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STUDIES
on the
DEVELOPMENT
of the
UPPER AIR PASSAGES

by

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STUDIES on the DEVELOPMENT of the UPPER AIR PASSAGES

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In this paper the writer proposes to give an account of the development of the nose, mouth, and pharynx. The methods of research employed in this piece of work have been mainly the use of wax plate reconstructions, while some embryos have been examined by the microscope alone. However, as the number of human embryos available was very limited, one has had to fall back on the literature for descriptions of some of the stages. It has been found necessary for the sake of clearness to repeat some of the facts occasionally.

Before going further, I wish here to acknowledge my indebtedness to Professor Robinson for his kindness in placing his material at my disposal, and also for much valuable advice.

The photographs for this paper have been taken by Mr. E.J. Henderson. The models from which the photographs were taken are to be seen in the Anatomy Department.

DEVELOPMENT of the NOSE.

Historical Survey of Literature.

Meckel (1818) considered the nasal and the buccal cavities to be developed as one single cavity, which is later subdivided into the two nasal fossae and the mouth cavity. Disproved later by the researches of Rathke, Reichert, v. Baer, &c.

Rathke (1838) was the first to describe the primitive nasal fossae in mammals.

Dursy (1869) described the formation of the olfactory pit in the human embryo on the lateral aspect of the head in front of the eye. The mesial and lateral nasal processes and the maxillary processes fuse below the pit to form what he called the primitive palate. Behind the primitive palate on each side a communication between the nose and the mouth is left, which is the primitive choana.

Kölliker (1882) studied the formation of the olfactory pits in the rabbit and found that their first appearance in the human embryo was in the fourth week. He stated that they were preceded by a considerable thickening of the ectoderm.

His (1880) gave the name Nasal Field (Riechfeld) to the ectodermal thickening, which occurs before the formation of the fossae, and showed the process of union of the various parts by reconstructions.

He /

He described the formation of the primitive choanae as due to a defective union of the maxillary and mesial nasal processes.

Hertwig (1891) described the formation of the external and internal nares, the palate, and the nasal conchae and sinuses.

Hochstetter (1891) as a result of researches on rabbits and cats disagreed with the foregoing authors with regard to the formation of the nasal fossae and the primitive palate. He stated that in man the maxillary process takes part in the formation of the external nasal orifice in the early stages, but that in the rabbit and cat, the mesial nasal process and the lateral nasal process unite and transform the nasal fossa into a cul de sac open in front. The primitive palate is formed from the union of these two processes while further dorsally the nasal cavities are separated from the buccal cavities by a thin lamina of epithelium, the bucconasal membrane. This membrane later ruptures and disappears and the opening thus formed is the primitive choana.

The same author in the following year discovered the bucconasal membrane for the first time in a human embryo.

Keibel (1893) confirmed the views of Hochstetter.

Zuckerkandl (1892) studied the development of the ethmoidal conchae in man. He occupied himself more especially with their later development and placed the number of ethmoidal conchae at three or sometimes four.

Mihalkovics (1899) divided the nasal cavity into three primary zones. The anterior zone corresponded with the vestibule and the concha inferior, the middle zone was the most essential, corresponding with the ethmoturbinals, while the posterior zone corresponded with the region of the sinus sphenoidalis and the naso pharynx. In the posterior zone the sinus sphenoidalis is formed by the apposition and fusion of the mesial and lateral walls of the nose, thus shutting off part of the nasal cavity.

Schönemann (1901) investigated the formation and growth of the nasal conchae. He divided the lateral nasal wall into three fundamental areas:- the maxillo-turbinal, the naso-turbinal and the basi-turbinal. He stated that one must distinguish between those conchae which arise from the basi-turbinal and those which belong to the lateral wall. He classified the conchae into c. obtectae and c. apertae according to their position. He stated further that the naso-turbinal takes a very small place in the adult nose in man, where it is represented only by the agger nasi. It is well formed in the cat, dog and rabbit.

Peter (1902) after working on the rabbit and man disagreed with Hochstetter upon certain points. Thus he found that both in the rabbit and man the primitive palate is composed solely of mesial nasal process and maxillary process in the very early stages. At a somewhat later period (9·5m.m.), the maxillary process does not reach quite to the front of the primitive palate, so that a small part of the palate is composed of lateral nasal process. "An diesem liess sich nachuweisen, dass der Oberkieferfortsatz bereits hinter dem Vorderrand des primitiven Gaumens sein Ende findet, dass demnach ein, wenn auch kleines, Stück dieses Gaumens vom lateralen Nasenfortsatz eingenommen wird."

In the same year he studied the development of the conchae and their homology in various vertebrates. The maxilloturbinal and the naso-turbinal arise from the lateral wall. The ethmoturbinal, on the contrary, arises from the mesial wall of the posterior part of the cavity. Separating the ethmoturbinal from the naso-turbinal is a deep curved fissure. He classified the conchae into those which arise from the lateral wall and those which arise from the medial wall.

Dieulafé (1905) studied the development of the nose in vertebrates. The two first conchae in mammals are the maxilloturbinal and nasoturbinal which should be classified together on account of

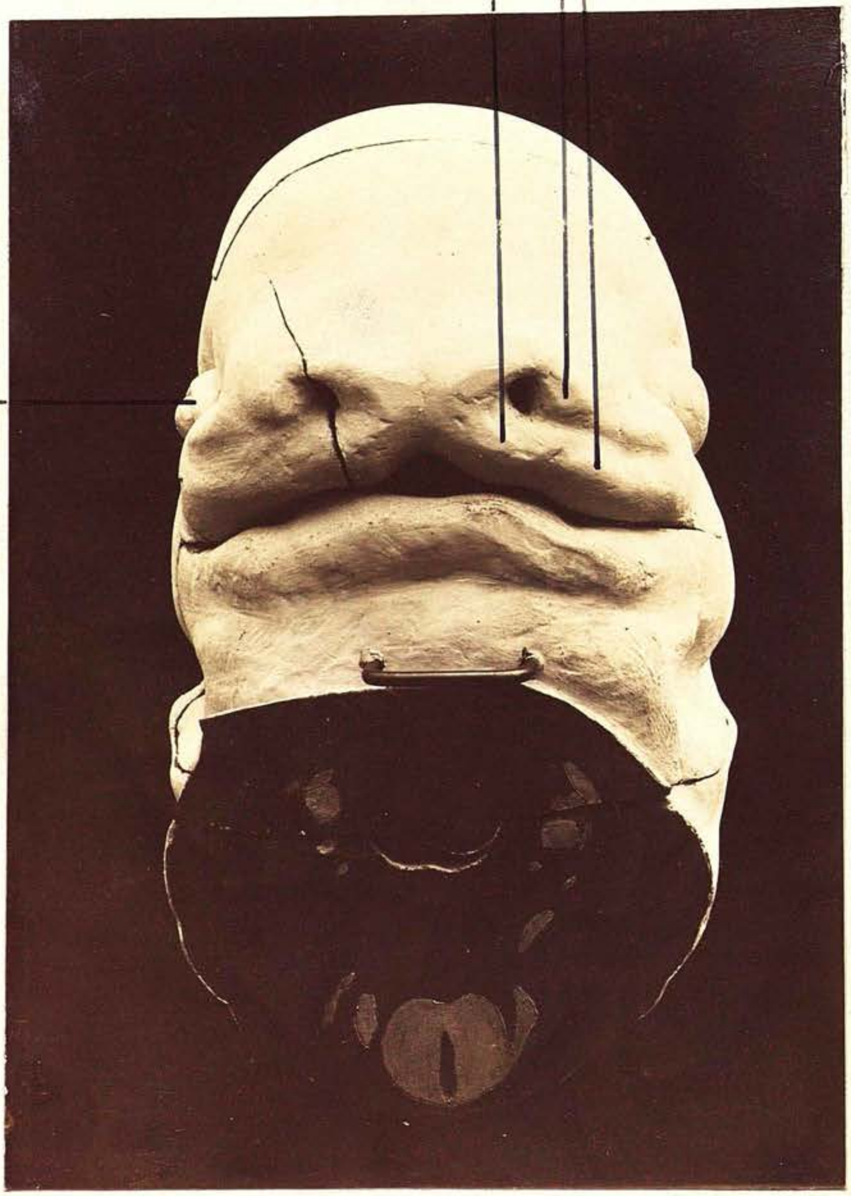
their /

their early appearance and common origin from the lateral wall of the nose. He confirmed the observations of Peter upon the development of the ethmoidal conchae. The conchae are classified into respiratory and olfactive groups. The former are disposed in the anterior part of the cavity, the latter more posteriorly.

Frazer (1911) studied the formation of the nasal cavities in man. He described an ingrowth from the deeper part of the maxillary process which is supposed to form part of the roof of the cavity and is applied as a superficial layer on the lateral wall of the septum. According to him the globular processes form the anterior extremities of the maxillary ingrowths.

Later stages of the development of the conchae and accessory sinuses have been fully studied by Killian in 1896 and by Schaeffer in 1910 and 1911, who found that on the average three to five ethmoidal conchae are differentiated before birth.

Fig. I.



Model od I4.5 mm pig embryo showing face. The three processes can still be distinguished in the upper jaw.

C 2 XXX

PERSONAL OBSERVATIONS.

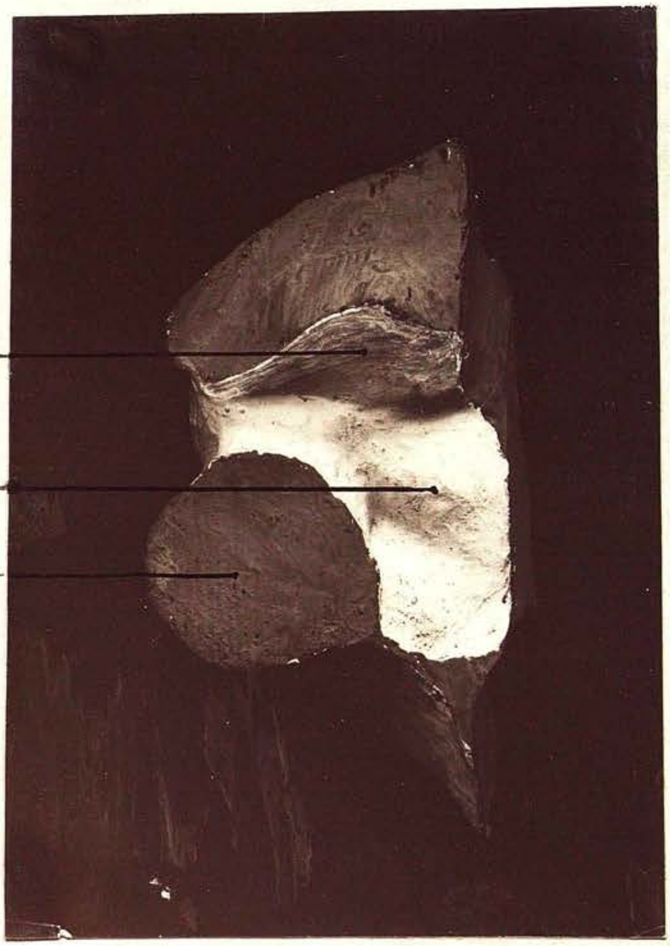
Pig Embryo 14.5 mm. V.B.

Fig. I.

The embryo was measured in alcohol. A wax plate reconstruction model was made of the head regions. It was thus seen that the head is flexed on the trunk so that the chin rests on the chest wall. The three flexures of the brain can be distinguished through the superficial tissues. The eyes are directed laterally and show as yet no trace of any eyelids. The two layers of the optic cup are still partially separated from each other, the outer layer having a well marked deposit of pigment, while the lens is hollow with a crescentic cavity. The primitive processes which form the upper lip and face have united into a definite snout. The anterior nares are widely separated from each other and directed forwards. The first and second visceral arches are still distinguishable on the outside of the neck. The external auditory pit is as yet only a simple depression with no indication of tubercles. The labyrinth has scarcely begun to coil and the semicircular canals are making their first appearance as small ridges on it.

The nose is a closed cavity somewhat retort shaped in profile. The vestibule of the nose is narrow and about 0·2m.m. in length, but immediately behind this the cavity increases both in height and depth. It is bounded below in its anterior portion by the fused globular and maxillary processes, further back it is separated from the buccal cavity by the

Fig.2.

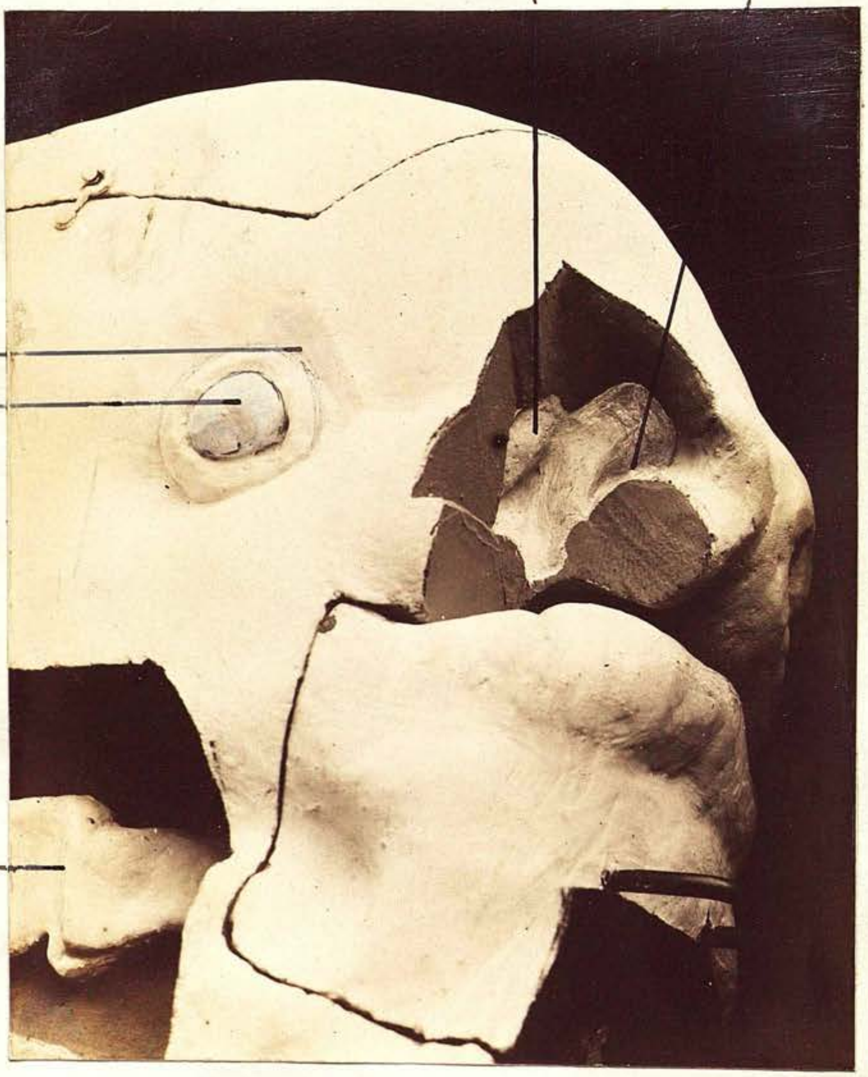


Lateral wall of nose of I4.5 mm pig embryo showing maxillo and nasoturbinals. C 2 XXX bucco-nasal membrane.

The lateral wall of the nose presents (Fig.2) several irregularities of surface. Running along the whole length of the wall near the roof from the anterior nares to the posterior or dorsal limit of the cavity is a distinct ridge which I take to be the naso-turbinal. Below this the maxilloturbinal or concha inferior is seen as a shorter and more rounded swelling, bounded below by a distinct horizontal furrow, which is much deeper at its anterior end. It terminates here in a small pit, which lies above the anterior limit of the bucconasal membrane. This depression is prolonged outwards into the mesenchymal tissue as a solid bud of epithelium which forms the nasal end of the naso-lacrimal duct. Below this again the wall is convex and is apparently composed of the mesial surface of the maxillary process. The bucco-nasal membrane is attached along its edge.

The naso-lacrimal duct in this embryo is interrupted. It commences as a linear bud of epithelium at the inner canthus of the eye and runs for a short distance (150 μ) parallel with, and connected by a stalk to, the bottom of the groove marking the line of union of the lateral nasal process with the maxillary process (fig.25). It then turns in mesially and becomes disconnected with the aforementioned groove and ends blindly in the mesenchymal tissue.

Fig.3.



Model of I4.5 mm pig embryo showing mesial wall of nose, primitive palate, and bucconasal membrane.

C_2XXX

The small bud which I have mentioned projecting from underneath the maxilloturbinal approaches it without actually meeting it, their ends being separated by a distance of .4 m.m.(400 μ) (fig. 26)

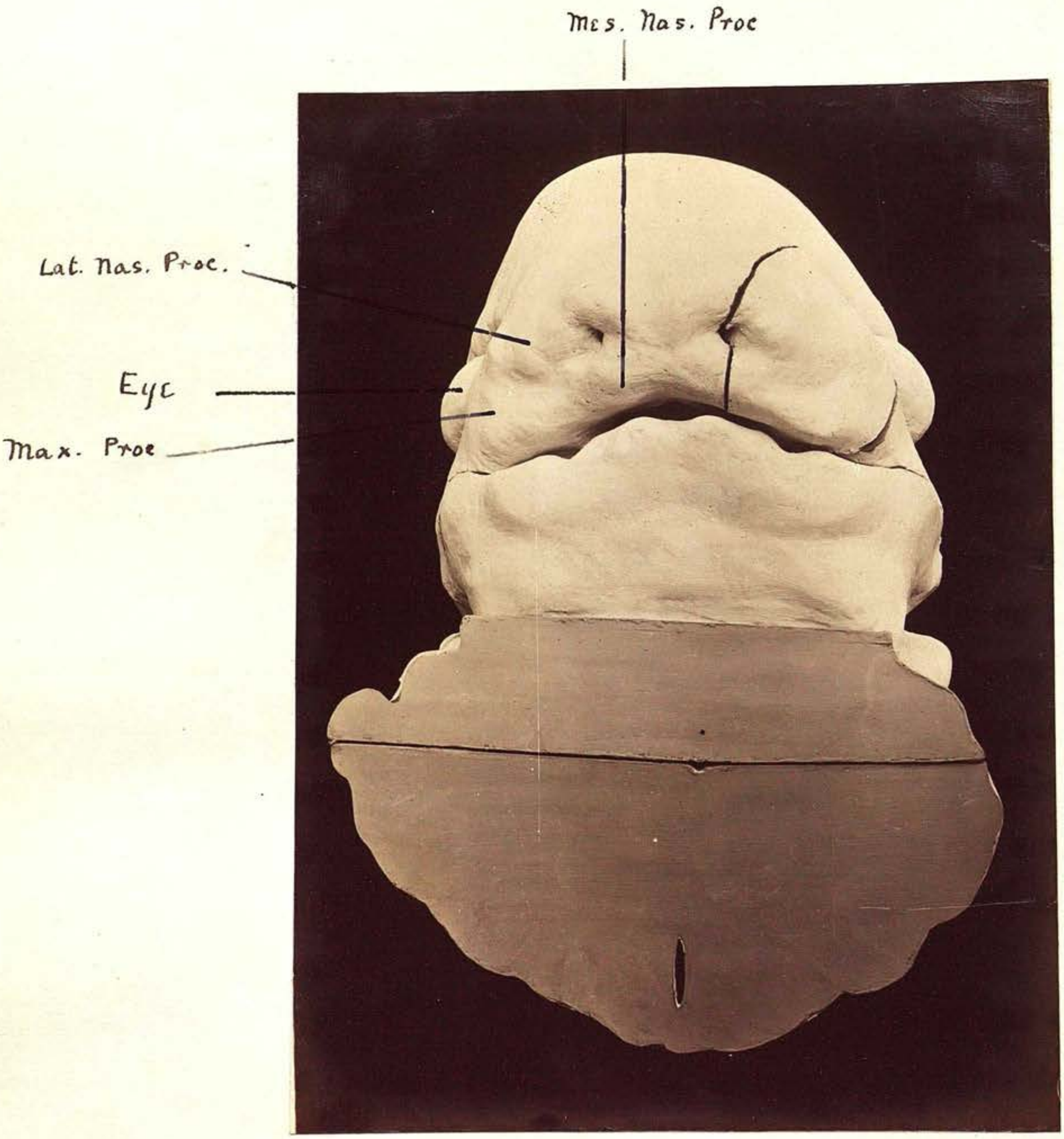
The mesial wall of the nose is more irregular than the lateral nasal wall. Immediately within (Fig.3) the anterior naris nasal orifice, the wall sinks in rapidly so as to widen the cavity from side to side. Thus the anterior part of the septum looks as much backwards as laterally. A little behind this is a thick prominent ridge overhanging the groove representing Jacobson's organ and running obliquely downwards and backwards to just behind the posterior or dorsal end of the primitive palate. Below this, the wall slopes outwards, coming to ~~be~~ lie more horizontally and forming part of the floor of the nose. The globular process is still quite evident and apparently forms the whole of the medial wall in front of and below Jacobson's organ. In order to open up the nose, the model has been divided through the primitive palate in that portion formed by the globular process. Dorsal to this, the cut edge of the bucco-nasal membrane is seen. In the model its thickness has been somewhat exaggerated through technical difficulties in reconstructing it of the proper thinness. Dorsal to the ridge bounding Jacobson's organ above is an angle, dorsal and superior to which

the /

the medial wall presents a rounded bulge, which also occupies part of the roof of the cavity. This swelling is lined by a thick layer of columnar epithelium and is richly supplied by nerves from the olfactory region of the forebrain. This, in the light of Peter's researches, I look upon as the rudimentary ethmoturbinal.

In this embryo there is as yet no nasal capsule. There is merely a slight condensation of the mesenchymal tissue in the middle of the septum nasi.

Fig. 4.



Model of I6.5 mm pig embryo from the front. To show general state of development. C 2 XXXII

Pig Embryo 16.5 m.m. V.B.

Fig.4.

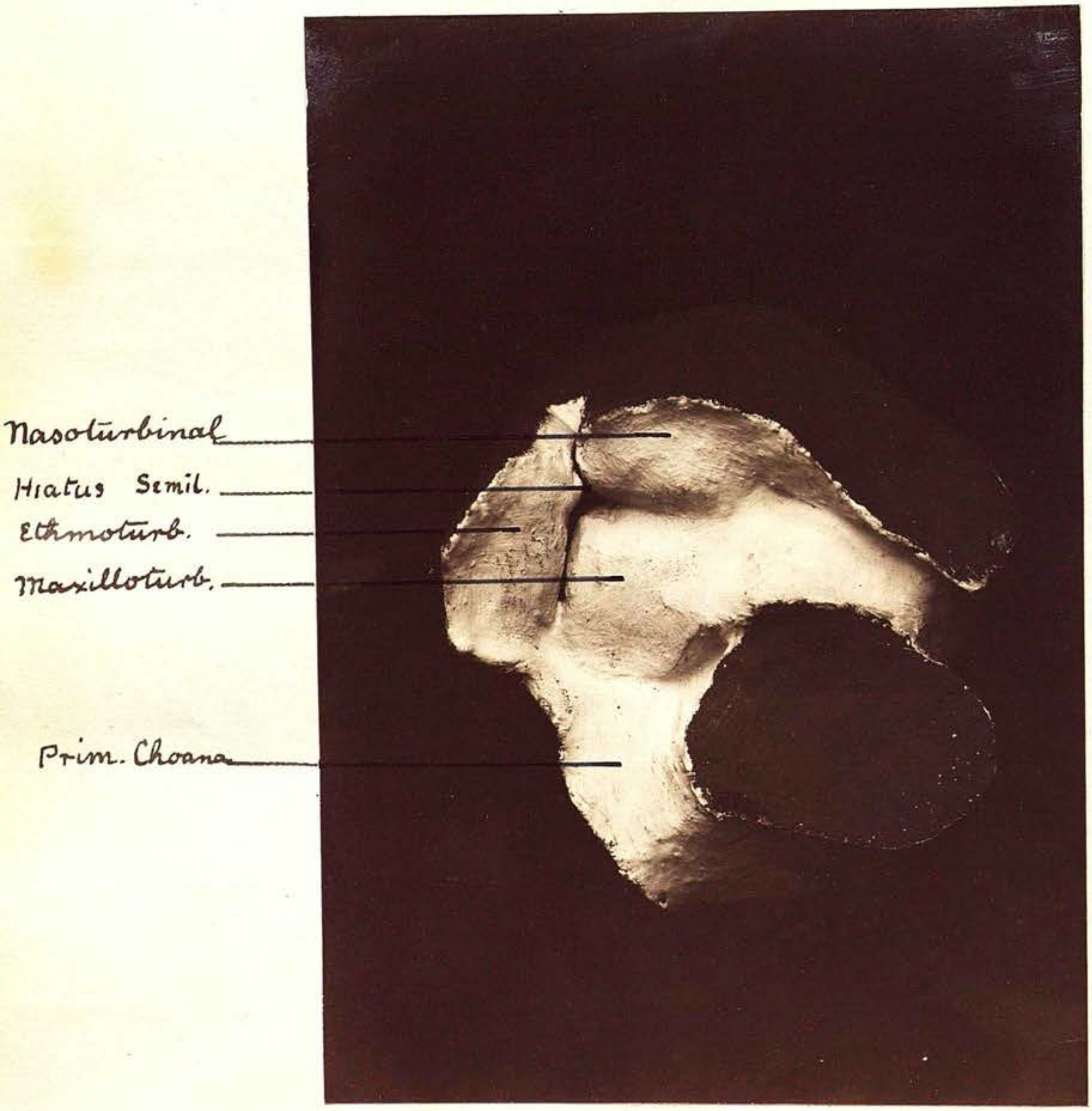
The embryo was measured in alcohol and has been reconstructed by the wax plate method at a magnification of 50.

The general form of the head is somewhat similar to that of the previous specimen, but the forebrain has grown considerably and the forehead is separated from the snout by a shallow fronto-nasal groove. The eyes are prominent and surrounded by a deep groove, but the eyelids are as yet absent. The snout projects beyond the mandible, and the nostrils, which are directed forwards and outwards, are overhung by distinct alae nasi. The second visceral arch can still be distinguished from the mandible on the outside of the neck. The ear pit is now an elongated depression whose ventral end burrows in deeply under an overhanging edge. The posterior margin of the pit shows a prominent projection, which is the beginning of the concha.

The nasal cavity has increased in length since the last stage and now communicates with the buccal cavity by means of the primitive choana, behind which the cavity extends still a short distance dorsally. On the lateral wall the nasoturbinal is more distinct, and is bounded behind by a deep fissure which is almost vertical in direction (Hiatus Semilunaris.).

Below /

Fig.5.

