XXIX.

THE MORPHOLOGY AND EMBRYOLOGY OF THE NASAL FOSSAE OF VERTEBRATES.

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(Continued from the March Annals.)

Mammals.

In all the series of mammals, the general plan of the structure of the nasal apparatus is almost the same, the variations being in the dimensions of the nasal cavity, the disposition of its orifices and turbinals and the amplitude of the sinuses.

NASAL CAVITY.—The usual shape of the nasal cavity is that of a quadrangular pyramid, with a base posterior and apex anterior. The turbinals modify the shape of the walls and lessen the lumen. The length of the cavity is generally proportionate to the length of the head and particularly to the length of the snout. The influence of the alimentary regimen is a large factor in these variations, while the height and size are dependent upon the extension of the respiratory apparatus.

EXTERNAL ORIFICE.—The anterior or external orifice is surrounded by a system of cartilages covered by skin, which forms the naris; to this, muscles are often attached. The musculature is often well developed and Wiedersheim (1890) reports the existence of sphincters and special valves in diving mammals. The orifices are often situated behind the end of the snout (*Quadrumana*), just at the end of the snout itself (*Carnivora*, *Rodentia*, etc.); sometimes they are prolonged into a tube, in which case a cartilaginous canal lies anterior to the nasal bones and articulates with them. This is the case in animals with projecting snouts (bears, moles). The snout of the pig is a rigid tube surrounded by circular fibres. Sometimes the nasal orifices end in a single tube of long dimensions, as the trunk of an elephant. The orifices may lie on the dorsal surfaces of the head (the blow holes of the cetaceans). The cartilaginous skeleton which surrounds them may be incomplete, as in the nose of the solipeds and ruminants. Finally the external orifice

may have rigid borders, as in *Ornithorhynchus*, in which it perforates the superior surface of the horny box which supports the maxillary.

BLOW HOLE OF THE CETACEANS.—There are certain whales which, on account of the single blow hole, are considered as monorrhinal. In reality, the blow hole leads into a chamber (spiracular cavity) in which the two nares end. Some valves (valves of v. Baer) separate the spiracular cavity from the nares. These cavities send diverticula in various directions (spiracular sacs and nasal sacs). The nares are provided with dilator muscles, retractors of the nasal alae and constrictors of the nose. In the sperm whale the nasal region is specially affected by the asymmetry of the cranium. The blow hole is to the side of the median line. The left naris has normal dimensions, the right is large, but it ends in a true nasal cavity (Pouchet and Beauregard, 1885). According to Pouchet (1889), the symmetrical position of the blow hole of cetodonts may be explained on the supposition that the latter is formed by the naris of the corresponding side (left in the sperm whale) into which, by special embryogenetic process, the nasal cavity of the opposite side opens. He noted in an embryo of the sperm whale, that the right naris was obliterated by epithelium, and the communication between the two cavities effected through the agency of the epithelial expansions, originating from the nares themselves and giving origin in a general way to the sacs of the blow hole.

Kükenthal found the nares fused together, forming a vestibule, in embryos of the dolphin.

Abel (1902) attributed to the position of the nasal fossa the cause of the cranial asymmetry in the odontocetes, but according to this author, this does not depend upon a superficial asymmetry, because the external nares, which are found in the skin, remain in the median line in the animals which he has studied. The deformity is in the bony system. The asymmetry of the cranium is greater in the varieties where the nares are placed higher up (*Platanistidae*, *Ziphiinae*); on the contrary, when the nares are placed more anteriorly, the bilateral symmetry hardly deviates (*Zeuglodon*, *Phocaena*, *Neomeris*, *Cyrtodelphis*); on the other hand, in young animals in which the nares are found much in advance of the cranium, the asymmetry is very slight or nil. The recession of the nares allows the animal to breathe when only a small portion of the head

is outside of the water. The principal bony modifications are in the nasal and interparietal bones, which become rudimentary.

CHOANAE.—The posterior orifices or choanae end in the pharynx behind the soft palate. The air which goes through the nasal cavity passes through the pharynx before reaching the larynx. In certain cases the air enters directly into the larynx, when it occupies a very high position and ascends just behind the soft palate (solipeds). The opening of the choanae is placed sometimes in a vertical plane (monotremes, marsupials, proboscidiens and primates), and sometimes in an oblique plane (carnivora, ruminants, solipedes). The two pterygoid processes limit a sort of fossa, very variable in its extent, into which the two choanae open.

NASO-PALATINE CANAL.—We find not only an incomplete palatal vault, as in birds, but also a communication persisting between the nasal and the buccal cavities in their anterior region. This is the canal of Stenson, incisor foramen or naso-palatine canal. It was discovered by Stenson and described by Bartholin, Verheyen and Santorini. It is not patent in all mammals. Lieutaud, Bertin, Heister, Holler, Portal, Boyer and Scarpa claim that it is impossible to enter the mouth from the nasal cavity through this canal, especially in man, in whom it is most atrophied. Jacobson and Cuvier are in accord with this opinion. According to Rosenthal, Weber, Huschke and Arnold, it is normally perforated. Leboucq (1881) has observed in several human fetuses (4th and 5th month), that the canal was precociously obliterated by the accumulation of an epithelial mass. The palatal papilla, which Merkel considers as a sensory organ, is placed between these two orifices or their remains in man.

SKELETON.—The internal wall is a septum formed by the vomer, a cartilaginous lamina and the vertical plate of the ethmoid. The inferior wall, slightly concave transversely, is composed of the palatal laminae of the superior maxillary and of the palate and a process of the intermaxillary. The roof or superior wall is formed by the nasal, the nasal spine of the frontal, the cribriform lamina of the ethmoid and the body of the sphenoid. The intermaxillary, the superior maxillary, the lachrymal, the lateral mass of the ethmoid and the vertical lamina of the palate constitute the external wall.

The osteology has been studied, with much detail, in the

works on human anatomy, comparative osteology and monographs on certain mammals (dog, cat and rabbit), so that we need not give, as in the preceding groups, a special description of each bone of the nasal framework. We will give details only of the arrangement of the bones. In the monotremes (*Ornithorhynchus* and *Echidna*) it is difficult to distinguish the sutures between the different bones of the cranium and the face. The facial wall is elongated, and in the *Ornithorhynchus* the superior maxillaries support a horny box.

The marsupials have nasal bones which are larger behind than in front, of which the anterior border is free and the external border articulates with the intermaxillary. The superior maxillary is very long and the posterior third of its inferior border is provided with tooth sockets. The palatal laminae of the palate bones are very extensive.

The cetaceans have bones which are very great in volume, the maxillary and intermaxillary being very large longitudinally. They have been studied by Abel (1902) in the *Eurhinodelphis* (dolphins of the upper Miocene). These animals possess a double orifice (*foramen olfactorium*) for the passage of the olfactory nerve, while the nerves no longer exist in the true delphinides.

In *Edentata* (ant-eater), the bones of the face have an excessive length, constituting a true cylindrical beak, which is flattened on its interior surface. The nasal fossae have the form of funnels; the nasal bones, which are very long, are narrowed towards their posterior part so as to pass between the anterior spine of the frontal and the superior maxillary, their anterior extremities reaching that of the superior maxillary. The palatal lamina of the palate bones are very large. The pterygoids aid, posteriorly, in forming the nasal floor. Anteriorly, the nasal cavities are separated by the vomer; posteriorly they communicate extensively with one another.

The nasal bones of the *Insectivora* (hedgehog) are only narrow bony bands, hardly perceptible. On the other hand, the intermaxillary are very well developed in size and form a part of the nasal roof. The nasal bone articulates with the internal border of the intermaxillary throughout the whole of its anterior extremity. The palate bones are joined with the superior maxillaries without distinct limits. The pachyderms have massive bones. In the tapir, the intermaxillaries are joined together in the median line; posteriorly they do not

reach the nasal bone. The internal or superior border of the maxillary ascends posteriorly and articulates with the descending process of the nasal. The intermaxillaries take only a very restricted part in the formation of the palatal vault. The nasal bone, large posteriorly, becomes thin anteriorly; the process which articulates with the maxillary passes from the posterior part of the external border. It is directed downward, then forward, forming a sort of prop which supports the nasal roof.

Among the proboscideans, the hippopotamus has very long nasal fossae, in conformity with the head. The anterior orifices are bordered by the lateral masses appertaining to the intermaxillary, which are not distinctly separated from the maxillaries in these animals. The nasal bones have a quadrilateral form; posteriorly it is difficult to distinguish them from the frontal.

In the elephant the intermaxillary is very large and very long. Its body is well developed and carries the anterior nasal orifice towards the middle of the face. The two anterior nasal orifices end in a large excavation which overhangs a median pyramidal ridge belonging to the nasal bones, which fuse completely with the frontal. At the bottom of this antrum, the vomer separates the two nasal fossae. The external wall is formed only by a thin bony lamella, external to which a large hollow cavity is found in the superior maxillary. Towards the middle portion of the cavity, the external surface is convex and the lumen narrowed. The floor of the nasal fossae is very narrow compared to the dimensions of the head.

In the solipedes (horse and ass) the intermaxillary does not reach the frontal. It reaches the external border of the nasal bone at the union of the anterior with the middle third.

The intermaxillary of the ruminants stops at the superior border of the maxillary without reaching the nasal junction, in which case it has the same disposition as in that of the solipedes.

Among the rodents the guinea-pig has very large nasal bones, which are in contact with the intermaxillaries throughout their external border. They lie between the nasal and the superior maxillary as far as the frontal.

In the bear (Carnivora) the nasal bones are long, and the intermaxillary passes backward to the frontal. The primates resemble man so much that there is little difference from an

osteologic point of view. The intermaxillaries are very distinct, as in other mammals, while in man they are completely fused with the superior maxillary. The nasal bones of the monkey are solidly united to one another and almost fused.

In man the internal wall or nasal septum, formed by the vomer, the perpendicular lamina of the ethmoid and the cartilage of the septum, does not always divide the nasal fossae into two equal cavities. It is often asymmetrical and inclined to the right or left. The septum is always symmetrical in the first years of life. In the adult, on the contrary, it is asymmetrical in more than half the cases. Cloquet expresses the opinion that the curvature depends upon a primitive law of organization. This deviation seems to us to be due to the asymmetry of the face, which may be considered normal and which is found in the most beautiful faces. Exaggerated, annoying deviations may be produced by inflammation of the mucosa, under the influence of which the physiologic curve of the subjacent cartilage is accentuated.

LUMEN OF THE NASAL CAVITY.—Ridges encumber, modify and complicate its form in various ways. These ridges, the turbinals, are inserted, on the external wall, and on the ethmoid. Between their bases of insertion are spaces in the form of fossae, known as the meatuses. Between the free border of the turbinals and the septum the lumen is more or less narrow, forming an irregular canal, dilated in its middle part and narrowed at its extremity. In viewing a transverse section of the nasal fossae, made at the region of their greatest vertical height (Fig. 20), one becomes immediately impressed with the reciprocal relations which exist between the respiratory and olfactory portions. The superior part of the lateral wall, in man, is so close to the nasal septum that there is only a narrow cleft between them. The mucosa which covers this region has a structure and appearance different from that covering other points of the cavity, and we shall study this under the name of the olfactory mucosa. The subjacent respiratory passageway, enlarged at the level of the meatuses and narrowed at the level of the turbinals, is separated, in man, according to Meyer (1885), from the olfactory cleft by the free border of the middle turbinal, which corresponds to a slight swelling of the nasal septum.

Nasal catarrh may easily cause an almost complete obliteration of this narrow hiatus, and one may therefore understand how this affection may occasion frequent interference with the perception of odors.

The nasal fossae of quadrupeds are not separated into two but into three cavities, because of the tremendous development and horizontal position of the terminal lamina of the ethmoid. They are the anterior, which encloses the inferior turbinal, the posterior, situated between the floor of the nose and the ter-

Fig. 20—X 34.3. Mouse (transverse section of the nasal cavity comprising the organ of Jacobson and showing the olfactory and respiratory regions). 1. Olfactory epithelium; 2. Ethmo-turbinal; 3. Superior maxillary; 4. Maxillary sinus; 5. Maxillo-turbinal; 6. Organ of Jacobson.

minal plate (nasopharyngeal canal of Dursy), and the superior, placed above the preceding and containing the olfactory margins (Zuckerkanndl).

Into the meatuses open the accessory cavities, true expansions of the nasal mucosa into the facial bones. In certain cases, in which one of these cavities, the frontal sinus or the maxillary sinus, is found open by some accident, it may be shown that the mucosa which covers it transmits no olfactory impression. These sinuses, therefore, should occupy a special

relation to the respiratory passageway. With the exception of the sphenoidal sinus and the posterior ethmoidal cells which open into the olfactory region (superior meatus and olfactory or ethmoidal fossa), all the other cavities, especially the most important (frontal sinus, maxillary sinus and anterior ethmoidal cells), open into the middle meatus below the middle turbinal.

Before undertaking the study of the nasal mucosa we shall study the ridges and the anfractuositities which they cover: 1, turbinals; 2, sinuses.

TURBINAL APPARATUS.—We may distinguish three turbinals in man: inferior, middle and superior. This division cannot be equally applied to all mammals. It is therefore preferable to differentiate the turbinals after the terminology of Schwalbe, Zuckerkandl, Seydel and Killian, into maxillo-turbinal¹, naso-turbinal and ethmo-turbinals.

The baso-turbinal of Schönemann is classed with the ethmo-turbinals.

MAXILLO-TURBINAL (Inferior turbinal, concha maxillaris).—This is a ridge, elongated antero-posteriorly, inserted upon the nasal surface of the superior maxillary. The lamina of insertion is directed towards the interior of the nasal cavity, and there it rolls up or branches, its form often becoming very complicated. Harwood distinguished two principal forms: twisted turbinals (*Herbivora*) and branching turbinals (*Carnivora*). Zuckerkandl (1887) divides the various forms of inferior turbinals of mammals into two types: coiled turbinals and branched turbinals. The coiled turbinals may present a one or two coiled laminae; in the latter case there is a superior and an inferior. The coiled turbinal always leaves a certain space between its free surface and the septum; the branched turbinal may completely obstruct the nasal lumen.

The monotremes studied by Zuckerkandl (*Echidna* and *Ornithorhynchus*) present differences in the disposition of the inferior turbinals. In *Echidna aculeata typica*, the inferior turbinal is an elongated projection which has two grooves upon its free surface; there is hardly a trace of rolling.

In an *Echidna* of undetermined species, two lamellae extended from the lamella of origin, one directed downwards and one directed upwards. The grooves placed upon the free

(1) Turbinal comes from turbo, turbinis, meaning rotation.

border of these lamellae are doubled by secondary lamellae, which is the beginning of a ramification. In *Ornithorhynchus paradoxus*, the surface of the turbinal is divided into 17 lamellae; here the secondary lamellae are branched into tertiary lamellae and these latter are rolled up at their extremities.

According to Allen and Otto Grosser (1902), the Cheiroptera of the Insectivora have an inferior turbinal in the form of a long band. We have studied the badger, which has a very well-developed inferior turbinal. Its pedicle is long and thin.

Fig. 21. Twice natural size. Badger (transverse section, showing spongy network formed by the ramifications of the maxillo-turbinal). 1. Naso-turbinal; 2. Maxillary sinus; 3. Maxillo-turbinal.

Upon its middle portion, and upon an extent equivalent to one-half of its length, it supports a large round mass, convex upon its superior, inferior and external surfaces, flattened upon its internal surfaces and cut into a very large number of lamellae extending antero-posteriorly.

We have here a beautiful type of branched turbinal. In a very interesting transverse section (Fig. 21) we may see that it fills up the nasal cavity, which is very spacious. The lamellae, which are irregularly branched a great number of times, include between them some spaces, areolar in appearance, which

give to the inferior turbinal a sponge-like aspect. The respiratory air is absolutely obliged to pass through this mesh-work. Similarly the inferior turbinal in the elephant is cut up into numerous vertical lamellae.

In the ruminants there are two coiled laminae, as in the pachyderms. In the sheep the antero-posterior extent of the turbinals is very large. The middle region forms a strong prominence which is flattened laterally, very high, and is

Fig. 22. Six-sevenths natural size. Sheep (transverse section showing double rolling of the maxillary turbinal). 1. Naso-turbinal; 2. Maxillo-turbinal; 3. Maxillary sinus; 4. Cartilaginous septum; 5. Vomer.

composed of two parts, one situated above, the other below the lamina of origin. In the transverse section (Fig. 22) it may be easily seen that each of these parts is a coiled lamina, the upper one describing about a turn and a half, the inferior one complete turn. The solipeds (horse and ass) have a very voluminous inferior turbinal, but it has only a single coil.

In the rodents (rat and guinea pig) the anterior extremity

of the turbinal reaches the level of the nares. There is only one roll, directed upwards.

The inferior turbinal is very complicated in the Carnivora (seal, otter, beaver), according to Cuvier. It is cut up into multiple lamellae in the dog; in the cat the turbinal is extended obliquely backward and downward. Its middle portion is voluminous and almost cylindrical, and is cut up into lamellae by antero-posterior grooves.

The same disposition is found in the tiger. In a large number of monkeys, the inferior turbinal is a ridge more or less prominent, rounded vertically, voluminous in its middle part (*Cercopithecus*). In the gibbons and cebus there are two rolls. In man it is a thin, curved lamina, slightly rolled, having a body and three processes (Henle). The anterior or lachrymal process serves to limit the osseous lachrymal canal; another, the posterior or the processus ethmoidalis, is articulated in several places with the uncinat process of the ethmoid; the third, or processus unciformis, is directed downward opposite to the two others. (See Zuckerkandl, *Anat. Foss. Nasal.* Pl. IV., Fig. 2.)

