosa a special respiratory character; the secretion must be abundant to keep moist a membrane which is subjected to very intense dryness while on flight. The epithelium of the surface is formed of high cylindrical cells, with a deep extremity containing the nucleus, intermingled with round elements, and a central extremity with finely granular and clear contents, limited towards the cavity by a granular border which is prolonged into very short cilia outside of the cell.

Glands are uncommon at the level of the nasal roof and the adjoining internal and external walls. The epithelium presents several layers of round cells lying close to one another, and a superficial layer of cylindrical cells. Max Schultze describes olfactory cells in birds, analogous to those in amphibia and reptiles, possessing tufts of long cilia and cylindrical non-ciliated epithelial cells.

In the air cavities we have not found a mucous investment covering the cartilaginous or fibrous walls.

Besides the numerous glands included in the corium of the respiratory mucosa, there are glandular masses in the neighborhood of the nasal cavity.

In the vestibular region, a group of cul-de-sacs is found between the two cavities, near the buccal roof, which are glands belonging to the buccal cavity.

Towards the anterior extremity of the principal cavity, glandular tubes are seen, on transverse section, placed some above and some below the palatal and maxillary sinues. The inferior group continues posteriorly along the external lip of the palatal fissure. The superior group (external nasal gland), which increases in importance at a more posterior level, is placed opposite the line of insertion of the middle turbinal, then disappears at about its middle portion. Some glandular tubes are found in the posterior region, external to the frontal sinus above the nasal roof.

These glands have a deep cubical epithelium, with a nucleus in the middle portion of the cell, with a clear, finely granular zone within. They are serous in character.

Most birds possess a special glandular apparatus, studied by Cuvier, Tiedemann and Jacobson. Nistch describes it under the name of nasal gland. Jobert (1869) made a very complete study of it in 1869. He made observations on the waders and the palmipeds. The gland is located in a hollow fossa in the frontal which limits it posteriorly and laterally, while the lachrymal bounds it anteriorly. The excretory duct discovered by Jacobson, then by Nistch, is double according to Jobert. The two excretory ducts, formed of long, laminated fibres, are directed from above downwards and from behind forwards; the superior passes under the nasal bone and opens at the superior and external portion of the nose. The other, deflected, descends behind the nasal and opens on the internal surface of the nose in the middle meatus.

According to Müller, all the glands of the nose have the same structure as the salivary glands. Jobert accepts this view for the nasal gland.

This gland has been considered by Cuvier and Nistch as a lachrymal gland; according to Tiedemann, it secretes an oily liquid and it is on this account well developed in birds which live in the water or on the shore.

No glands below the corium are found in the interior of the septum. It contains only connective tissue and the vessels of each side of the cartilaginous axis. There is no trace, in the pigeon, of invagination of the mucosa, nor of an isolated tube which might represent an organ of Jacobson. Ganin and Mihalkovics have described an invagination of the mucosa in the septum at the level of the anterior extremity of the middle turbinal which, in certain transverse sections, is isolated and closed in the form of a tube. According to their view this represents an organ of Jacobson. Mihalkovics compares this formation with the canal of Jacobson in the human fetus. There is evidently a great resemblance between them.

Birds form an aberrant group between saurians and mammals which possess a well-developed organ of Jacobson. The absence of the organ coincides, in these, with a greatly reduced olfactory sense. Whether or not this organ has the function of exercising a sensory control upon the contents of the buccal cavity, it is found largely replaced by olfactory epithelium itself, which is directly affected by virtue of the communication established between the buccal and nasal cavities by the long palatal fissure.

(To be continued in the June number.)