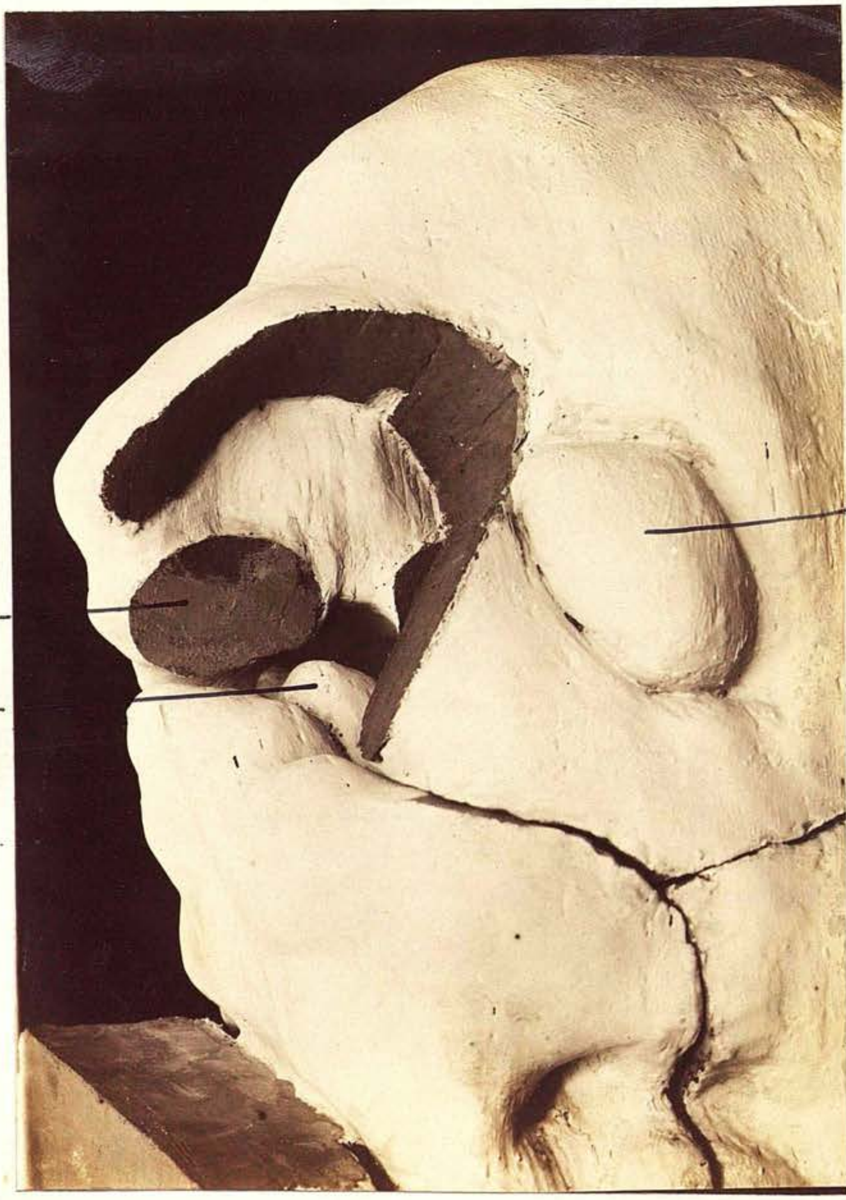


Lateral wall of model of nose of 16.5 mm pig embryo showing ethmo-,naso-,and maxilloturbinals. The primitive palate also seen in section. C 2 XXXII

Below the nasoturbinal the maxilloturbinal has also grown and extends from near the anterior naris to the lower end of the hiatus. It is separated from the nasoturbinal by a sulcus which runs into the hiatus at right angles. It is also bounded by another sulcus, which, at the hinder end of the primitive palate, deepens suddenly and is connected with the solid lacrimal duct, the two ends of which have now united. The eye end of the lacrimal duct in this specimen is bifurcated. In the upper and hinder part of the lateral nasal wall a prominent swelling is seen which is bounded in front by the deep fissure of the hiatus semilunaris already mentioned. This is the ethmoturbinal and it will be noticed that it has migrated from its former position on the mesial wall and roof to one on the lateral wall and roof. It is covered by a thick layer of columnar epithelium which is richly supplied with olfactory nerves, which stream down from the forebrain. These olfactory nerves do not reach the nasoturbinal but stop short at the edge of the ethmoturbinal.

The mesial wall of the nose shows a well developed Jacobson's organ, which consists of a small canal opening into the nose at the dorsal end of the primitive palate, and bounded above and behind (cranio-dorsally) by a projecting margin. (Fig.30).

Fig. 6.



Model of 16.5 mm pig embryo with lateral nasal wall removed showing septum and choana. C 2 XXXII

In front of (ventral to) Jacobson's organ the mesial nasal wall is concave but dorsal to it the wall shows a uniform convexity. The surface of the septum on the whole is more simplified than in the 14.5 m.m. embryo.

(Fig.6) The nasal capsule is now making its appearance as a prechondral condensation which is now quite distinct in the septum. The roof and lateral plates are however still rather indefinite. The paraseptal cartilages are merely condensed mesenchyma.

Pig Embryo. 20 m.m. V.B.

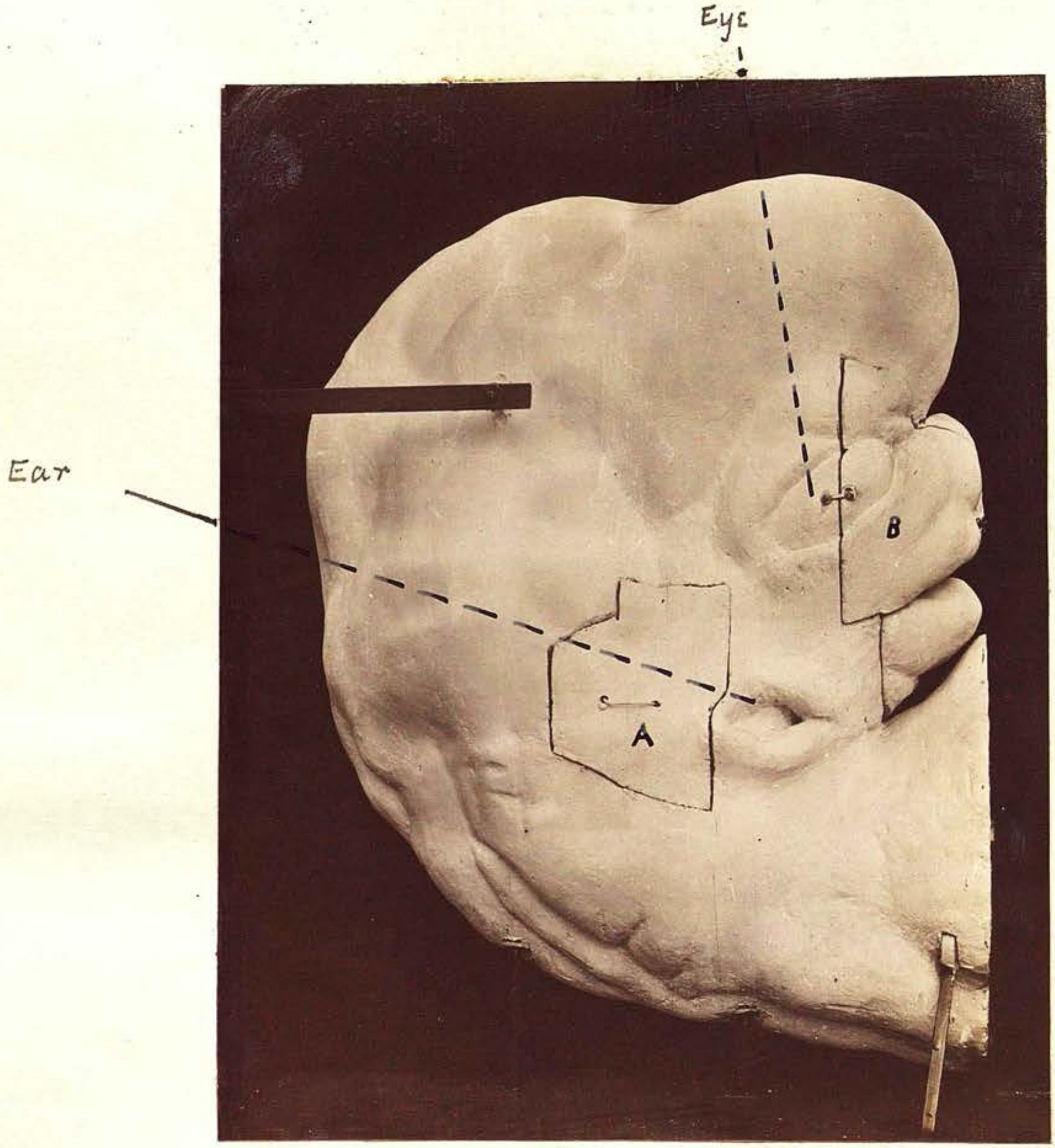
Figs.31,32,33.

The maxilloturbinal has now grown considerably and projects much more distinctly from the rest of the nasal wall than before. It is bounded below by a groove which extends also laterally to it, thus freeing its lower edge. The nasoturbinal is also more distinct, and, as before, bounds the hiatus semilunaris ventrally. Turning off ventrally from the deep part of the hiatus semilunaris one sees a small diverticulum. This I look upon as the commencement of the infundibulum ethmoidale (fig.32)

The mesial nasal wall is, if anything, a little flatter than in the last stage but Jacobson's organ shows very little change.

The nasal capsule is now very distinct although still in the prechondral stage. The septum is connected above and in front with two thin lateral plates which arch over and close in the sides of the nose. The capsule is quite open below.

Fig. 7.



Model of head of 20 mm human embryo showing general form. The same model is shown in fig 34 with the parts A & B removed to show the interior. C2XXXV

Human Embryo 20 m.m. V.B.

Fig. 7.

The embryo was obtained by operation and measured fresh. Reconstructed at a magnification of 50. The head is markedly flexed on the trunk so that the chin lies almost in contact with the front of the pericardium. The three primary flexures of the brain are well seen and the cerebral vesicles form a prominent frontal region which is sharply divided from the nose by a deep fronto-nasal groove. The nose is in the form of a snout, there being no bridge and the tip being directed upwards. The nostrils are widely separated from each other and directed forwards. They are partially occluded by epithelial plug and are bounded by broad alae nasi. The mouth is open and allows the tip of the tongue to be seen. The lower lip has underneath it a distinct double chin, probably due to the second arch. The eyes are directed laterally and are partly covered by eyelids. The external ear is a wide oval pit deepest at its ventral end and surrounded by a raised slightly irregular edge.

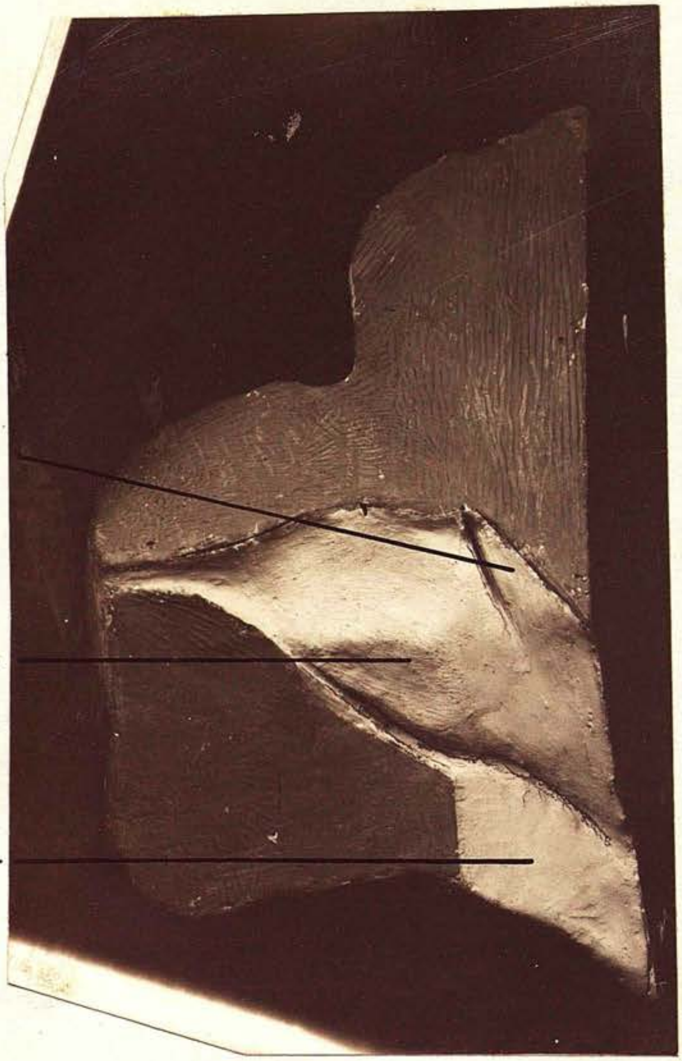
The nasal cavity opens on to the face by means of a narrow vestibule, which is partly occluded by epithelial plug. More dorsally the cavity increases in depth, the floor sloping down rapidly to the posterior edge of the primitive palate. The /

Fig. 8.

Ethmoturbinal I.

Maxilloturbinal.

Palatal Process.



Lateral wall of nose of 20 mm human embryo.

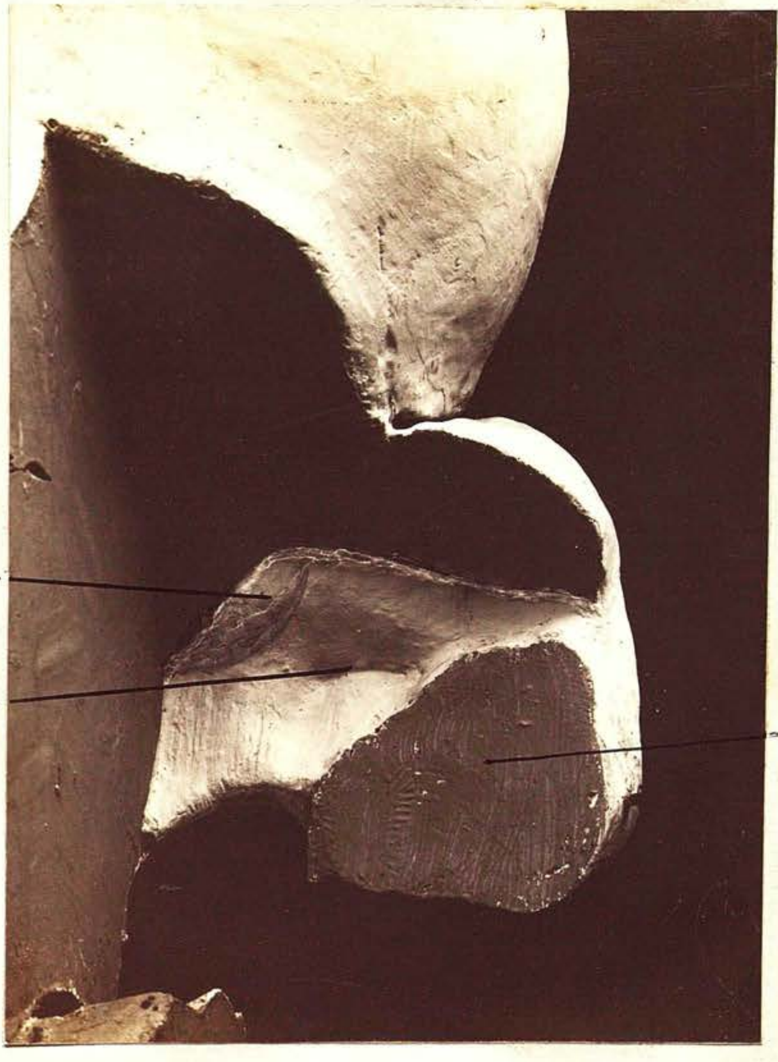
C 2 XXXV

The buccal and nasal cavities communicate by means of the primitive choana, from which all trace of bucco-nasal membrane has disappeared.

The lateral nasal wall is still fairly (Fig.8) simple. The maxilloturbinal is seen as a ventro-dorsal ridge about its middle and is bounded below by a narrow groove. The latter is the inferior meatus and its deepest part is connected with the solid naso-lacrimal duct. Above the maxilloturbinal the wall shows a uniform concavity in its ventral two thirds. The hiatus semilunaris is a short deep fissure in its posterior third, running obliquely from the roof caudally and also to a lesser extent dorsally. The ventral boundary of this is rounded a little and is the only representative of the nasoturbinal. The dorsal and cranial corner of the lateral wall separated off by this fissure represents the ethmoturbinal. In this region the epithelium is thicker than elsewhere on the lateral wall and numerous olfactory nerve fibres can be seen to supply it. The lateral boundary of the choana is seen to be formed by the palatal process of that side. It is sharply divided off from the maxilloturbinal by an extension of the groove representing the inferior meatus.

On the mesial nasal wall Jacobson's organ is an open groove in the bottom of a depression. In the upper and hinder part of the septum is a rounded swelling with a definite lower margin. (Fig.9).

Fig. 9.



Mesial wall of nose of 20 mm human embryo.

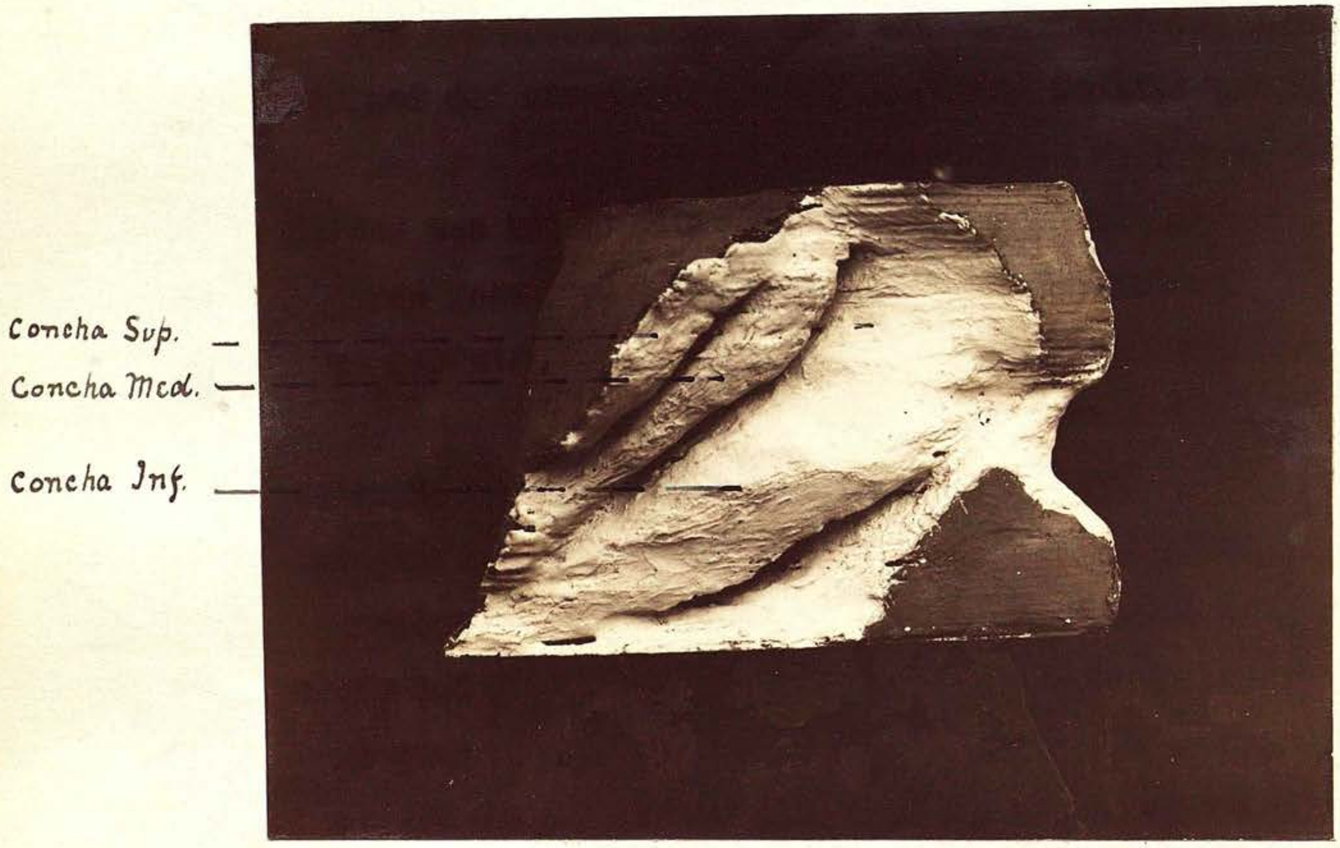
C 2 XXXV

The epithelium here is thick and supplied by olfactory nerves. Possibly this may be the commencment of a second ethmoturbinal. (Figs.35 - 36).

The nasal capsule is very rudimentary, being only a condensation of mesoderm which is most distinct in the septum. The lateral plates are still very indefinite.

On comparing the foregoing models and taking into account the state of development of the other organs on is struck by the poor development of the nose in man as compared with the pig.

Fig. IO.



Lateral wall of model of nose of 30 mm human embryo showing the conchae inferior, middle and superior. C 2 XXXI

Human Embryo, 30 m.m. V.B.

Fig. 37.

The head is now extended and the brain and cranium have grown very large in proportion to the face. The fronto-nasal groove is now absent although the nose is still very short and somewhat upturned. The nostrils are placed close together but are still directed forwards. The eyes look forwards and are partly covered by the eyelids. The lower lip begins to show some slight indication of a chin.

The nasal cavities are large and are taking on the adult form. They open at their dorsal ends into the naso-pharynx, which has become delimited by the half united palate.

The lateral nasal wall (fig.10) is occupied in nearly half of its area by the maxilloturbinal or concha inferior, which commences a short distance behind the anterior naris and extends along the whole length of the cavity. Its lower edge hangs free in the cavity in the greater part of its length but is attached at each end. The inferior meatus is wide and its lateral wall slopes in a smooth curve down into the floor of the nose. There is a large atrium meatus medii behind which the concha media (Ethmo-turbinal I) hangs down. The latter presents a distinct genu in its lower border at its anterior end. The mesial nasal wall is almost quite smooth.

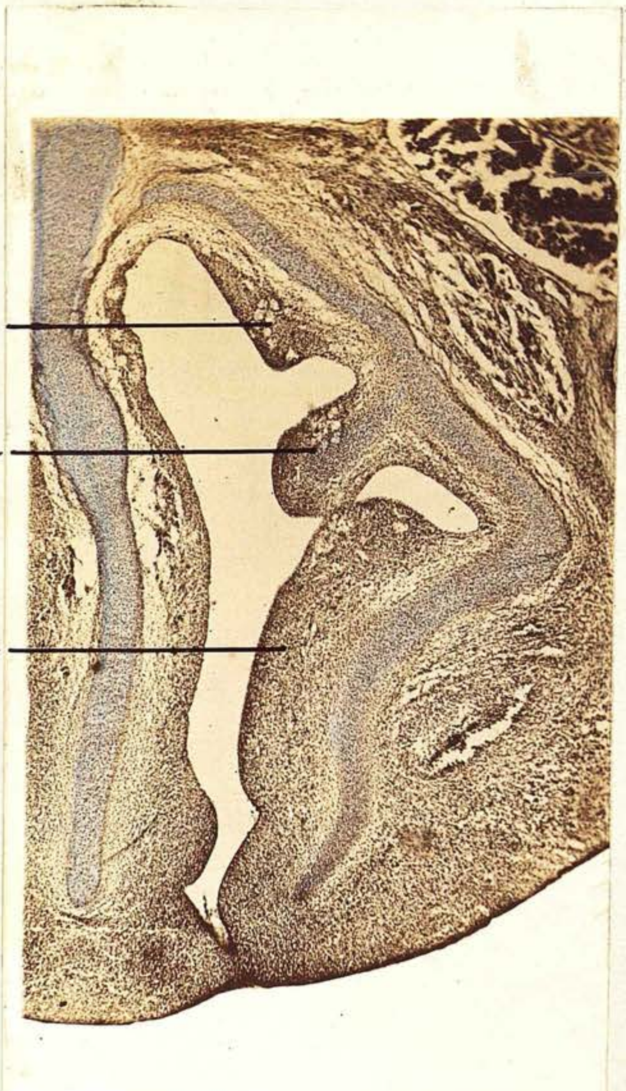
There /

Fig. II.

Concha Sup.

Concha Med.

Concha Inf.



Section of nose of 30 mm human embryo showing nasal capsule and conchae.

There is just a faint groove indicating the position of Jacobson's organ.

In this embryo there is a fairly complete cartilaginous skeleton of the nose. The Septal cartilage is roughly quadrilateral and is attached to the sphenoid by its postero-inferior (dorso-caudal) angle. Its upper edge is free and projects up in front to form the crista galli. The anterior or ventral edge in its upper half is continuous with the lateral plates of the nasal capsule, while its lower half is free and curves down into the inferior or caudal edge. The lateral walls of the nasal capsule are continuous with the septum in front. From there they arch outwards over the nasal cavities to lie lateral to them. Seen from the outside each is markedly convex, its posterior border curling round to meet the back of the septum. The lesser wing of the sphenoid lies in contact with its upper edge but apparently has not united with it. The cribriform plate has not yet appeared, there being still a gap in that part of the capsule. The mesial surface of the lateral plate is concave and presents two prominent ridges projecting from the surface. These are the skeletal bases of the conchae inferior and media. Projecting caudally from the antero-inferior angle of the plate there is a pointed projection or spur which curves in mesially underneath the nostril. See Figs. II & 38 - 41.

In the angle between this space and the inferior turbinal the nasal duct curves inwards. At the antero-inferior corner of the septum there is on each side a small flat plate of cartilage (Cart. Parasept). The vomer is a short wide gutter in which the cartilage of the septum rests. It is a membrane bone and is partly ossified. It occupies a position just behind the paraseptal cartilages and is over-lapped to a certain extent by them.

Development of the Nose.

In the study of the development of the nose it has been shown by Kölliker (1863), Peter (1911) and others that its first appearance is in a form of thickening of the epithelium on the side of the anterior end of the forebrain in front of the optic vesicle. This thickened olfactory area (Riechfeld of His) appears in the human embryo of about the third week. In the fourth week the olfactory area becomes converted into a shallow depression by the growth of the tissues round its edges. The growth of the margins of this primitive olfactory pit continuing, in the fifth week the mesial and lateral nasal processes are formed bounding it on either side. At the same time the Maxillary process has grown forwards and is separated from the lateral nasal process by a short groove.

The older embryologists, Kölliker, Dursy, His, &c, believed that these processes fused together, leaving a communication behind, between the primitive nasal fossa and the mouth cavity, and this constituted the primitive choana. The roof of the buccal cavity in front of the choana is the primitive palate. (Dursy) His in Anatomie menschlicher Embryonen H.III, P. 33, says: /

says:- "Die Nasenhöhlen entstehen, in später zu beschreibender Weise, aus den flachen Nasengruben, und sie nehmen dabei die Form zweier Spalten an, die mit einem schrägen Schlitz nach vorn und nach unten hin sich öffnen. Unter einer jeder dieser Spalten bildet sich, vermöge einer direkten Verbindung des mittleren Stirnfortsatzes mit dem Oberkieferfortsatz, eine Querbrücke und es haben nun dieselben je zwei getrennte Oeffnungen, das nach vorn gekehrte <u>äussere Nasenloch</u> und die nach abwärts sehende <u>primitive Choane</u>. Die Brücke welche sich durch Verbindung des mittleren Stirnfortsatzes mit den beiden Oberkiefern gebildet hat, und welche die Mundspalte von oben her begrenzt, bezeichnen wir mit Dursy als <u>primitiven Gaumen</u>."

This was disproved in 1891 by Hochstetter, who, working on cat and rabbit embryos, showed that the nasal and buccal cavities are shut off from each other by a thin epithelial membrane (Membrana Bucco-nasalis) and do not at first communicate. This membrane later ruptures, and the primitive choana is thus established. In 1892 Hochstetter discovered for the first time the bucco-nasal membrane in a human embryo. The date of rupture is placed by Schaeffer at the 35th to the 38th day. Hochstetter also stated that the primitive palate was formed by the union of the mesial nasal process with the lateral nasal process. These observations were confirmed by Keibel (1893) who summarised as follows /

follows:- " (1) Die Nasenhöhle ist bei den von mir untersuchten Säugern (Katze, Meerschwein, Schwein) und dem Menschen in frühen Entwickelungsstadien, ein blindes Säckchen.

In diesem Stadium giebt es also keine Rinne, welche die primitive Mundhöhle mit der primitiven Nasenhöhle verbindet, und die Choane entsteht in der von Hochstetter geschilderten Weise secundär.

(2) Die erste Anlage des primitiven Gaumens kommt durch die Anlagerung des lateralen Nasenfortsatzes an den medialen Nasenfortsatz zu stande, nicht durch die Anlagerung des Oberkieferfortsatzes an den medialen Nasenfortsatz."

With the regard to the closing in of the nasal fossae and the development of the face, the view of Höchstetter, that the maxillary process was not directly concerned in the formation of the anterior naris, was opposed by Peter (1902) who held that the maxillary process did take part in the limiting of the nares. In 1911 Peter again demonstrated that in a 10.3m.m. human embryo the maxillary process formed the outer part of the floor of the anterior naris. The lateral nasal process was completely shut off from the primitive palate by the union of the maxillary process with the mesial nasal process.

On the question of the formation of the

primitive /

primitive palate, I wish to associate myself with Peter when he states that the mesial nasal process and the maxillary process together form the primitive palate. This is so in an 8.5 m.m. human embryo, which I have examined, the lateral nasal process being quite separated from the primitive palate . Peter also asserts, however, that in a slightly later stage the lateral nasal process forms a small part of the front of the primitive palate. This is also borne out in a 14.5 m.m. Pig embryo. When one examines the face one sees that the greater part of the primitive palate is formed by the mesial nasal process.(fig. I) It is difficult to say whether the lateral nasal process or the maxillary process forms the rest of the palate, but when one examines a section through the snout just behind the anterior nares, one sees that both lateral nasal and maxillary processes enter into its composition. The edge of the lateral nasal process covers the maxillary process and forms the floor of the nose at this part. (fig.26) A little further dorsally, however, the primitive palate is formed entirely of mesial nasal and maxillary processes.