NASO-TURBINAL (Middle turbinal of certain mammals, anterior turbinal of Schwalbe, *agger nasi* of man, first ethmo-turbinal of the writers).—This turbinal is placed above the maxillo-turbinal, inserted upon the external portion, partly in the ethmoid region and partly in that of the superior maxillary. Zuckerkandl (1895) describes in it a free portion in the cavity (*pars libera*), and a posterior portion covering the ethmoidal turbinals (*pars tecta*).

In certain mammals (rodents) its situation places a middle turbinal between the maxillo-turbinals and the ethmo-turbinals (Fig. 23); in others (carnivora and ruminants) it lies throughout its extent above these different turbinals. Schwalbe, Seydel and Killian consider it the first ethmo-turbinal; Peter (1902) separates it from this group. His classification, based upon their origin, separates them from one another, and distinguishes those which arise from the external nasal wall (maxillo-turbinal and naso-turbinal) from those which arise from the internal wall (ethmo-turbinal).

The naso-turbinal, being a turbinal quite distinct in its anatomic relations, is reserved for a special description.

In the guinea-pig (Fig. 23), it is a lamina placed above the inferior turbinal, the superior border of which it covers, ex-

tending from the anterior extremity of this turbinal to the anterior extremity of the ethmoidal turbinals. Its lamina is simple, without rolling.

In the rat it is inserted upon the most elevated portion of the external wall, and is folded inferiorly; it begins a little behind the anterior extremity of the inferior turbinal and terminates at the same level as the latter. Its posterior border is notched by the anterior extremity of the superior ethmoidal turbinal.

In the cat the naso-turbinal presents another appearance; it is inserted along the entire nasal roof; it runs along it, and does not descend towards the inferior turbinal to form a ridge be-

Fig. 23. Twice natural size. Guinea-pig (Sagittal section, passing external to the median line, showing the external nasal wall. 1. Naso-pharyngeal canal; 2. Ethmo-turbinal; 3. Naso-turbinal; 4. Maxillo-turbinal.

tween it and the ethmoidal turbinals. Its anterior extremity is situated between the nasal roof and the inferior turbinal. Schönemann represents it thus in the embryos of the cat, calf and rabbit. In this disposition it is not a middle turbinal, but an anterior, or, better, an antero-superior turbinal. It is the ethmo-turbinal I.

In the sheep and badger, the naso-turbinal is a simple, slightly projecting margin, placed along the nasal roof. It is represented in man, but it does not correspond to the middle turbinal.

Schwalbe (1887) has shown that the ridge which v. Meyer called the *agger nasi* is a vestige of it; Zuckerkandl describes

the agger nasi as the pars libera, and the uncinatè process as the pars tecta of the naso-turbinal of man. The agger nasi is a ridge placed upon the frontal process of the superior maxillary, joined to the middle turbinal (Zuckermandl, Pl. IX., Fig. 4; Schwalbe, *Anat. der Sinnesorgane*, 1887, Fig. 27). Schwalbe considers it the rudiment of the anterior turbinal.

So the naso-turbinal is, in certain cases, a middle turbinal, intermediate to the maxillo-turbinals and ethmo-turbinals (guinea-pig, rat); in other cases it is an anterior turbinal (cat, rabbit), and in others (monkey, man) it is reduced to a simple ridge.

ETHMO-TURBINAL (olfactory turbinals or projections, baso-turbinal of Schönemann, conchae obiectae, ethmoidal volutes, middle and superior turbinals of man).—The number of olfactory turbinals varies in mammals from three to nine, the number five being most common (carnivora, rodents, insectivora, lower monkeys). Zuckermandl distinguishes the lateral olfactory projections from those which freely arise from the median wall. Seydel names them principal and accessory turbinals. They all have a simple lamina of origin from the ethmoid (Schwalbe). Karl Peter (1902, 1) distinguishes them from the lateral turbinals (maxillo-turbinal and naso-turbinal) by the generic name of medial turbinals. Schwalbe (1883), Seydel (1891), Killian and Zuckermandl consider the naso-turbinal as an ethmoidal turbinal, regarding the olfactory projection as more important than Peter does.

The ethmo-turbinals are characterized as ridges inserted upon the anterior surface of the ethmoid, and are free in the nasal cavity. Together, they form a triangular mass with attached base (baso-turbinal). This ridge may be cut by grooves of the external surface into the form of projections, or completely subdivided into distinct lamellae. The different turbinals are generally parallel to one another, their volume is not uniform and their length diminishes from above downwards.

Among the monotremes, *Ornithorhyncus*, according to Simon Paulli (1900), has a very much reduced ethmoid, while in *Echidna* it is well developed and very complicated.

In the marsupials, the carnivora are recalled (Chatin). According to Simon Paulli, it is divided into five turbinals, a number typical in mammals (including naso-turbinal). In *Cheiropteres vespertilionides*, Otto Grosser describes two

series of ethmoidal turbinals. A rudimentary naso-turbinal exists in the median series. The second is the largest, the third and fourth the smallest. They are very simple, being thick lamina in the form of a club on their free border.

The badger has a large middle ethmoidal turbinal with a pointed ending anteriorly. Superiorly and inferiorly it ends in a series of fine lamellae disposed antero-posteriorly.

The sheep is provided with a large turbinal inserted by its base upon the median portion of the ethmoid in the form of a triangular pyramid with apex anterior. Its inferior surface is applied against the posterior border of the maxillo-turbinal, its superior surface answers to the other ethmoidal turbinals. Internally it has a plane surface, externally a round border. It may be described as a middle turbinal on account of its situation.

Above and behind this turbinal, the ethmoid supports four others, which are almost cylindrical projections separated from one another by deep longitudinal grooves; they are free on their anterior extremities. There are four turbinals in the goat. According to Simon Paulli, the fissure formation is at a minimum in the ruminants, but in the other ungulates the number may reach eight (horse). It is the same in the rhinoceros, tapir, pig and the peccary.

Among the rodents the guinea-pig has three ethmoidal turbinals (Fig. 23); they are not completely separated from one another, the superior and middle being united at their anterior extremity; the inferior has a free anterior extremity. They form together a triangular ridge inserted by its base upon the anterior surface of the ethmoid, being free on all other sides.

The rat has four ethmoidal turbinals; the superior is longest and reaches greatly beyond the second, which reaches beyond the third. The first three turbinals are curved and directed downward at the level of their anterior extremity. The fourth or inferior turbinal has a free pointed anterior extremity.

The cat has a well-developed collection of ethmo-turbinals. We may distinguish a superior turbinal, parallel to the roof of the nose; a second turbinal, parallel to the preceding and applied along its inferior surface, united anteriorly to two laminae extending downwards and backwards. Between these laminae and the anterior portion of the ethmoid, a triangular ridge is interposed which is flattened transversely and placed between the ethmoidal lamellae and the septum. In all there

are three turbinals, one of which is divided into two. According to Simon Paulli, bears have seven olfactory projections and the Mustelidae six to seven. In Pinnipedia the number is five to six.

In the prosimians (*Lemur cotta*) Seydel describes four olfactory projections, besides the naso-turbinal. They arise from three basal lamellae, the first of which has two rolls. There are three principal and two accessory turbinals, of which the superior limits the frontal sinus below, while the other lies between the first and second principal turbinals.

In the lower monkeys the number of ethmoidal turbinals, according to Zuckerkandl, varies from one to three; the mycetes have only a single turbinal.

The anthropoid apes exhibit a striking resemblance to man in respect to the ethmoidal turbinals. These turbinals are no longer inserted by distinct pedicles. The nasal surface of the ethmoid labyrinth presents, as in man, a furrow, which determines the formation of two or three turbinals, ending in a point posteriorly. Zuckerkandl found in *Hylobates concolor* three turbinals on the left and two on the right side; in the orang one and rarely two; in the chimpanzee three in one instance and four in another; in the gorilla sometimes three and sometimes two.

In man, Zuckerkandl (1895) finds, on the median wall of the ethmoid labyrinth, two or three clefts dividing the osseous lamina into three segments, and exceptionally into four. Three typical ethmoid turbinals are designated under the name of inferior, middle and superior. The inferior ethmoidal turbinal resembles the maxillo-turbinal; the posterior extremity terminates in a point beyond the labyrinth; the anterior extremity, which is truncated vertically, is shorter by one to two centimeters than that of the maxillo-turbinal, and it is continuous with the *agger nasi*. The anterior extremity of this turbinal may be transformed into a large vesicle (*concha bulbosa*). The middle ethmoidal turbinal is placed above the inferior and is shorter by 7 to 15 mm.; its form and extent are very variable and it is sometimes rudimentary.

The superior ethmoidal turbinal, irregularly quadrangular, is placed between the superior ethmoid cleft, the cribriform plate and the anterior wall of the sphenoid sinus. It may be transformed into a vesicle or in other cases it may have a spherical ridge limited in one place.

The fourth or supreme ethmoidal turbinal is found by Zuckerkandl in 6.7 per cent of the cases. When it is well developed it has the form of the middle ethmoidal turbinal, but it is sometimes reduced to a simple ridge.

Behind the uncinatè process, which, with the *agger nasi*, represents the naso-turbinal, is found constantly, says Zuckerkandl, an osseous, hollow, round projection, which forms part of the ethmoid labyrinth. Its convexity is towards the middle meatus and it is covered by the inferior ethmoidal turbinal. This is the *bulla ethmoidalis*. This projection corresponds to an atrophied olfactory projection.

RESUME.—The maxillo-turbinal, the most inferior and anterior of the turbinals, exhibits only two types in the series of mammals: rolled or branched.

The branched turbinal presents every degree from the simple turbinal crossed by longitudinal grooves, as in the *Echidna*, to the branched turbinals of the third degree, disposed in every direction, as in the badger. The rolled turbinal may present a single lamellar coil (*solipeds*, rodents, man) or two laminae, one above and one below the lamina of insertion (*pachyderms*, ruminants).

The naso-turbinal placed above the maxillo-turbinal may be parallel to it and may insinuate itself between its posterior extremity and the ethmo-turbinals (*guinea-pig*, rat), or it may be parallel to the roof of the nose and pass backward above the ethmo-turbinals (ruminants, carnivora). It is reduced to a simple ridge (*agger nasi*), anterior to the middle turbinal, in man.

The ethmo-turbinals, varying in number from three to five, are inserted in the posterior part of the nasal cavity, upon the body of the ethmoid. Their form is that of a triangle with a base posterior. They are sometimes united together (*guinea-pig*), sometimes completely separated from one another (badger). At other times one of the turbinals may be very voluminous and entirely detached from the others, which are united together (*sheep*). The typical number is five, as found in the marsupials. In man the ethmoidal turbinals are represented by the middle and superior and accessory turbinals and by vestiges such as the *bulla ethmoidalis*.

The presence of turbinals greatly augments the surface of the olfactory and respiratory regions. This augmentation is:

In the sheep, 4.9 times for the olfactory and 1.52 times for the respiratory surface;

In the dog, 2.46 times for the olfactory and 1.48 times for the respiratory;

In man, 1.30 times for the olfactory and 1.39 times for the respiratory.

ACCESSORY CAVITIES OR NASAL SINUSES.—These are the hollow cavities of the bones of the face and head in the neighborhood of the nasal fossae, with which they communicate. They are covered by a mucous membrane continuous with that of the nasal apparatus.

We have already stated that, as a general rule, their orifices open into the respiratory region with the exception of the sphenoidal and some ethmoid cells which open into the olfactory region.

The older writers who make mention of the sinuses appeared to be greatly interested in the nature of their contents. A large number insisted on the presence of a green membrane, *membrana viridis*; e. g., Laurentius (1628), Spigel (1645), Bauhinus, Olhafius, De Marchettis (1654).

Schneider claimed that this was a cadaveric phenomenon. Others held that these spaces had medullary contents. The following may be cited as holding this opinion: Albertus Salomon (1583), Bartholinus (1658), Jessen (1601), Kyper (1660), Veslingius (1637), (Palfyn (1712), Vesalius (1725) Fallopius (1562) and Diemerbroeck (1685) held that the frontal sinus and the other accessory cavities were alternately filled and empty.

Fallopius claimed that only air and mucus were present.

According to Valverde, Columbus, Riolan (1618), Vereheyne and Schneider, the sinuses contained air.

Highmore (1681) advanced the idea of the pneumatisation of the sinuses. Riolan (1649) was the first to make a study of the cavities together.

Vieussens and Haller thought that the sinuses had the function of secreting mucus.

After the latter, anatomists were divided into two camps: Those holding his view, Arnold, Bidder, Haarwood, Huschke, Hyrtl, Magendie, Rudolphi and Walter; others holding that the sinuses and cavities were pneumatic, Braune, Clasen, Langer, Meyer and Weber.

Zuckerkindl remarks that we have not gone beyond the accurate observations of Columbus, Fallopius, Riolan and Schneider.

The volume of the sinuses varies greatly in the different species of mammals. While Richerand states that the sinuses are tremendously developed in all animals which excel in the acuity of olfaction, Müller claims, on the contrary, that the principle which presides over the formation and modification of the organ of olfaction is the multiplication of the olfactory surfaces in a small space.

Braune and Clasen (1877) have measured the volume of the nasal cavities and the various sinuses in man. The average figures corresponding to them are as follows:

Right frontal cavity.....	3.1 cc.	left,	3.4 cc.
Right sphenoidal	4.0 cc.	left,	1.8 cc.
Right ethmoidal	3.1 cc.	left,	4.5 cc.
Right maxillary	12.5 cc.	left,	11.6 cc.

The total volume of the two sides was 44 cc., of the two nasal cavities 30.5 cc. The ratio was 144 to 100.

Zuckerkindl and Seydel, without according to the sinuses a role in the phenomenon of olfaction, claim, especially as to the frontal and sphenoidal, that these cavities include portions of the powerful ethmoid labyrinth in animals with great olfactory power.

In microsmatic animals and in man, the nasal cavity is sufficient to contain the reduced ethmoid, and the sinuses, thenceforth free, disappear or remain as empty cavities.

Simon Paulli does not accept this view, which is erroneous, for Zuckerkindl has confounded portions of the nasal cavity with the pneumatic spaces.

According to Simon Paulli, pneumatization of the cranium is missing in monotremes and marsupials.

The kangaroos, however, according to Cuvier, have a frontal sinus.

SINUS MAXILLARIS.—The maxillary sinuses, according to Cuvier, are smaller in the *Quadrupedia* than in man. They are reduced almost to nothing in the carnivora, the rodents and the edentates. In most of the other ungulates they exist, but are a part of the nasal cavity, from which they are not separated by a narrow opening. The pachyderms have no sinus maxillaris, but they have a malar sinus.

In the insectivora the maxillary sinuses are the only pneumatic cavities. They are very large in the ruminants, and open into the nose by an oblique and narrow cleft situated behind the inferior turbinals. Those of the sheep are long antero-posteriorly; upon transverse section they have an elliptical form, but their inferior wall makes a large ridge in the cavity because of the dental alveoli. They are relatively very large.

The maxillary sinus of the horse is divided into two compartments by the supermaxillo-dental canal which traverses it. The internal compartment communicates with the sphenoidal and ethmoidal sinuses, its wall making a ridge in the interior of the nose.

In the elephant the sinus maxillaris is immense, separated from the nasal cavity by a very thin, bony wall. It is partitioned into a multitude of very large cells.

In the carnivora the ethmoid labyrinth, according to Zuckerkandl, forms a projection into the sinus and narrows it. We have not seen a sinus maxillaris in the cat.

In the monkeys the sinus maxillaris is very spacious. In the orang it forms, with the hollow space which replaces the ethmoid cells, a large single cavity, which leads into the sphenoidal sinus.

In man this is the largest of the accessory cavities. It is external to the lateral walls of the nasal cavity and below the floor of the orbit. Its form is that of a triangular pyramid with a base superior, or to the orbital side. It opens into the nasal cavity by two orifices, a principal (ostium maxillare) joining with the frontal opening in the region of the infundibulum, in the middle meatus, lying behind the bulla ethmoidalis. This will be discussed in connection with the frontal sinus. The other accessory orifice (ostium maxillare accessorium) is inconstant, occurring once in ten times. It was discovered by Giralde's; it is situated in the posterior part of the middle meatus (Zuckerkandl, 1895).

FRONTAL SINUS.—The frontal sinuses are lacking in a large number of animals. Among the ruminants, the deer is unprovided with them. In cattle, sheep and the goat they are very extensive. The sheep's frontal sinuses are very large cavities, occupying almost the whole extent of the frontal bone, provided at their antero-internal angle with an orifice which is directed towards the nasal cavity and prolonged upward into the bony

processes which support the horns. The mucosa which covers them forms, in the vicinity of the median line, one or two folds which isolate some small spaces.

The rodents generally are not provided with frontal sinuses, but we have seen a small one in the Indian hog. Cuvier reports very large ones in the porcupine, in which they penetrated into the depths of the nasal bones.

The horse's frontal sinuses extend into the frontal bone and open into the posterior or internal compartment of the sinus maxillaris.

Baum (1894) has examined sections from the heads of 80 horses, and considers the communication established by the large opening between the frontal sinus and the maxillary to be physiologic.

They are very large in the elephant, and extend not only into the frontal, but also into all of the bones of the cranial vault. Anteriorly, the nasal and the intermaxillary bones are hollowed out by air spaces.

All of these bony cavities, partitioned and subdivided into cells, communicate with one another. A horizontal section across the head of an Asiatic elephant, to be seen in the new galleries of the Museum of Paris, shows beautifully the extent of all of these spaces.

Among the Carnivora, dogs, wolves and hyenas have very extensive frontal sinuses, which descend to the posterior wall of the orbit. They are less developed in the cat, being limited to the median part of the frontals.

They are less extensive in the cercopithecus, and are wanting in many monkeys.

Zuckerkindl (1887), after a comparative study of the frontal sinuses, established a distinction between the macrosmatic mammals and the microsmatic primates. The former have at least one excavation in the nasal portion of the frontal bone. The irregular distribution of the frontal sinus in the series of mammals does not appear to justify this classification.

In man the frontal sinus has the form of a triangular pyramid, its base being formed by the passageway between the squama and the roof of the orbit, and by the excavation of the nasal portion of the bone. A median sagittal partition separates the sinuses from one another. The volume varies considerably, even constituting a racial characteristic. In southern negroes it is greatly reduced. According to Steiner (1874)

the frontal sinuses may have ethmoid cells included within them.

Boege (1902) considers the frontal sinuses as extensions of the ethmoid mucosa. They communicate rarely through the partition, 1 per cent of the cases. Two frontal cavities are rarely found on a single side, 1.5 per cent. They are absent in 4.9 per cent of the cases, an opinion which Poirier (1892) accepts.

Mouret (1902) has found several double frontal sinuses independent of one another; each of these opens singly into the corresponding nasal fossa; the more anterior one is considered as the principal sinus, the other, the nasal orifice of which is posterior to that of the former, is the supplementary sinus. The supplementary sinus, according to this author, is formed by a dilatation of the anterior ethmoidal cell, which he calls the posterior frontal bulla.

The frontal sinus opens, in common with the maxillary sinus, in an excavation of the middle meatus, situated upon the ethmoid and bounded by the bulla ethmoidalis and the uncinate process. Boyer has given to this depression the name of infundibulum. Zuckerkandl calls it the hiatus semilunaris. This space is accessible on account of the disposition of the inferior turbinal, which, at the level of its anterior extremity, is not adherent to the external wall, but hangs in the form of a triangular strip. (Raugé, 1894.)

ETHMOID CELLS.—The ethmoid cells, which occupy the thick portion of the ethmoid bone, are spaces of small dimensions, communicating with one another; their number is very variable.

Simon Paulli remarks that the number of pneumatic cavities in the ethmoid has no relation with the total volume of pneumatization nor with the size of the animals. In several carnivora, in the prosimians and platyrrhinans, the number of the cavities is restricted; it is important in many of the ruminants, and may be much reduced in many of the large animals (horse and hippopotamus).

Zuckerkandl found shallow ethmoidal cells when the ethmoidal turbinates were slightly developed (lower monkeys). In the orang a large hollow space is found, instead of cells, between the lamina papyracea and the wall of the ethmoid turbinates, communicating with the maxillary sinus.

Zuckerkandl has described these cavities in man; they are spaces situated between the ethmoidal turbinates, being of the

nature of interturbinal meatuses. They are hollow cavities in the thick portion of the turbinals and the bulla ethmoidalis.

SPHENOIDAL SINUS.—The sphenoidal sinus is absent in a large number of animals, otter, seal, pole-cat, ruminants and cetaceans; it is very small in the pig and hippopotamus; in the horse it is the smallest of the sinuses and is partitioned; it is very small in the carnivora and in the monkeys. The rudimentary development in mammals, as remarked by Zuckerkandl, depends generally upon the fact that the sinus usually has no anterior wall and does not exist as a true sinus, but simply as a form of excavation or anfractuosity of the olfactory region of the nasal cavity. It is thus in the echidna, the marsupials, the edentates, the artiodactyles, with the exception of the pig, the rodents and the insectivora, which have a sphenoidal sinus in the form of a niche.

It often has for its function the lodgement of the olfactory projection. In microsmatic animals the sinus, which is empty, has an anterior wall with an ostium sphenoidale (Zuckerkandl).

In man it is a hollow cubical cavity in the body of the sphenoid, divided into two parts by a median partition, each cavity having an anterior orifice which opens into the corresponding nasal cavity.

The sphenoidal sinus is often limited anteriorly by lamellae called sphenoidal turbinals, which are portions of the ethmoid.

RESUME.—Most of the accessory cavities open into the nasal cavity at the level of the respiratory region (frontal, maxillary sinuses and anterior ethmoidal cells).

The maxillary sinus is very much reduced in the carnivora, the rodents and the edentates. It is replaced by a malar sinus in the pachyderms. It is very large in the ruminants, the solipeds, proboscidiens, primates and man.

The frontal sinuses are absent in certain groups or in certain species (absent in the deer, well developed in cattle, sheep and the goat). They are absent or very small in the rodents. They open into the maxillary sinus in the horse, and they are very large in the elephant. They are absent in many of the monkeys. In man their volume is variable (absent in negroes of the south). They are formed by ethmoidal cells enclosed in the frontal (Steiner). The ethmoid cells are spaces of small dimensions communicating with one another. They are numerous in the ruminants, being much reduced in the horse and hippopotamus. They form a single cavity in the orang.

The sphenoidal sinuses are often lacking (otter, seal, ruminants and cetaceans) or much reduced (pachyderms, proboscideans, carnivora and monkeys). They often have for their function the lodgement of the olfactory projections.

The total volume of the accessory cavities in man is greater than that of the two nasal cavities, the relation being 144 to 100 (Braune and Clasen).

ORGAN OF JACOBSON.—Ruysch (1703), Sömmering (1809) described in man a canal corresponding to the organ of Jacobson, but without giving to it its significance. Jacobson gave a description of it in 1811 and it was studied by Cuvier and Gratiolet (1845).

Huschke noticed the paranasal cartilage or the cartilage of Jacobson. Dursy described this organ in 1869 and Kölliker (1877) noted the presence of the organ of Jacobson in the human adult. Remy (1878) made some observations in different mammals and confirmed the description of Cuvier. The orifice of the receptacle of Jacobson in the canal of Stenson has the form of a linear furrow, which recalls the orifice of the nasal canal in the middle meatus. Its mucosa is analogous to that which covers the nasal fossae.

Klein (1881) studied this organ in the India pig. It is a tube opening frontally into the canal of Stenson; behind it terminates in a cul-de-sac. It is enveloped by a hyaline cartilage which forms an incomplete capsule. The wall consists of epithelium, a fibrous subepithelial coat, a layer of cavernous tissue and a glandular layer. The epithelium, like that of the nasal cavity, is composed of a superficial layer of cylindrical or conical cells, between the extremities of which are placed fusiform or inverted conical cells. The superficial surface of the cells is provided with fine cilia.

Balogh has found the same epithelium in the sheep. The alveolar glands are more developed in the region where the capsule is deficient.

In the rabbit Klein (1881) found an organ of Jacobson longer than that of the India pig. In the latter the organ is distinguished, moreover, by direct communication with the nasal cavities.

Harvey (1882) describes an analogous orifice in the mouse. The organ has no relation with the canal of Stenson. In the cat and hedgehog, on the contrary, there is a direct communi-

cation between the anterior extremity of the organ of Jacobson and the canal of Stenson.

Klein (1882) described the organ of Jacobson of the dog, which is placed in the inferior part of the septum, corresponding to a small prominence above which a larger one lies; it is the special ridge of the cartilage of Jacobson which causes the superior prominence. In a dog of average size the length of the organ is 3 cm. It does not open directly into the nasal cavity, but into the canal of Stenson by its anterior extremity. The latter is covered by stratified pavement epithelium; in the upper, large region, the most superficial cells are cubical. The intermaxillary bone has an important role in supporting the organ of Jacobson.

The cartilage which surrounds this organ is curved crescentically on transverse sections. The structure of the organ, studied in extensive detail by Klein, does not differ from that of the India pig or the rabbit, except that the cavernous tissue, so well developed in the latter animals, is absent in the dog.

Gegenbaur (1886) advances the opinion that the obliterated tube, which is considered in the adult man as a rudimentary organ of Jacobson, is an excretory canal of a nasal gland situated in the septum. It is removed from the cartilage of Jacobson, with which it should be in relation, and its situation corresponds to that of the septal gland of acinous structure, which is well developed in the prosimians.

Herzfeld (1888) published a very important work in which he discusses the presence or absence of the canal of Jacobson and of the naso-palatine canal, and the structure of the different parts of this organ. The following are his conclusions:

1st. The canal of Jacobson opens into a distinct naso-palatine canal in the ruminants (sheep, goat, ox), pig, dog, cat, mole, lemur, macaco and *Hapale penicillata*;

2d. No naso-palatine canal exists, but a diverticulum is found into which the canal of Jacobson opens (horse, ass);

3d. The naso-palatine canal exists, but the canal of Jacobson opens into the nasal cavity (rabbit, hare and rat);

4th. The nasal cavity is united to the buccal cavity by an open naso-palatine canal, the organ of Jacobson being wanting (bat, *Pteropus edwardsi*, *Cercopithecus fuliginosus*);

5th. Canal of Jacobson and naso-palatine canal both absent (seal). Man forms a group apart, for he possesses, at the level of the septal wall, the canal of Ruysch, which in other mammals is replaced by glands.

Herzfeld, in reference to the structure of the organ, notes the presence of a venous sinus situated laterally between the mucosa and the cartilage.

Symington (1891) describes the organ of Jacobson in marsupials; it is very well developed and resembles that found by Parker in the monotremes. It is a simple epithelial tube, communicating anteriorly with the naso-palatine canal, and surrounded by a cartilage in the shape of a "U." In the *Ornithorhynchus*, also studied by this author, the cartilage forms a complete tube in a large part of its extent. The organ extends anterior to its opening into the naso-palatine canal.

Potiquet (1891) studied, in the human adult, the canal of Jacobson, a vestige of the organ of the same name. It is found easily enough in the cadaver, at least when lesions of the mucosa do not cause its obliteration. He examined for it in the living. Although it is not as easy to discover it as in the cadaver, it was found quite often.

It is situated above a projection, elongated from before backwards, and constituted in part by the cartilages of Jacobson; it occupies the antero-inferior portion of the septum. A large number of affections of the septum (syphilides, ulcerations, perforations, repeated epistaxis) attack the region of the canal of Jacobson, perhaps indicating the localization of the pathologic process at this place.

Mathias Duval and Gernault (1895) made observations on the organ of Jacobson in the *Cheiroptera*; they noted its absence in the murin and in the horseshoe bat and they found traces of it in the embryos of the pipistrel. The canal of Stenson is closed early in the murin and horseshoe bat, but persists in the pipistrel.

Broom (1896) studied the organ of Jacobson in *Echidna*; the palatal cartilage contributes to form the cartilaginous framework. The cartilage has the shape of the letter "C" in its anterior part, and then takes the form of a complete ring.

A band of cartilage, the turbinal cartilage, in relation with the external wall of this cartilaginous tube, supports the glandular tissue.

The epithelium described by Broom is sensory in character. This author also examined the organ in the *Ornithorhynchus*, finding differences in the disposition and extent of the cartilages.

Mikalhovics (1889) studied the organ of Jacobson, or

vomero-nasal organ, in a certain number of mammals. In the mole the organ is located in a fossa of the vomer; the cartilage of Jacobson or paranasal cartilage is situated above the canal, and is not in relation with it. Some serous glands lie on the lateral side of the organ. On the caudal part, the glands are more numerous and the tube more narrow. Anteriorly it opens into the canal of Stenson and has a common cylindrical epithelium.

In the mouse it is independent of the paraseptal cartilage; anteriorly it opens into a groove placed above the canal of Stenson; it lies partially in the intermaxillary and partially in the vomer.

In Ungulata and Carnivora the organ of Jacobson is analogous to that of the rodents; it lies in the "C" shaped cavity formed by the paraseptal cartilage. In man the canal of Jacobson is present during embryonic life. Later it is represented only by the paraseptal cartilages.

Mangakis (1902) has observed in the human adult the organ of Jacobson, first described by Kölliker, then by Merkel and Anton. It was in a young soldier that Mangakis found this organ, which had the form of a canal and was 6.2 cm. long. The anterior orifice was visible without rhinoscopy. It communicated with that of the opposite side through the septum, the posterior opening, narrower than the anterior, lying free in the pharynx. Histologic examination of three fragments showed the presence of olfactory cells like those described by Merkel.

We made a microscopic study of the organ of Jacobson in the sheep. It is located in a longitudinal fossa of the vomer, opened considerably externally and superiorly. It is surrounded by a complete cartilaginous tube, which comes in contact with the nasal cartilage on its superior border. This cartilaginous canal is 3 mm. wide transversely, and 5 mm. vertically; its circular cavity has a diameter of 2 mm.

The organ of Jacobson, which fills it completely, is a cylindrical tube, the walls of which are 0.5 mm. thick and the lumen 1 mm. in diameter. The total length is 7.6 cm. The head of a sheep is 23.5 cm. long, and the nasal fossa 11 cm.

Anteriorly, the tube of Jacobson opens into the naso-palatine canal. It is widely opened, and at the level of the roof of the mouth it is widened into a fossa, and is directed towards the nasal cavity, obliquely across its floor. The opening of the

organ of Jacobson lies concealed behind a mucous fold of the internal border, at the anterior extremity of the buccal opening of the naso-palatine canal.

We have studied the organ in the mouse, by histologic sections (Fig. 20). Its situation is, as in the sheep, in a fossa of the vomer. We found no cartilaginous envelope, but a thick fibrous wall. The organ presents walls of great thickness on transverse section, 128 mikra at the level of the internal wall, and 185 at the level of the external. In toto, it forms an elliptical mass, the diameters of which measure 400 mikra vertically and 357 transversely.

The lumen, elongated vertically and narrowed transversely, has the form of a crescent with concavity external, with a height of 178 mikra and a width of 28. The external wall forms, in the cavity, a convex ridge analogous to the ventral ridge of the organ in reptiles.

The walls are uniform throughout, and are formed by a thick cellular mass of closely applied polyhedral or round cells provided with a large nucleus.

The cells which border the lumen of the organ are much elongated and present two very distinct portions, one deep and dark, containing the nucleus, and an internal, very clear and homogeneous. The cells are not so high on the external wall as on the internal.

The organ of Jacobson in the cat lies below a large ridge of the septum. Its anterior opening does not enter a permeable naso-palatine canal, as this is closed by the buccal roof.

NASAL MUCOSA.—(a) *Macroscopic Aspect*.—Schneider (1645) gave the first exact description of the pituitary membrane. He refuted the ancient view which ascribed the flow to the discharge of liquid humors of the brain through the cribriform plate.

This mucosa covers the entire extent of the nasal fossae and sinuses; behind it is continuous with the pharyngeal mucosa, anteriorly with the skin. It is very adherent to the subjacent periosteum. Nevertheless it can be separated from it, and Remy rejects the expression "fibro-mucosa."

Its thickness varies according to the region; it is thinner in the olfactory fossa than in the respiratory portion, thicker over the inferior turbinals than over the other turbinals, with the exception of the inferior border of the middle turbinal in man.

Its internal surface is covered with mucus; it is smooth,

but in the posterior portion Kölliker observed folds and ridges, directed from above downward and from behind forward. These folds are found only in the infant and disappear later. Its color is an intense red in the living, but it is not uniform. In the superior part it shows a yellowish color, noticed for the first time by Todd and Bowmann. The yellow color marks a region which the writers name *regio olfactoria*, and which Ecker has called *locus luteus*. It is in this region that the branches of the olfactory nerve end (M. Schultze, Ecker, Eckardt and Rémy). The color may be brown or yellow, depending on the animal.

The topographic situation of the olfactory region is easy to determine on account of this coloration, and besides, the histologic examination fixes it at about the same limits. We may say in general, that the olfactory mucosa covers the entire extent of the ethmo-turbinals and of the grooves which separate them, the nasal roof and the septum in the corresponding region. It extends only to the level of the naso-turbinal upon its posterior extremity; upon the external wall it never reaches the meatus subjacent to the inferior ethmo-turbinal.

In man this rule is verified, since the sensory mucosa comes to the inferior border of the middle turbinal (inferior ethmoidal turbinal). However, according to the researches of Max Schultze and Hermann Suchannek, it is less extensive upon the middle turbinal and covers only the superior half, while Battista, Grassi and Castronovo (1889) found upon this turbinal a transitory investment between the olfactory mucosa and the respiratory mucosa.

The extent of the olfactory mucosa, expressed in absolute figures, whether dependent upon the number or dimensions of the ethmo-turbinals, is too much connected with the total volume of the head to give any exact notion. It is more interesting to compare it with that of the respiratory mucosa.

This relation will give a better idea of the peripheral extent of the olfactory organ. We have measured the extent of the two regions, olfactory and respiratory, in different animals. For this purpose we have cut paper squares of 4 mm. on each side, and, fragment by fragment, we have covered the entire surface to be measured, taking account of the hollows and ridges. If we do not arrive at absolute exactness, at least we have a sufficient approximation, for the points of error remain the same for both regions. The following are the figures which we have found in certain animals:

	Respiratory Surface.	Olfactory Surface.	Ratio.
Sheep	33.00 cc.	8.84 cc.	3.73
Guinea-pig	2.08 cc.	1.12 cc.	1.85
Rat	1.60 cc.	1.12 cc.	1.33
Cat	6.08 cc.	5.76 cc.	1.055
Dog	12.08 cc.	9.76 cc.	1.23
Monkey	9.76 cc.	4.16 cc.	2.34
Man	10.40 cc.	3.08 cc.	3.37

According to these figures, the dog, cat, rat and guinea-pig are macrosmatic; the sheep, monkey and man are microsmatic.

This classification agrees with those of Broca and Turner, which are based upon other anatomic conditions, such as the extent of the olfactory region of the brain.