The true or definitive palate is developed as two folds, which grow in from the lateral wall of the primitive buccal cavity. These palatal folds are at first directed downwards and lie at each side of

the tongue,/

tongue, which arches up between them. Later on, the floor of the mouth and tongue sink away from the roof, and the palatal processes now assume a horizontal position, and, growing towards the middle line, begin to fuse with each other from before backwards. The nasal septum grows downwards from the roof of the bucco-nasal cavity to meet the palatal processes, which it does also from before backwards. This growth of the septum and palate causes the choanae to change their position to one further back, which they retain permanently.

Before going further it may be advisable to study the rôle played by the mesial nasal, lateral nasal, and maxillary processes in the formation of the various parts of the nasal cavity.

Frazer (1911) has advanced a theory in which the postero-inferior part of the primitive nasal septum is developed as an outgrowth from the maxillary process. He writes as follows:- "But there is another process of the maxillary mass which has not been mentioned so far: this is a solid ingrowth from its highest or deepest part, extending inwards over the roof of the general cavity, and turning downwards and forwards on the lateral and back aspect of the septum to reach the globular region.

The septal ingrowth is found in the early

stage /

stage figured in this paper (5 weeks), and, by its lower and front enlargement, seems to be responsible for the existence of the globular process.

In the sixth week the ingrowth is a thick condensation with a well marked border, forming the roof of the deepened groove and approaching the middle line as it is traced forwards and downwards."

If this be so, then the bilateral character of the vomer with its relationship to the septal cartilage is explained, as is also the course of the naso-palatine vessels and nerve. I think, however, that the actual facts of the case are scarcely sufficient to justify the theory. I have examined with great care the region in question in 15 m.m. and 20 m.m. human embryos, as well as pig embryos of 14.5, 16.5 and 20 m.m., a sheep of 15 m.m. and a series of ferrets at a corresponding stage of development. I have been unable to find evidence of a process such as Frazer describes. I have made reconstructions of several of the embryos and the others I have examined with the microscope alone and find it impossible to differentiate two layers on the septum.

As has already been mentioned, the maxillary process fuses with the mesial nasal process to form the primitive palate. From the primitive palate the premaxilla develops and its posterior limit is at the

canal /

canal of Stenson, which is connected with the organ of Jacobson. Now the hinder end of the organ of Jacobson reaches the posterior margin of the primitive palate, and so I think one may say that the premaxilla corresponds with that portion of the primitive palate formed by the mesial nasal process.

The definitive palate is developed, except for the premaxillary part, as the palatal processes from the mesial aspect of the maxillary processes and first visceral arches.

The lateral nasal process is responsible for the origin of the maxilloturbinal and nasoturbinal. In pig, human and ferret embryos the line of fusion between the lateral nasal processes and the maxillary process is oblique, the inner surface of the lateral nasal process extending to a much lower level than its outer surface. One can see the line of fusion to a certain extent as the mesenchyma of the lateral nasal process is much denser than that of the maxillary process, and shows a fairly clear line of demarcation. The position of the nasolacrimal duct also helps to make clear the line of fusion. It is seen in a 14.5 m.m. pig embryo that the whole of the lateral wall of the nose is formed by the lateral nasal process, and that the maxillary process only forms the lateral wall of the inferior meatus. In a

16.5 m.m. /

16.5 m.m. pig, a 15 m.m.sheep and a 20 m.m. human embryo the conditions are the same, except that the palatal processes are more developed and form part of the floor of the nasal cavity. The ethmoid region has also begun to encroach on the lateral nasal wall.

The ethmoidal region is derived from the mesial wall of the nasal cavity in mammals as was shown by the work of Peter (1902) who followed the stages in a series of rabbit embryos. In a rabbit of 3.5 m.m. headlength there is an angle on the medial wall of the nose (Knickung der medialen Wand) dividing the surface into an upper and a lower part. The upper area bulges into the cavity and is covered by thick epithelium. This area is seen to bend more and more outwards till it forms the roof of the cavity, still later it comes to lie on the lateral wall, and from it the two lower ethmoidal turbinates are developed. Further ethmoidal turbinates are developed as separate ingrowths from the hinder part of the roof of the cavity.

As regards the origin of the primitive ethmoidal conchae from the septal wall, from observation of a series of ferret and pig embryos I can confirm the statements of Peter. In a pig of 14.5 m.m. V.B. the ethmoturbinal is on the hinder and upper part of the mesial wall. That part of the nasal wall

is /

is composed of a layer of epithelium much thicker than elsewhere in the nasal cavity. The olfactory nerves also are seen to spread out on the roof and mesial wall and are not seen on the lateral wall. In a pig of 16.5 m.m. the ethmoturbinal occupies a position partly on the roof and partly on the lateral wall of the nose, but mostly on the latter. It is separated from the naso-turbinal by a very deep fissure. As in the previous specimen the olfactory nerves spread out over the ethmoid region, but do not supply the naso-turbinal. The epithelium also is much thicker there than in the lower parts of the nose.

Schönemann (1901) derived the ethmoturbinal from what he called the Basiturbinal, which lay along the roof of the cavity, and correspond with some of the stages described later by Peter, and with my specimens. However, he thought that all the ethmoturbinals came from the same swelling, viz, the Basiturbinal.

Dieulafé (1908) agrees with Peter in asserting that the ethmoturbinals are developed from the medial wall. He places the maxilloturbinal and naso-turbinal in the same group, his reason being that the nasoturbinal and maxilloturbinal are the earliest to appear. This I cannot agree with, as in mammals the ethmoturbinal is the first to appear, while in man the maxillo-turbinal is the first, followed by the ethmo-turbinal, while the nasoturbinal does not become dis-

tinct /

distinct till very much later.

In the human embryo Peter was unable to trace the growth of the ethmoturbinal from the medial wall, owing to lack of material. The youngest specimen of his, in which the ethmoturbinal was seen showed it on the lateral wall.

In a 20 m.m. human embryo, whose nasal region I have reconstructed, the mesial wall in its postero-superior part presents an angle at and above which the epithelium becomes very much thicker than below. Above the angle the medial wall bends outwards and that part is richly supplied by olfactory nerves. On the lateral wall two swellings are seen divided by a deep fissure running from the roof obliquely downwards and backwards. The thickened epithelium of the roof is prolonged down to line both sides of the fissure. The upper swelling I take to be ethmoturbinal I, while the lower one is the maxilloturbinal or concha inferior. The lower margin of the fissure is all that represents the nasoturbinal in this embryo.

Development of the Septum Nasi.

The mesial wall of the nasal cavity at first presents a more irregular surface than the lateral wall. In its early stages the organ of Jacobson occupies a relatively large part of its area. It is represented about the period of the rupture of the bucconasal membranes by a deep curved groove, which extends from near the anterior naris backwards and downwards to the ventral end of the primitive choana. It is bounded above by a thick projecting fold. The groove later becomes converted into a canal with an opening at its ventral end. As the septum grows, the projecting ridge above it gradually disappears, and finally the ventral end of the organ itself disappears. Its dorsal end, however, which is placed at the posterior end of the primitive septum on either side, persists and becomes identified with Stenson's canal (Röse 1893, Harvey 1882, Peter 1902-1903)

Lateral Nasal Wall.

In the earliest stages of its development the lateral nasal wall is more simple than the mesial nasal wall. In a 35 day human embryo it is quite smooth and the turbinates have not yet begun to appear. (Schaeffer.) About the 40th day the concha inferior or maxillo-turbinal makes its first appearance as a smooth bulge on the lower part of the lateral wall (Schaeffer.) Paulet describes the head of a human embryo of 14·7 m.m. whose age he gives as 35 days or a little more. In this the inferior turbinate has already appeared. This swelling is bounded above and below by shallow grooves, the inferior meatus and part of the middle meatus. Peter describes the nose of a 15 m.m. human embryo (37-38 days) as follows:- "Die laterale Wand lässt zwei Wülste erkennen: einen grossen, fast bis zum Hinterende des Sackes reichenden, aus welchem sich die untere Muschel, das Maxilloturbinale, formt, und im vorderen Teil einen schwächeren, durch eine Rinne von dem ersten getrennten Wulst, in dem ich eine frühe Anlage des später verschwindenden Nasoturbinale sehe."

The slightly varying results of these authors are probably due to the embryos being measured in some cases before, and in others after fixing.

It will thus be seen that in the human embryo the maxilloturbinal is the first to appear.

Peter (1902) describes an embryo with a headlength of 5 m.m.. In it the maxilloturbinal and the ethmoturbinal are already formed. The nasoturbinal has not yet appeared. In an older embryo (28 m.m.) there is still no appearance of the nasoturbinal. My own observations coincide with those of Peter. In a human embryo of 20 m.m. total length (seven and a half weeks) the maxilloturbinal and the ethmoturbinal are well developed (fig. 8). Immediately below the ethmoturbinal is seen a deep curved cleft bounded below by a fairly sharp margin, This, I take it, is the beginning of the infundibulum ethmoidale. The lower edge of this cleft is thicker in front than behind & is separated from the maxilloturbinal by a very shallow groove. This is all that represents the nasoturbinal in the human embryo of this age. The thick epithelium of the roof of the cavity extends down on the lateral wall to the upper part of the maxilloturbinal.

I was unfortunately unable to obtain a human embryo between 20 and 30 m.m. In the latter however, the concha inferior is large and overhangs a roomy meatus inferior. Two other turbinals are present, the first and second ethmoturbinals. The nasoturbinal has not yet appeared.

In other mammals, such as the pig, rabbit, ferret, &c, the ethmoturbinal is the first to appear (Peter 1902.) Soon /

Soon after this the maxilloturbinal becomes distinct, followed rapidly by the nasoturbinal. In other mammals also the nasoturbinal is much better developed than in the human embryo. In the pig it forms a well marked longitudinal swelling extending from the anterior naris back to end below the ethmoturbinal in the posterior part of the cavity.

With regard to the homology of the nasoturbinal Seydel (a), Schönemann (b), and Peter (c) are firmly of the opinion that the nasoturbinal has nothing in common with the ethmoturbinals either in its origin or adult relations. Killian, (1896) on the other hand classifies the Nasoturbinal with the ethmoturbinals as his "erste Hauptmuschel".

I am strongly inclined to agree with Seydel, Schönemann and Peter that on account of its origin, the nasoturbinal ought not to be grouped with the ethmoturbinals but with the maxilloturbinal. The fact that the naso and maxilloturbinals are developed from the lateral wall, and moreover probably from the same primary division of the face, viz the lateral nasal process, while the ethmoturbinals are developed from the medial wall, are, I think, sufficient grounds to justify this view.

A.B.C. - see next page.

(a) Seydel (1899) writes:- "Das Nasoturbinale einschliesslich seines Processus uncinatus ist von den übrigen echten Siebbeinmuscheln scharfzu trennen. Wie in Form und Lage im erwachsenen Zustande, so ist es auch in seiner ontogenetischen Entwicklung von diesen verschieden. Es stellt sich als eine erst im Säugetierstamme selbst entstandene Bildung dar."

(b) Schönemann (1901)says:- "am besten wird man wohl unterscheiden zwischen Muscheln, welche dem Basiturbinale und solchen, welche den äusseren Wänden der Nasenhöhle (inclus.Nasoturbinale) angehören, also zwischen conchae basiturbinales und conchae parietales incl. nasoturbinales."

(c) Peter (02) "das Nasoturbinale mit den Ethmoturbinalia nichts gemein hat, sondern mit dem Maxilloturbinale in eine Gruppe, die der vorderen seitlichen Muscheln zu vereinigen ist."

The Nasolacrimal Duct.

With regard to the development of the nasolacrimal duct there was considerable diversity of opinion among the early investigators. K.E. v. Baer † advanced the theory that it was an outgrowth from the primitive buccal cavity, while Burdach * thought that it was an epithelial fold growing in from the inner canthus. Erdl (1845) was the first to point out that it developed in the line of fusion between the lateral nasal process and the maxillary process. Legal (1883) made a series of careful observations in pigs a a few other mammals and concluded that the duct originates as a thickening of the epithelium in the floor of the groove marking the site of union of the maxillary and lateral nasal processes. This thickened line of epithelium becomes constricted off from the surface in the greater part of its length.

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† In Ueber Entwickelungsgeschichte der Tiere. T.II.P. 219, he states:- "Der Thränengang stulpt sich auch hier (bei Säugethieren) aus der Rachenhöhle gegen das Auge hervor und liegt Anfangs hinter den Muscheln,die nur, indem sie sich verlängern, sich über ihn ziehen."

* In Physiologie als Erfahrungswissenschaft writes:- "schon in der achten Woche erscheint in ihm (i.e.der innere Augenwinkel) die Karunkel und eine zur Mundnasenhöhle sich senkende Hautfalte als Anfang des Thränenkanals."

forming a cord of epithelial cells lying parallel to the surface and connected with it by a thin membrane. On section this shows as a pear shaped bud connected with the groove by a thin stalk. Towards its ventral end this bud sinks inwards curving toward the inferior meatus of the nose. It now meets with a bud growing from the inferior meatus and in this way the continuity of the duct is established. He further states that the duct is originally single at the eye end and that the other canaliculus grows later from the original one.

From my own observations I can confirm Legal's results. In a pig of 14·5 m.m. (figs. 25,26) the duct is represented by a linear bud connected with the surface epithelium along its whole length while parallel to the surface. The length of this part of the duct is 160μ. Ventral to this it sinks in and approaches a solid projection from the inferior meatus but does not meet it, so that the duct at this stage is completely interrupted. In a sheep of 15 m.m. the two ends of the duct have united, as they have also in a pig of 16·5 m.m. In the 16.5 m.m. pig also the eye end of the duct has bifurcated although in the previous stages it was single. This was described by v. Ewetzky in cow embryos, but Legal had not seen it in a pig of about the same age. In a human 20 m.m. embryo the

continuity /

continuity of the duct is established but it is rather difficult to say whether it is bifurcated at the eye end or not as the sections are rather damaged in this region. The duct is a well formed structure in a 30 m.m. human embryo and arches out from the inferior meatus under the edge of the nasal capsule and up towards the eye. It presents a fair lumen but that is due in this case probably to the epithelium having become detached.

Development of the Skeleton of the Nose.

As is seen from the description of the detailed stages, the skeleton of the nose is laid down at first as a slight condensation of the mesenchyma, which later becomes prechondral tissue, and still later true cartilage. The septal condensation is attached behind to the basis cranii and in front is connected with two vertical lateral plates which arch over to meet the septum and form part of the roof in front, The lower edges of the septum and lateral plates are free so that the capsule is open below.

The paraseptal cartilages make their appearance as early as the septal cartilage and lie below and somewhat in front of Jacobson's organ. According to Röse, Anat.Anzeiger 1893, "Der sogannte Jacobson'sche oder Luschka'sche Knorpel ist lediglich der Basalteil der ursprünglich einheitlichen knorpeligen Nasenkapsel, welches sich secundär vom gemeinsamen Knorpelgerüste differenzirt hat," They have nothing to do with Jacobson's organ and really become secondarily separated off from a common mass. Spurgat (93) names them Cartilagines basales narium. I cannot agree with Röse where he says that the septum and paraseptal cartilages are derived from a single mass and only secondarily separated. As far as my own observations go, the septum and paraseptal cartilages are developed

separately /

separately from the beginning. Into the question as to whether they have any connection with Jacobson's organ I am not prepared to enter.

The shape of the nasal capsule remains very much the same until the 9th or 10th week; beyond this stage I have not gone. At this age (9-10 weeks), the capsule is completely chondrified (fig II). On the inner surface of the lateral plate are seen two prominent ridges which form the skeleton of the conchae inferior and media. The vomer has appeared as a shallow bony gutter in which the lower edge of the septum lies. The paraseptal cartilage of each side is a flat plate of cartilage, the dorsal edge of which encloses the ventral end of the vomer. The cribriform plate is formed eater by an extension from the plate of cartilage representing the lesser wing of the sphenoid. Certain of the bones of the nose, such as the vomer, sup. maxilla and the palate bone, are laid down in membrane. Figs. 38 - 41.

The later stages in which ossification takes place in the cartilage do not come within the scope of this paper, which is only intended to cover the period during which the turbinals make their first appearance.

Summary.

(1) The olfactory organ makes its first appearance in the form of a localised thickening of the epithelium on each side of the forebrain. This later becomes a depression or pit bounded by three raised edges, the mesial nasal, lateral nasal and maxillary processes.

(2) The olfactory pits are bounded laterally by the lateral nasal processes, mesially by the mesial nasal processes and inferior by the united mesial nasal and maxillary processes. They are blind sacs, their deepest extremities approaching the roof of the mouth.

(3) The primitive palate is formed by the fusion of the mesial nasal process with the maxillary process, its greater part being composed of the former. The lateral nasal process in the early stages does not enter into its conposition at all, but somewhat later it grows inwards to form a small part of the floor of the nose in its most anterior part. The line of fusion of the maxillary and mesial nasal processes dorsally becomes a thin lamina called the bucconasal membrane, which finally ruptures and thus establishes the primitive choana.

(4) The premaxillary part of the permanent palate is derived from the mesial nasal process,

while /

while the rest of the palate is derived from the maxillary process, excepting part of its posterior edge (**Uvula and** ant. pillar), which come directly from the mandibular arch.

(5) The lateral wall of the inferior meatus of the nose is developed from the maxillary process, while the maxilloturbinal or concha inferior, and the nasoturbinal are derived from the lateral nasal process. The ethmoturbinals, however, come originally from the deepest and most dorsal part of the mesial nasal process.

(6) In man the first turbinal to appear is the maxilloturbinal, followed somewhat later by the ethmoturbinal. The nasoturbinal is quite a late development.

In other mammals (pig, ferret, &c.) the ethmoturbinal is the first to appear. Next in order comes the maxilloturbinal, followed quickly by the nasoturbinal.

(7) I am of opinion that the maxilloturbinal and the nasoturbinal should be classified together in one group on account of their common origin from the lateral nasal process. The nasoturbinal has nothing in common with the ethmoturbinals, which have their origin from the mesial wall of the nose.

(8) The nasolacrimal duct is developed in the line of fusion of the lateral nasal process with

the maxillary /

maxillary process as a solid cord of epithelial cells lying a short distance below the surface. This cord commences at the inner canthus and runs parallel to the surface and connected with it by a thin lamina. At its forward end it sinks in deeply, and, losing its connection with the surface, it unites with a solid epithelial bud, which grows out from the anterior end of the inferior meatus of the nose. A short time after the continuity of the duct is established, the eye end of the duct bifurcates to form the canaliculi. From this time onwards the duct remains almost unchanged, its lumen not being established until late foetal life.

(9) The nasal capsule consists at first of a bar of condensed mesenchymal tissue, running down from the basis cranii to the anterior end of the septum and giving off two lateral wings, which arch over the nasal cavities and form their lateral walls. The paraseptal cartilages are also present from the beginning as prechondral condensations. Later on the capsule becomes chondrified and still later partially ossified, while additional membrane bones are laid down, which also form part of the nasal skeleton.

Development of the Buccopharyngeal Cavity.

Historical Survey of Literature.

Born (1883) in studying the floor of the mouth described a median swelling between the first and second arches. It had a forward prolongation on each side into the first or mandibular arches and appeared to be mainly derived from first arch elements. He named it the "Schaltstück" and asserted that the whole of the body of the tongue was developed from it. The root of the tongue grew from the second arches and the epiglottis from the third.

His (1885) described a swelling similar to the Schaltstück and named it Tuberculum impar. the two ends of the second arches united to form another swelling which he named the Copula. He agreed with Born in stating that the body of the tongue was formed from the tuberculum impar and the rest of the tongue from the copula.

Hammar (1901) working on human embryos went into the development of the tongue and salivary glands. He concluded that the tub. impar. was only a transitory structure, but stated further that it formed a small area in front of the foramen caecum. The root of the tongue was formed from the second arches. The third arches did not enter into its composition at all.

Kallius (1905) studied the development of the

tongue /

tongue in birds, and in 1910 in the pig. In the latter the tub. impar. is a small triangular slightly raised area on the floor of the mouth between the first and second arches in the middle line. Later it extends laterally into the under side of the first arches, where it ends in two raised tubercles which develop into the papillae foliatae. The ventral angle of the tub. impar is enclosed between the two lateral tongue rudiments, which grow in from the first arches. The tip and sides of the tongue develop from the lat. tongue rudiments, while the dorsum as far back as the foramen caecum develops from the tub. impar. The root of the tongue grows from the copula and second arches.

Moldenhauer (1877) in investigations on the development of the mouth and pharynx described a Colliculus palatinus which grew from the upper jaw and passed backwards to end in the under surface of the first arch. It was bounded dorsally or aborally by a deep groove running out into the first visceral pouch and named by him Sulcus tubo-tympanicus. This sulcus later became the Eustachian tube and part of the tympanic cavity.

His (1885) was of the opinion that the second pouch gave rise to the tonsillar fossa and the fossa of Rosenmüller. Some years later (1901) he changed his views & denied that the fossa of Rosenmüller was derived from the second pouch.

Kastschenko (1887) also thought that the

fossa/

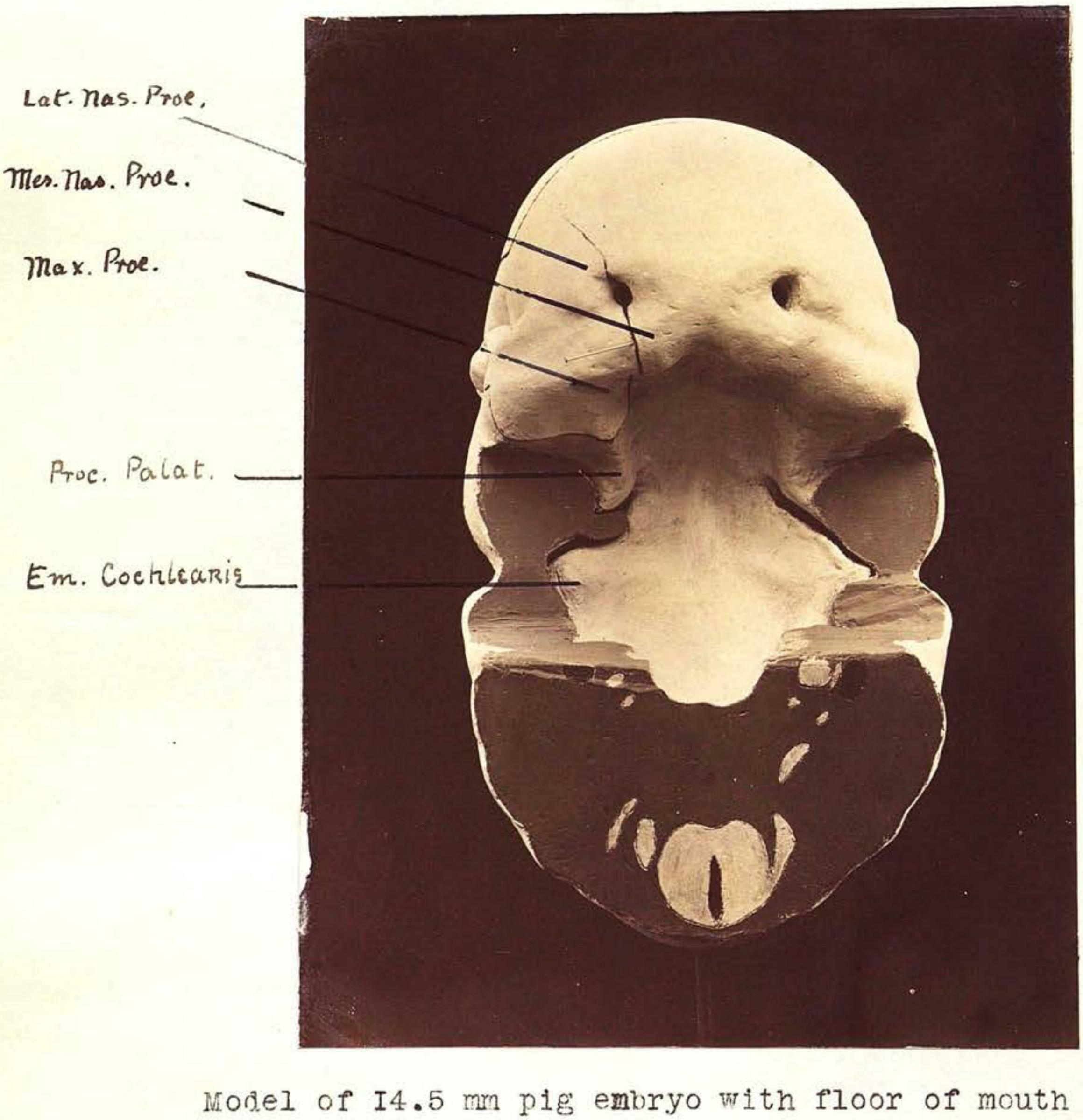
fossa of Rosenmüller was derived from the second pouch.

Hammar (1902) studied the fate of the first visceral pouch in man. In addition to the Sulcus tubo-tymp. he described a Sulcus tymp. post., and a Sulcus tensoris tympani. The middle ear and tube are developed from these three sulci which are all derived from the dorsal extension of the first pouch. The dorsal extension of the second pouch also enters into the composition of the ear. He stated also that the handle of the malleus is derived from the second arch and not from the first.

In the same year he took up the development of the tonsil, which he found to develop from the second pouch, its first appearance being in the third month.

Sudler (1901) studied in the human embryo the buccopharyngeal cavity as a whole, at the same time following the development of the derivatives of the pharyngeal clefts. Most of his attention was devoted to the latter.

Fig. I2.



Model of I4.5 mm pig embryo with floor of mouth removed to expose buccopharyngeal cavity. Note eminentia cochlearis and palatal processes.

Personal Observations.

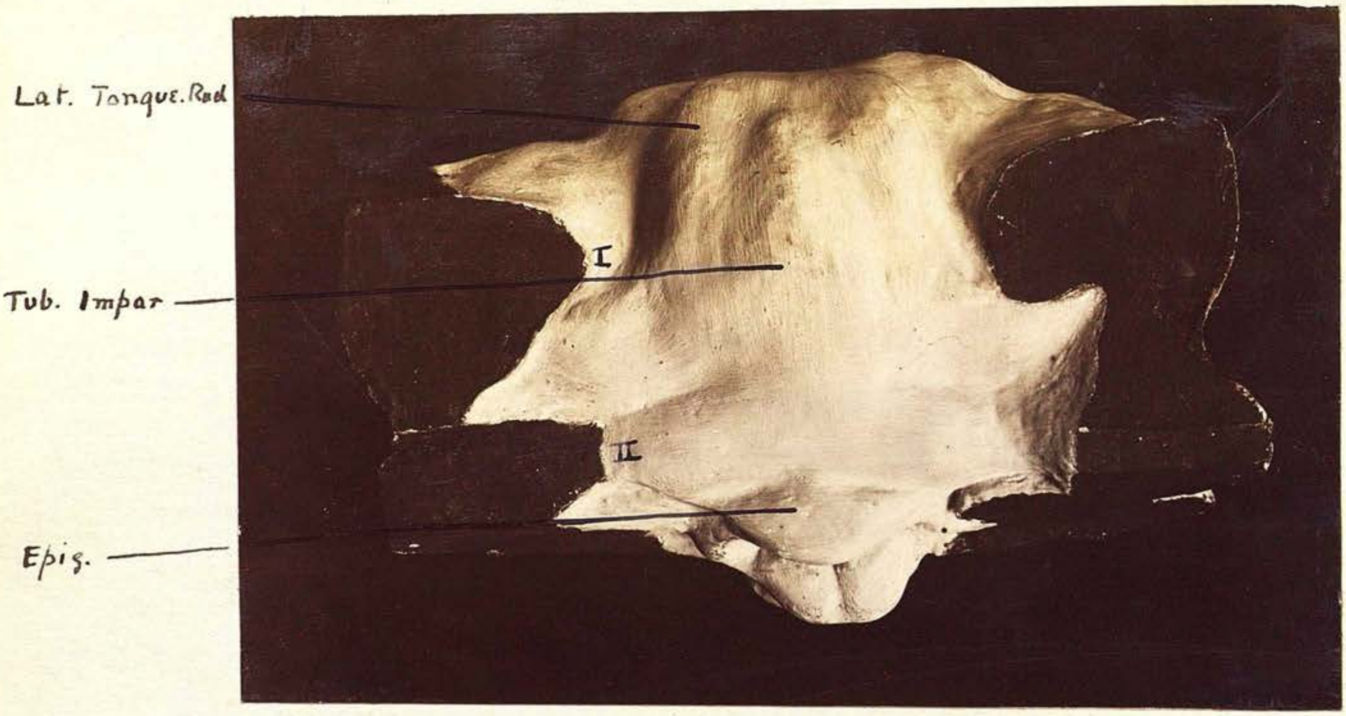
Pig Embryo 14.5 m.m. V.B.