Braune and Clasen, who measured the volume of the nasal cavities, found that the amount of air entering the olfactory region during sniffing was one-tenth of that passing through the respiratory region.

(b) *Structure*.—We can distinguish an epithelium and a corium containing glands, vessels and nerves.

EPITHELIUM.—The epithelium is the place in which the differences between olfactory and respiratory regions reside.

The epithelium of the respiratory region is composed of long, cylindrical cells, enlarged at one extremity and attenuated at the other, with a nucleus in the middle of the cells. The enlarged extremity of the cell has vibratile cilia, generally curved outwards. Below and between the deep prolongations are round cells. At the level of the nares, this mucosa is united to a covering which has all the characteristics of the skin. The transition is abrupt, according to Rémy.

According to Eckhardt, Ecker and Max Schultze, the epithelium of the olfactory region possesses two kinds of cells, viz., cylindrical and fusiform cells. Max Schultze described the fusiform cells as characteristic of olfactory epithelium. They are in intimate relation with the fibres of the olfactory nerve and are the peripheral ends of this nerve.

Cisoff (1874) saw the prolongations of the olfactory cells penetrate into the subepithelial layer, into which the fibres of the olfactory nerve also enter. It is rarely possible to demonstrate the fine nervous fibrils in communication with the olfactory cells, but Sidky (1877) admits this communication.

Von Brunn (1880) describes the fusiform cells as sensory cells in direct union with the branches of the olfactory nerve; he describes, on the surface of the epithelium, a homogeneous membrane (*membrana limitans*) which permits the peripheral prolongations of the sensory cells to pass through the pores.

Delavan (1880) and Tourneux (1883) found the same elements as Von Brunn.

Grassi and Costranovo (1889) studied the distribution of the varicose fibrils of the olfactory nerve of the dog; upon their entrance into the connective tissue of the mucosa, they divide into horizontal branches parallel to the epithelial layer; of these branches, there are divisions which enter into the olfactory cells, but some fibrils end directly in the cells without following a horizontal course.

Hermann Suchannek (1890) gives an entire series of distinctive characteristics between the two epithelia, olfactory and respiratory, but he does not find the *membrana limitans* of Von Brunn. Ramon y Cajal finds that each olfactory fibril preserves its absolute independence from the olfactory bulb to the cell in which it terminates. It never anastomoses with the neighboring fibrils, and does not divide at any point in its passageway. The olfactory cell is a bipolar nerve cell, and its internal prolongation is a fibre of the olfactory nerve.

Fusari (1894), like Grassi and Costranovo, finds the same nerve fibrils passing into the basal prolongation of several olfactory cells. In the epithelium of the organ of Jacobson he observed that one portion of the fibres of the olfactory nerve entered directly into relation with the basal process of the epithelial cells. The others, at the base of the epithelium, were in relation with a globular nerve cell, which sent towards the periphery slender prolongations scattered between the epithelial cells.

Van Gehuchten (1890) agrees with Ramon y Cajal, that the fibrils pass directly into the olfactory cells without ramification, and after a slightly waving course. The nerve prolongation is continuous insensibly with the cellular mass, and at the other pole the protoplasmic substance forms a thick peripheral prolongation, which extends to the free surface of the epithelium.

The ordinary epithelial cells present a cylindrical peripheral portion and an irregular central portion, often terminating by bifurcation at the internal limits of the epithelium.

Disse (1900) has found, in the calf, olfactory buds lying upon the internal wall of the ethmoidal labyrinth, and upon a field corresponding to the septal wall. They are spherical in form and present a pore, open upon the surface of the mucosa, and enclose replacing and sensory cells.

The olfactory epithelium is thicker than the respiratory epithelium; in the mouse it attains a thickness of 128 mikra at the level of the olfactory fossa, and 21 mikra at the level of the external wall, below the naso-turbinal. The cells are of two kinds: fusiform, sensory united by varicose prolongations with the fibres of the olfactory nerve, and epithelial, supporting cells of cylindrical form.

The deeper shade of the olfactory region results, according to Tournoux, Hermann Suchanek, etc., from the presence of colored granules in the epithelial cells, and according to Rémy, from infiltration of the corium by the fusiform bodies filled with yellow matter.

CORIUM.—*Glands*.—The connective tissue corium contains glands and vessels, distributed in an irregular manner.

The glands are particularly compact at the level of the lateral and inferior wall, where they attain a large size.

In the respiratory mucosa, according to Max Goerke (1897), there are numerous mucous as well as serous glands. The mucous secretion, by becoming dry, checks the movement of the vibratile cilia, so the very fluid serous secretion is of great utility in holding the humidity of the mucus. Schmincke (1902) has studied minutely the glands of the respiratory region in man, which are of a mixed type. He has followed the process of secretion in two kinds of cells; during the period of repose the albuminous and mucous cells are similar.

The lachrymal canal pours out the aqueous secretion of the lachrymal glands at the level of the inferior meatus; the humidity is still further increased in this region if exposed to the passage of a current of air.

In the olfactory region numerous glands are found (Bowmann's glands). In the mouse they form an important supero-internal group. According to Max Goerke, these glands never secrete mucus, an opinion concurred in by Heidenhein, who considers them as serous.

Von Brunn considers all of them as albuminous glands. Their excretory ducts open upon the superior nasal wall, and

upon the portions in the vicinity of the lateral wall and the septum, in the recesses covered by ciliated epithelium.

The adenoid tissue, under the form of small follicles, is quite abundant in the respiratory mucosa; the migratory cells belonging to it are very much diffused (Stöhr), as are those in the olfactory region (Von Brunn). In the dog, cat, sheep, deer, pig, hare, horse and calf the diffused adenoid tissue is very abundant. The follicles attain a large size in the dog (Zuckerkindl).

VESSELS.—Erectile Tissue.—The arteries of the nasal mucosa have several trunks; the anterior nasal comes from the facial, the sphenopalatine from the internal maxillary, and the ethmoidal arteries from the internal carotid. Their ramifications have the type of spiral arteries. We have not undertaken their study in mammals. For the description of arteries in man see Zuckerkindl and works on anatomy.

The veins form efferent plexuses accompanying each of the arterial branches. Interest in the vascular system of the nasal fossae lies in the formation of venous networks, situated between the corium and the periosteum, and having the character of cavernous tissue.

Kohlrausch has described a venous network, rich in anastomoses, situated between the periosteum and the mucosa; Volto- lini considers these networks as composed exclusively of veins and announced a theory of erection. Zuckerkindl's study (1895) in man is very complete. He observes that the nasal mucosa is thicker in such places as it comes in contact with a large quantity of air. For this reason, a true cavernous body is developed only on the inferior turbinal, on the border of the middle turbinal, and at the posterior extremities of the middle and superior turbinals. In the places where the mucosa is thin there is only a dense venous network, but no cavernous tissue. These cavernous bodies in the nose are formed of two networks; an external, composed of large venous vessels in communication with efferent veins, and a more delicate internal, in relation with the capillaries, which are placed in the system of laminous trabeculae, containing also some muscular fibres. The glandular culs-de-sac penetrate into the vascular layer, so that, while Langer compares the erectile tissue of the nose to the corpus cavernosum, Zuckerkindl compares it to the cavernous tissues of the urethra.

In the cavernous bodies of the penis, the trabeculae repre-

sents disassociated vascular walls and the muscles are irregularly scattered and have more the disposition found around veins. In the nasal mucosa the expansion of the veins into a vascular system is not so marked, and the muscular layer appears more regular.

Kiesselbach reports cavernous tissue on the nasal septum in man, in the region where the organ of Jacobson should lie. This is the locus kiesselbachi, which is very frequently attacked by hemorrhages.

Arviset (1887) and Isch Wall (1887) consider the erectile tissue of the nasal fossae as constituted primitively of capillaries, which later take on considerable development and undergo important modifications.

Isch Wall also found these capillary dilatations in the embryo of the pig, cat and mole.

In the human adult, he studied the cavernous tissue in an executed criminal. The middle turbinal was entirely occupied by lacunae which were very numerous in the corium, and which were distinguished from those of the penis by lessened thickness of the layer of smooth fibres. Towards the surface the tissue is formed by fine vascular meshwork; towards the depths by very large lacunae.

Herzfeld (1889) found that the cavernous body of the nasal mucosa is rich in smooth muscles and elastic fibres. The cartilages of the turbinals are spongy, and their lacunae communicate with the efferent veins of the cavernous tissue.

Pilliet (1891) found the erectile tissue composed of large, irregular cavities, the larger ones situated against the bones, the smaller in the corium. These are neither arteries, veins nor dilated capillaries, such as C. Robin describes.

The muscular elements are disposed in two different planes around the connective tissue walls, the more internal being longitudinal; but it is difficult to establish their direction, by reason of the bendings of the cavernous sinuses.

In the human fetuses examined from the fifth month to birth, no trace of erectile tissue is found. In the younger embryos of the sheep, horse, pig and rat there is found, between the cartilage and epithelium, only a thick layer of connective tissue with stellate or elongated cells, studded with capillaries; the true erectile organs are developed in this manner (Nicholas). The observations of Retterer (1887) and those of Tourneux (1887) demonstrate that the region which is to be the

seat of the erectile organ is for a long time characterized by the complete absence of blood vessels.

According to Boulai (1896) the vessels which groove the nasal mucosa are very muscular veins, but not erectile tissue; the development of these networks does not in any way resemble erectile tissue, the period of appearance being too early.

In the newly born dog and in the mouse, we have found, beneath the mucosa, a layer of connective tissue containing round and fusiform cells pressed together, between which are placed very large vessels with thin walls, running in various directions. On transverse section, some are found running transversely and others longitudinally or obliquely. These lacunae lie particularly at the level of the external surface, and especially along the free border of the inferior turbinal. At this point there are only venous dilatations.

Arvise found large vascular dilatations in the armadillo. In the buck, the corium of the mucosa contains arteries surrounded by a large number of capillary dilatations, which have neither muscular nor elastic coat. The glands of the mucosa are very rare in the region of the vascular dilatations; elsewhere they are abundant.

The camel, at the level of the septum, presents numerous glands, between which the vascular dilatations are distributed. The rabbit has only a train of dilated capillaries at the level of the septum; likewise the rat.

Pilliet found erectile tissue in the rodents and endentates. In the dolphin and cachelot, the corium, on the contrary, is thick, white, fibroid and very dense.

Arvise has observed that animals living in a wild state have a more abundant cavernous tissue than the domestic animals. This fact is in accord with the general development of the olfactory faculty.

The turgescence of the cavernous bodies of the nose is dependent upon the nervous system: the sphenopalatine ganglion, according to Zuckerkandl, is the vasodilator center for the nasal mucosa.

Hack has well shown the role of the nervous influence. Before Hack, Voltilini explained the erection without nervous intervention. According to his view, the vessels which constitute the cavernous tissue pass from the bony canaliculi, at the level of which the venous walls are wide open, and the blood

enters the cavernous tissue constantly, through the vessels, which are always open.

But if the blood enter easily, it could leave easily, and erection is impossible, so Zuckerkandl judges this theory untenable.

En résumé, Are we dealing with erectile tissue in the nose or not? The true erectile tissue is composed of lacunae, interposed between arteries and veins, whose walls contain smooth muscle fibres (Robin, Tournoux). According to Retterer (1902) the adherence of the capillaries to a dense fibrous tissue especially characterizes the erectile tissue.

Arviset, Isch Wall and Herzfeld consider the vascular network of the nose as capillary dilatations. According to the observations of Kohlrausch, Zuckerkandl, Pilliet and Boulai, who corroborate our observations on the dog and mouse, the dilated veins and lacunae are not identical with those of the corpus cavernosum of the penis; Zuckerkandl compares them to the spongy tissue of the urethra. From a histologic standpoint, the vascular tissue is not true erectile tissue, but it may be said that it is a lacunar tissue, capable of increasing its volume.

By virtue of the presence of the spiral arteries and of a special vaso-dilator system, the afflux of blood into the lacunar tissue may be suddenly increased and the turgescence which results is sometimes considerable. Certain reflexes may provoke it.

The most interesting observations are those which connect the olfactory with the genital apparatus. In animals, olfactory excitations precede genital excitations, so erectile tissue is more developed in wild animals in which the sexual phenomenon is most intensely manifested.

Mackenzie has studied the relation between the nasal and genital organs in man and woman, which, according to him, will depend on the analogy of structure. The turgescence of the nasal mucosa, by a hyperesthetic effect on the nerve terminations, makes the most delicate impressions perceptible, on account of which the cavernous tissue is more developed in wild animals which have the need of great sensibility in order to smell their prey or to scent the female at great distances.

The influence of odors on the generative apparatus is very marked in the human species, according to Cloquet. "The care, which many women take in using perfume, seems to be a proof; she is wise in the art of pleasing, who does not allow anyone to see her until after she has aided her charms by the use of odors."

Fliess, and after him Schiff, Malherbe and other clinicians, have treated the painful attacks of dysmenorrhea by application of cocain tampons to the nasal fossae; they also destroyed, by cauterization, certain zones in the nasal cavity (genital points), and obtained satisfactory results. This is particularly effective in nervous dysmenorrhea. Malherbe, in cases of genital asthenia, excites the genital points in the nose by electric stimulation.

The inverse influence seems better demonstrated. Mackenzie has shown that excessive venery in man causes coryza, due to obstruction of the nares by the dilated cavernous bodies. According to this writer, repeated sensual excitations may cause inflammations of the nose. Isch Wall reports the case of two young people who were affected with epistaxis at each coitus, at the beginning of their genital life.

The accelerated, noisy respiration in the course of the venereal orgasm seems to indicate that there is a partial obstruction of the nasal fossae by the turgescent mucosa.

We have seen chronic coryza in several women affected with retroversion of the uterus, which is always accompanied by utero-ovarian congestion.

It is only rarely that women breathe normally through the nose, but sleep with their mouth open, during their menstrual periods.

LYMPHATICS.—Well studied in man by Sappey and then by Simon (1859). The latter found in the nasal fossa the justification of a law proposed by Sappey, that the lymphatics of a region are more abundant as its sensibility is more developed.

The lymphatic network of the septum ends by six to eight trunks in the lymphatics of the lateral walls. There it exists as a superficial network at the level of the superior turbinal, of the anterior half of the middle turbinal and of the space in front of the turbinals; a deep network with larger meshes is in the remaining portion of the lateral wall. The efferent trunks converge in a fossa placed between the Eustachian tube and the posterior ends of the turbinals. In the nares there is a network independent of the preceding, the efferent trunks of which run parallel to the facial artery.

NERVES.—The trigeminal (branches of the ophthalmic nerve and of the spheno-palatine ganglion) innervates the respiratory region. The branches of the spheno-palatine ganglion are the vaso-dilators of the nasal mucosa.

The olfactory nerve, divided into numerous branches, is distributed to the olfactory mucosa, and we know its relations with the epithelial cells of this region. Its branches pass into the nasal fossae through the cribriform plate of the ethmoid. They are covered by prolongations, in the form of sheaths, of the coverings of the brain, which accompany them into the mucosa. It is a true nerve center placed at the periphery.

The olfactory cells are nerve cells derived directly from the ectodermic cells. Their protoplasmic prolongations form the olfactory cilia: the prolongation of the axis cylinder is a fibre of the olfactory nerve. It goes to form the connection with the protoplasmic prolongation of the interpolated neuron, the cellular body of which lies in the olfactory bulb. This last establishes the relations with the cerebral centres.

The central olfactory nerve apparatus varies according to the osmotic power of the animal, and this depends upon the olfactory bulb with its convolutions. According to Zuckerkandl, the following organs are reduced in animals with rudimentary olfactory lobes and in man: the gyrus hippocampi, the lobe of the corpus callosum in the region of the isthmus and the fold of the retrolymbic passage, the convolution of the corpus callosum, the anterior perforated lamina, the horn of Ammon, the external marginal convolution, and finally the internal marginal arc. In the dolphin, which is truly an anosmotic animal, in opposition to the preceding, which are microsmatic, the brain presents: complete absence of the olfactory lobe, a decided regression of the basal portion of the limbic lobe, complete absence of the anterior perforated lamina, reduction of the horn of Ammon to an extremely faint rudiment, complete absence of the fimbria, and a considerable regression of the external marginal arc.

CHAPTER II.

EMBRYOLOGY.

Amphioxus.

Hatschek (1884) asserts that the ciliated fossa corresponds to an ectodermic recess in which the anterior neuropore opens; it persists for some time without closing. The depression is united with an evagination of the left intestinal diverticulum which fuses with it. Thus constituted, the olfactory organ of *Amphioxus* represents two organs of *Craniata*: the olfactory organ and the hypophysis.

In this last homology, Hatschek finds a difficulty in the entodermic establishment of the hypophysal tube in *Amphioxus*.

According to Dohrn, the anterior primitive olfactory invagination becomes dorsal by the extraordinary development of the upper lip.

Willey considers the ciliated fossa of Klliker as the homologue of the hypophysis of *Craniata*.

According to Kupffer this fossa corresponds to the median olfactory plate of the embryo of *Acipenser*. *Amphioxus* is the only primitive monorrhinal vertebrate.

Legros (1897) has extensively studied the morphology of the head of *Amphioxus*. The stomodeal fossa is, at the beginning, a large cavity (preoral fossa) which is separated into two parts by a fold of the entoderm. The antero-superior portion gives origin anteriorly and to the right, to a short diverticulum, the fossa of Hatschek, which is directed forwards; behind and to the left, to a narrower diverticulum, the nephridium of Hatschek, which is directed backwards. These two organs are the respective homologues of the olfactory fossa and of Rathke's pocket of the *Craniata*. Klliker's fossa represents the portion of the ectoderm which corresponds to the neuropore of the embryos of *Craniata*. But it is not, as claimed by Hatschek and Willey, the homologue of the hypophysis of *Craniata*.