On removing the floor of the buccopharyngeal cavity of the model it is seen that its shape is roughly triangular. The widest part or base of the triangle is the oral fissure, while its apex is at its junction with the oesophagus. To describe it in a little more detail :- The thick mandibular arches encroach on the cavity at its oral end causing a sudden narrowing (fig. 12). Aboral from this the cavity widens considerably into the first pair of pouches. At the level of the second pair of pouches, which are deep, it is still very wide, but aboral from this the cavity becomes suddenly much narrower, owing to the projection of the third pair of arches. The third pouches are small, and below this the cavity tapers rapidly into the oesophagus, whose lumen is uniformly narrow. The cavity, seen from the side, presents a fairly uniform curve with a ventral concavity.

On looking at the floor of the mouth, the lower lip on each side of the middle line presents a rounded elevation bounded laterally by a distinct sulcus. On the floor of the mouth the developing tongue forms a large elevation (figs. 13,14), in which the various elements entering into its composition are

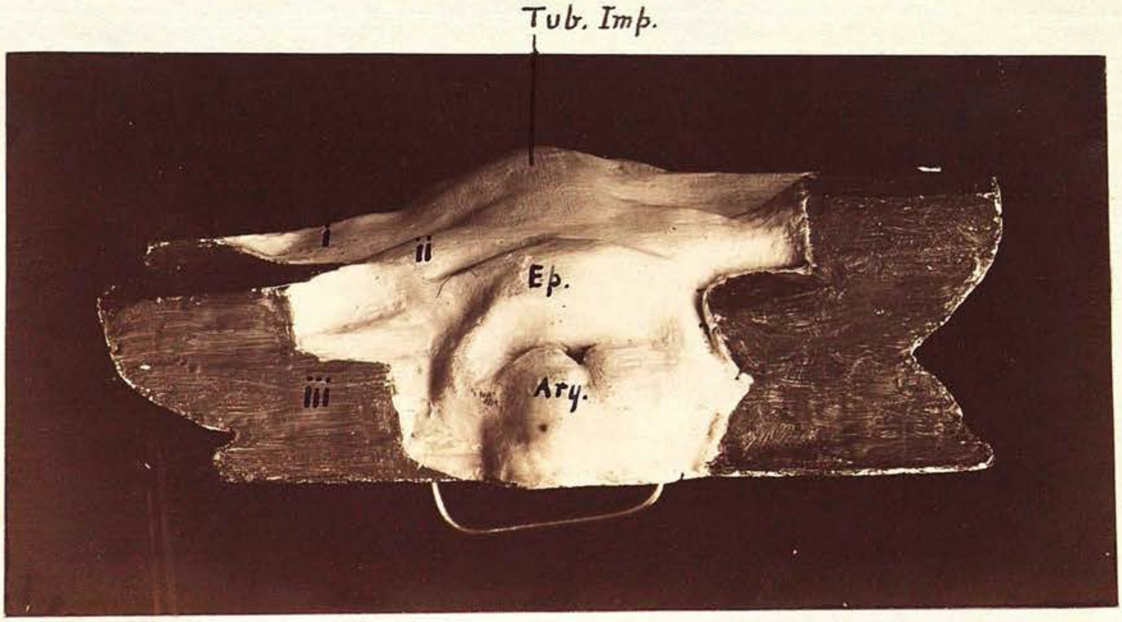
clearly /

Fig. I3.



Floor of mouth of I4.5 mm pig embryo showing tub. impar, lateral tongue rudiments, and root of tongue. Epiglottis and aperture of larynx also seen. FITS INTO C2XXX

Fig. I4.



Same model seen from behind. FITS INTO C2XXX clearly visible. Thus, the tip of the tongue, which is not yet distinctly separated from the mandible, is seen to be formed from two lateral swellings, growing from the mesial ends of the first arches. These have been called by various investigators the lateral tongue rudiments (seitliche Zungenwülste). These lateral tongue rudiments enclose the tip of a pointed median elevation. The posterior part of this ridge broadens out into two lateral extremities which end on the under or aboral surface of the first arches. In the light of the researches of Kallius, I take this to be what was originally tuberculum impar. Immediately aboral from this the root of the tongue is seen to be formed by the second arches which are separated from the tuberculum impar by a shallow groove.

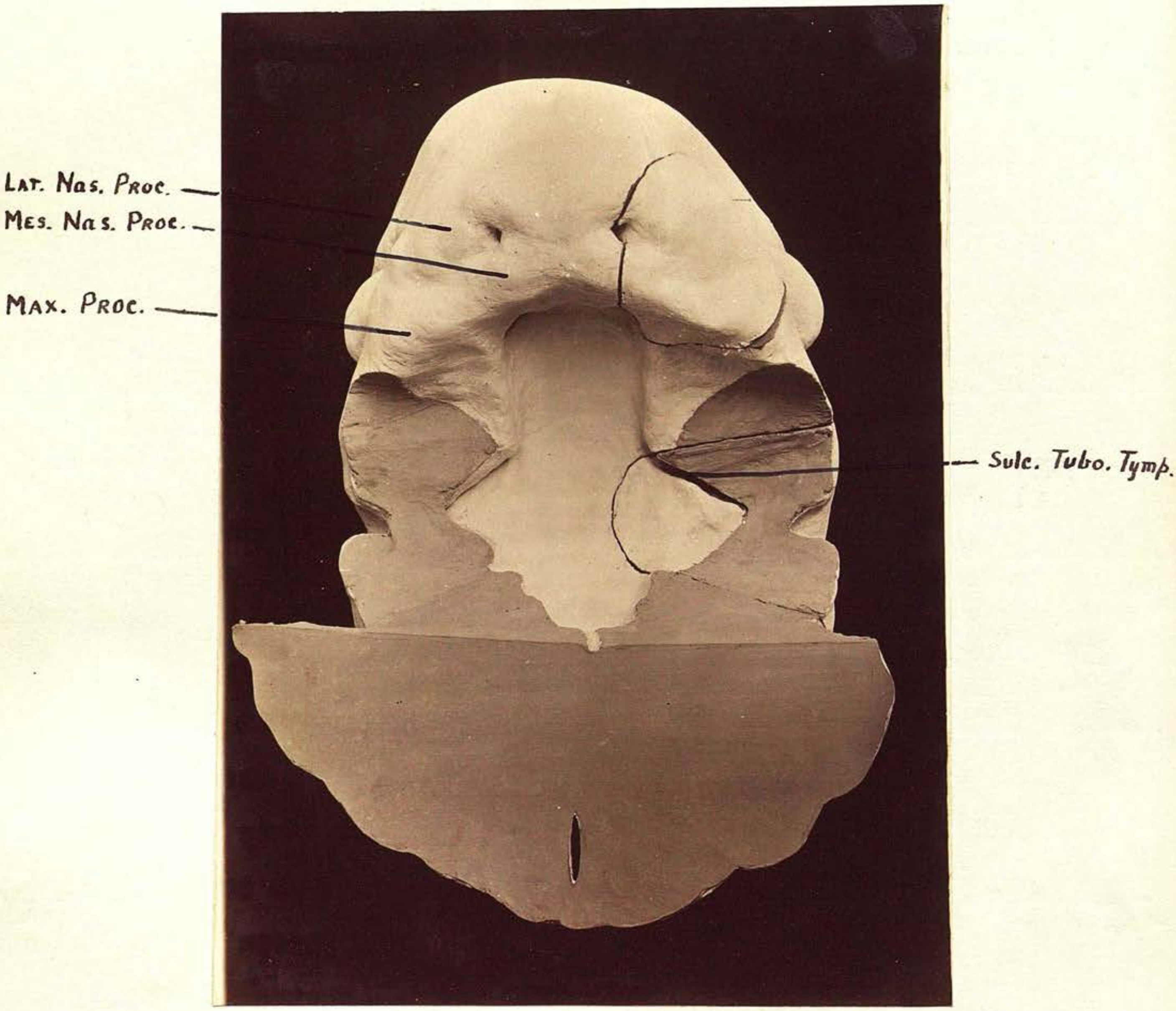
T he epiglottis is well formed and projects back over the upper aperture of the larynx, It is connected with the root of the tongue by a median glosso-epiglottic fold. Two lateral glosso-epiglottic folds also run out into the second arches. The laryngeal aperture is bounded laterally by well marked aryepiglottic folds, while posteriorly two large rounded swellings lying in contact with each other are seen. These structures form a very prominent projection on the ventral wall of the pharyngeal Cavity. The ventral extensions of the first, second and third /

third pouches are still visible while attached to the III pouches are seen the thymus buds.

The margin of the upper lip shows a median notch. On either side of this are the globular processes, which are limited laterally by a less distinct notch marking the line of fusion with the maxillary process. At the oral end of the roof of the mouth on either side there is a depression marking the site of the future primitive choana which is still closed by the bucco-nasal membrane. Lateral to and aboral from these two depressions one sees on each side a ridge (processus palatinus) running from before backwards along the roof of the mouth. (fig. I2). It begins in front on the under surface of the maxillary process, and as it passes back it becomes more elevated till it reaches the level of a deep fissure (sulcus tubo-tympanicus), which runs in a latero-aboral direction. At this point it takes a bend outwards and loses itself in the under surface of the first arch. It is seen to form the lateral wall of the sulcus tubo-tymp. The palatal process is much more distinct where it is attached to the first arch, than where it is connected with the maxillary process. Bounding the sulcus tubo-tymp. aborally there is a prominent swelling on the roof of the pharynx which is caused by the underlying tip of the cochlea (eminentia cochlearis). From this a distinct ridge runs backwards to meet the

third /

Fig. 15.



Model of 16.5 mm pig embryo showing roof of buccopharyngeal cavity. Note that the palatal process bounds the sulcus tubo-tympanicus. C 2 XXXII third arch and is caused by the internal carotid artery which lies deep to it. At the level of the third cleft the posterior pharyngeal wall presents a striking peculiarity. A shallow median pouch is seen here with a wide transverse orifice directed orally, (fig.42). It is to be noted also in connection with this that it lies at a considerably lower level than the laryngeal aperture. Below this point the pharynx passes down uneventfully into the œsophagus.

<u>Pig Embryo 16.5 m.m. V.B.</u>

General form of the Buccopharyngeal Cavity. (fig.I5).

As in the 14.5 m.m. pig the cavity is widest at the angle of the mouth. Behind this it is constricted by the massive mandibular arches, while opposite the first clefts it again widens. From this point backwards or aborally it narrows with only faint indications of the third and fourth pouches at its lateral borders. It ends just behind the fourth pouch by narrowing suddenly into the Oesophagus, the lumen of which is crescentic and uniformly narrow.

Several changes have occurred in the roof of the cavity since the 14.5 m.m. stage. The bucco-

nasal membranes /

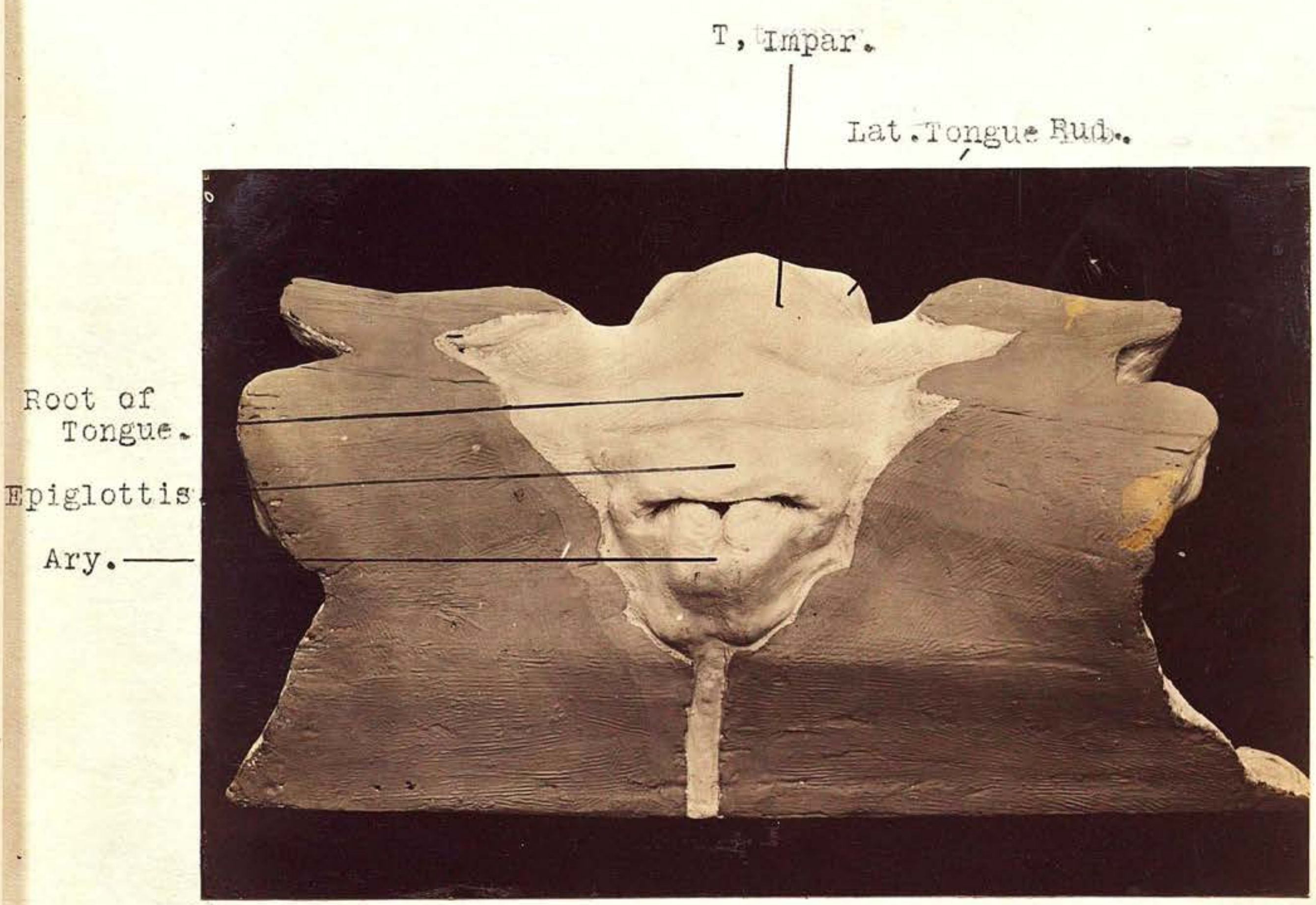
membranes have disappeared and the primitive choanae are thus constituted. The primitive palate and lip margins have grown so as to increase the depth of the cavity. The free edge of the septum lies distinctly more deeply than the primitive palate and is delimited from it by a transverse groove. The palatal processes also have grown downwards into the cavity more than before. As in the 14.5 m.m. pig their aboral ends are seen to fade away on the under surface of the first arches, and to constitute the ventro-lateral wall of the first cleft. The latter has not altered much from the last stage. The cochlear eminence on one side is a little more prominent than on the other. From the cochlear eminence also a low ridge passes aborally into the third arch , partly due to the internal carotid artery which underlies it. On the middle of the posterior pharyngeal wall there is a fairly large pouch or diverticulum,(fig. 43), which has a wide transverse orifice directed upwards i.e. orally. The pharynx ends abruptly a short distance below this in the commencement of the oesophagus.

A dental lamina is present in the upper and lower jaws, but as yet no tooth buds have formed.

The shape of the under lip is very similar to that of the 14.5 m.m. embryo. There is still a raised median area on the lower lip bounded laterally by two deep wide depressions. Two shallow grooves

containing dental /

Fig. 16.

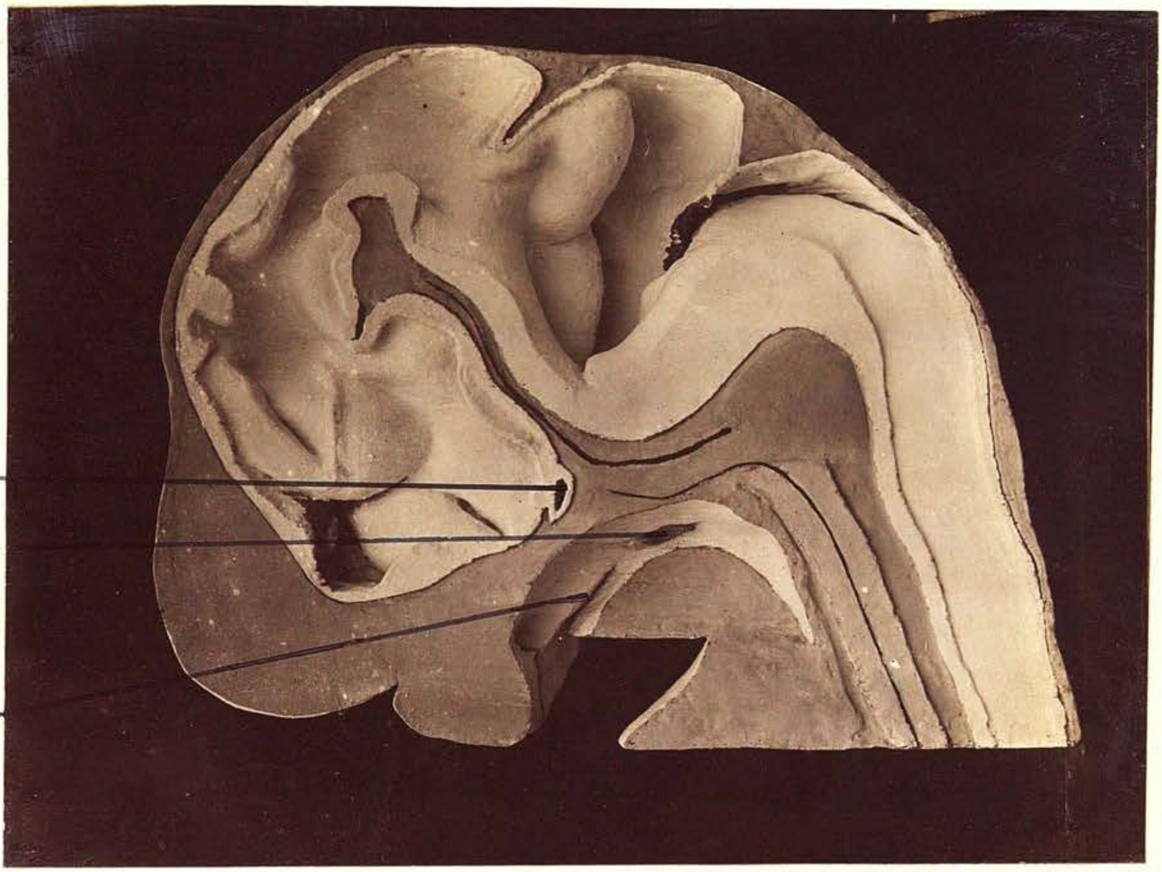


Floor of mouth and pharynx of 16.5 mm pig embryo showing root of tongue and laryngeal aperture. C 2 XXXII

"FITS INTO C 2 XXXII"

dental laminae are present laterally but they do not reach to near the middle line. The tongue has now developed considerably since the last stage and is separated from the floor of the mouth by an alveolo-lingual sulcus. The tip is bifid and here again one sees distinctly how the tip and sides are developed from the lateral masses, (fig.). The middle of the tongue shows a raised triangular area, the apex of which reaches to near the tip in the middle line. The two lateral angles are prolonged out on to the under surface of the first arches where they end in two slightly raised tubercles. The triangular area I take to be the tuberculum impar, and its two aboral angles show the beginning of the papillae foliatae. Behind the tuberculum impar the second arches are prolonged across to the middle line and form the root of the tongue, (fig. 16). The epiglottis is a broad flat structure connected with the second arches by a median and two lateral glossoepiglottic folds. The upper aperture of the larynx is nearly closed by the overhanging epiglottis. The arytenoid and cricoid region projects markedly into the pharynx. At the lateral angles of the pharynx also the ventral extensions of the third and fourth pouches are seen.

Fig. 17.



Model of 20.mm human enbryo showing pharynx from the side. The tongue has been removed, the Eustachian tube is seen as a wide cleft in the lateral wall of the pharynx. The palatal process is seen stretching between this and the primitive choana.

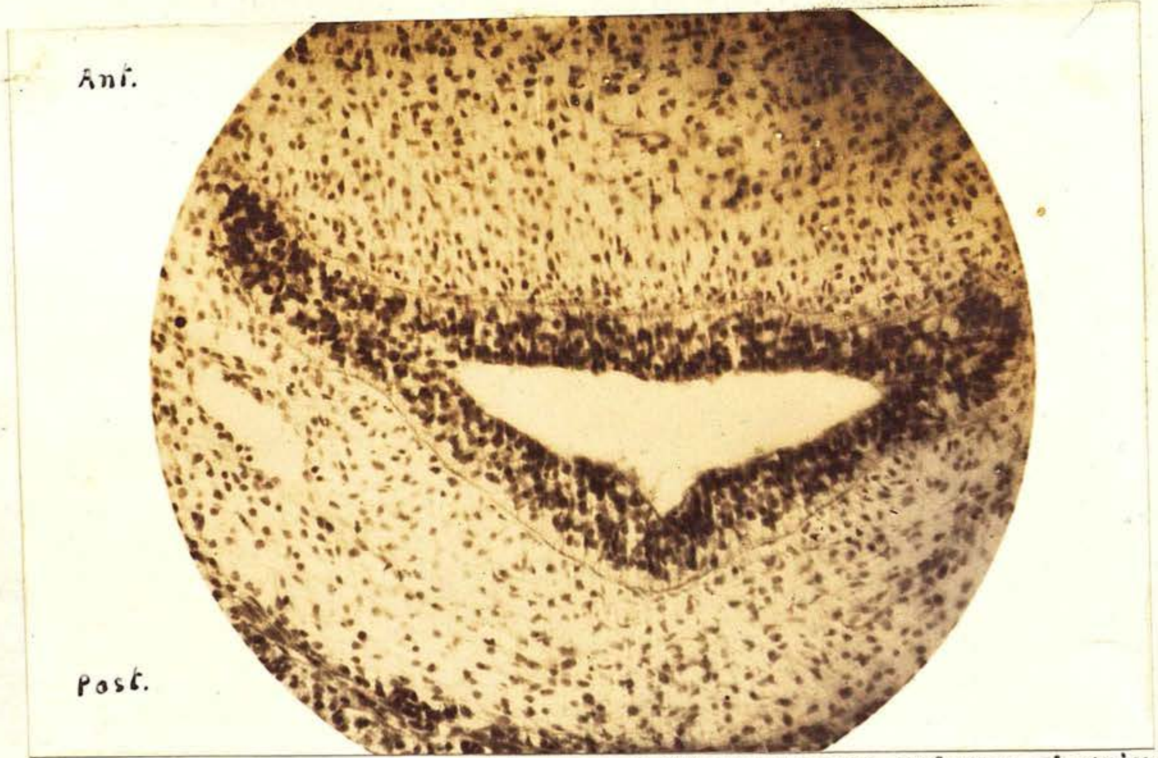
Human Embryo 20 m.m. V.B.

The cavities of this embryo have been reconstructed as a solid model as well as being shown in a model similar to the others. The bucco pharyngeal cavity seen from the side presents a uniform curve from its oral to its œsophageal end,(fig.17). The cavity is widest at the mouth and from the angle of the mouth it narrows rapidly as it is followed back. It again widens suddenly behind the first arches due to the large first and second pouches, from here to its aboral termination it tapers smoothly into the mouth of the oesophagus. (figs. 44 - 46).

The roof is more advanced than in the 16.5 m.m. pig. The primitive choanae are seen in front, bounded laterally by the palatal processes, which are thinner and more prominent than in the pig, though still directed downwards. They are higher orally and fade away at their aboral ends into the lateral walls of the Eustachian tube. Each palatal process is limited laterally from the rest of the roof of the mouth by a groove. Lateral to this groove again is another rather shallower groove which runs round parallel to the lip margin towards its fellow of the opposite side. In the floor of this groove is a thickened band of epithelium (the dental lamina) from which the teeth later develop. The roof of the mouth is divided by

the palatal /

Fig. I8.



Microphotograph of section of 20 mm human embryo showing lower pharynx with pit in posterior wall.

Fig. I9.

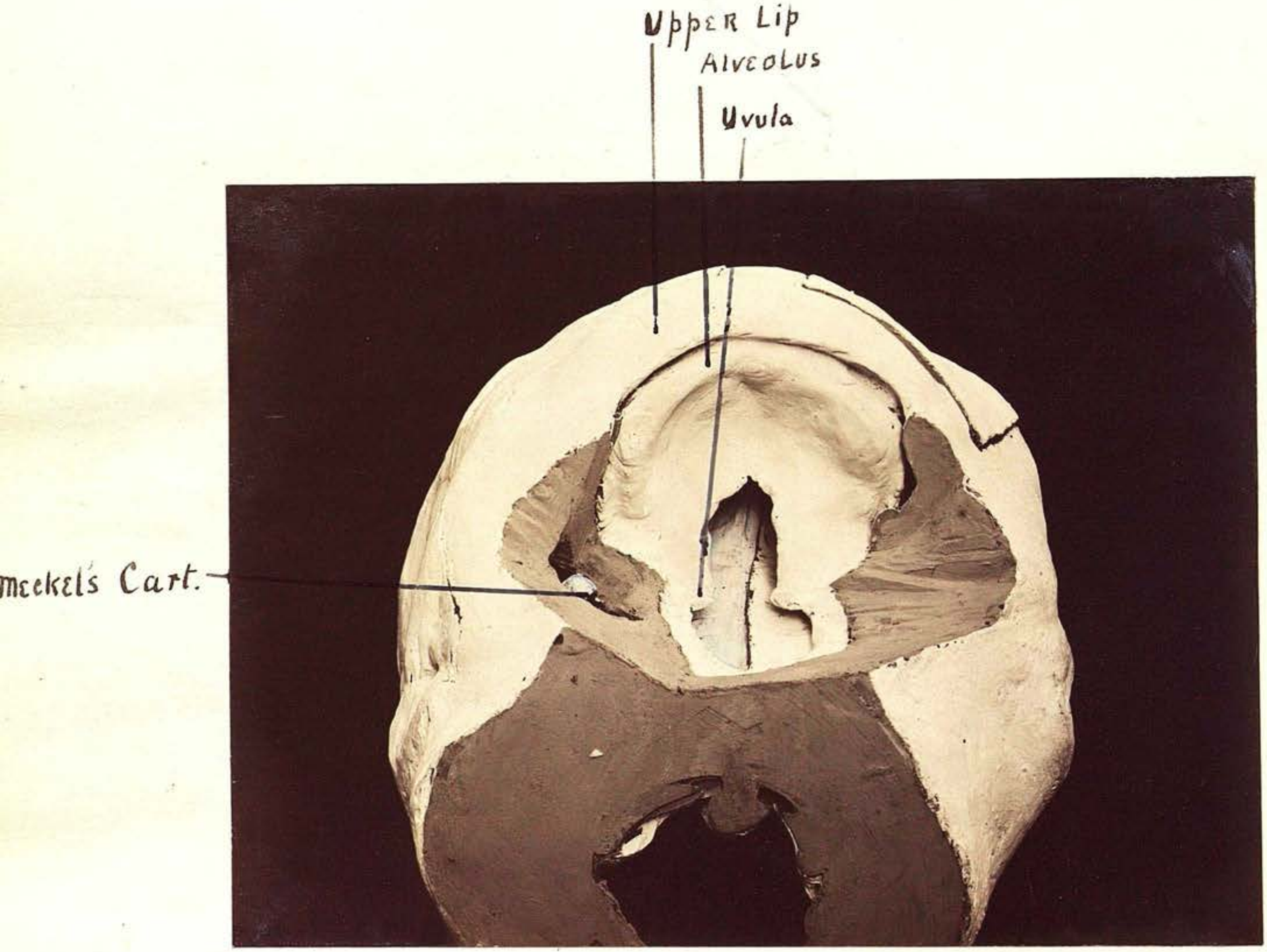
Section of same embryo showing band of thickened epithelium on posterior pharyngeal wall.

palatal processes into three parts, a median and two lateral parts. The median part of the roof is deeply concave from side to side and the concavity is filled by the dorsum of the tongue. The remains of Rathke's pouch is still present as a solid column of cells reaching from the roof of the mouth to the pituitary. The middle ear recess is a wide wing shaped lateral extension of the pharynx at the summit of its curve composed of the dorsal extensions of the Ist & IInd pouches. Its pharyngeal orifice is narrowed by the eminentia cochlearis on the roof. Its aboral end shows a depression due to the dorsal extension of the second pouch. (Fig 44) None of the other pouches are visible in the lateral angle of the pharynx. The posterior pharyngeal wall caudal to the opening of the larynx shows a well defined band of thickened epithelium in the middle line (figs. I8, I9) which passes down into the Oesophagus. The epithelium of the anterior pharyngeal wall is also thicker here than above, but the thickening has not such a definite edge. Near the mouth of the oesophagus the band of epithelium on the posterior wall dimples in so as to form a tiny pharyngeal pouch. This is perhaps a little lower in position than the pouches seen in the pig and is not so large, but is probably homologous.