Fish.

1. CYCLOSTOMES.

The study of the morphology of the olfactory apparatus shows a great difference between the cyclostomes and the other vertebrates; it is the monorhinals against the amphirrhinals. This anomaly exists during embryonic life, even from the beginning of their development.

HISTORICAL.—Scott (1882), contrary to Calberla, describes the primitive imparity of the olfactory outline. This appears as a slight depression above the mouth—the common invagination of the nasal fossa and the hypophysis. The ectoderm, simply thickened at first, has very high cells; then, when the fossa is formed, those at the bottom are increased in height, while those of the opposite walls remain very low.

Kupffer (1894) was concerned in demonstrating the primitive amphirrhinal character of the Monorhina and found two series of plakodes on the head; a dorsolateral and an epi-bronchial series. The two series converge anteriorly upon a terminal anterior plakode, which exists in the amphirrhina as well as in the Monorhina. But in the Monorhina it is invaginated, becoming a groove. At the passage which it forms there is a point of continuity between the brain, before its complete isolation, and the ectoderm.

In *Petromyzon* larva of 3.5 to 4 mm. in length, a fibrillary cord is found, destined soon to disappear, which unites the summit of the olfactory sac to the single olfactory lobe.

This disappears, and paired olfactory nerves are formed, which, without doubt, are homologous with those of Amphirrhina. But these paired nerves correspond to a single olfactory sac.

Calberla had already expressed the opinion that these nerves, which come from two symmetrical halves, are an index of the duplex character of the nasal organ.

Kupffer, from the standpoint of the single plakode, finds paired plakodes which are at first feebly developed and distinctly separated from the terminal plakode. Invaginations, which are produced and prolonged from them, are utilized for the formation of the olfactory sac. These paired portions affect the duplex character of the olfactory nerve in Petro-

myzon. No difference exists between the Monorrhina and the Amphirrhina.

Wilhelm Lubosch (1902), in *Ammocetes* of the eighth day, found the brain completely detached from the ectoderm. At the passage where the last point of union existed, the ectoderm was thickened and formed a single olfactory plate. On the 12th day a groove appeared in this olfactory lamina. Between this thickening and the hypophysal plate, an intermediate plate was found. This lies lower and permits the olfactory plate to project.

In the myxinoids, Kupffer found as the olfactory beginning a median plakode, placed ventrally in relation to the orifice of the neuropore. The final development does not differ from that in the *Petromyzon*. However, in place of terminating in a cul-de-sac, the cavity opens on the roof of the digestive cavity and communicates with it.

According to Götte, this canal of the Monorrhina is conserved in the Amphirrhina under the form of the cerebral prolongation, called the hypophysis; but Dohrn separated the two formations from one another.

OBSERVATIONS.—We have studied some young stages of *Petromyzon planeri* of 2 to 6 mm., but we have not been able to conclude our series. The nerve tube is well outlined in embryos of 4 to 6 mm. On its anterior extremity, it is in relation with a thick cellular mass, which, moreover, is connected with the ectoderm. This is the single plakode of Kupffer. On transverse and frontal sections, we have not seen the lateral thickenings of the ectoderm in connection with the single epithelial mass. Thus we find in the cyclostomes and in *Amphioxus* an olfactory beginning different from that of other mammals.

This same observation has been made by Scott and Wilhelm Lubosch, who describe only a single outline.

This is not the opinion of Kupffer, who describes three plakodes as the primordial olfactory outline in vertebrates.

Amphioxus, according to him, is the only one to possess a single plakode; all the others have a single plakode and paired plakodes.

Thus, in the Monorrhina (cyclostomes), the single plakode plays a great role in the formation of the olfactory organ, the

others taking little part in the extension and becoming fused to the first.

On the contrary, in *Amphirrina* (gnathostomes), the single plakode is visible only during a short period of development.

However, Kupffer represents the single plakode as present in *Acipenser*, *Acanthias*, frog and sheep.

But many observers contradict this. In the figure of *Acanthias* by Miss Platt there is no local thickening of the horny layer and no plakode. The ectoderm in the anterior region of the head is almost wholly thickened and the opinion of Kupffer is not verified (Karl Peter).

In the amphibians, Götte describes a median thickening which he considers as the outline of the hypophysis. Corning and Hinsberg thought that this thickening was a frontal ray.

In birds, Van Wijhe did not find any median thickening.

Peter (1901), in the lizard, found a thickening upon the ventral portion of the lips of the neuropore, but this thickening did not have in its structure any characteristics of the sensory plakode; besides, it was never in relation with the lateral olfactory region. Moreover, it appeared in its formation to be related to a mechanical cause, as it is found at the place where certain organs (crystalline lens, auditory vesicle) are detached from the ectoderm; there is, therefore, no special significance in its formation at the level of the anterior cerebral vesicle. Karl Peter, on the other hand, denies the existence of this median ectodermic thickening in mammals.

Two facts, only, remain in favor of the primitive parity of the nasal organs of the cyclostomes: the duplex nature of the olfactory nerve, announced by Calberla, and the presence of a median septum, presented by Langerhans in support of this idea.

We have very distinctly observed the existence of two olfactory nerves in *Ammocetes* (see *Morphology*, Fig. 3) and the presence of a median septum (Fig. 2). It is, therefore, necessary to admit that two distinct areas give origin by their precocious fusion to the formation of the median single thickening. The mesoderm is only interposed between the two olfactory fields, as in the other vertebrates. The primitive dorsal situation of the areas favors this evolution.

In résumé, the *Monorrhina* are vertebrates with dorsal olfactory anlage, while in all the other groups we will see that it is primarily ventral.

The origin of the hypophysal diverticulum is due to the neuroporal thickening, according to Götte, Scott, v. Wijhe (1884, 1886) and Wiedersheim (1902). The naso-palatine canal in lampreys and mixinoids appears to correspond more to this nerve formation than to the choanal canal of air-breathing vertebrates.

SELACHIANS.

HISTORICAL.—Balfour (1878), in his monograph on Elasmobranchia, speaks of the first appearance of the olfactory organ as a double thickening of the ventral epiblast. Milnes Marshall (1879) found a pair of thickenings of the external layer, below the surface of the anterior brain and immediately above the mouth. Each thick point evolved as a fossa; the bottom of this is very close to the brain. Ziegler indicates also the olfactory area. Holm (1894), in the torpedo, showed the origin of the olfactory organ depending upon ectodermic thickenings, placed laterally in relation to the neuropore. They are united to the brain by a cellular cord formed of elongated elements, while those which constitute them are formed of round embryonic cells. The brain, which is separated from the thick ectodermic zone, retracts and leaves it, and forms an olfactory nerve or ganglion. Hoffman (1896) indicates the zone of fusion between the anterior extremity of the medullary tube and the epidermis as the point of departure of the olfactory outline. Above the neuropore, this point of fusion is absorbed in part, but it persists as bridges of delicate plasma, at the place where the olfactory nerves are formed. In young embryos, the beginnings of the olfactory nerve are very close to one another, then they separate. The olfactory nerves can be well seen in an embryo of 13.5 to 14 mm. Up to this period, the olfactory groove lies close to the medullary wall. Mesenchymatous tissue is interposed between these two formations, and the olfactory nerve is increased in length in embryos from 18 to 20 mm. At the same time the groove is deepened. The borders of the groove approximate in embryos of 22 mm. and in embryos of from 27 to 28 mm. the base of the groove begins to be provided with folds.

Kurt Berliner (1902) published a long work on the development of the olfactory organ of selachians. He examined some embryos of *Acanthias*, *Pristiurus* and *Spinax niger*.

The olfactory beginning appears in *Acanthias* of 3 mm. length. In a *Pristiurus* of 5 mm. the outline is represented by a cellular plate of two or three layers. The ectodermic condensations have no relation with the neuropore; there is no possibility of a monorrhinal beginning, according to the idea of Kupffer. The olfactory plates increase by cellular multiplication, and it is the deep sensorial layer which alone enters into this development.

There is an invagination which increases progressively in depth and forms a cul-de-sac. Its borders are constituted by two cutaneous cushions. The olfactory organ, at first in the neighborhood of the neuropore (*Acanthias* of 3 mm.), is directed more and more towards the ventral side, and always retains this situation. The formation of cutaneous folds is due to an active proliferation of the indifferent ectoderm in the neighborhood of the olfactory organ.

The ridges of the mucosa, or folds of Schneider, appear in *Acanthias* at the stage of 25 mm. of length. Their formation appears to be due to the spontaneous multiplication of the internal wall of the sensory groove, rather than to the pressure of the mesodermic tissue.

DESCRIPTION OF STAGES.—We have examined a series of embryos of *Pristiurus* in the youngest stages, from 2 mm. in length, and some specimens of *Scyllium canicula* from 3 to 3.5 cm.

PRISTIURUS MELANOSTOMUS, 3 mm. in length.—The central nervous system is represented by an elliptical tube, flattened laterally, with walls of regular thickness formed of round cells crowded against one another. The ectoderm is formed by several layers of round cells. The optic vesicle is present, and is placed behind and below the nervous system. There is no trace of the olfactory anlage.

7 mm. in length (Fig. 24).—The nervous system is a tube of very large lumen with slightly thickened walls. The optic vesicle is well developed. Below this, and at the level of the latero-ventral part of the nervous tube, the ectoderm presents a considerable thickness very much extended in the dorso-ventral direction. The thickness has the form of a disc, the borders of which are confounded gradually with the surrounding ectoderm. This is the olfactory anlage, which is composed of very small round cells. The central region of the

disc is slightly depressed and is of maximum thickness. The nuclei of the most superficial layer are far removed from the surface, so that the outline is bordered posteriorly by a layer of clear, finely granular protoplasm.

12 millimeters (Fig. 25).—The nervous tube and the optic vesicle have attained a high degree of development. The ectoderm is composed of several layers in regular order. The mesenchyme below the ventral surface of the nervous system is more compact, and surrounds an elliptical mass composed of round cells analogous to those of the ectoderm. A very large

Fig. 24—X 95. *Pristiurus melanostomus* 7 mm. (right side).
1. Eye; 2. Olfactory outline; 3. Central nervous system.

cavity occupies the center of this mass, thus transformed into a vesicle, as seen in transverse section, passing 40 mikra behind the preceding. The cells which border the lumen of this vesicle present the same characteristics as those which lie at the surface of the olfactory outline in the 7 mm. stage; their central part is clear and they are of cubical form. This cavity changes in form and becomes more irregular in proportion as we approach the posterior regions, situated at a

distance of 140 mikra from the anterior extremity. The ventral surface penetrates into the cavity under the form of a conical ridge, and at each of the antero-external and postero-external extremities, the epithelium rises in very low folds, into the interior of which the mesenchymatous cells are insinuated.

Behind and above the ridge of the ventral wall, a large epi-

Fig. 25—X 34.3. *Pristiurus melanostomus*, 12 mm. long (appearance of lamellae in the olfactory cavity; left side). 1. Eye; 2. Nervous system; 3. Olfactory cavity.

thelial tract unites the vesicle with the ectoderm. Behind this epithelial tract, the vesicle communicates freely with the exterior. This orifice is limited by the borders of the primitive fossa. It is narrow, and it forms a sort of canal of an average height of 170 mikra. At this level, which is almost the middle region of the olfactory cavity, the epithelial folds are very numerous and occupy a very large portion of the bottom

of the cavity. In the most posterior sections (Fig. 25), the entire bottom is found occupied by folds, the height of which varies from 30 to 60 mikra, and which are separated from one another by plainly visible, deep fissures. The external orifice of the olfactory cavity is opened at the level of the border of the head, upon the ventral surface.

A little behind, the groove is less deep and opens freely externally, its borders not being limited by the canal. The walls are simple and without folds. Then, behind the groove, lies a slight depression, at the edge of which the ectoderm is unmodified.

The buccal depression begins a short distance behind the olfactory cavities.

In the regions where no folds exist the epithelial cells have still the embryonic character, while they lose it at the level of the folds, where they are more elongated, but still without a well defined form.

22 Millimeters.—As in the preceding stage, the olfactory outline begins anteriorly by a solid cellular mass. At the center of this the cells converge by their clear, finely granular extremities. The cavity appears in this cellular mass 110 mikra behind. The cavity in frontal sections is seen closed over an extent of 50 mikra, and then it opens externally by a large orifice. In passing from before backward, the fossa is enlarged and becomes less and less deep, its borders becoming attenuated and confounded with the neighboring ectoderm. Our frontal sections do not manifest any folds of the epithelial wall.

The cells of the superficial layer are quite cylindrical, and have an average height of 24 mikra. Their central portion is finely granular and clear, their color is rose gray (colored by alum carmine), while the peripheral portion is deepened and contains a strongly colored nucleus.

The nasal organ has not undergone displacement towards the lateral surface of the head; it is always situated under the infero-external border of the central nervous system. There is still no trace of cartilaginous skeleton.

SCYLLIUM CANICULA, 30 Millimeters (Fig. 26).—The external forms are those of the adult animal; the nasal orifices are hollowed upon the ventral surface of the head, anterior to the buccal opening, and are placed at a level anterior to

that of the eye. The nervous system is completely developed; below the ventral surface of the anterior cerebral vesicle, in the midst of the mesenchyme, is seen a series of small cavities elongated in a dorso-ventral direction, constituting the anterior extremity of the olfactory apparatus. These cavities are increased upon more posterior sections, and are finally united to form a single cavity. The common portion is extended transversely and the preceding cavities run vertically. The walls

Fig. 26—X 70. *Scyllium canicula* (transverse section showing the lamellae inserted on the dorsal wall of the nasal cavity; right side). 1. Lamellae; 2. Nasal orifice.

which separate these cavities are nothing more than epithelial folds which have become higher and transformed into large lamellae.

A large cartilaginous tract, placed transversely, separates the ventral surface of this cavity from the ectoderm.

In the external third of the cavity, a large epithelial cord unites this wall with the ectoderm, and posterior to this the cavity opens externally (Fig. 26).

The nasal opening is contracted on account of the development of its borders, which approach one another and limit it into a narrow slit only 35 mikra wide at the point of greatest contraction. They are in the same plane as the ventral surface of the head. At a more posterior level, the borders of the groove limit an irregular canal with thin epithelial walls, which run obliquely into the nasal cavity. This is prolonged posteriorly from the orifice of entrance and is arranged as above.

The cartilaginous capsule is quite incomplete, only a portion of the ventral and dorsal walls being present. There is a trace of the septum.

The epithelium at the level of the ventral wall, and upon the border of the canal of entrance, is formed of round or cubical cells crowded together, and arranged in two or three layers. The lamellae, which are inserted perpendicularly upon the dorsal wall of the cavity, have a height varying from 178 to 500 mikra. At the level of the lamellae, and in the bottom of the grooves which separate them, the epithelial layer presents a superficial stratum of cylindrical cells. The axis of the lamellae is formed by the mesenchyme, composed of fusiform same as mesenchyme cells. The posterior portion of the nasal cavity is subjacent to the bulbus oculi.

OLFACTORY BEGINNING.—The olfactory organ appears in a very early stage in the selachians. Ziegler found it in the torpedo 3 mm. long; Balfour in *Pristiurus* and *Scyllium* of 6.5 mm.; Berliner in *Acanthias* of 3 mm. and *Pristiurus* of 5 mm.

We find in *Pristiurus* of the 7 mm. stage a very extensive olfactory outline, under the form of ectodermic thickening in several layers, occupying a large portion of the latero-ventral surface of the embryo.

This outline has been found by Holm and Hoffmann under the lateral portions of the ectodermic thickening of the neuropore.

Milnes Marshall (1879), Ziegler and Berliner (1902) found the outline placed below the central nervous system.

This ventral situation, or, more exactly, latero-ventral, can be well seen in Fig. 25; it remains during the stages of evolution.

According to Berliner, the olfactory outline is constituted by the multiplication of the deep or sensory layer of the cells of the ectoderm. Our observations indicate that the entire

thickness of this layer is indifferently employed in the development of the nasal thickening. In fact, the most superficial cells of the outline of the stage of 7 mm. present the characteristics which we find later in the cells which limit the olfactory cavity (Fig. 24). These are the cells of the surface which border the depression or olfactory fossette, and at a stage somewhat advanced, the cavity results from the union of the borders of the groove.

Moreover, at no point of the ectoderm is it possible to distinguish two morphologically different layers.

EVOLUTION OF THE OLFACTORY ORGAN.—The surface of the olfactory plate is grooved, and, by virtue of the continued deepening, it becomes a deep cul-de-sac. This last is surrounded on all sides by thick ectoderm. Anteriorly, the cellular mass grows into the mesenchyme, and the cavity is enlarged so as to form a sort of vesicle. The depth of this cavity presents a series of folds of the epithelial wall, into the center of which the mesenchymatous cells penetrate. These folds, which are the outlines of the folds of Schneider, appear in *Pristiurus* of the 12 mm. stage; Berliner finds them in *Acanthias* of 25 mm.

From the time when the modifications of the epithelium appear, it is cylindrical at the level of the superficial layer of the folds, at the intermediate grooves in the 12 mm. stage, and at the orifice of entrance. The borders of the latter are elongated under the form of thick ridges converging in such a manner that the external border is concealed by the internal border; the external nasal orifice, instead of opening largely externally, is found transformed into a narrow and oblique canal.

Berliner (1902) shows, with great detail, the role played in the development of the nasal cavity by the multiplication of the cells in the olfactory outline and the elevation of the indifferent ectoderm.

It is to the cellular multiplication of the olfactory thickening that he accords the primordial role. The edges of the groove are developed, not in order to increase the cavity, but to increase the ventral wall and accordingly to narrow the external opening.

The olfactory organ, situated ventrally in the beginning of its appearance, holds this situation and is always found anterior to the buccal cavity.

III. TELEOSTS.

HISTORICAL.—His, Hoffmann, Holm and Kopsch studied the olfactory apparatus in Salmonidae family, Balfour and Parker in *Lepidosteus*, Kerr and Semon in the Dipnoi.

The organ begins as a thickening of the ectoderm placed on the ventral surface of the embryo, in front of the eye. According to Holm (1894) the cells of this outline are distinguished at an early stage from the neighboring embryonic cells by their elongated form. This writer studied the connection of the olfactory nerve lobe with the ectodermic thickening and assisted in the understanding of the olfactory nerve by separating its two formations. The organ begins in the salmon (*Salmo salar*) from the 28th to the 30th day. Kopsch (1898) recognized its first appearance in the trout at the stage of eighteen primordial segments.

The ectoderm being composed of two layers, the deep layer alone gives origin to the olfactory plates, and the superficial layer passes above their rudiments but does not participate in their formation any more than it participates in the formation of the crystalline lens and the auditory vesicle. Three processes are involved in the changes taking place in the olfactory organ: the growth of the organ, the modifications in the surrounding epidermis, and the changes in the sensory epithelium itself.

The organ is displaced from the ventral to the dorsal side. At first it is placed below the eye, later, anterior to it. On both sides of the groove are developed two prolongations, which confine at first the nasal orifice, then by fusion give rise to the two orifices. While the posterior orifice remains simple, the anterior becomes a long canal which, according to His, is formed by two median folds.

Balfour and Parker in *Lepidosteus* show the beginning of the olfactory organ as a marked thickening of the sensory layer without participation of the superficial.

Semon finds, in *Ceratodus*, ridges dividing the olfactory grooves, directed towards the buccal cavity. One of the orifices of the nasal cavity will sink into the buccal region—it is the first step towards the adaptation of the nasal cavity to the respiratory function.

Our investigations were made on the salmon trout, and on the rainbow trout for older stages. There is considerable dif-

ference in the duration of the evolution of these two species. At Clermont, the eggs of the salmon trout, placed in running water at 9° , are hatched in sixty days. At Pointis-Inard, at the home of our friend, Dr. Cardeilhac, the rainbow trout was developed in thirty days in water of 14° ; thus, the specimens of one and two months which we have examined correspond to the much older stage of the salmon trout.

STAGES OF DEVELOPMENT.—*Salmo trutta*—22nd day (After fecundation.)—The external covering, well developed, presents several layers of cells, but it is impossible to distinguish two different strata. The interior of the embryo is occupied

Fig. 27—X 70. Egg of salmon trout, 34 days after fecundation (olfactory outline presenting differentiation of the cells of the superficial ectodermic layer; left side). 1. Nervous system; 2. Eye; 3. Olfactory outline.

by agglomerated round cells without differentiation, and by the outline of the nerve tube. There is no optic vesicle or olfactory field.

34th day (Fig. 27).—The optic vesicle is large and well-formed and the neural tube is of large dimensions. The inferior surface of these formations is very close to the ventral ectoderm. In the short space between the optic vesicle and neural tube, the ectoderm shows a thickening in the form of a disc (Fig. 27). This is the olfactory anlage, its transverse extent is 285 mikra and its thickness 57. The superficial cells, at this level, have already undergone differentiation; they take

on a cubical or cylindrical form, and their protoplasm is similar to that of the embryonic cells.

52nd day.—The anterior part of the outline is a simple ventral thickening of the ectoderm; the cells which constitute it are elongated, perpendicular to the surface and distinguished easily from the adjacent ectodermic cells. No distinction is possible between the superficial and deep layers—the entire thickness of the ectoderm is concerned. A little posterior, the surface of the outline is depressed into a fossette and this grows, taking the form of a vesicle at a more posterior level. Then the mass becomes solid and is separated from the corresponding ectoderm. The buccal fossette does not correspond to the region of the olfactory outline, but is shown only a little more behind. The olfactory cavity lies between the optic vesicle and the lateral wall of the neural tube.

55th day.—There is little difference from the preceding stage; the olfactory vesicle is a little larger, its walls are uniformly thick. The length of the solid olfactory mass which prolongs the cavity is very considerable, and the ectodermic covering is detached for a greater length.

3rd day (after hatching).—No modification up to this time. The olfactory organ, which is always ventral, is placed on a transverse plane anterior to that of the eyes.

9th day.—The lumen of the nasal cavity is enlarged; the cartilaginous skeleton makes its appearance. The nasal organ begins to be directed towards the lateral surface of the embryo.

30th day (Fig. 28).—The nasal cavity is placed somewhat towards the middle of the lateral surface; it has the form of a simple pit, 100 mikra in extent from its anterior extremity. The borders which limit it are considerably elevated, due to the increase of the indifferent ectoderm. The cavity is closed and of cylindrical shape, with a length of about 70 mikra, then, behind, it is prolonged by a solid cellular mass. The epithelium which covers the bottom and the lateral walls of the fossette, and further the entire cavity, presents a superficial layer of cylindrical, much elongated cells. The buccal cavity has advanced to the region of the olfactory organ; the ventral wall of the latter is about 280 mikra distant from the buccal roof.

The cartilaginous skeleton has acquired a great development and has the form of an X on transverse section. An inferior branch separates the organ from the buccal roof, the superior branch separates it from the central nervous system and the

point of union of the four branches forms a sort of median septum some distance from each olfactory cavity (Fig. 28). The optic vesicle is in relation with the posterior extremity of the nasal apparatus behind which it is situated.

30th day (Fig. 29).—The body of the animal has the form of the adult. The olfactory cavity opens on the dorsal surface by a large orifice (172 mikra transversely), and it lies on the anterior extremity of the olfactory organ, the solid cellular

Fig 28—X 68.5. Salmon trout, 30 days after hatching (olfactory fossette presenting differentiated sensory cells throughout; left side). 1. Olfactory fossette; 2. Outline of cartilaginous skeleton.

mass which existed in the preceding stages, being distinctly hollow. The ventral wall makes a projection into the cavity under the form of a thick fold, 228 mikra at the base and 321 mikra high across its middle portion. This ventral fold lies only in the opened portion; behind the nasal orifice, the lateral walls have each a narrow, slightly elevated fold. The epithelium is thick throughout the ventral wall and the fold comprised by it; it is thin over the lateral and superior walls.

2 months.—The nasal sac has an irregular, triangular form; its walls sink into the cavity. A very long fold lies on the internal wall at the level of the external orifice. Behind, the folds are numerous (3 or 4 depending on the section considered); they are all inserted along the bottom of the cavity. Their folds or lamellae have the structure which we have described in the adult. The dorsal situation of the nasal organ is definitely acquired; it is entirely in front of the eye.

Fig. 29—X 68.5. Rainbow trout, 30 days after hatching (olfactory cavity presenting ventral folds with the outline of the lamellae; left side). 1. Nasal cavity; 2. Folds of ventral surface; 3. Cartilage.

A bony arrangement separates it from the buccal cavity, from which it is henceforth very far removed.

EVOLUTION OF THE OLFACTORY ORGAN.—The olfactory apparatus is exceedingly simple, a solid outline which is transformed into a pit and vesicle. Its origin from the ectoderm is very well marked by the differentiation of the epithelial cells in this region. We have been unable in any stage to

distinguish, at the level of the ectodermic thickening, the superficial epithelial layer from the remainder of the ectoderm. This layer appears concerned in its entire thickness in the development of the nasal anlage. The increase in size of the cavity and its displacement towards the dorsal surface are the principal transformations. At an advanced stage, the wall is raised and forms the lamellae, which are better developed in the adult. There is no trace of glands or of diverticula in the cavity. Madrid Movenó (1887) has studied the histologic transformations of the nasal mucosa in a series of fishes having the olfactory buds described by Sophie Pereyaslawzeff and Blaue. (Belone, *Trigla hirundo*, *Zoerus viviparus*, *Cyprinodon californicus*.)

A disc of homogeneous sensory epithelium is primitively in the bottom of the olfactory fossette.

Soon an islet of pavement epithelium appears in the middle of the disc; this later becomes a fold. Other islets are established, extend and unite with one another in such a manner as to divide the olfactory epithelium into small fields. These olfactory fields, more or less small and numerous, are composed of supporting and sensory cells.

The neighboring pavement epithelium surrounds them in such a way that they communicate with the exterior only by a narrow orifice.

In fish such as the trout, eel, perch, etc., in which the epithelium is deprived of olfactory buds, the modification of the epithelium consists mainly in the appearance of folds, such as Kopsch has observed in the trout.

The olfactory fossette, on the 52nd day of incubation, is covered with long cells which circumscribe the lumen, while the deep cells preserve the characteristics of round embryonal cells. The differentiation of the round cells is extended throughout the groove. In the posterior region, where the olfactory outline is represented by a small vesicle with thick walls, the differentiation does not extend to the external wall of the vesicle.

On the ninth day after hatching, the long olfactory cells do not occupy a large portion of the olfactory cavity; the external portion only is covered with round cells.

The disposition of the elements is still the same on the 30th day in the salmon trout (Fig. 28). On the 30th day folds may be seen on transverse section, passing through the middle of

the vesicle (Fig. 29) in the rainbow trout. The whole internal portion, folds and intervals, and a portion of the dorsal and ventral wall present a very thick epithelium with superficial, long, cylindrical cells. The other portions of the cavity are covered with epithelial cells, round in the bottom and flat towards the lumen. This arrangement remains definite.

The enlargement of the olfactory cavity, after the ninth day, results not only from the multiplication of the cells of the olfactory mass and their membranous disposition to cover the fossette of invagination but also from the growth of the borders of the fossette, which are only welded together after forming extensive folds.

Amphibia.

HISTORICAL.—Born, Burckhardt, Seydel, Bawden, Brauer and Sarazin studied the evolution of the nasal cavity in old embryos.

Goette (1875) made a complete study of the series of stages in a remarkable work on the development of *Bombinator*.

He found the ectodermic cells, at the beginning of the development, arranged in two layers: the covering or superficial layer, and the sensory subjacent to it. The beginning of the olfactory organ is a thickening of the sensory lamina. On each side, this appears as a depression in front of the fore brain and below the inferior portion of the primitive optic vesicle. Portions of the middle layer are placed between the eye, the brain and the olfactory organ, but its situation remains lateral in relation to the anterior extremity of the brain. The external layer is invariably separated from the basal layer formed of cylindrical cells; soon they are fused into a single cellular mass, in such a way that the entire external coat forms the bottom of the olfactory organ. The ectoderm adjacent to the posterior border of the thick olfactory lamina is raised into a fold which increases the external wall of the nasal fossette, while the olfactory lamina forms the median wall. The superior portion of the olfactory cavity remains open, the bottom directed backward is narrowed in the form of a slit and is fused with the anterior portion of the buccal roof. The posterior orifice opens in this place.

In opposition to Rusconi and Van Bambecke, who claim that the whole nasal fossette forms the olfactory organ, Goette

considers only the thick part forming the median wall as the sensory organ.

Corning (1889) describes the two layers of ectoderm, the superficial and the nervous, and indicates in detail their individual characteristics.

The olfactory thickening is established as a medullary plate. At this level, the two layers of the ectoderm are at first distinct, then they are intermingled so that it is difficult to determine what part of the formation is derived from the superficial and what from the nervous layer.

The olfactory organ thus differs from the auditory, the crystalline lens and the organ of the lateral line.

The fusion of the two layers is already effected in embryos of 6 mm.

Strasser (1901) reports only the role of the mesoderm in the situation of the olfactory organs.

Hinsberg (1901, 1902) gives a long description touching all the stages of development of *Anura*, *Urodela* and *Gymnophiona*.

The olfactory thickening of *Rana fusca* comprehends only the sensory layer of the ectoderm, the superficial layer regressing at this level. The olfactory lamina increases its ventral portion and reaches the buccal epithelium. By the removal of the cells, a round lumen appears at the postero-superior pole of the olfactory lamina, as well as in the ventral prolongation, and then a communication is established between the buccal groove and the nasal lumen. The choana thus formed lies behind the vestige of the pharyngeal membrane, consequently in the ectodermic region of the buccal cavity.

The olfactory fossette, increased in dimensions, takes on a funnel-shaped form; it is continued posteriorly and internally by a canal terminating in a cul-de-sac. Ultimately the cul-de-sac enlarges, becoming the middle lumen.

En résumé, the nasal cavity is composed of three genetically different parts: 1. The dorsal lumen, a round canal situated at the superior pole of the olfactory lamina, covered on all sides by sensory epithelium. 2. A slit made by dehiscence, which forms across the ventral prolongation of the olfactory lamina and communicates with the buccal groove—the ventral lumen. 3. The middle lumen, constituted by the differences in growth between the olfactory lamina and the epidermis.

The ultimate changes at the neighborhood of the external

orifice consist in an increase in the length of the middle lumen, and a retraction of the orifice itself, which has an annular thickening on its circumference, having the function of a valve. The choana is modified by enlargement transversely.

Hinsberg does not attribute to the cul-de-sac the value of an organ of Jacobson, accorded to it by Born and Seydel.

The establishment of the middle lumen is simultaneous with the lachrymal opening and we must therefore think of a causal coincidence between these two facts. A large glandular conglomeration appears at the beginning of the metamorphosis on the lateral nasal wall, anterior to the lateral appendix. A second forms on the posterior border of the choana, corresponding to the pharyngeal gland of Born.

The formation and evolution of these different culs-de-sac have been studied at length by Hinsberg.

The beginning of the olfactory lamina in Urodela, as well as Anura, is a thickening of the sensory lamina; the disappearance of the superficial layer is also more distinctly recognizable. The primitive nasal cavity is more simply established; it increases longitudinally, while in Anura it increases dorso-ventrally.

The lumen of the olfactory fossette corresponds to the middle lumen in Anura. The external orifice is displaced towards the lateral part by a sort of rotation of the axis of the nasal canal. On account of this rotation, the external cul-de-sac of the triton corresponds to the inferior cul-de-sac of the frog.

Hinsberg has studied the development of the olfactory apparatus in Gymnophiona, the first stages in *Hypogeophis rostratus*, the more advanced stages in *Ichthyophis glutinosus*.

The sensory lamina is still alone the site of thickening. While Brauer, insisting on the development of the external forms, finds a persistent groove between the lateral and median frontal buds, forming a slit between the mouth and the nasal cavity, Hinsberg has not observed a canal of this kind, but finds the naso-pharyngeal canal formed later into a cellular cord which at first was entirely solid. Nevertheless, by the formation of the choanae, *Gymnophiona* approach more nearly the *Mammalia* than any other *Amphibia*. Hinsberg also noted an inferior cul-de-sac, which had been described by Sarazin as an organ of Jacobson, but he does not accept the opinion of this writer.

Peter's (1902) article in Hertwig's work on comparative and

experimental embryology is principally based on the investigations of Hinsberg.

DESCRIPTION OF THE STAGES.—We have examined two series of embryos, *Bufo vulgaris* from the 2.5 mm. stage to the complete disappearance of the tail, and *Rana esculenta* from 4 mm. to the beginning of the metamorphosis.

BUFO VULGARIS.—*Tadpole 2.5 mm. in total length.*—The ectoderm is formed by several layers of cells pressed upon one another, all round and without regular disposition in the successive strata. The most superficial are filled with pigment, which forms a brown border, the pigmentation sinking in places and forming spots in the deep portion.

The ectoderm is very thick on the ventral surface of the embryo.

The nervous system is represented by a small tube with a thick wall detached from the ectoderm. A compact cellular mass fills up the remainder of the body. A separation exists between this mass and the external coat, marked by a circular fissure. There is no trace of sensory outline.

Tadpole of 3 mm.—The nervous system represented by a round tube with thick walls throughout its circumference; appearance of the optic outline, an evaginated vesicle of the neural tube, of which the walls are very thick anteriorly and posteriorly; no trace of olfactory outline.

Tadpole of 4 mm. (Fig. 30).—The ectoderm presents a strongly pigmented external border and a layer of round cells, between which short, pigmented cells extend. The nervous system is represented by a tube, very high on transverse section, with thick lateral walls. The buccal invagination is well-marked. The olfactory outline exists under the form of a thick zone projecting inwards from the ectoderm. The cellular multiplication is especially active at the level of the deep layer, but the pigmented cells constituting the superficial layer do not disappear at the level of the thickening.

The surface is slightly depressed on the anterior part of this olfactory zone. The olfactory outline is placed at the level of the latero-ventral angle of the neural tube. The middle and posterior part are subjacent to the cellular mass which becomes the optic vesicle (Fig. 30).

Tadpole of 6 mm.—The anterior extremity of the olfactory outline is a solid cellular mass, into which the ectodermic depression penetrates with an increasing growth from before backwards. The pigment is localized in the superficial layer but is found in the bottom of the depression.

The buccal invagination, which is large and deep, has a roof formed by a thick epithelial layer. The olfactory region, depressed into a fossette, has a length of 80 mikra; then its borders approach and limit a closed cavity. It has a narrow lumen, and its dorsal, internal and ventral walls have an

Fig. 30—X 95. Toad, tadpole, 4 mm. long. 1. Central nervous system; 2. Outline of the eye; 3. Olfactory outline.

average thickness of 70 mikra, while the external wall is only 14 mikra in thickness. Its ventral extremity is elongated towards the buccal epithelium, and the two walls, nasal and buccal, are fused to an extent of 40 mikra, antero-posteriorly. Behind, the nasal cavity, in the form of a fissure, opens into the buccal cavity, the first appearance of the choana.