The lower lip shows a dental lamina like that on the upper lip. The greater part of the floor of the mouth is occupied by the tongue (fig. 47),

which /

Fig. 20.



Roof of mouth of 30 mm human embryo showing the palate and alveolus.

C 2 XXVI

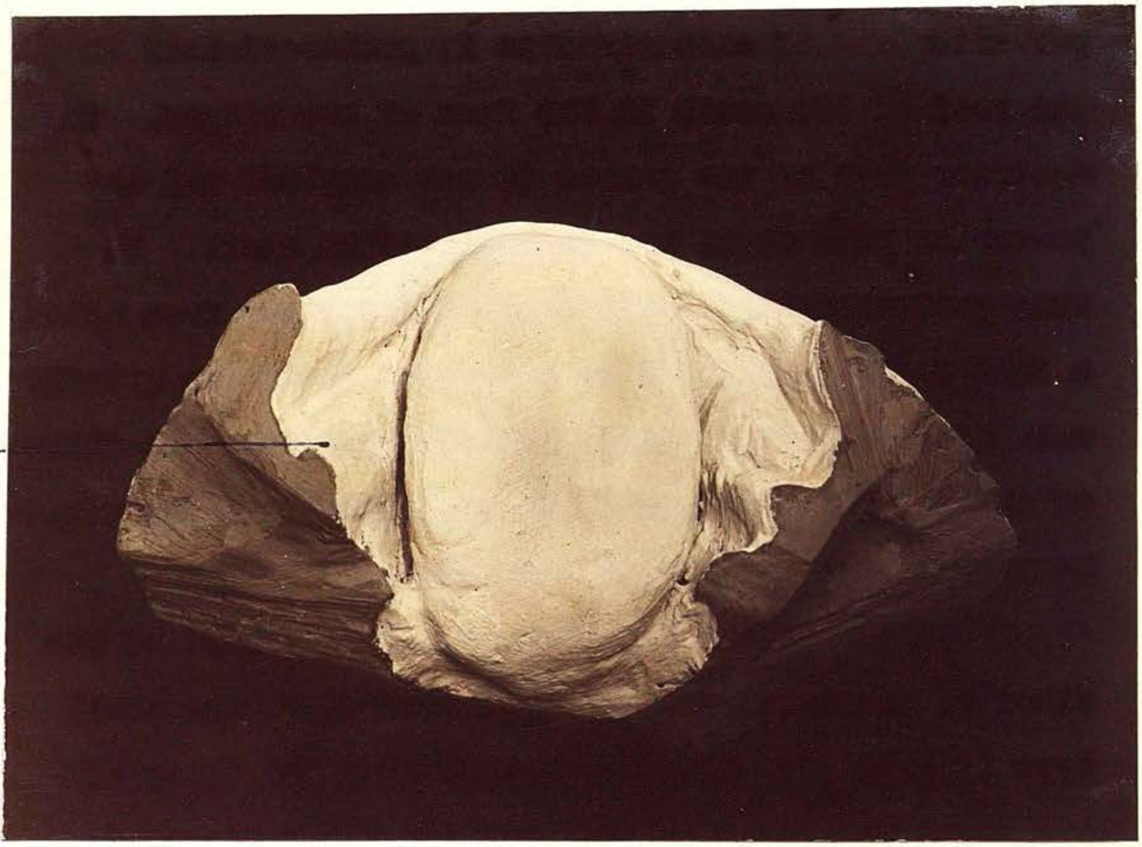
which is long and bounded at the sides and in front by a deep alveolo-lingual sulcus, from the bottom of which the submaxillary gland is growing as a solid pear shaped bud of epithelium. The tip of the tongue is free and is no longer bifid. A shallow median groove traverses the dorsum in its long axis and there is practically no indication of what is tuberculum impar area and what lateral tongue rudiment. The second arch element, however, can still be distinguished at the aboral end of the tongue. The epiglottis projects backwards, overhanging the upper aperture of the larynx. The arytenoid swellings are large, and below them the wall passes smoothly down into the oesophagus.

Human Embryo 30 m.m. V.B.

The bucco-pharyngeal cavity is now divided by the growing permanent palate,(fig. 20). The naso-pharynx is a fairly roomy space bounded dorsally by the cartilaginous plate representing the basioccipital and the basisphenoid. The hinder part of the cartilaginous septum is in one continuous piece with it and bounds the cavity above. Below, the cavity is partly open owing to the incomplete fusion of the palatal processes. There is as yet no sign of adenoid tissue

on the posterior /

Fig. 21.



Floor of mouth and tongue of model of 30 mm human embryo.
The alveolar ridges are divided from lip by a sulcus.
Tongue now has adult form. PART OF C 2 XXXI

posterior pharyngeal wall. The orifice of the Eustachian tube is a narrow vertical slit in the lateral angle of the nasopharynx just above the posterior end of the palate. There is as yet no sign of the fossa of Rosenmüller.

The upper lip is divided by a deep sulcus from the alveolus, which is now well formed. The posterior end of each alveolus is prolonged back on the roof of the mouth in the form of two ridges. The anterior part of the palate is now complete but the posterior part still has a large median cleft. It ends posteriorly in two pointed extremities from which a fold passes downwards on each side on to the lateral wall of the pharynx (post. faucial pillar). The floor of the mouth in the model has been removed along a line between the two pillars of the fauces.

The tongue fills up nearly the whole of the floor of the mouth and has now attained to the adult type (fig.21). It is separated from the floor of the mouth by a deep sulcus, and its tip projects forwards and reaches to the lip margin. The dorsum shows a shallow median groove. The lower alveolus is not so definite as the upper one. It is most distinct at the sides, where its posterior ends are each divided into two by a short deep fissure running obliquely backwards and outwards. The significance of the splitting is uncertain.

The tongue is connected with the lateral wall of the cavity /

cavity by means of the anterior faucial pillar, in the fossa posterior to which the tonsil can be seen in the form of an irregular mass of darkly staining cells. It is mainly attached to the posterior surface of the anterior pillar, but part of it is also attached to the posterior pillar, while there is also a prolongation on to the root of the tongue. Several distinct crypts can be seen lined by a single layer of squamous epithelium.

General Outline of Buccopharyngeal Cavity.

Sudler 1901, has described the changes in form of the bucco-pharyngeal cavity of the human embryo during the first seven weeks of its development. His data were obtained by solid reconstructions of the cavity. He writes :- "The shape of the human pharynx changes from a more or less rounded cavity, and one without many distinguishing characters, at the end of the second week, to an angular, much differentiated cavity, during the fourth week. After that time it gradually loses its angularity, until it is a curved and well rounded cavity in the embryo of the seventh week." In none of his reconstructions was the oral aperture a five sided opening, such as His figures and describes, but in all the earlier stages, was a mere slit. Hammar made similar observations in 1901. During the second week the cavity is flat and triangular and is closed in ~~in front~~ a short distance from the oral aperture by the bucco pharyngeal membrane. During the fourth week the cavity bends at a right angle opposite the third and fourth visceral pouches. In the fifth week a second angle has appeared oral to the first mentioned one. At the level of this angle the nasal cavities communicate with the mouth. In the stages mentioned hitherto, Rathke's pouch has been a marked feature of the roof of the cavity: Early in the sixth week this pouch becomes shut off from the pharynx.

The first /

first visceral pouch, destined to form the future middle ear and Eustachian tube, is now a broad flat projection from the side of the pharynx. At the end of the sixth week, the state of the parts is very similar. There is still a solid epithelial projection from the roof of the mouth marking the site of Rathke's pouch. The laryngeal cavity, which hitherto had been patent, has now become occluded. In the seventh week the bucco-pharyngeal cavity is curved on itself so that the oesophagus and the ventral end of the mouth are in the same plane. The Eustachian tube is placed on the summit of the curve and projects laterally and dorsally. Seen from above the cavity as a whole is oval.

In a solid model of the buccopharyngeal cavity, which I have reconstructed from a human embryo of about the seventh week a very similar state of affairs ia seen (figs.44-46). Viewed from the side its curvature is not quite so marked as that of Sudler's of the same period. Its cranial aspect, excluding the part representing the oral fissure,presents a somewhat oval outline. It is arched from side to side especially in front where that part of the model representing the vault of the nasopharynx is bounded laterally by two deep grooves corresponding with the palatal processes. Lateral to these the cavity broadens out rapidly into the oral fissure. Projecting laterally

from /

from the cavity at the most cranial part of the arch are two broad wingshaped processes representing the Eustachian tubes and tympanic cavities. On the cranial aspect of each of these is a depression caused by the tip of the cochlea (impressio cochlearis). This will be described in detail on another occasion. Immediately dorsal to the Eustachian tube is another much smaller projection, the remains of the dorsal extension of the second pouch. From this point the cavity tapers rapidly down into the oesophagus. Projecting upwards from near its oral end, are seen the nasal cavities. On the caudal surface of the model a large concavity for the tongue is seen. More dorsally a wedge shaped projection represents part of the laryngeal cavity.

The Floor of the Mouth.

During the second week of development the primitive oral aperture or stomodaeum is separated from the pharynx ~~mouth is closed~~ by the buccopharyngeal membrane. In the fourth week the buccopharyngeal membrane has completely disappeared. The floor of the mouth is composed of five pairs of visceral arches with the corresponding visceral clefts. In the middle line between the first and second pairs of arches there is a small rounded swelling, the Tuberculum Impar. Born in 1883 described a similar swelling which appeared to have two roots from the first pair of arches. He named it the "Schaltstück" and writes as follows:- "der ganze Körper der Zunge aus dem Schaltstücke, das zwischen den Unterkieferfortsätzen der ersten Kiemenbogen und den nach hinten convergirenden Enden der zweiten gelegen ist, hervorwächst, während die zweiten Schlundbogen sammt dem sie verbindenden Theile des medianen Längskammes nur die Zungenwurzel liefern." Joining the medial ends of the second arches is another swelling, the Copula of His. The median Thyroid rudiment is situated between the Tuberculum impar and the Copula. Dorsal or aboral to the Copula there is a pit formed by the lung diverticulum. Later on the tuberculum impar and the Copula enlarge and merge into each other, till by the end of the 5th week they can only be distinguished by the position of the median

thyroid /

thyroid rudiment. In the fourth week also two swellings appear on the first arch, one on each side of the middle line. These swellings are the lateral tongue rudiments (seitliche Zungenwülste) which were observed by Rabl, Köllmenn and Kallius. The lateral tongue rudiments grow together to meet in the middle line in front, and blend with the tuberculum impar. The eminence on the floor of the mouth caused by the fusion of these elements is the rudimentary tongue.

According to His the whole of the body of the tongue in front of the foramen caecum is formed from the tuberculum impar, while the root of the tongue behind the foramen caecum is developed from the Copula. Most authors are agreed, however, that the tongue is derived from three main elements, namely : (a) the tuberculum impar, (b) the lateral tongue rudiments from the first pair of arches, (c) the copula and the mesial ends of the second arches. There is some difference of opinion as to how much of the tongue is developed from the tuberculum impar. As already mentioned, His thought that the whole of the tongue in front of the foramen caecum was tuberculum impar. Hammar (1901)* believed that the tuberculum impar is only a transitory structure. He also says, however, that it corresponds with a small area in front of the foramen caecum. Kallius (1910) working on pigs gives a very full account of the development of the tongue.

According /

*See next page.

According to his results the Tub. impar is at first a small median elevation between the first and second arches. In its growth it increases much more rapidly in breadth than in the dorso-ventral direction,* becoming triangular with two lateral angles, which extend into the first visceral cleft. Its pointed oral extremity is embraced by the lateral tongue rudiments. These latter have united with each other in front of the tub. impar and from their continued growth form the tip, the sides, and part of the dorsum of the tongue of the adult. The lateral extensions of the tub. impar subsequently become the Papillae Foliatae. The root of the tongue i.e. that part behind the Caecum is developed from the second arches.

Peter (1911) in a number of reconstructions shows a similar series of changes in the human embryo. In the fourth week there is a small tub. impar and aboral from it is a small copula uniting the second and third arches. Four arches are distinct in the

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* In Anat. Anz. 1901 he states:- "Aus dem Obigen erhellt, dass das Tub. impar die Anlage des Zungenkörpers und der Zungenspitze <u>nicht</u> ausmacht. Es ist eine transitorische Bildung und entspricht nur einem beschränkten Gebiete des vor dem For. coecum gelegenen Zungenkörpers.--Die Zungenwurzel geht nur aus der ventralen Verbindung der 2 Bogen hervor. Das Mittelstück des 3 Bogenpaares hingegen bildet die Anlage der Epiglottis."

floor of the mouth while the fifth is only partially seen. In the sixth week the tongue is much further advanced. The tub. impar and the lateral tongue rudiments form a large mass which is delimited from the floor of the mouth in front by a groove. The second arch elements are still quite distinct. In the ninth week the tongue has taken on the adult type, being raised from the floor of the mouth and separated from it by a deep alveolo-lingual groove.

As far as my own observations go, the fate of the tub. impar as described by Kallius seems to be borne out by my models of pig embryos.

In a 14.5 m.m. pig the dorsum of the tongue presents a raised triangular area whose two posterior angles are lost in the underside of the Mandibular arches, This I take to be the Tub. impar. On each side of the pointed anterior part of this area is a swelling forming the tip and sides of the tongue. The part of the tongue formed by the second arches is also distinctly marked off from the rest. (figs. I3, I4)

In a 16.5 m.m. pig the same subdivisions are seen with some slight changes due to increased growth. The lateral tongue rudiments have grown considerably and make the tip of the tongue slightly bifid. The lateral extensions of the tub. impar end on the under surface of the first arch as rounded projections, which Kallius says are the developing papillae foliatae.

The second /

The second arch is still distinct though not so much so as in the last stage. The three arches are now disappearing, the third, fourth and fifth being only just distinguishable. (fig.I6).)

In a 20 m.m. human embryo the tongue is well formed and is separated from the floor of the mouth by a deep sulcus, its tip projecting forward. Down the middle of the dorsum is a shallow groove, and there is practically no trace of the conditions seen in the pigs. The epiglottis is flat and projects backwards over the aperture of the larynx. T he visceral arches can no longer be distinguished in the floor of the mouth. (Figs.)

In a 30 m.m. human embryo (9-10 weeks) the tongue is practically identical with that of Peter's 28 m.m. embryo. Its dorsum also presents a shallow median groove. (fig. 2I).

In comparing the developing tongue of the pig with that of man, one is struck by the fact that in the early stages the tuberculum impar is not nearly such a definite structure in the pig as in man. According to Kallius's researches the tuberculum impar at first is not nearly such a definite structure in the pig as in man, but rather a small slightly raised triangular area blending with the copula, from which it can however be distinguished by the position of the thyroid rudiment. In man in corresponding phases

of development /

development the tuberculum impar and the copula are quite distinct.

The epiglottis is developed from the third arches, as is well seen in 14.5 and 16.5 pig embryos. Frazer (1910) has described the development of the arytenoid swellings from the fourth and fifth arches, and this is borne out by my models which show them connected with the arches in question. Each arytenoid swelling shows a shallow vertical groove which appears to indicate its formation from the two pairs of arches.

The Roof of the Mouth.

At the end of the second week the ~~buccal~~ stomodaeum ~~cavity is closed in ventrally~~ is separated from the pharynx by the bucco-pharyngeal membrane. By the beginning of the fourth week this has disappeared and the roof of the mouth is continuous with the upper lip. In the middle of the roof of the mouth Rathke's pouch is present as a wide pit. The dorsal extension of the first visceral pouch is a deep cleft. Immediately to its mesial side is a small swelling on the roof of the pharynx caused by the developing cochlea. In the fifth week the hypophysial opening has contracted considerably. The palatal processes are just appearing and the bulge of the cochlea is still marked. The bucco-pharyngeal cavity is very wide in front of (oral to) the second arch, behind which it narrows rapidly. In the sixth week the roof has become more arched in the dorso-ventral plane. The palatal processes are now more distinct, while mesial to them on each side is a depressed oval field composed of the bucco-nasal membrane. Further dorsally the hypophysis is still a narrow pit. The first visceral cleft or future tympanum and tube is now very deep. Its opening is partly obstructed by the bulge of the cochlea (Eminentia Cochlearis). In the seventh week as shown by my model, the palatal processes are well defined with a sharp free edge which is directed

more /

more downwards than inwards. The dorsal extremity of each palatal process fades away in the lateral wall of the first cleft. The primitive choanae are now established as oval openings immediately medial to the oral ends of the palatal processes. Rathke's pouch has now disappeared, but its position is still marked by a solid cord of cells leading up towards the infundibulum. The middle ear cleft is a wide elongated opening situated opposite the summit of the curve of the buccopharyngeal cavity, (figs.44 - 46). It is narrowed from above by the cochlear bulge, which, however, is not so marked as in the previous stages. Aboral from this a small depression is seen marking the position of the second pouch, from which the tonsil regions will later develop, (Hammar). The other pouches have now disappeared and their derivatives, namely, the lateral thyroid and the thymus are now separated from the pharynx and have migrated to a lower level. From the level of the first cleft the cavity tapers back smoothly into the oesophagus. In both the upper and lower lips there is a thickened band of epithelium, the dental lamina. As yet no tooth-buds have formed. In a 30 m.m. embryo (aprox.9-10 weeks), whose head I have constructed, the most striking change is the growth of the palate. The palatal processes have fused with each other in about the anterior half of their extent while dorsally they

are separated /

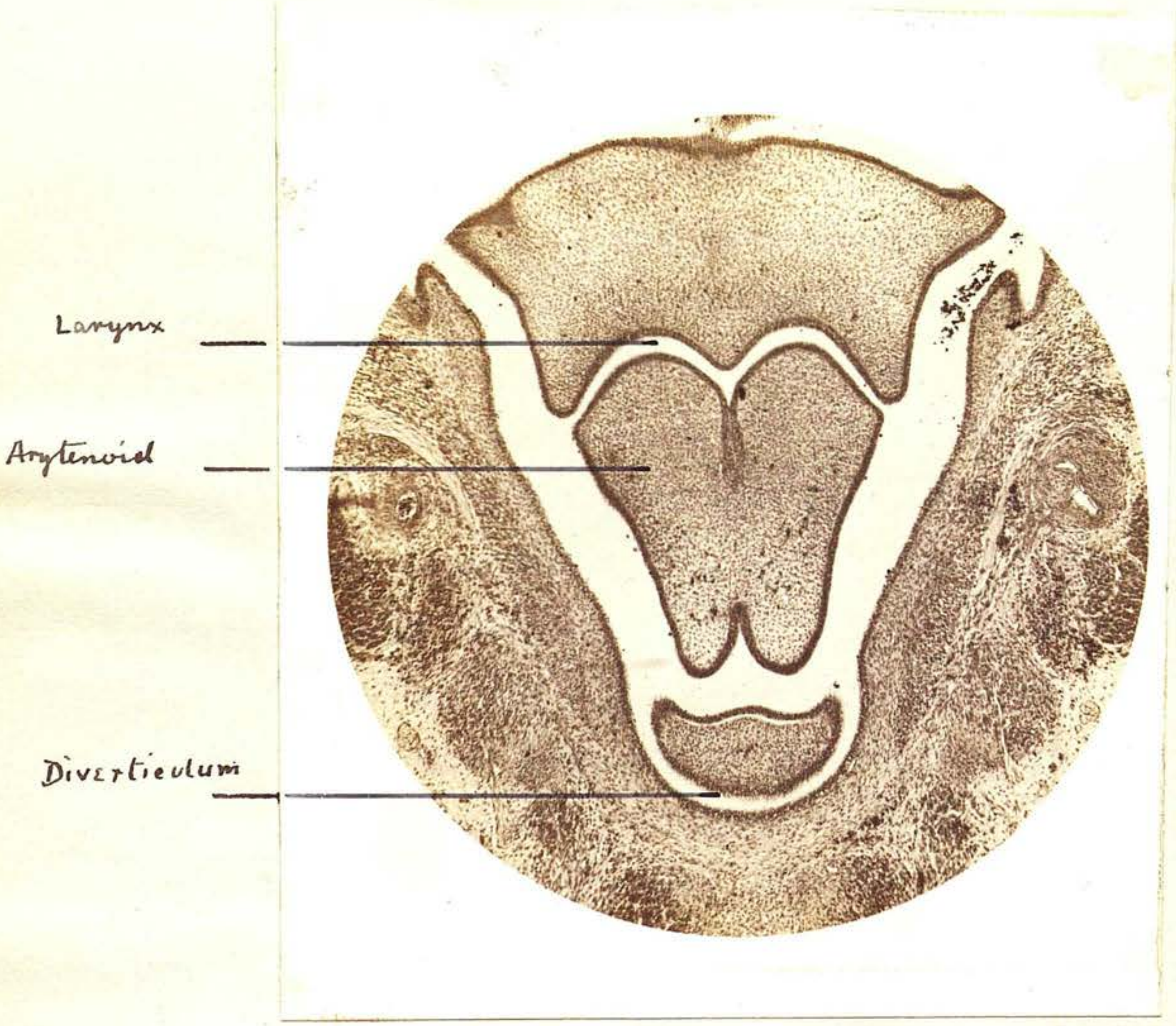
separated by a wide cleft. Their dorsal or aboral ends are pointed and from these points two folds run down the lateral wall of the pharynx, the one to reach the root of the tongue, the other to end in the pharynx. These are the anterior and posterior faucial pillars between which the tonsil has begun to appear. There is a well developed alveolar ridge separated from the upper lip by a deep sulcus. The posterior extremity of each alveolus is traversed by a shallow groove dividing it into a medial and a lateral portion. This subdivision is not nearly so well marked as in the lower alveolus. The nasopharynx is roomy and presents in its lateral walls the oval openings of the Eustachian tubes, which have now attained almost to the adult type. The lower part of the pharynx and the larynx could not be reconstructed as the specimen was unfortunately damaged in the neck region.

The fate of the visceral clefts has been worked out by many investigators, notably His, Hammar and Sudler. I may be permitted to summarise their results, thus :- The first visceral cleft becomes the Eustachian tube and tympanum. The second cleft gives rise to the tonsillar fossa and tonsil. The third cleft gives off buds which form the thymus and parathyroid. The fourth gives rise to the lateral thyroid rudiments and also another parathyroid.

With regard to the median pouches in the

posterior /

Fig. 22.



Section of throat of 20 mm pig embryo showing pharynx, larynx and pharyngeal diverticulum.

posterior pharyngeal wall, the only reference in literature which I have so far discovered is where Keith (1910), in a paper on oesophageal diverticula, quotes Fawcett as having seen one in the pig. I have seen these pouches in seven pig embryos whose vertex breech measurements varied from 10 to 20 m.m. (fig.22) and from this I should think that they are constantly present in pig embryos of this age. I have not examined the pharynges of older pigs as I had none cut and stained in time. No such pouches were observed in the sheep or the ferret but in a human embryo of 20 m.m. there was a small pit in the centre of a band of thickened epithelium on the posterior pharyngeal wall. This, although not nearly so distinct as in the pig, appears to me to be homologous with it. It seems to me possible that malignant disease and pharyngo-oesophageal diverticula may owe their origin in part to this developmental condition. However, I have not yet had time to follow up this subject more fully, but intend to do so at an early date.

Summary.

(1) The tongue is developed from three roots, viz. tuberculum impar, lateral tongue rudiments and copula.

The tuberculum impar is itself mainly derived from the first pair of arches, and ultimately forms a triangular area on the dorsum of the tongue in front of the foramen caecum. The lateral tongue rudiments grow up from the anterior edges of the first arches and enclose the tip of the tuberculum impar between them. The tip and sides of the tongue are formed by the lateral tongue rudiments. The copula is a swell-ong caused by the union of the second arches in the middle line. It along with the parts of the second arches immediately lateral to it form the tongue root, i.e. the portion between the foramen caecum and the epiglottis.

In this way the whole of the tongue in front of the foramen caecum is derived from the first arch, while behind the foramen caecum it is derived from the second arch.

(2) The epiglottis is developed from the third arches and the arytenoid tubercles from the fourth and fifth arches.

(3) The palatal processes, from which most of the permanent palate develops, are derived partly from the maxillary processes but also to a large extent direct-

ly from /

from the mandibular arch.

(4) The middle ear and Eustachian tube are developed from the dorsal extensions of the first and second visceral pouches. Thus elements of the first, second and third arches enter into the composition of its walls.

(5) The faucial tonsil is developed from the remains of the second and appears a considerable time before the pharyngeal tonsil.

(6) Median diverticula in the posterior pharyngeal wall near the mouth of the oesophagus are a common occurrence in the pig and may also occur in the human embryo. Their position is pretty constant in the pig, viz. between the third and fourth visceral pouches. They are situated in a position in which malignant disease is very liable to occur and where the so called "pressure pouches" are not uncommon. These facts are sufficient to suggest that there may be an embryological element in the causation of the pharyngo-oesophageal diverticula met with occasionally in the adult.