There are to be recognized in the nasal walls pigment cells

which indicate well the participation of the superficial ectodermic layer in the olfactory development. Within the nasal cavity there are some cartilaginous intervals.

Tadpole of 7 mm.—The olfactory outline presents an anterior portion detached from the ectoderm. The nasal cavity is more prolonged posteriorly and the dorsal and internal walls attain a very great thickness. There is a very slight diverticulum of the external wall, which is very thin.

Tadpoles of 8 and 9.5 mm.—The olfactory outlines do not present any important modification.

Fig. 31—X 68.5. Toad, tadpole, 13.5 mm. (left side). 1. Olfactory fossette; 2. Buccal cavity.

Tadpoles of 10 mm.—Olfactory mass very voluminous, lumen spacious, dorsal and lateral walls thick. The expansion of the cavity which penetrates the ventral cellular mass is large; the lateral diverticulum is of slight depth. Some cells of the internal wall are cubical, the nuclei are far removed from the surface and the protoplasm is clear.

Tadpole of 13.5 mm. (Figs. 31 and 32).—Anterior to the ectodermic depression corresponding to the olfactory fossette, the cellular mass which limits the bottom of it is prolonged as a cylindrical mass, isolated from the ectoderm for a distance

of 40 mikra. The olfactory fossette is of large dimensions, 250 mikra deep and 164 in width (Fig. 31). The opened portion extends antero-posteriorly 120 mikra, then the cavity is closed. The internal and ventral walls are very thick. The lumen is formed of two diverticula, one of small importance directed outward, the other directed downwards. The latter is arranged as in the stage of 6 mm. It increases in depth from before backward and opens into the buccal cavity (Fig. 32).

In its anterior part, the nasal cavity presents a lumen formed

Fig. 32—X 68.5. Toad, tadpole, 13.5 mm. (transverse section of the posterior region of the nasal cavity, passing through the choana; left side). 1. Nasal lumen; 2. Choana; 3. Buccal cavity.

by an almost elliptical central portion and three diverticula; a dorsal, an external and a ventral. Behind, it is elongated dorso-ventrally and narrowed from above downwards. It is situated entirely in front of the eye, and its posterior extremity is in relation with the central nervous system.

Tadpole of 16 mm.—The dorsal region of the olfactory vesicle has undergone a transverse enlargement, which is represented in transverse sections by external and internal culs-de-sac. The nasal cavity is behind the choana, shown in an antero-

posterior direction. Over the whole internal wall there are long cells, some cylindrical, some cubical.

Tadpole of 20 mm.—"The olfactory fossette appears to acquire a position more and more dorsal. The mass constituting the

Fig. 33—X 68.5. Toad, tadpole, with four feet and a long tail (transverse section, showing the inferior cul-de-sac, glands and the lachrymal canal; left side). 1. Principal nasal cavity; 2. Lachrymal canal; 3. Gland of Jacobson; 4. Organ of Jacobson; 5. Inframaxillary cul-de-sac; 6. Palatal glands.

ventral prolongation is hollowed into a lumen by the simple removal of the cells at the level anterior to the choana.

The first differentiation is effected in this cellular mass while it is exclusively composed of round cells. Throughout the in-

ternal wall, the superficial cells elongate, become cylindrical and are arranged in regular layers.

Tadpole having four feet and a long tail. (Fig. 33) The nasal orifice is placed on the border of the dorsal surface of the cephalic region; it gives access to a deep fossette, the epithelial wall of which has a more regular thickness than in the preceding stages.

Behind the external opening, the cavity has an elliptical form in transverse sections, and it sends out an external diverticulum, of small importance. Its long axis is directed transversely.

The nasal cavity communicates through the middle of its ventral wall with a small cavity which is subjacent to it (Fig. 33). The orifice of communication is situated 250 mikra from the anterior extremity of the organ. It has an antero-posterior extent of about 80 mikra; transversely, its extent is increased as we pass backward. The inferior cavity, to which it gives access, is nothing but the ventral diverticulum seen in the preceding stages, which has acquired now a large expansion and a disposition approximating that of the adult. This diverticulum extends anterior to the orifice of communication for a distance of 120 mikra, and passes parallel to the ventral surface of the nasal cavity.

In the largest portion, the lumen of this diverticulum has a transverse extent of 357 mikra. Its internal wall is much thicker. The canal, by which it communicates with the nasal cavity, opens at the middle of its superior wall. It has this disposition for a distance of 150 mikra and then it forms a large groove opening upwards into the nasal cavity. This enlarged portion ends in the choana.

The superficial cells have a cylindrical form throughout the nasal cavity, those of the dorsal and internal walls being the highest (from 57 to 71 mikra). In the vicinity of the ventral diverticulum, the cells gradually lose their height, becoming cubical and then flat. The epithelial investment of the inferior diverticulum has still the embryonal characteristics.

Numerous glandular culs-de-sac lie below the inferior diverticulum, throughout the transverse extent of the palatal vault. They are separated from the nasal organ by an incomplete cartilaginous lamina.

Others, less numerous, lie between the internal border of the inferior diverticulum and the nasal septum, and another group against the external wall of the nasal cavity.

In the middle of these last glandular tubes, the section of the lachrymal gland is distinguished (Fig. 33).

The glandular cells, of cubical form, have a basal extremity containing the nucleus, and a clear central extremity with homogenous contents; they appear to be of a mucous nature.

The metamorphosis comes to its end; the animal already adapted to amphibian existence, perfects the respiratory apparatus by the appearance of these glands.

We may see the relation of the olfactory apparatus to the neighboring organs, by a series of sagittal sections. It is always situated in front of and below the eye, and above the buccal roof. The length, dorso-ventrally, of the olfactory mass establishes the continuity between this mass and the buccal epithelium, then the nasal lumen discards the cells of inferior prolongation, the epithelium is resorbed and the communication is established. The antero-posterior extent of the nasal cavity and of its ventral diverticulum is inconsiderable; this latter appears destined to establish the bucco-pharyngeal communication. In a series of horizontal sections comprising all of the body of the embryo, we have seen that the choana opens into a true fossa of the buccal epithelium. In its middle portion, the nasal cavity is separated from the buccal region by a cartilaginous wall.

We see it open externally; at this level the cartilaginous wall of the cranium separates it from the nervous system. A little higher, an interruption in the cartilaginous capsule permits the passage of the olfactory nerves, which arising from the anterior pole of the anterior cerebral vesicle, already divided into two hemispheres by a sagittal groove, enters the internal wall of the olfactory vesicle at the level of its anterior third.

In a more dorsal section, the olfactory apparatus is represented only by a solid mass situated in front and only a very short distance from the brain. At this level, the eye seems far behind the olfactory mass.

RANA ESCULENTA. Tadpole of 4 mm. On the lateral surfaces of the cephalic region, there is a lightly depressed ectodermic zone; the entire thickness of the ectoderm is involved. At the level of the groove, the deep layer, composed of round cells, crowded upon one another, presents a distinct thickening, which is continued backwards and downwards into the mesenchyme. The neural tube exists, and the olfactory fossettes correspond to its latero-ventral surfaces. The buccal depression does not exist in this stage.

Stage of 5 to 9 mm. Evolution of the olfactory outline analogous to that of the toad. The choana is plainly shown in the 9 mm. stage; in the preceding stages, the lumen already penetrates into the ventral cellular mass and comes in contact with the buccal epithelium.

Tadpole with two feet. The spacious nasal cavity presents, anterior to the choanal region, three diverticula of large antero-posterior extent: one is directed externally and opens into the superior part of the cavity; another, directed internally and superiorly opens in the middle portion and is surrounded by a very thick epithelial wall; finally the inferior diverticulum ends in the choana. Numerous glandular culs-de-sac lie internal and below the internal diverticulum.

APPEARANCE OF THE OLFACTORY OUTLINE. Corning found the cells of the two indistinct ectodermic layers participating in the formation of the olfactory epithelium in an embryo of *Rana fusca*, 6 millimeters long.

Hinsberg observed the first condensation of the sensory layer in a tadpole of *Rana fusca*, 3 mm. long.

Our results in *Rana esculenta* and *Bufo vulgaris* are almost identical. The first traces of the olfactory mass appeared in tadpoles 4 mm. long.

It is a thickening of the ectoderm which represents the olfactory beginning; it is composed of a mass of round cells having the characteristics of the deep cells of this coat. The superficial pigmented cells preserve their characteristics at this level.

The ectodermic zone, thus modified, lies upon the lateral portions of the head on each side of the neural tube (Fig. 30); the buccal depression still does not exist at this period, but the eye is already formed; it is placed dorsally in relation to the posterior extremity of the olfactory mass.

EVOLUTION OF THE NASAL OUTLINE. During the first stages, the olfactory apparatus of the Amphibia appears as that of fishes; it is formed as a thickening of the ectoderm which is depressed into a fossette. This increases in depth and its borders approach by cellular multiplication, limiting a narrow orifice, the external nasal opening. The groove penetrates the cellular mass, the elements of which disappear, the internal and posterior walls alone remaining thick.

The lumen appears in the zone which results from the growth posterior to the nasal outline and which remains isolated

from the neighboring ectoderm, and at this level the nasal cavity has the appearance of a vesicle, isolated in the mesenchyme. The olfactory mass, hollowed in its middle portion, solid anteriorly and especially behind, approaches the buccal roof by its posterior extremity. It is situated below the eye and central nervous system. Up to this point there is no difference from animal's breathing water exclusively. Little by little, the animal is prepared for air breathing; the olfactory mass is elongated in its ventral portion and forms a solid prolongation. Then a lumen appears in this latter—the ventral diverticulum.

The ventral prolongation joins the buccal epithelium and the diverticulum lengthens, the two cavities, buccal and nasal communicating with one another. First there is cell proliferation, then fissuration with removal of the cells appears, increases and ends finally with the formation of the choana.

The bucco-nasal relation is established by a peculiar, one might say, intrinsic process, without participation of the ectoderm as in Amniota, which have an external naso-buccal fossa or groove. Götte (1875) observed the beginning of this process in young specimens of the toad. Hinsberg (1901) could not find this process in *Rana fusca* and we have not seen any trace of it in the frog or toad.

Two processes must be admitted in the appearance of the nasal lumen: the ectodermic folds which limit the olfactory fossette and the hollowing of the olfactory mass by the removal and compression of the cells. We must not be exclusive as Götte, who attributes all importance to the first factor and as Hinsberg who accepts the second only.

The first process is concerned in the beginning, for the purpose of forming the superficial fossette in the thickness of the ectodermic mass and then, when the pigmented layer is indistinct, the second process is brought into play to increase the cavity, already acquired.

It is this process of fissuration which creates a lumen in the ventral bud. This latter becomes hollow from its anterior portion, and in the posterior region, where it unites with the buccal epithelium, it is completely perforated and constitutes the canal of communication between the two cavities. The lumen which exists anterior to the choana has the form of a groove, opening above into the nasal cavity. In old tadpoles, with four feet, this is only a simple groove, which is hollowed in its inferior prolongation—a diverticulum extended transversely.

This is evidently the inferior cul-de-sac of Born. We have, in the chapter on Morphology, shown the importance of the inferior cul-de-sac, which is a formation destined to increase the respiratory region. In a series of embryos, we have observed in fact that this inferior lumen appears by a hollowing in a cellular bud, which has no other purpose than to reach the buccal epithelium so as to establish bucco-nasal relations, and in consequence to open an air passage. And it is in the vicinity of this respiratory zone, which must be lubricated and moistened, that the first glandular formations appear.

The advanced stages have been well studied by Born in *Pelobates fuscus* and *Rana fusca*. He devotes a long description to the buds of the nasal cavity and to the diverticula which perforate them. These are superior, lateral and inferior; the superior corresponds to the true nasal cavity, the lateral receives the opening of the lachrymal canal and the inferior constitutes the maxillary cavity.

Hinsberg finds these culs-de-sac and insists upon their significance. He does not accept the opinion of Born with regard to the inferior cul-de-sac; it also appears to him difficult to consider it as the homologue of the organ of Jacobson, as Fleischer, Sarazin, Burckhardt (1891) and Seydel (1895) claim. The points of difference in the development and the later appearance in Amniota do not permit homology with this organ. But because of the sensory epithelium which this cul-de-sac contains, Hinsberg attributes to it the same functions as the organ of Jacobson. There is analogy but not homology between these two formations.

Besides, in the course of development, he observed "a lateral appendix" arising from the postero-superior wall, appear and disappear.

Our sections show the inferior diverticulum, and external to it a lateral diverticulum, which pushes into the region where the glandular evaginations of the external gland (superior of Born) are formed.

EVOLUTION OF THE NASAL CAVITY OF URODELA AND GYMNO-PHIONA. In these two groups, Hinsberg (1901, 1902) studied the beginning of the development. The olfactory outline is constituted, as in Anura, by a thickening of the ectoderm, localized in the sensory layer. Brauer observed in *Gymnophiona* the nasal apparatus begin in a very slight fossette of almost triangular form. The buds of the facial mass distinctly participate in the constitution of the olfactory apparatus.

Between the median and lateral frontal buds, a groove is gradually formed, which brings the nasal fossa in direct communication with the buccal cavity. The choana, by an earlier establishment, will utilize a naso-pharyngeal ectodermic canal in its constitution. According to the researches of Sarazin, there is, in the ventral portion of the cavity, a sensory epithelial mass which corresponds to the organ of Jacobson in form and location. Hinsberg found this diverticulum representing the inferior cul-de-sac in other Amphibia.

Fig. 34—X 68.5. Triton, still having branchia (transverse section, left side). 1. Nasal cavity; 2. External furrow.

The ectodermic thickening in Urodela appears more in the form of a button than in Anura, and the dorso-ventral addition does not exist. Hinsberg explains this difference by the form of the head and the location of the olfactory outline. The head is flatter, and the outline lies at the point of the anterior extremity of the buccal cavity, and not dorsally as in Anura. The increase in the direction of the axis of the body brings the primitive nasal cavity in contact with the buccal epithelium by removal of the mesoderm.

The caudal prolongation will be hollowed out of a lumen, like the ventral prolongation of *Anura*, and later the naso-buccal communication will appear. A cul-de-sac arises from the inferior wall, which ultimately acquires a lateral position by displacement of the axis of the nasal cavity; this is the inferior cul-de-sac. A slight evagination exists on the lateral wall which is to receive the lachrymal canal, but it remains in the state of a simple groove, while in *Anura* it forms the lateral cul-de-sac.

Burckhardt (1891), in old embryos, and Seydel (1850) and Born (1838), in the adult, homologized the inferior cul-de-sac with the same cul-de-sac of *Anura* and the organ of Jacobson of *Mammalia*.

We have been able to examine only the triton, in advanced stages of evolution, but still provided with gills. The external nasal orifice lies almost exactly in the middle of the lateral surface of the head, and corresponds to the anterior extremity of the nasal cavity. This has the form of a vesicle with thick walls, circular on transverse section; it opens into the buccal cavity by its posterior extremity. At this level, the ventral wall, very near to the buccal roof, is united to the latter; the nasal lumen penetrates into the zone of union and communication is established by a very simple process (Fig. 34).

The nasal lumen is prolonged radially by narrow diverticula or canaliculi which force away the constituting cells from the wall. Certain zones have the appearance of a cavity cut out by lamellae, as in fishes. At the level of the infero-external angle, the cavity sends out a lateral diverticulum which is hollowed into an evagination of the epithelial wall (Fig. 34). This diverticulum, which is very extensive antero-posteriorly, constitutes a groove enlarging the nasal cavity, and terminating behind in the choana. This is the inferior cul-de-sac of Born, Seydel and Burckhardt. It retains the same situation in the adult, and we have already indicated its functional significance.

REPTILES.

HISTORICAL. Rathke (1839) published a monograph on the development of the lizard; Parker (1879) studied the skull of the common snake; Born (1883) described the development of the nasal cavity of *Lacerta agilis* and *Tropidonotus natrix*.

The beginning of the olfactory organ, as described by Rathke, is a small circular zone found on the ectoderm, under the cerebral hemispheres. A fossette is formed in this zone. External modifications are brought about by the development of the face (frontal and maxillary bud). A groove appears at the ventral extremity of the median wall of the nasal cavity in the stage of 47 intervertebral segments in the lizard; this is the first appearance of the organ of Jacobson. The external and internal nasal buds are formed at the expense of the frontal and approach one another; the point of the external nasal buds unites with the external surface of the internal nasal bud. Above this is only a punctiform orifice, which is the external nasal orifice. Below the bridge of fusion, the internal nasal orifice is formed and the bridge of fusion forms the primitive palate, which is increased in such a manner that it pushes the internal orifice more and more posteriorly. This transformation is well seen in Fig. 2, Pl. IX (1883).

Born (1883) gives a lengthy description of the formation of the palate; the superior maxillary bud sends out a median prolongation which unites with the septum except in its anterior portion, where the organ of Jacobson opens. These formations and their line of fusion extend backward, increasing the length of the palate and displacing the choana. The turbinal, a ridge which penetrates into the cavity, is formed on the external wall of the nasal cavity at the level of the maxillary bud. The formation of the lateral nasal gland, the relation of the lachrymal canal with the space subjacent to the turbinal, and the distribution of the sensory and stratified epithelium are the subjects of detailed study. Plates IX and X of his work (1883) show the relation of the different buds of the face and their changes as well as their orifices and the relation of the cavity with the organ of Jacobson.