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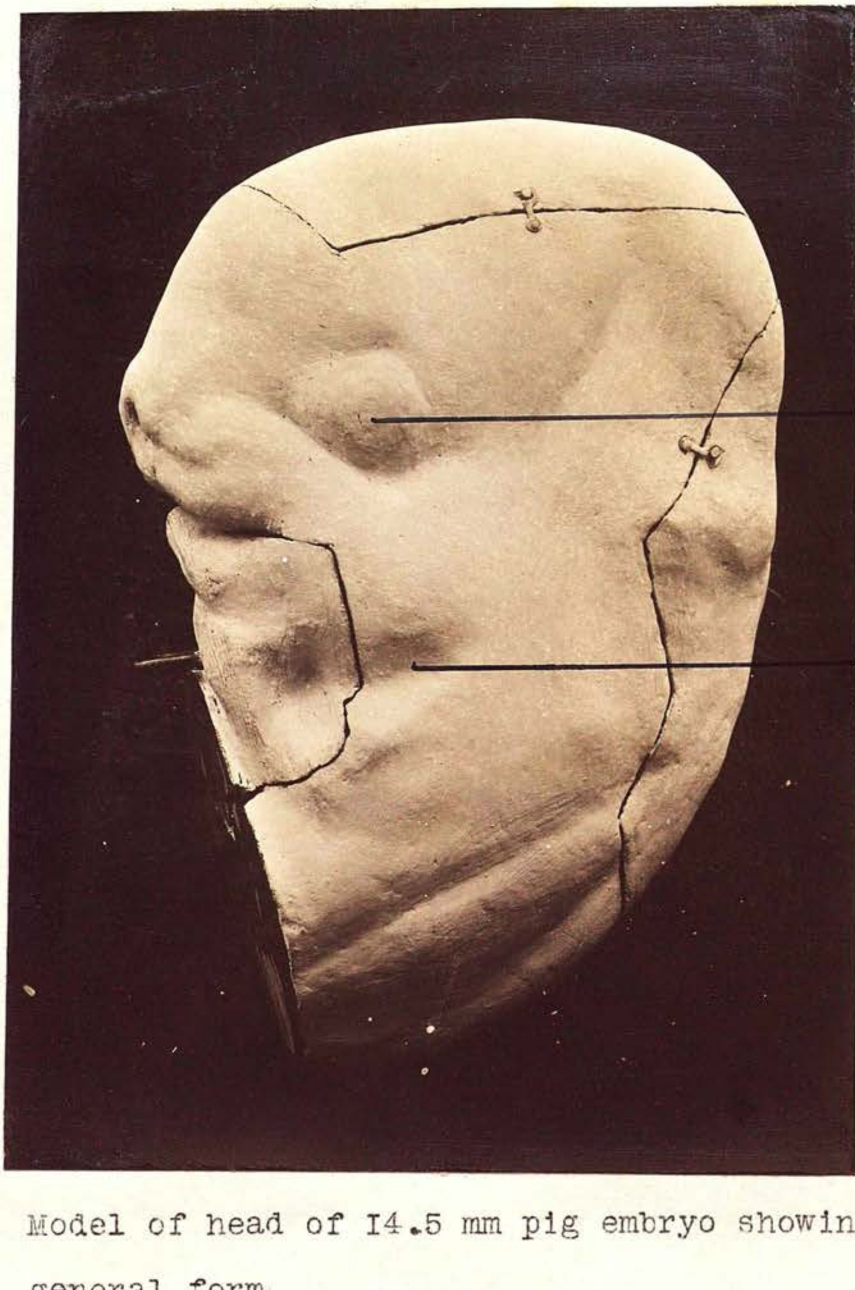
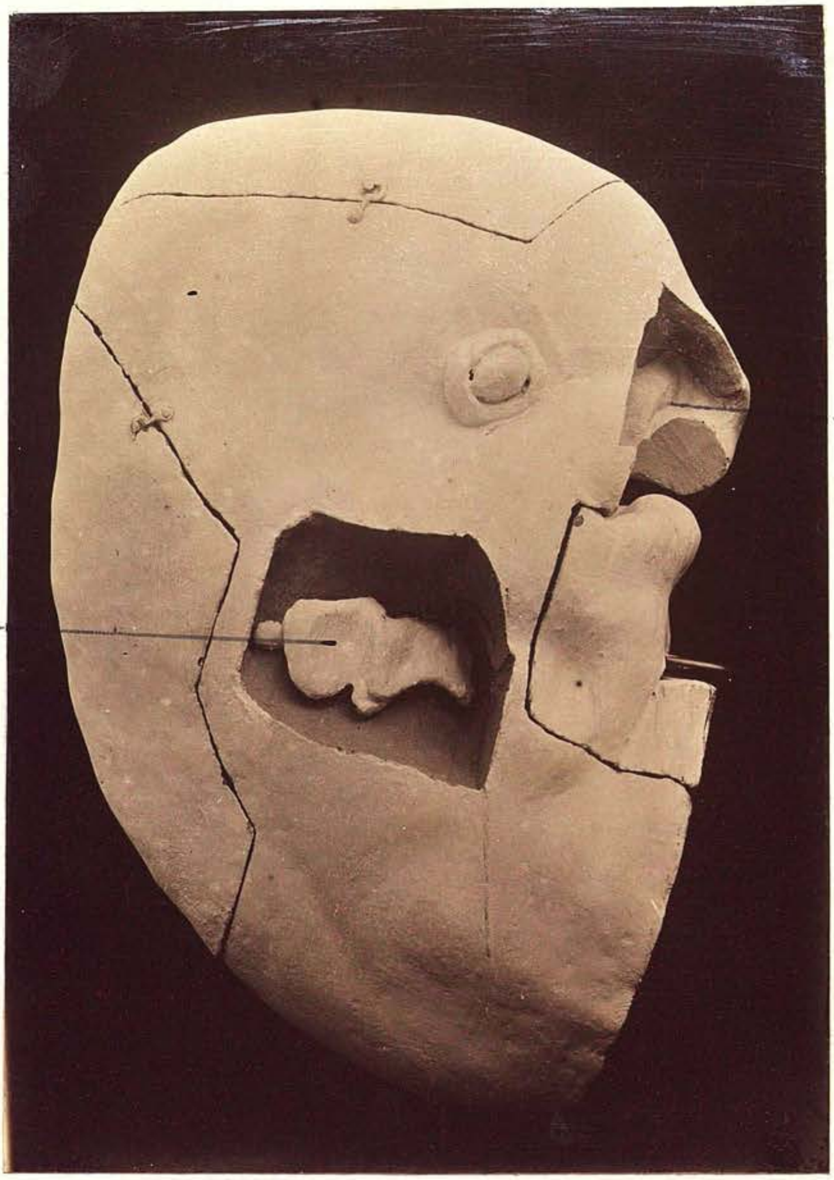
Fig. 23.



Model of head of 14.5 mm pig embryo showing general form.

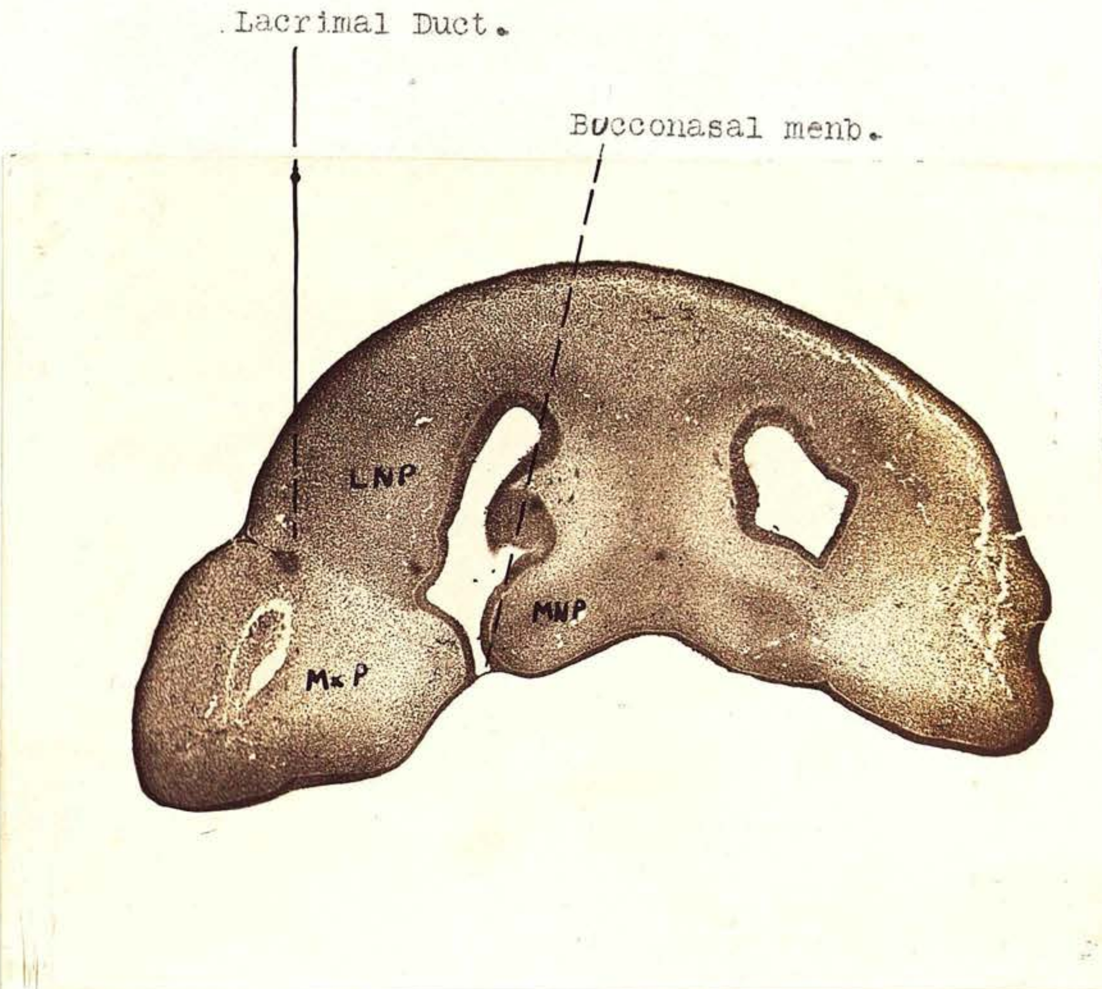
C 2 XXX

Fig. 24.



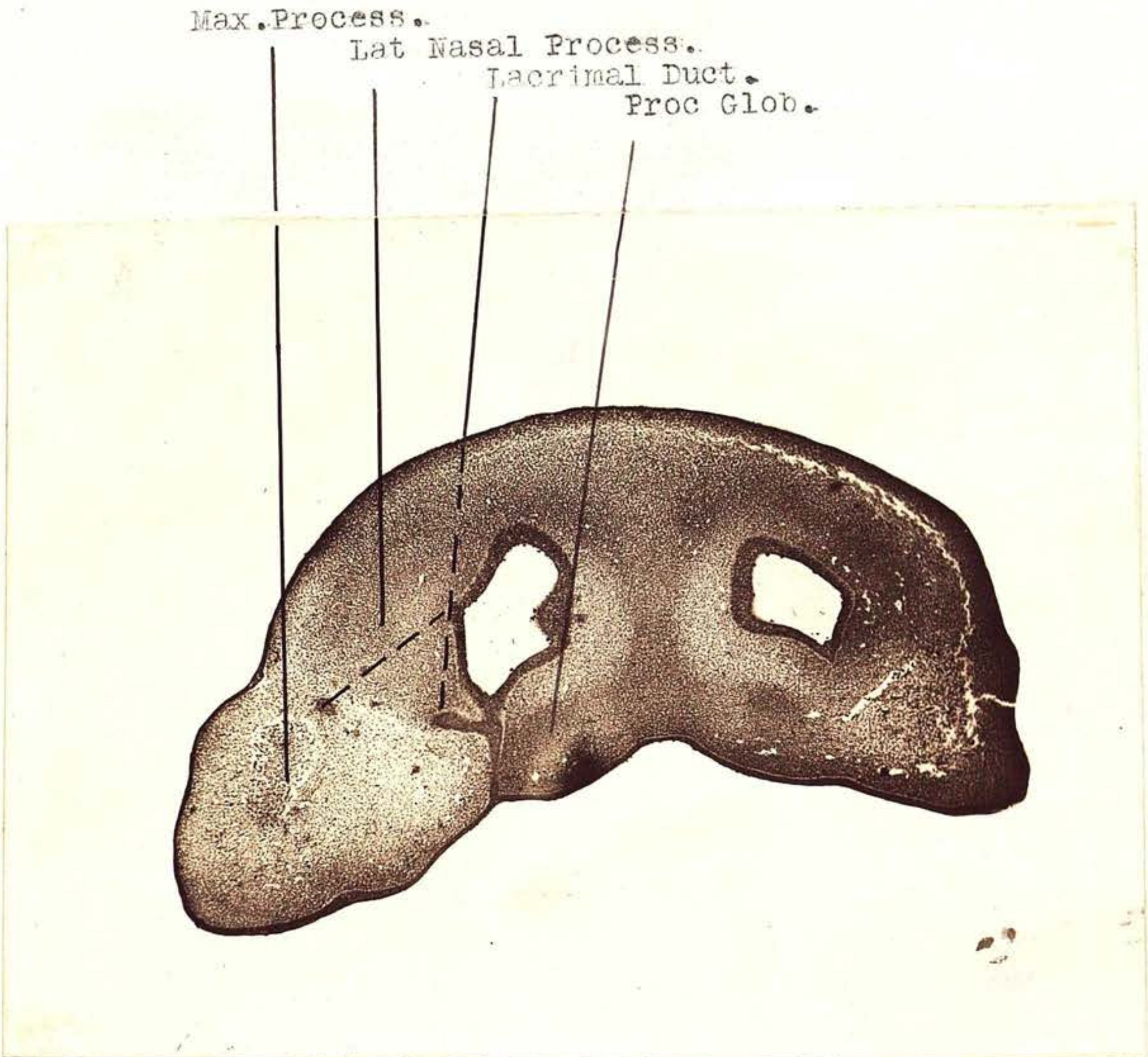
Model of head of 14.5 mm pig embryo showing labyrinth. The lateral nasal wall also has been removed. The same model as fig 23.

Fig. 25.



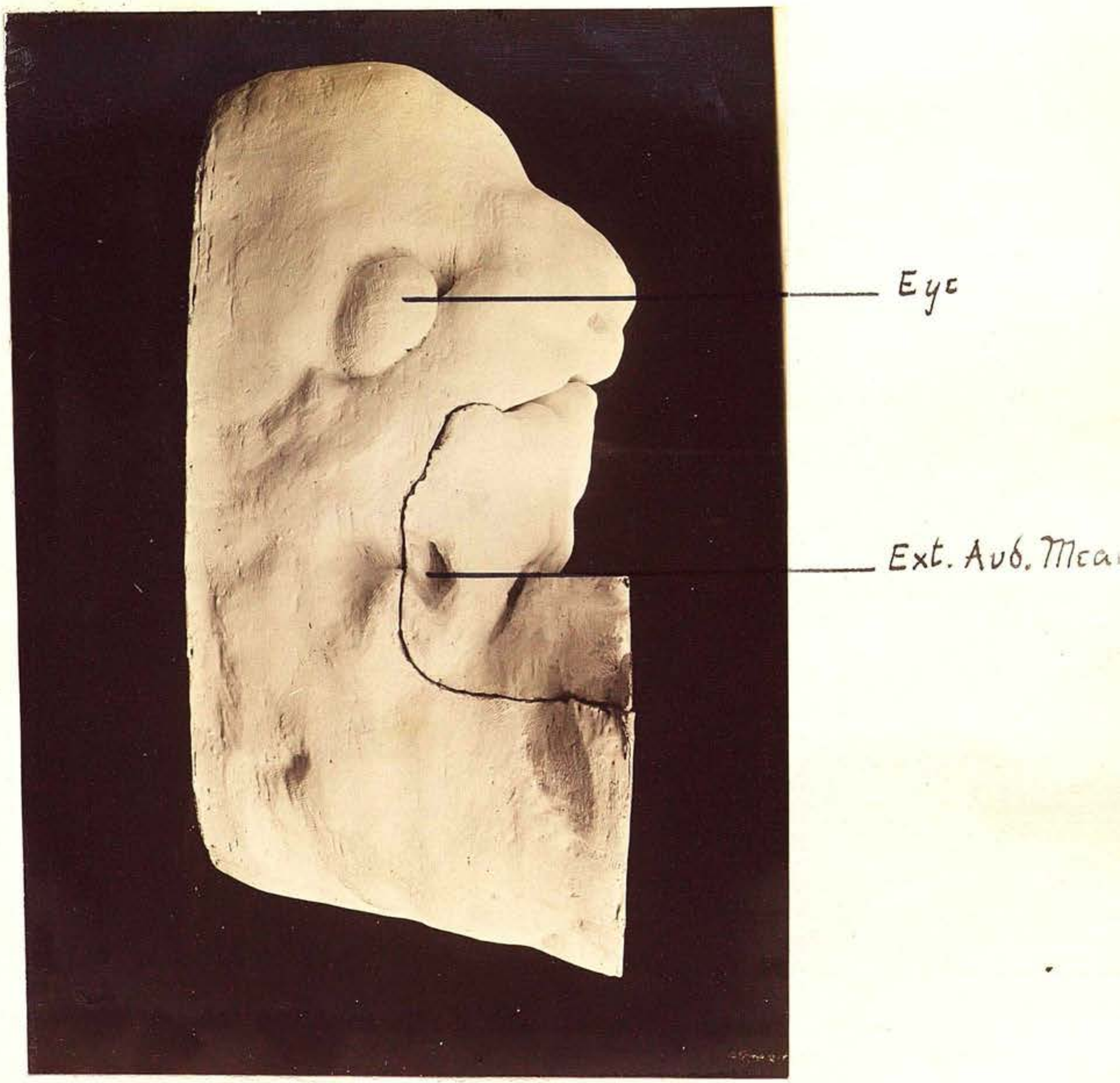
Sectiin of I4.5 mm pig embryo showing the lacrimal duct connected with the surface by a thin lamina. The line of fusion of the maxillary and lateral nasal processes is well seen.

Fig. 26.



Section of I4.5 mm pig embryo showing the two ends of the lacrimal duct. It is seen that the lateral nasal process forms part of the floor of the nose.

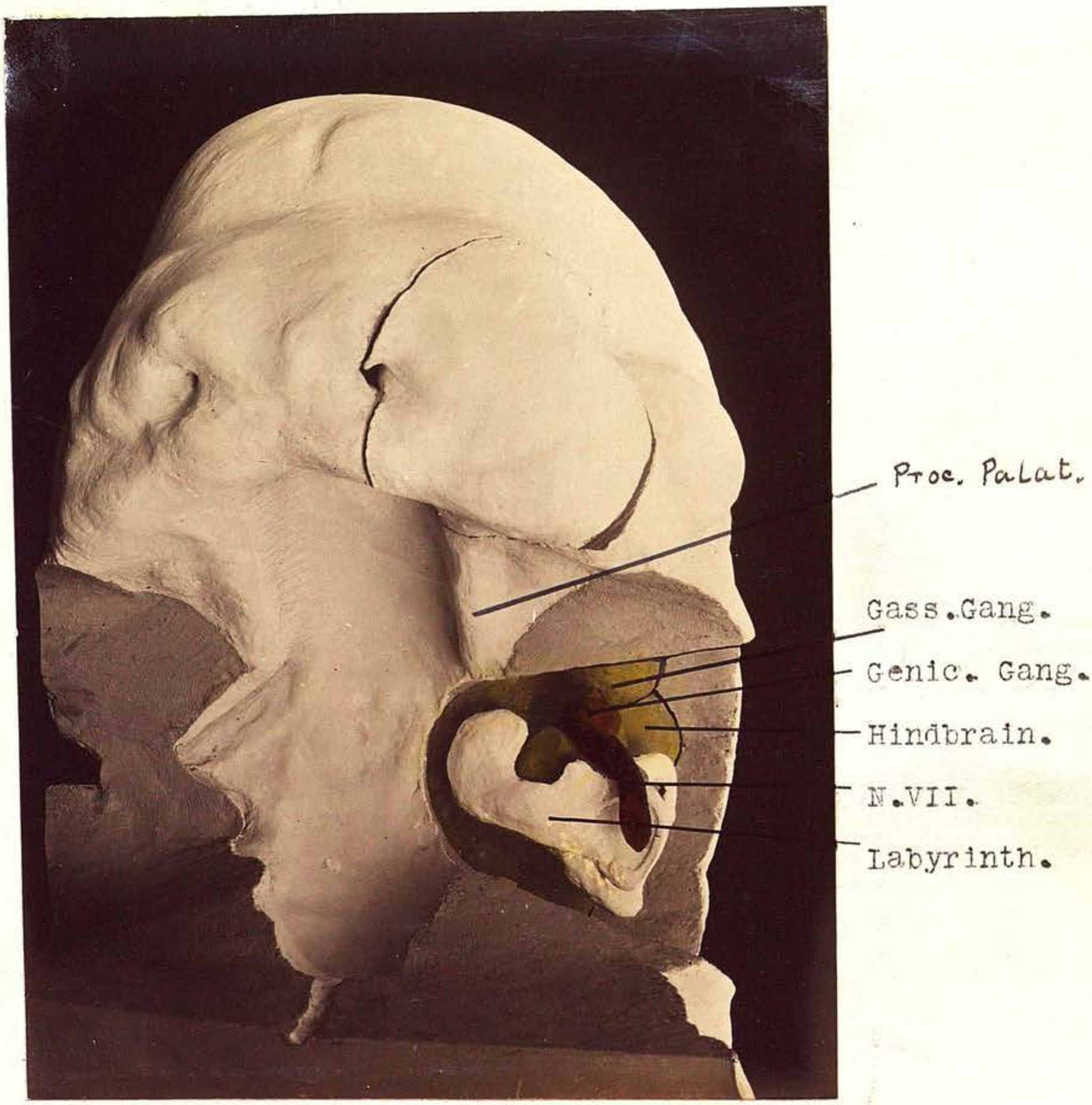
Fig. 27.



Profile view of model of face of
16.5 mm pig embryo to show general form.

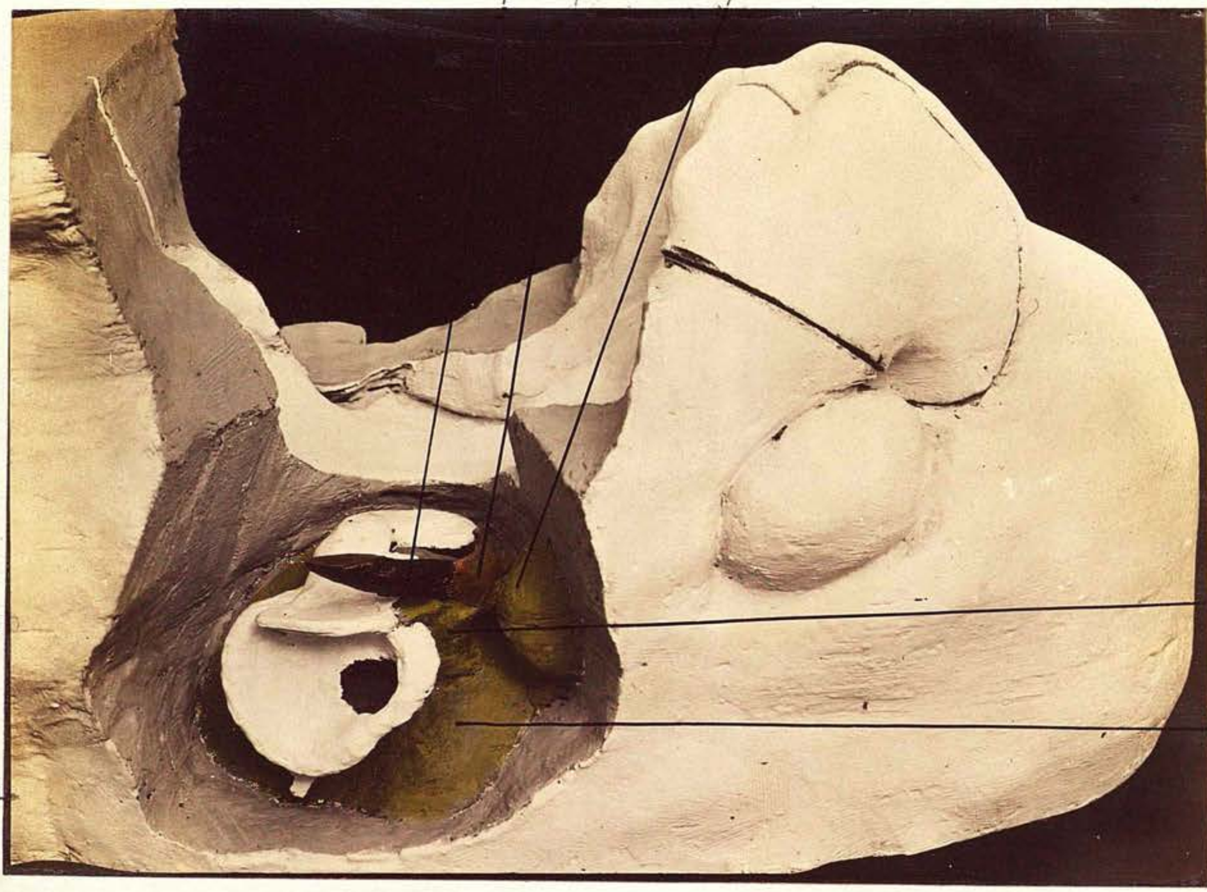
C 2 XXXII

Fig. 28.



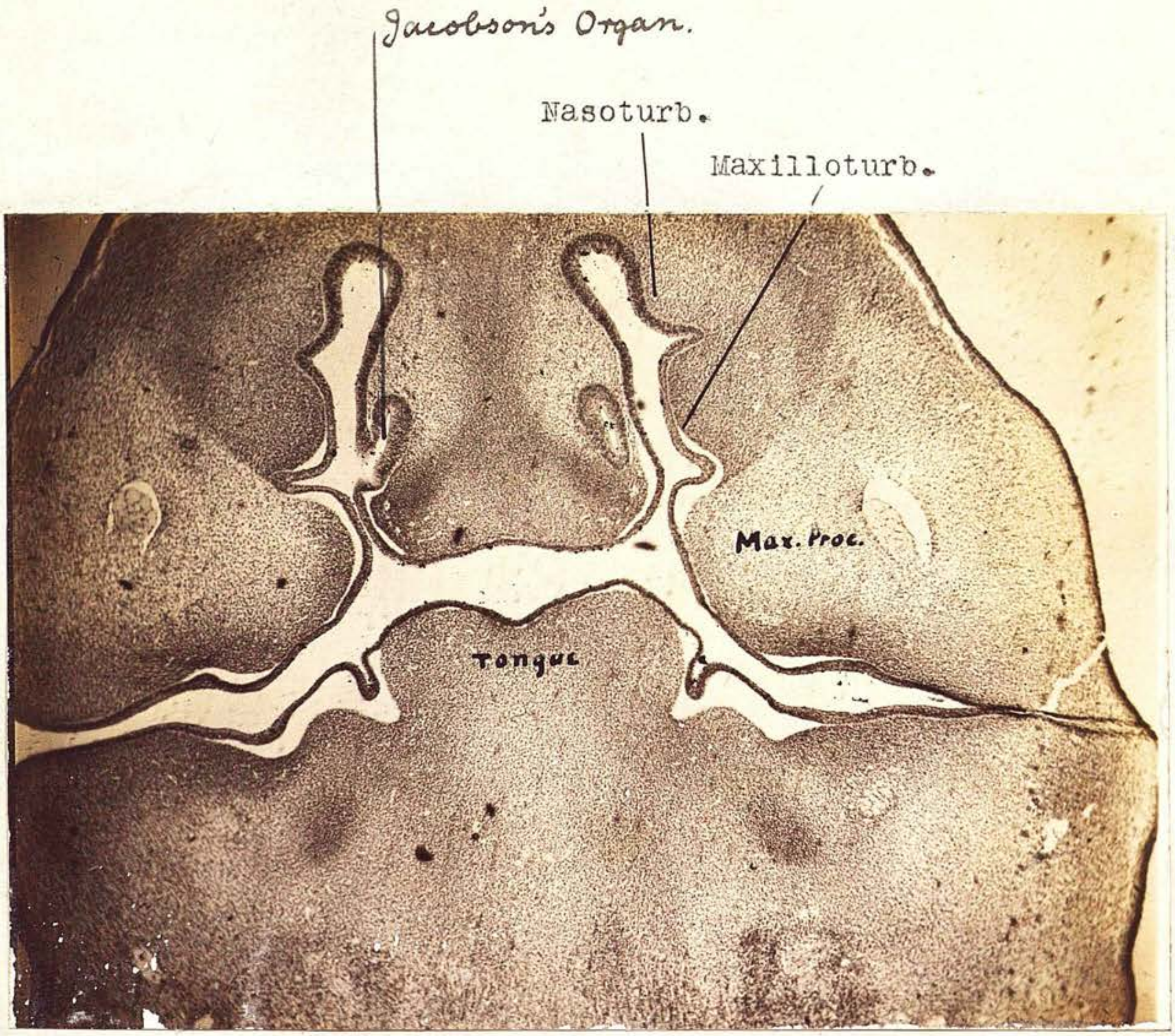
Model of 16.5 mm pig embryo showing buccopharyngeal cavity opened up. The model also shows the relation of cochlea to pharynx. The palatal processes run into the under surface of I arch. C 2 XXX II

Fig. 29.