Orr (1887) represents the olfactory beginning in the lizard as a thickening of the epiblast, which is gradually transformed into a round depression.

Keibel (1893) deduced no conclusions from the study of a series of *Anguis fragilis* but agreed with those of Born, and admits that in important points there is analogy with mammals.

Voeltzkow describes, in the Madagascar crocodile, the formation of an olfactory cavity, as in the saurians. The differences lie mainly in the development of the palate. The palate prolongations are formed of large laminae which come in

Voeltzkow describes, in the Madagascar crocodile, the formation of an olfactory cavity, as in the saurians. The differences lie mainly in the development of the palate. The palate prolongations are formed of large laminae which come in contact through the middle portion of their length; the palatal laminae and the pterygoid, behind, limit a long nasopharyngeal canal.

Meek (1893) describes, in the early stages of the *Crocodilus porosus*, the nasal cavity and its diverticula, particularly a closed groove of the internal wall, which is a vestige of the organ of Jacobson.

Sluiter (1892) and Röse (1893) in a series of young embryos of the crocodile, studied a cul-de-sac of the postero-inferior extremity of the nasal cavity, which they considered as the organ of Jacobson.

Seydel found the olfactory beginning in the turtle (*Chrysemys picta*), as a fossette, which is deepened and limited by nasal buds which are fused as in the lizard. It forms on the median wall a groove covered with olfactory cells, and separated by a projection of indifferent epithelium from the sensory epithelium situated above. Seydel compares it to the inferior cul-de-sac of Amphibia, and considers it the organ of Jacobson.

Karl Peter (1900), studying the development of the olfactory organ of the lizard, shows the part which should be accorded to the corrugation of the ectoderm and the predominant role played in the active development of the olfactory thickening by multiplication of the cells. The organ of Jacobson is thus established by the intrinsic activity of an invagination localized on a limited portion of the median wall of the nasal sac. In later works, Peter (1902) was concerned with the ectodermic thickening of the anterior neuropore and concluded that it has no relation with the paired lateral olfactory outlines.

Beecker (1903) studied the development of the nasal region in several reptiles: *Platydactylus guttatus*, *Tropidonotus natrix* and *Lacerta agilis*. He observed that the nasal canal was divided into the vestibule and the zone of the turbinals. The nasal sac and choanal canal are largely developed transversely and compressed dorso-ventrally. The choanal canal has a horizontal and a descending branch. The horizontal branch forms an internal lateral pocket; the descending branch has a small angular pocket directed obliquely upwards.

The organ of Jacobson opens into the oral extremity of the choanal groove. The true turbinal of reptiles originates from the lateral wall of the principal portion.

DESCRIPTION OF THE STAGES. *TROPIDONOTUS NATRIX*, 4 cm. in total length, the embryo being unrolled (Fig. 35). This is the only stage which we have been able to examine; we have studied it in transverse sections.

A depression of the lateral wall of the head gives access to the olfactory cavity; this is entirely filled in its anterior portion with a cellular mass, composed of polyhedral or round cells with a large nucleus; this is the vestibular region. Passing to the posterior portion, a lumen is encountered which

Fig. 35—X 60. Adder, 4 cm. in total length (transverse section of the nasal cavity and the organ of Jacobson; right side). 1. Nasal cavity; 2. Sensory epithelium; 3. Organ of Jacobson; 4. Choana.

pushes the cells towards the periphery, in the form of an epithelial wall. The dimensions of the cavity are increased as we pass from before backwards; an enlarged dorsal region and an elongated ventral portion may be recognized under the form of a fissure. The epithelium differs in these two zones. In the superior portion it is provided with a superficial layer of cylindrical cells, while in the inferior part it is much thinner

forms a septum, larger below on account of the obliquity which each cavity attains from above downward and from within outward.

At a distance of 280 mikra from the anterior extremity of the cavity, and 428 below the nasal roof, the internal wall sends out a diverticulum which sinks into the septum, constituting the organ of Jacobson (Fig. 35). It communicates with the nasal cavity by an antero-posterior extent of 60 mikra. It is prolonged longitudinally in front of and behind its union with the olfactory organ, 120 mikra anteriorly and 130 posteriorly; its total length is 310 mikra. Its anterior and posterior extremities are solid cellular masses. The entire anterior segment is greater in width than in height; its dorsal wall is very thick (114 mikra), while the ventral wall is only 21. The lumen has the form of a crescent, with concavity inferior, on account of the convex ridge made by the ventral wall on the interior of the cavity. The dorsal wall presents a superficial layer of greatly elongated cells having the characteristics of sensory cells. The ventral wall is provided only with cubical or round cells. The posterior segment of the organ of Jacobson is a cylindrical canal with walls of uniform thickness and covered throughout with sensory epithelium.

At the level at which the ventral region of the cavity forms the evagination of Jacobson, its vertical extent increases and it attains the buccal wall so as to form the choana.

The external wall of the nasal cavity is strongly convex and corresponds to a concavity of the internal wall. In the portion situated behind the choana, the convexity of the external wall is of less extent vertically; it is localized in the middle portion of the wall and forms a very slight ridge, representing the outline of the turbinal.

The posterior extremity of the cavity forms a cul-de-sac, and the wall is prolonged posteriorly in the form of a solid epithelial mass.

The sections including the posterior extremity of the organ of Jacobson and of the nasal cavity pass through the olfactory bulbs and show the branches of the olfactory nerve divided into two groups, one for each of these organs. The disposition of the olfactory apparatus in the viper is the same as that in the adder.

ANGUIS FRAGILIS, 25 mm. long (Figs. 36 and 37). The general form of the cavity is similar to that of the adder. It

is long vertically, in transverse sections, and oblique inferiorly and externally. The superior portion, which is spacious, is covered with very thick epithelium; the ventral portion, which is narrow, is covered with an indifferent, thinner epithelium.

Fig. 36—X 68.5. Blind-worm, 25 mm. total length (transverse section passing through the nasal cavity and the organ of Jacobson, showing an epithelial bud of the external wall sinking into the mesenchyme; left side). 1. Nasal cavity; 2. Epithelial bud; 3. Mesoderm of the turbinal; 4. Organ of Jacobson; 5. Choana.

A central cartilaginous lamina begins to be differentiated in the septum. Between this septum and the inferior extremity of the nasal cavity, is the organ of Jacobson, a solid epithelial mass anteriorly and posteriorly (Fig. 37) and a cylindrical

canal in the remaining portion (Fig. 36). The communication with the nasal cavity is placed, as in the adder, on the internal wall of the choana. The cylindrical cells begin to differentiate at the level of the dorsal wall of the organ of Jacobson, which is composed of very thick epithelium. The thin ventral wall is raised slightly towards the cavity (Fig. 36).

Fig. 37—X 60. Blind-worm, 25 mm. long (transverse section passing behind that presented in Fig. 36; the turbinal is limited above by a fissure which has replaced the epithelial bud of the preceding section. The organ of Jacobson is represented only by a cellular mass; left side). 1. Superior fissure; 2. Turbinal; 3. Eye; 4. Organ of Jacobson; 5. Choana.

A turbinal, already well developed, is found on the external wall of the olfactory cavity. It is possible here to see distinctly how a turbinal is formed (Figs. 36 and 37). The external wall presents a convexity limited above by the nasal lumen, which penetrates into it in the form of a fissure. This

increases and is directed outward and then downwards, thus causing a ridge on the external wall—a mass of mesenchyme covered by an epithelial layer projecting into the cavity. The base of this mass has a height of 250 mikra and a transverse extent of 285.

The fissuration is effected in an epithelial mass, resulting in a budding of the external wall (Fig. 36). The cells which form these buds are round, packed closely together, having a distinct border, a finely granular protoplasm staining well with carmine, and a deep nucleus, often seen dividing. The buds are not separated from the mesenchyme by a limiting membrane; their borders are indicated only by peripheral elements arranged in a regular layer. The nasal lumen penetrates into the mass, destroys the cells and arranges them in two epithelial layers, which border then on one fissure (Fig. 37).

The nasal cavity terminates in a cul-de-sac, behind the posterior extremity of the organ of Jacobson. Nerve fibres are seen passing from the olfactory bulb into the two organs, those of the organ of Jacobson being the most anterior.

Three centimeters. The nasal cavity and the organ of Jacobson increase in length, and their lumen is of greater extent. The turbinal is much more evident, a round ridge with thick pedicle. The nasal epithelium is very thick on the superior border of the turbinal and upon the walls throughout their extent, subjacent to the latter.

All portions with thick epithelium have a superficial layer of cylindrical cells. The inferior border of the septum is enlarged transversely; the inferior portion of the internal wall of the choanal fissure takes part in the buccal roof, thus the organ of Jacobson, completely separated from the nasal cavity is seen opening directly into the mouth.

Four centimeters (Figs. 38 and 39). The nasal cavity is large and of elliptical form on transverse sections. It has a floor slightly concave in place of being elongated to a point towards the buccal roof as in the preceding stages. The turbinal is greatly developed, beginning 340 mikra from the anterior extremity of the cavity and having a length of 360 mikra. Its anterior extremity is a slightly elevated ridge with a large base, but its height increases little by little and its pedicle is contracted. The thickness of the pedicle towards the middle portion is 107 mikra; the height of the turbinal (distance from the base of the pedicle to the free border) measures 378 mikra

(Fig. 38). It becomes thin and low gradually towards the posterior extremity.

The fissure which circumscribes it ventrally sinks into the axial mesenchyme at first from below upward and then from without inward. The surface of the turbinal is thus defined,

Fig. 38—X 68.5. Blind-worm, 4 cm. long (transverse section passing through the nasal cavity in which a pedunculated turbinal projects and through the organ of Jacobson opened directly into buccal cavity; right side). 1. Nasal cavity; 2. Turbinal; 3. Organ of Jacobson.

the free border is displaced and the organ has the appearance of being rolled on its axis.

The nasal cavity is surrounded by a cartilaginous capsule, still in fair way of development, at the level of the inferior wall. The external wall sends out a lamina which penetrates

into the turbinal and lies in the middle of the mesenchyme which it follows up to the level of the free border, being subjected to beginning rolling.

Fig. 39—X 68.5. Blind-worm, 4 cm. long (transverse section, posterior to that represented in Fig. 38, showing the choana which has acquired a definite arrangement; right side). 1. Nasal cavity; 2. Turbinal; 3. Choana.

The organ or Jacobson has a length of 370 mikra and the lumen occupies it almost entirely. It communicates with the buccal cavity, 220 mikra from its anterior extremity by a small fissure which arises from the internal border of its floor (Fig.

38). It presents throughout its extent a thick dorsal wall covered with sensory epithelium and a thin ventral wall, projecting into the cavity, formed of cubical or polyhedral cells.

The posterior extremity of the organ of Jacobson appears at the level of the choana. This last is a narrow canal directed obliquely from above downward, and from without inwards, arising at the infero-external angle of the nasal cavity (Fig. 39). The choanal canal and the nasal region subjacent to the turbinal are covered with flat epithelium; all the other regions, including the turbinal, are provided with thick epithelium, the superficial layer of which has cylindrical elements. The organ of Jacobson is in relation with a cartilaginous groove, opened externally, which covers its internal and inferior walls; this is independent of the nasal septum.

Seven centimeters. (Embryo has two small posterior members.) The nasal cavity is large at its anterior extremity; it opens externally through the middle of the external wall. The region of the opening is covered with pavement epithelium on the inferior wall and the parts adjoining the external and internal walls, while the other portions are covered with cylindrical epithelium. The relations of the nasal cavity and of the organ of Jacobson are as in the adult. The bony skeleton is already well developed; external to the cartilaginous capsule are seen the vomer, maxillary and nasal and, towards the middle portion of the external wall, the external nasal gland. The turbinal is clearly pedunculated and it describes a half turn of enrolling.

LACERTA MURALIS. The olfactory fossette in a 6 mm. embryo is deep and opened below. The primitive palate is not formed at this stage. The organ of Jacobson opens on the internal wall of the fossette near its inferior extremity. It has for a certain distance the form of a groove, then forms a cylindrical tube isolated from the nasal wall.

At the stage of 7.5 mm., the ridge of the external wall is developed, being formed, as in the blind-worm, by fission of a solid epithelial mass; the internal and external nasal cushions are fused for a certain extent. The opened portion, situated behind the primitive palate, receives the end of the canal of Jacobson. The 10 mm. embryo already presents the characteristics of the adult. The cartilaginous skeleton is well differentiated; the ridge which becomes the turbinal now occupies the superior surface, and forms an enormous prominence

in the olfactory cavity, which is reduced to the two fissures limiting this ridge. The organ of Jacobson is prolonged in front of the anterior extremity of the olfactory cavity and opens directly into the buccal cavity.

BEGINNING OF THE OLFACTORY OUTLINE. Born, in an embryo of *Lacerta agilis* with ten primordial segments, observed a zone of ectoderm between the anterior neuropore and the primitive ocular cavity, in which the cells take on a cylindrical form; this is the olfactory plate.

Peter studied the evolution of this olfactory plate in the lizard, and accorded to the multiplication of the cells constituting it the most active role in the growth of the organ. He found the olfactory fields well marked in the stage of eleven primordial segments. He found on the ventral wall of the anterior neuropore, in the stage of sixteen primordial segments, an ectodermic thickening analagous to that described by Kupffer, but it had none of the characteristics of the sensory plakode and never was in relation with the paired olfactory outlines.

EVOLUTION OF THE OLFACTORY ORGAN. The olfactory fossette resulting from the invagination of the corresponding ectodermic thickening, grows particularly by the mitotic activity of the cells constituting this outline, as was well noted by Peter (1902). The neighboring, indifferent epithelium forms only the bordering portions. Rathke (1838) and Born (1879) described at length the ultimate changes of these portions.

The thick postero-superior border is prolonged, in the form of a curtain, anteriorly and inferiorly into the area of the nasal depression. The free border of this fragment (nasal roof of Rathke) is entirely straight at first, then advances further at its middle portion and is prolonged as a rounded ridge.

At a period at which the nasal sac is still largely open (*Lacerta agilis* with 47 primordial segments), Born observed the appearance of a groove indicating the organ of Jacobson, from an active depression of the ventral extremity of the median wall of the nasal sac.

The space between the two nasal fossae forms the frontal bud of Rathke and each of its parts forms the internal nasal bud of Koelliker. The external border of the fossette is formed by the external nasal bud, which a groove (lachrymo-nasal) separates from the superior maxillary bud. Fusion of the

nasal buds caused at first by the crowding together of the epithelium, then by the union of the two subjacent masses of mesenchyme, separates the nasal groove into two orifices. This fusion is effected in the adder with a head length of 4 mm. The external orifice, in the form of a fissure, is placed upon the plane of the face and the posterior orifice of the choana is situated on the palatal plane.

The bridge of fusion which forms the primitive palate grows, the palatal prolongations of the superior maxillary are united with the nasal septum, and the choanae are displaced backward. We have observed that the inferior part of the septum which divides the choanae from one another grows transversely in such a manner as to separate them. As a consequence of this growth, which causes a transverse enlargement, the orifice of the canal of Jacobson, which opens on the internal wall of the choana, is carried along the palatal surface, and the definite opening of the choana is finally external to the communication between the canal of Jacobson and the buccal cavity. The two organs are then independent of one another; this process is effected in the blind-worm at the stage of 4 cm. of total length.

The organ of Jacobson does not remain here in the state of a groove communicating throughout its length with the nasal cavity as in the Anura; it is transformed into an isolated, well-defined canal, entirely independent of the olfactory cavity.

Two interesting points are found in the nasal cavity: the formation by growth antero-posteriorly of a vestibular region, and the delimitation of a ridge on the external wall in the form of a turbinal. While the turbinal is a simple ridge in the adder, in the blind-worm it is comparable to those of the mammals.

We have seen how it is established by the growth of the fissure of the nasal lumen. Some epithelial buds begin to isolate a region of the mesenchyme, then the fissure penetrates into the bud and the mesenchymatous mass, covered by the epithelium of the cavity and of that which is organized along the fissure, forms a free ridge in the nasal cavity, simply united to the external wall by a base, more or less large, forming the pedicle of the turbinal.

The round, embryonic cells, which constitute the walls of the nasal cavity, are differentiated into cylindrical cells at the

level of the nasal roof at the beginning of development; their territory is already large in the blind-worm of 2.5 cm.

The differentiation takes place on the internal wall and the turbinal; the region, subjacent to the turbinal remains covered with indifferent epithelium. The sensory cells in the organ of Jacobson, limited to the dorsal wall, are completely differentiated at the stage of 2.5 cm.

The lateral nasal gland, of which Born found the beginning in the form of an epithelial bud on the external wall, exists in our sections of the blind-worm of 7 cm. It is formed by a group of culs-de-sac, situated external to the capsule, near the middle part of the external wall.

In the Crocodilia, according to Voeltzkow, the development is analogous to that of the sauropshidians. According to Meek (1863), in the 5 mm. stage of *Crocodilus porosus*, the nasal sac is completely formed and the anterior and posterior nasal orifices approach very closely to one another. A depression of the frontal wall represents the origin of the organ of Jacobson. At the stage of 7 mm. an evagination corresponding to the lachrymal canal is the beginning of a simple accessory cavity of the nose. The invagination representing the canal of Jacobson is absent in specimens of 7.75 mm. in length. Sluiter (1892) and Röse (1893) found an outline of the organ of Jacobson always present in their investigations. Seydel and Voeltzkow gives but slight indication of it in the chelonians. The organ of Jacobson, according to Seydel, is represented by a groove on the median wall, while Mihalkovics sees this organ in a canal which opens on the septum and has glands in its blind extremity.