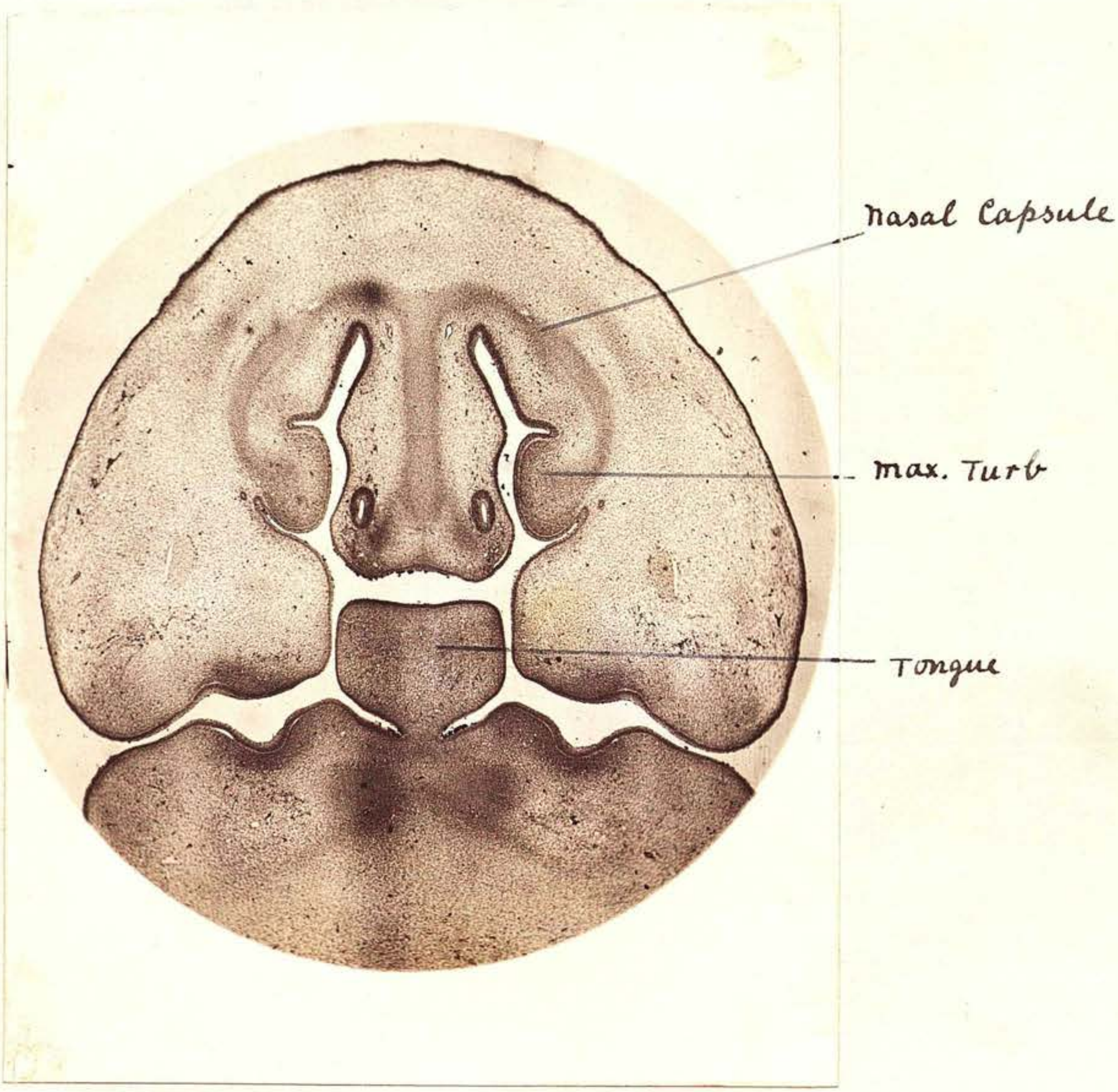
Model of 16.5 mm pig embryo showing relation of labyrinth to pharynx. C2 XXXII

Fig. 30.



Section of 16.5 mm pig embryo showing maxillo and naso-turbinals and Jacobson's organ. The line of union of maxillary and lateral nasal processes is seen.

Fig. 31.

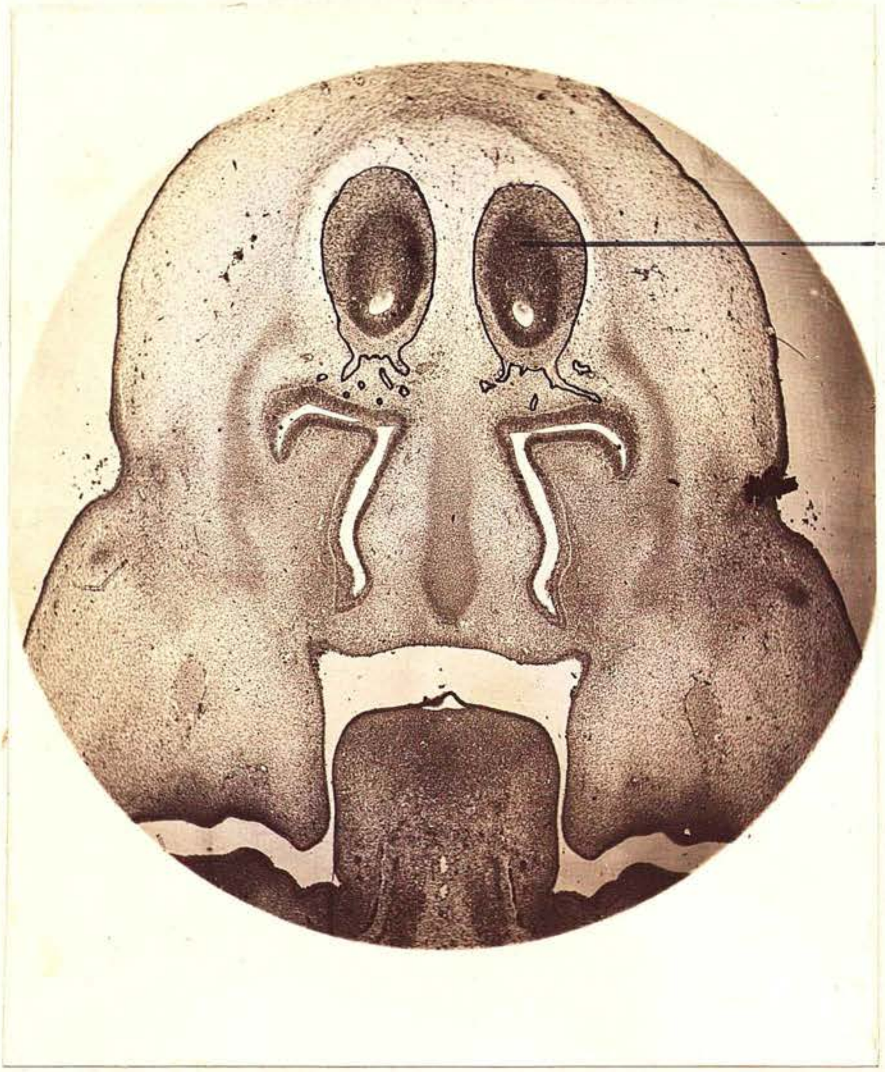


Section of 20 mm pig embryo showing conchae, nasal capsule and Jacobson's organ.

Fig. 32.

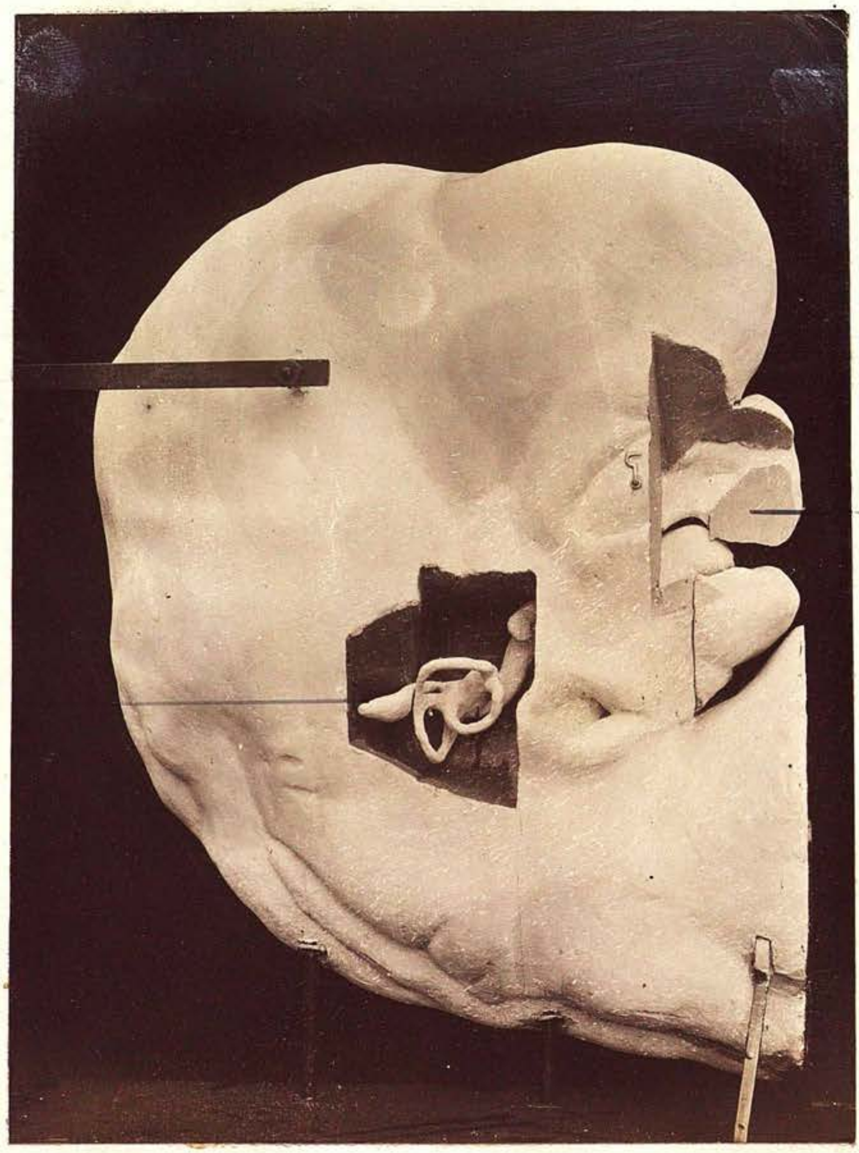
Section of 20 mm pig embryo showing ethmoturbinal and infundibulum. Nasal capsule also seen.

Fig. 33.



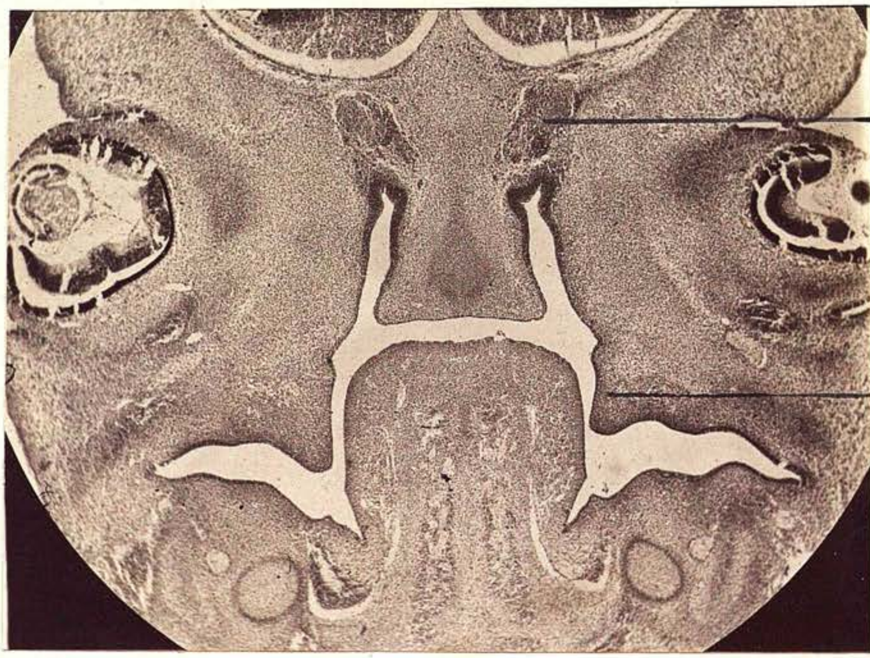
Section of 20 mm pig embryo showing olfactory nerves reaching ethmuturbinal.

Fig. 34.

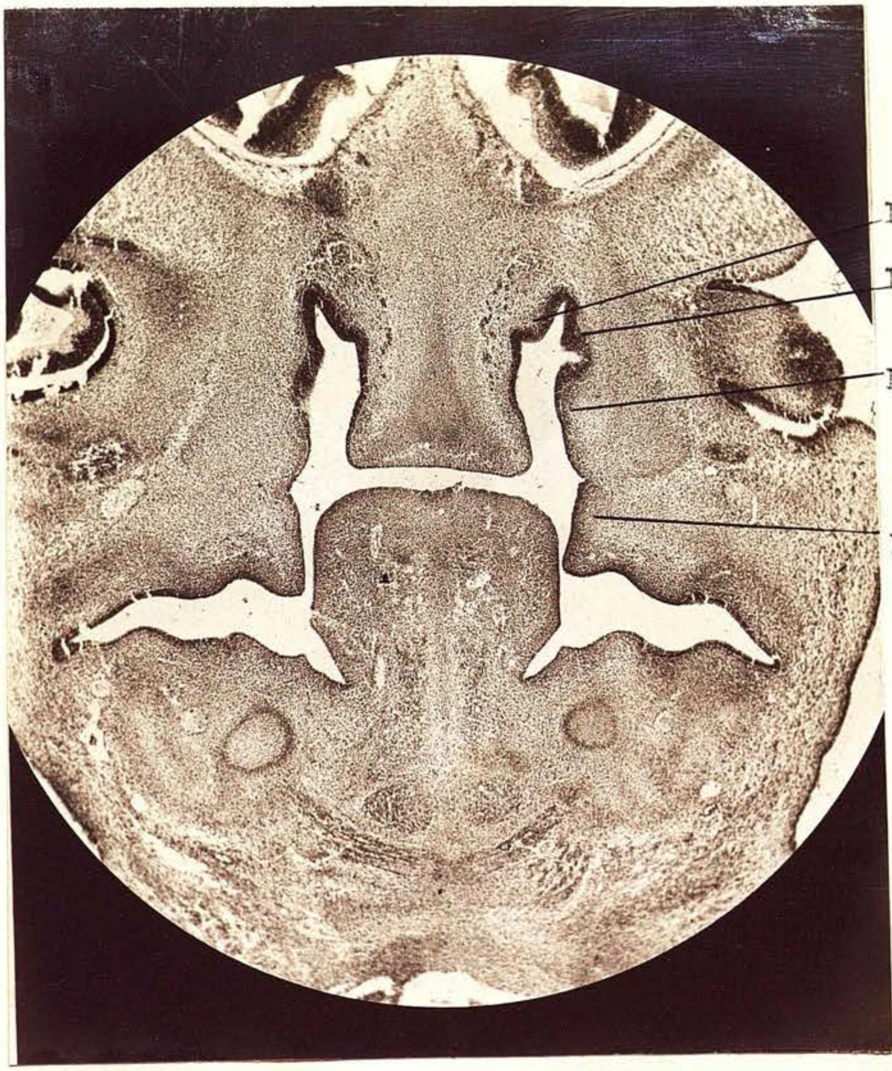


Same model as fig.7. with labyrinth exposed and lateral nasal wall removed. C_2 xxxv

Fig. 35.

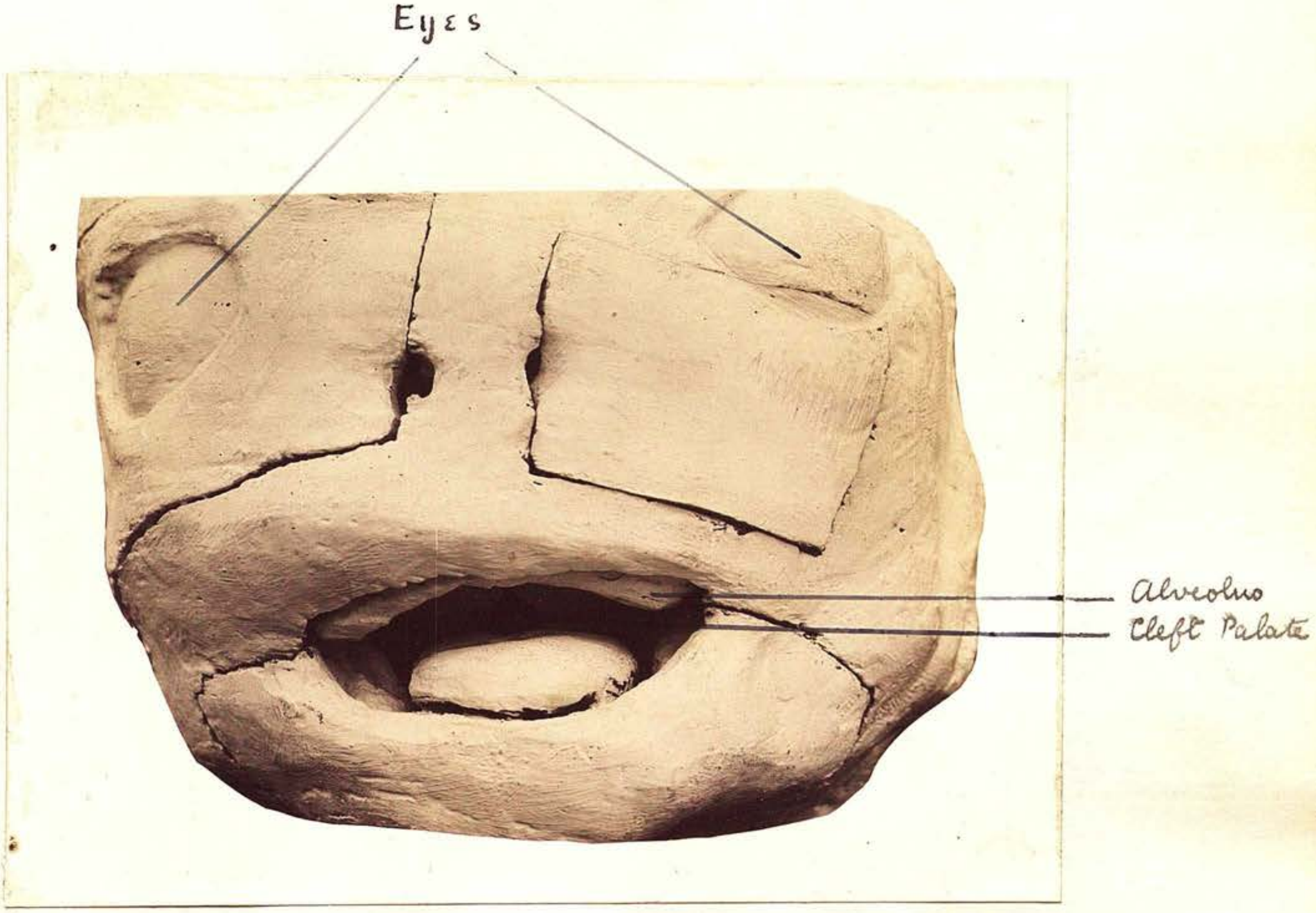


Section of 20 mm human embryo through hinder part of nose showing olfactory nerves reaching nose.



Section of 20 mm human embryo somewhat further forwards showing Maxillo and Ethmoturbinals.

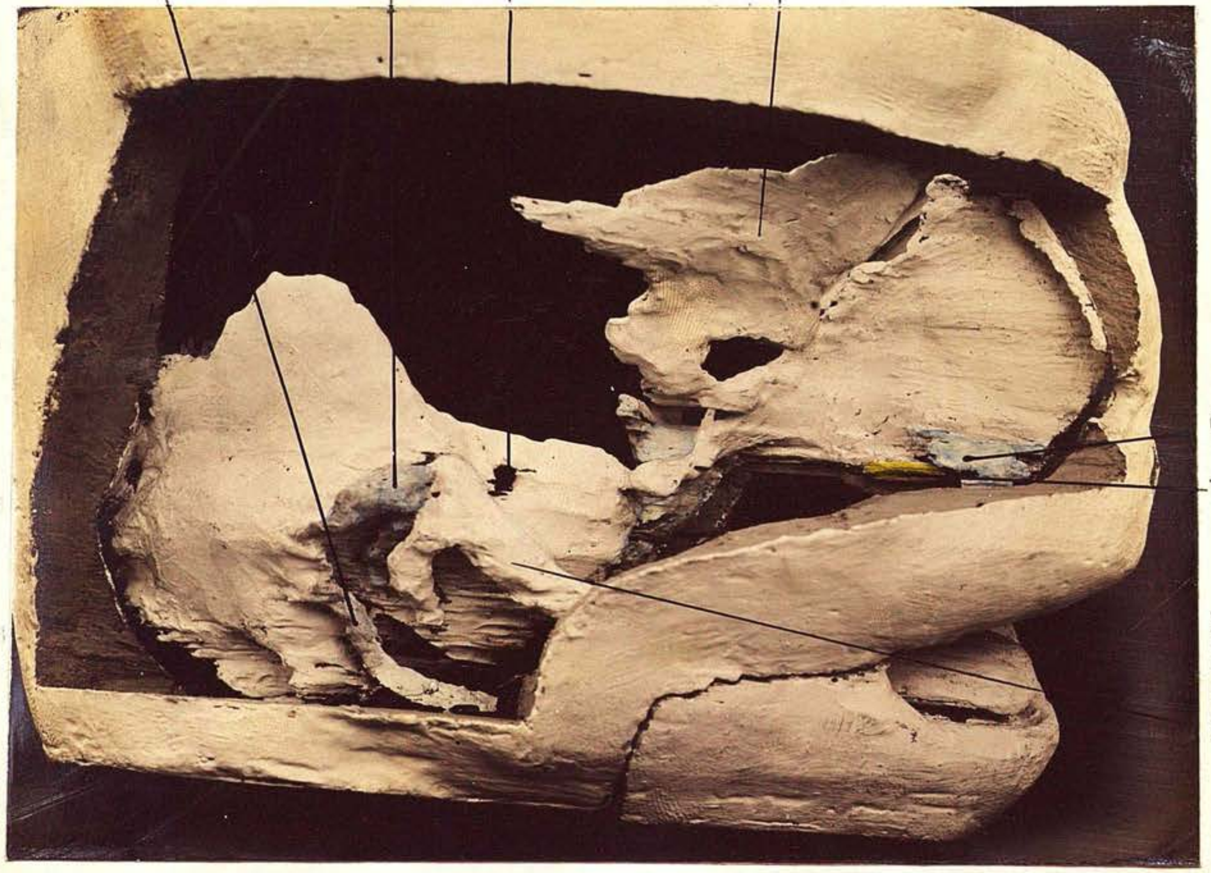
Fig. 37.



Face of 30 mm human embryo. The tongue, alveolar ridges and cleft palate can be seen. See fig 20.

C 2 XXXI

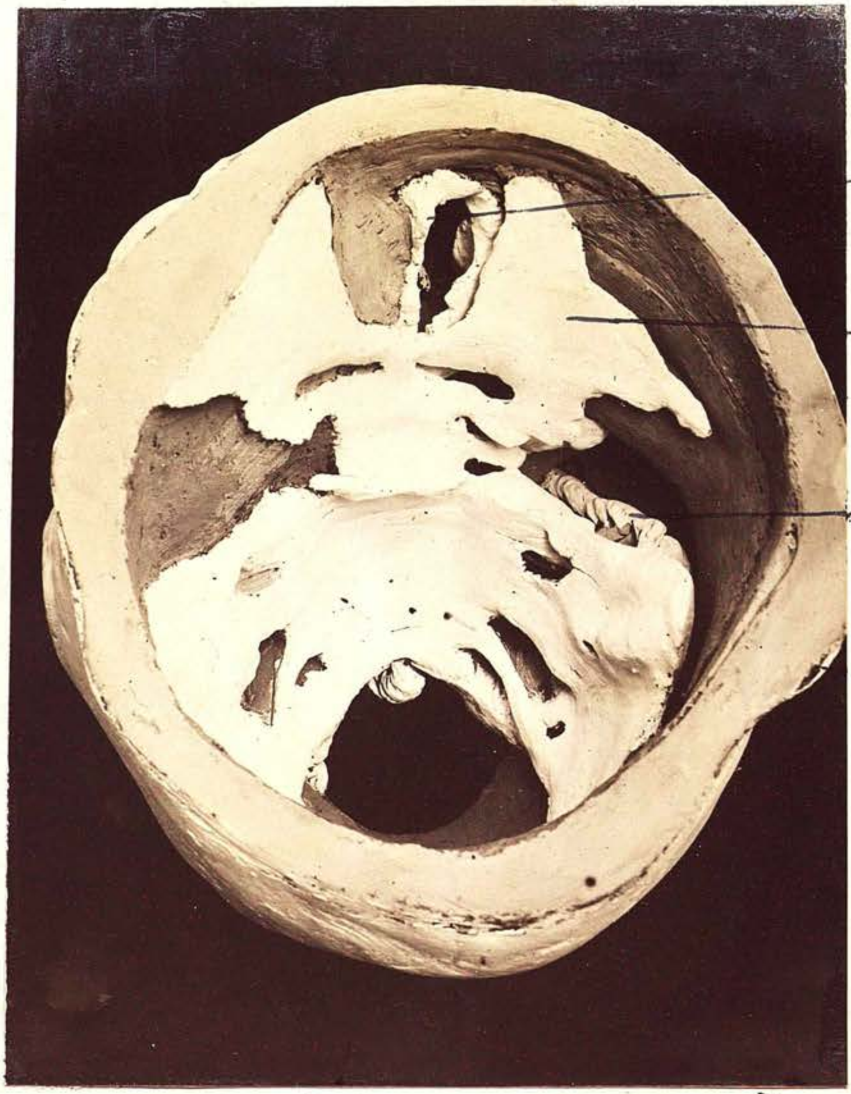
Fig. 38.



Model of cranium of 30 mm human embryo showing nasal septum with vomer and paraseptal cartilage. The auditory ossicles can also been seen.

C 2 XXXI

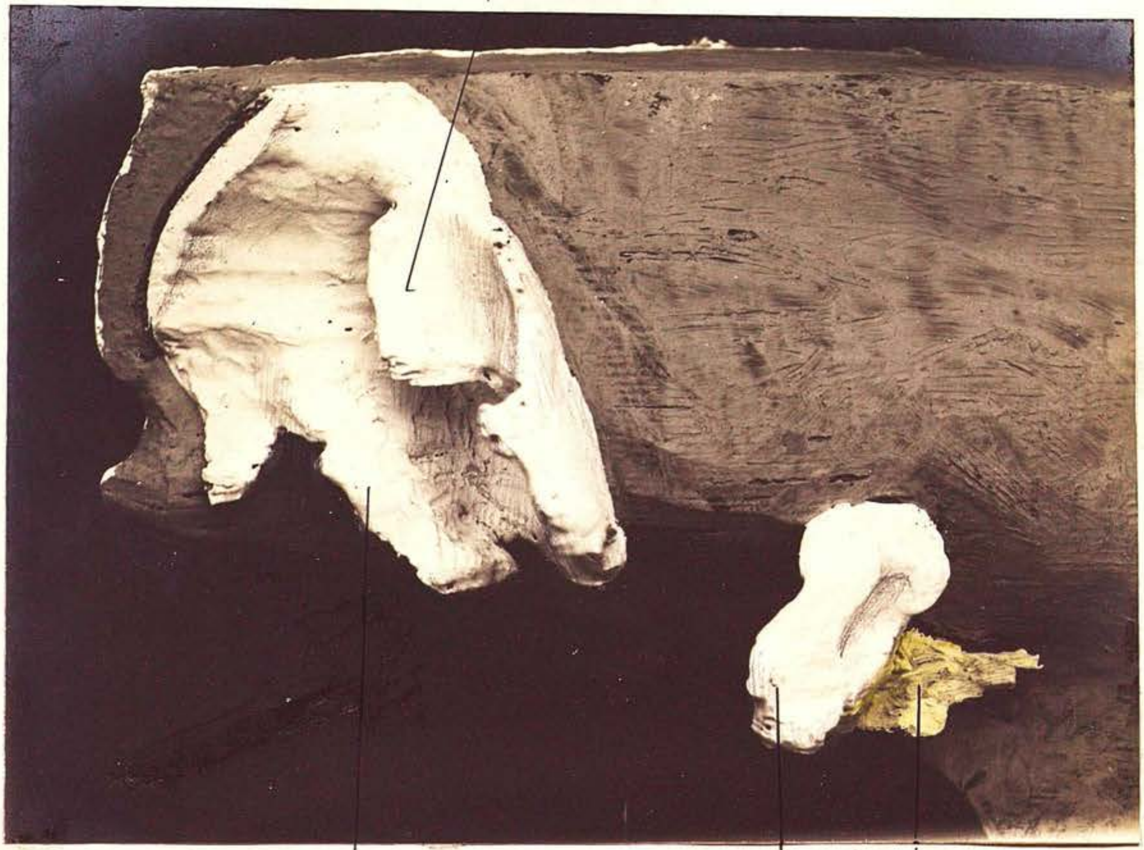
Fig. 39.



Model of 30 mm human embryo showing cartilaginous cranium.
The top of the nasal capsule is shown on the right side with the large lesser wing of the sphenoid in contact with it.
The ear capsule has been modelled in detail on the right side.

C 2 XXXI

Fig. 40.



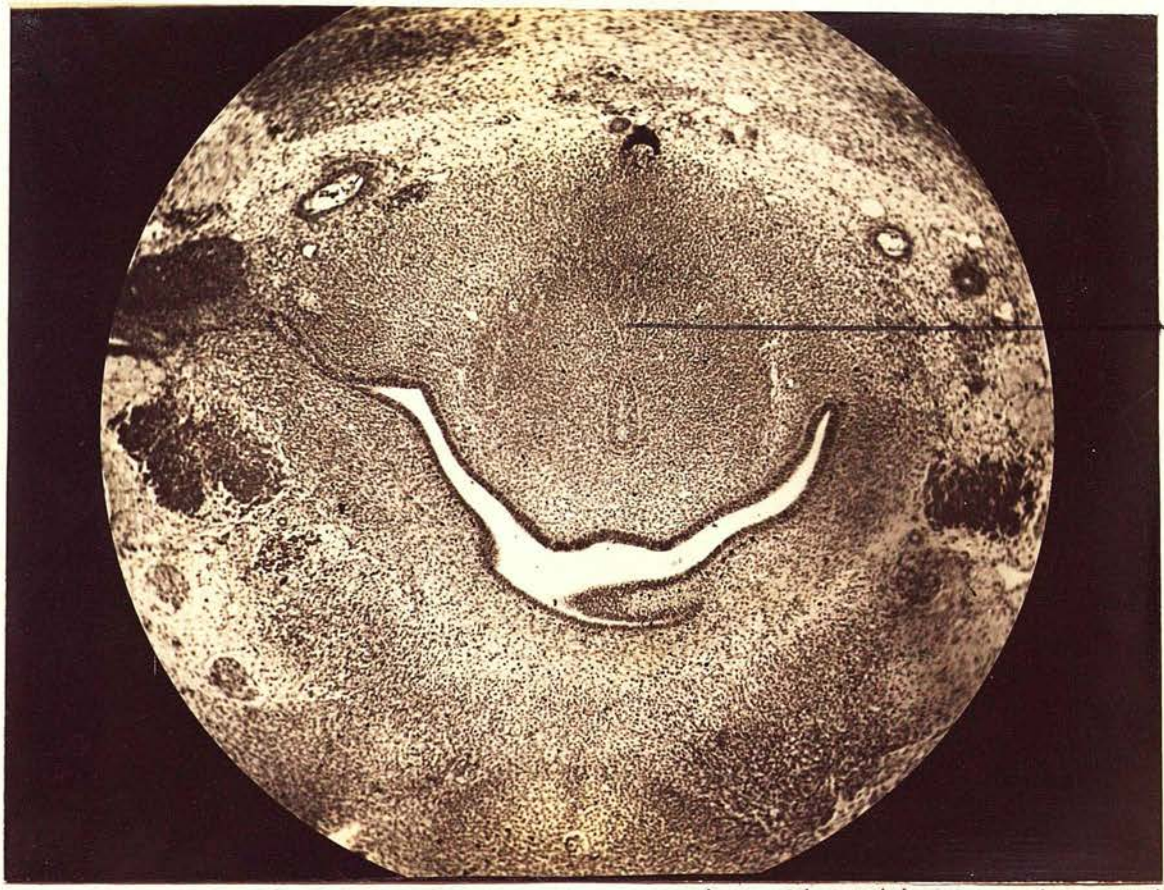
Lateral wall of nasal capsule of 30 mm human embryo.

C 2 XXXI

Fig. 41.

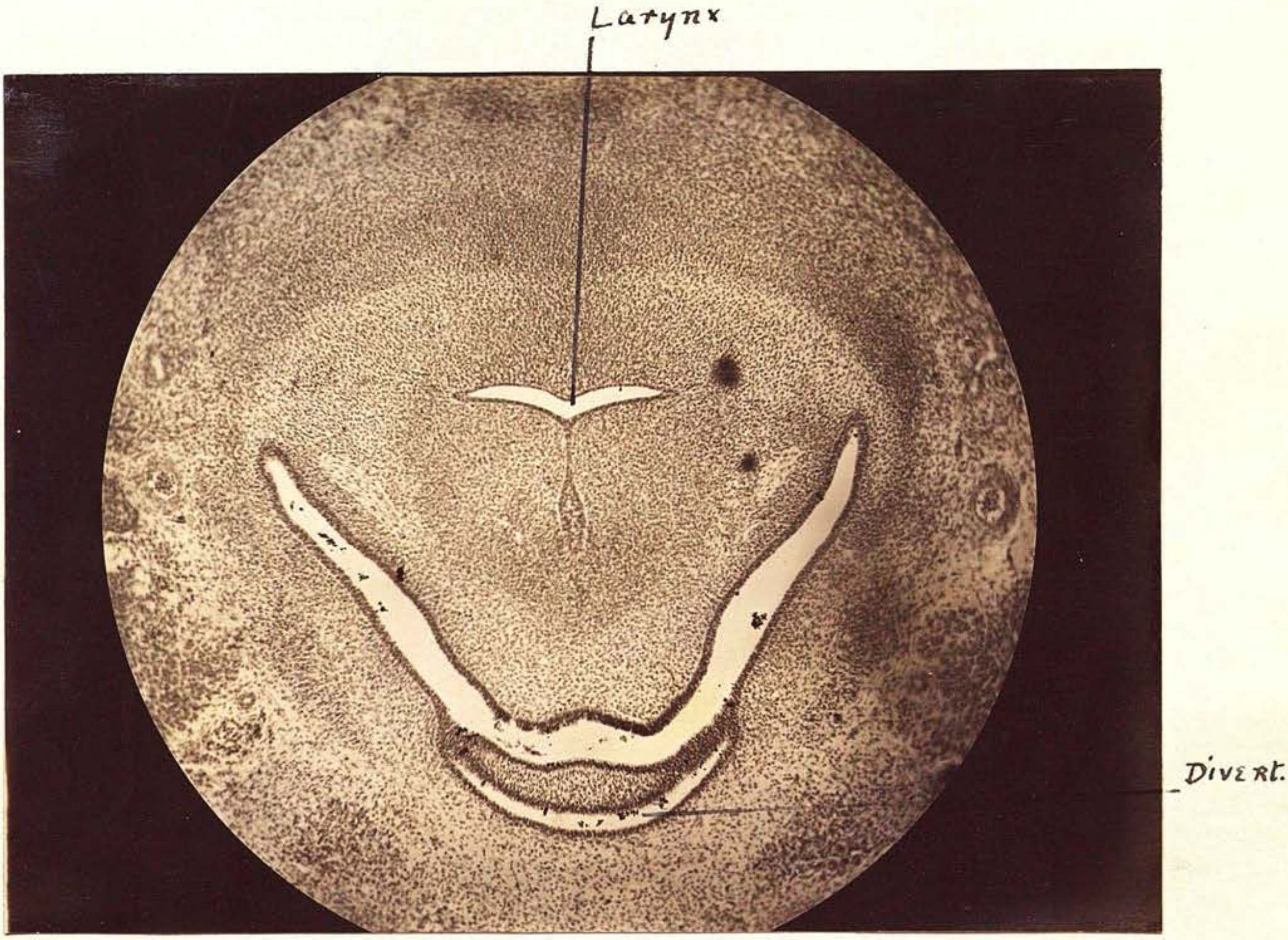
Sectiin of 30 mm human embryo showing lower part of nasal septum. The section is oblique. The lower edge of the septal cartilage is enclosed on each side by a thin lamina of bone representing the vomer. The paraseptal cartilages are seen in front of the vomer.

Fig. 42.



Section of 14.5 mm pig embryo showing diverticulum in posterior pharyngeal wall. Also shows thyroid and thymus buds and the two walls of larynx in apposition. The section is oblique.

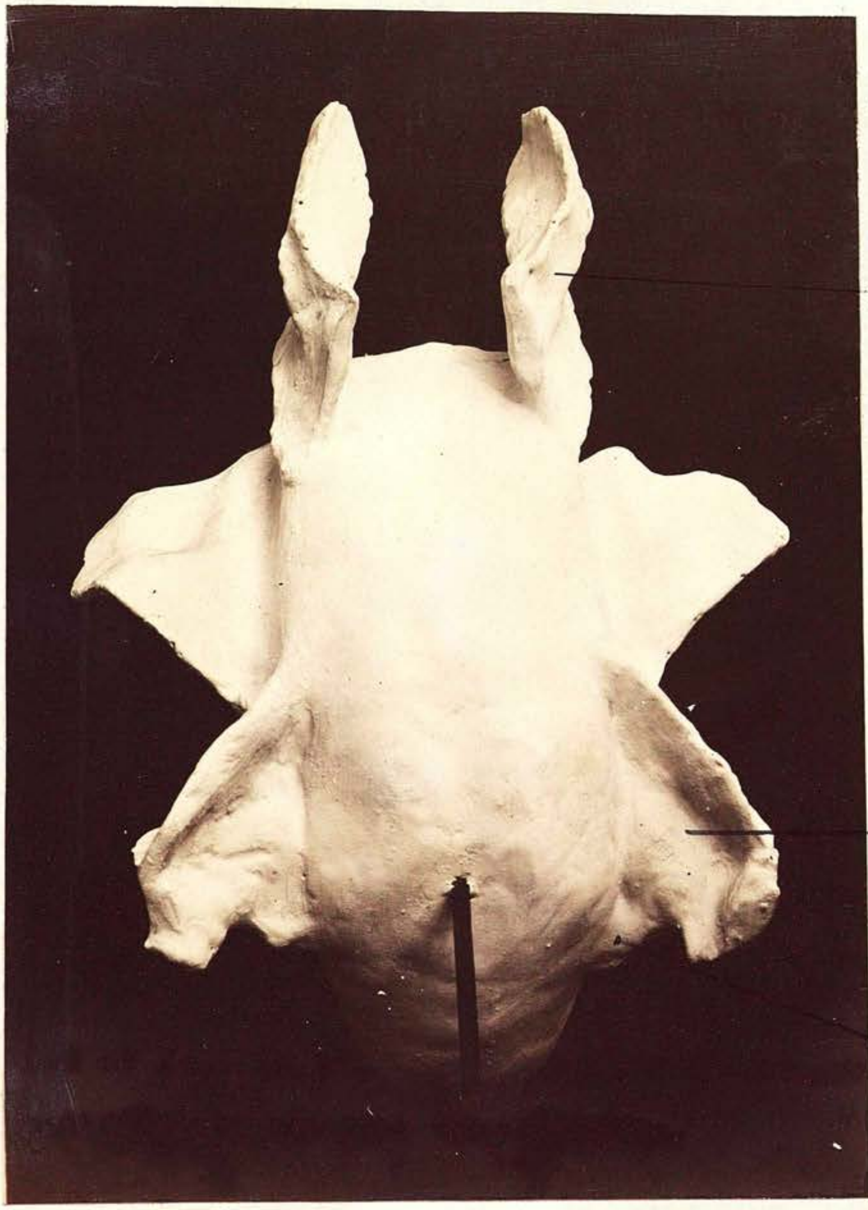
Fig. 43.



Section of 16.5 mm pig embryo showing larynx, pharynx and posterior pharyngeal diverticulum.

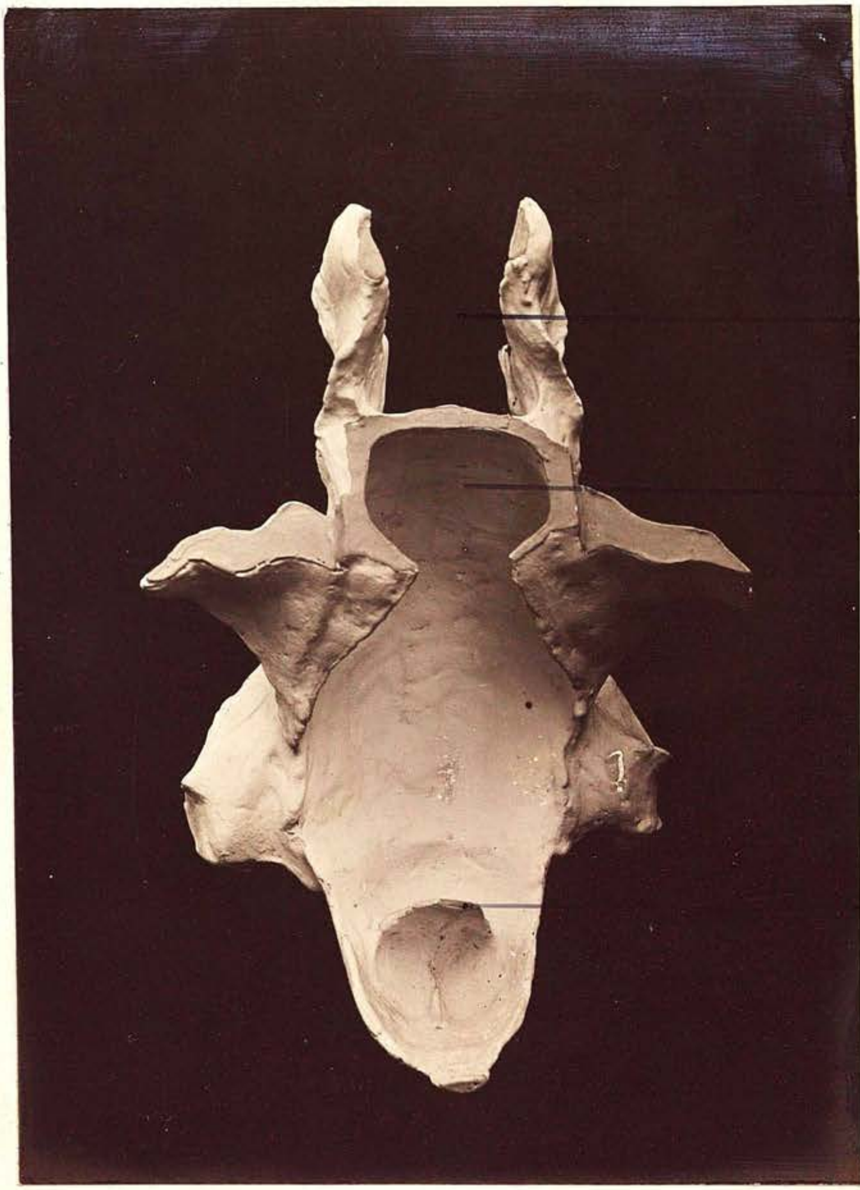
Fig. 44.

Model of air passages of 20 mm human embryo, cranial aspect The nasal cavities are seen as projecting from the top of the model. Lateral to them are two grooves representing palatal



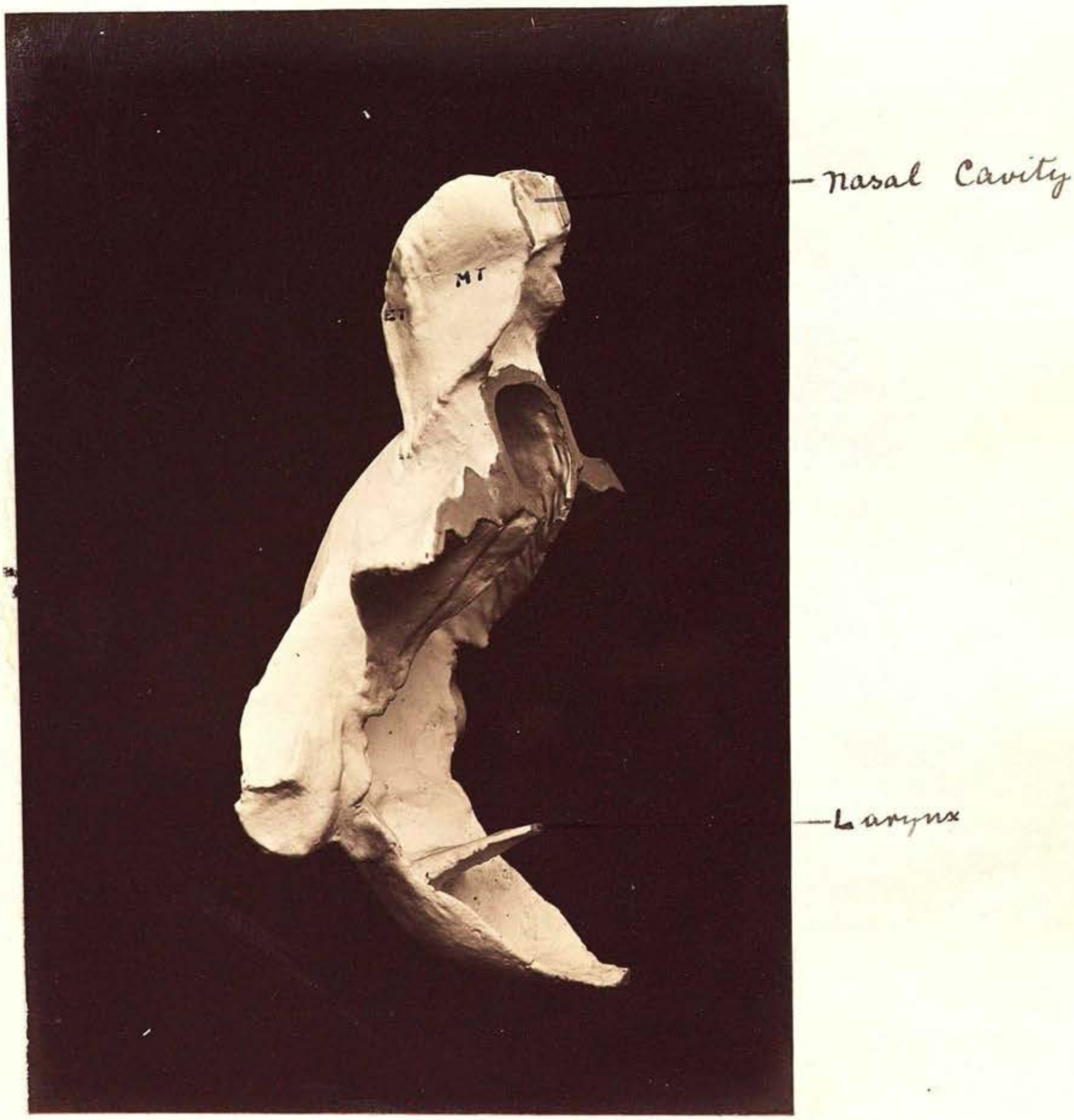
processes. Just behind where the cavity narrows the middle ear cleft is seen as a wing-shaped projection with a concavity on its upper surface representing the impressio cochlearis. The dorsal extension of II pouch also seen to form part of the middle ear projection. C 2 XXXV - adapted to

Fig. 45.



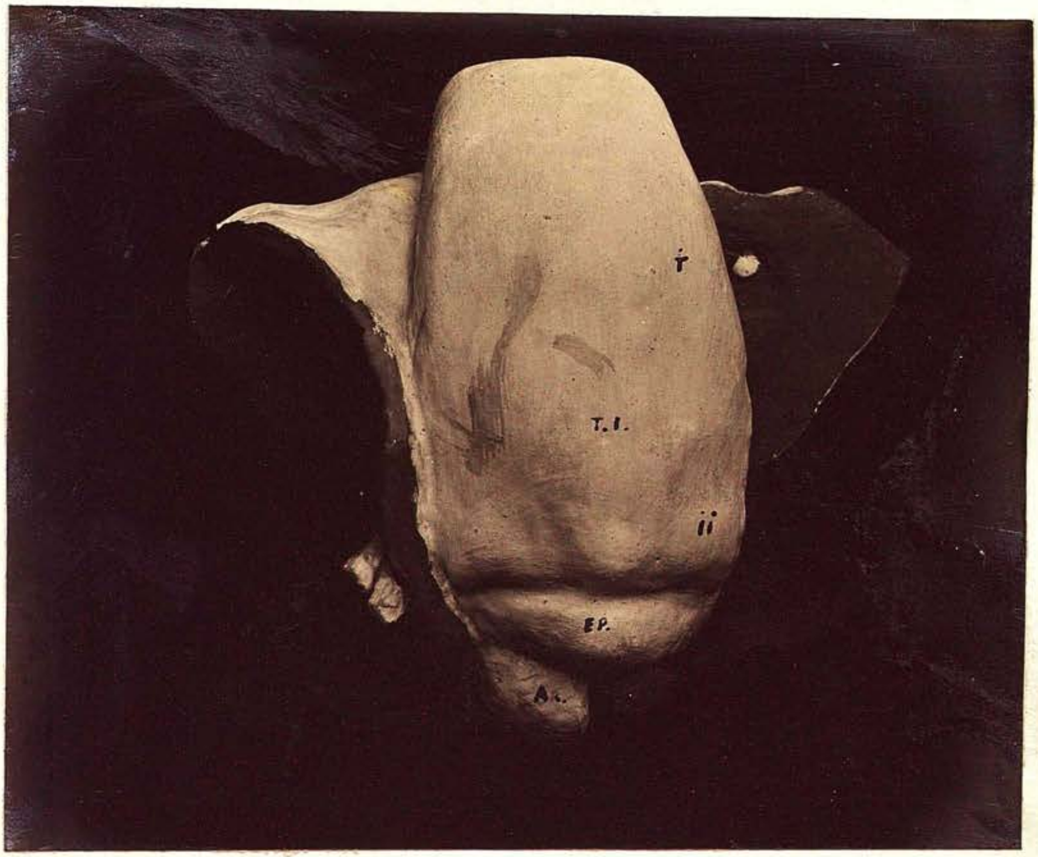
Same model as fig. 44. The large concavity underneath is due to the tongue and below it is the wedge-shaped projection caused by the laryngeal cavity.

Fig. 46.



Side view of same model as figs. 44 & 45. Shows on nasal part of model two concavities representing the maxillo and ethmoturbinals.

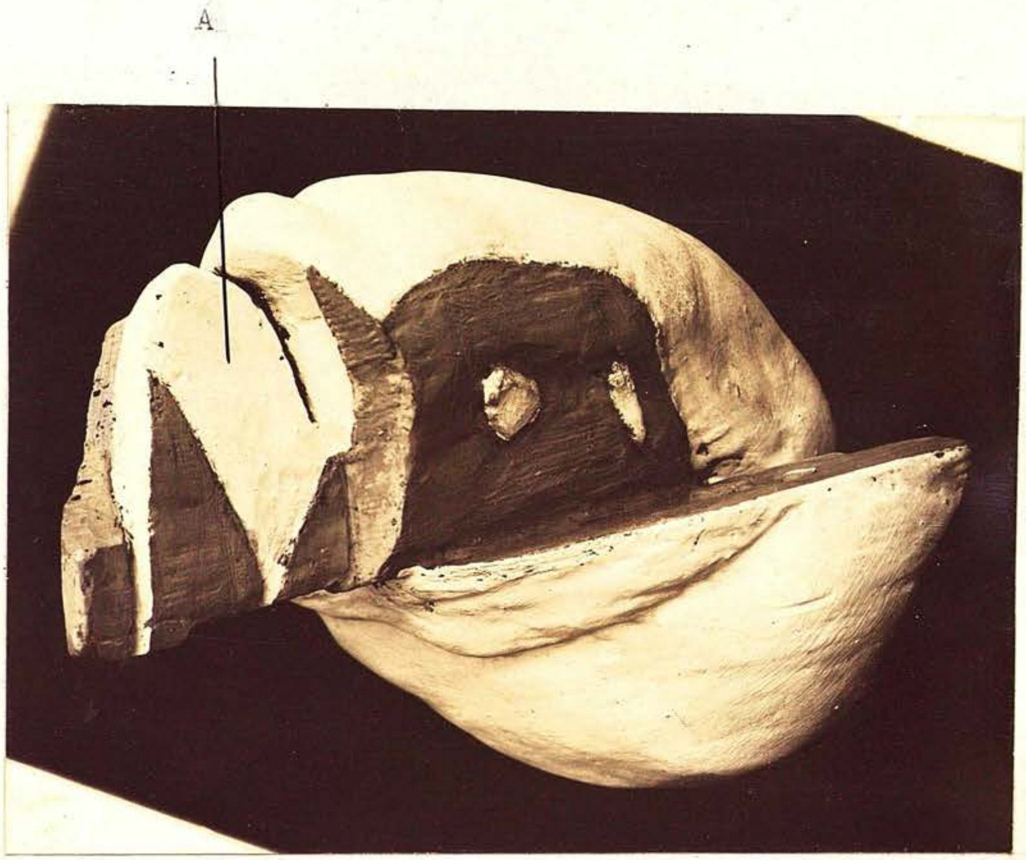
Fig. 47.



Model of tongue of 20 mm human embryo seen from above. The second arches can still be faintly made out in front of epiglottis. Half of the larynx has been removed.

C 2 XXXIII

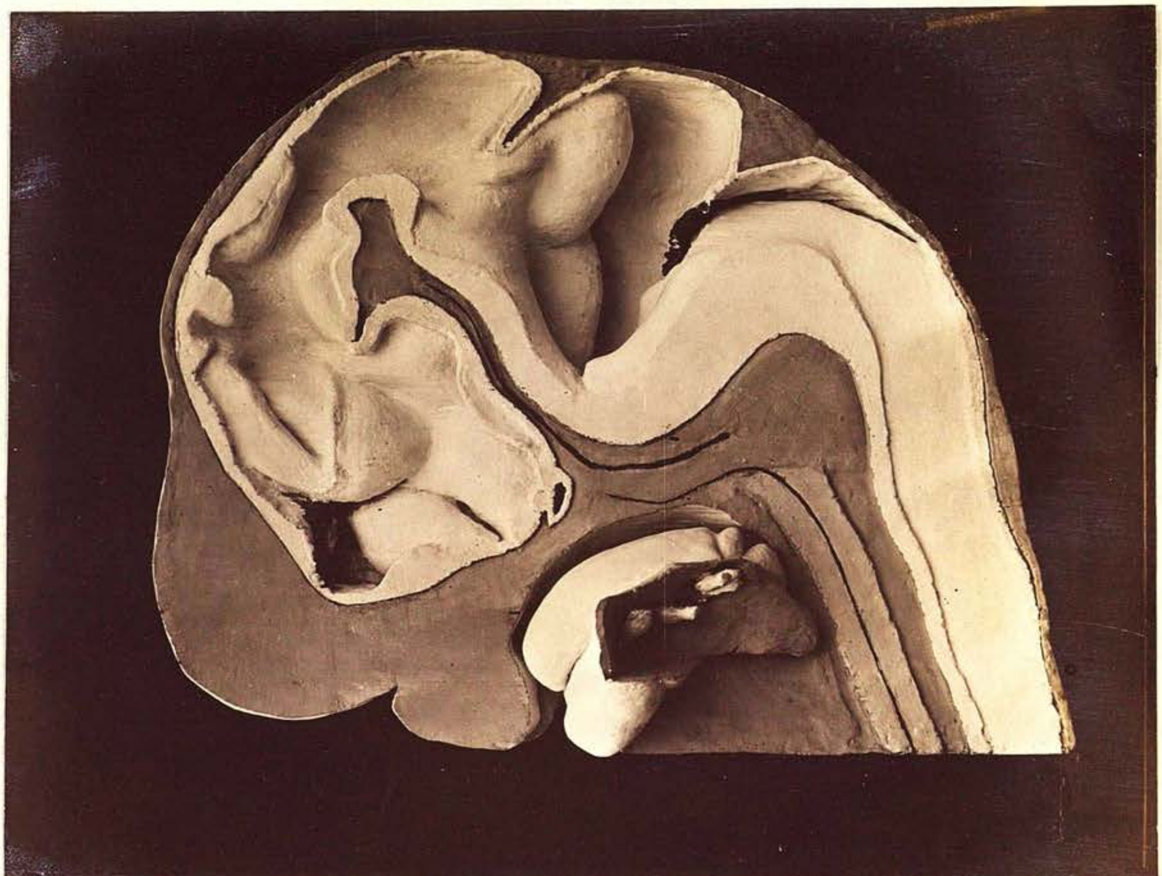
Fig. 48.



Model of tongue and larynx of 20 mm human embryo showing laryngeal cavity opened up by removal of one side. The part A is only a potential cavity, its walls lying in apposition.

C 2 XXXIII

Fig. 49.



Model of 20.mm human embryo with floor of mouth in situ.

The lingual, glossopharyngeal, and hypoglossal nerves are seen under tongue. The brain has also been modelled in this specimen. See fig 17.

C2 XXXV and C_2 XXXIII