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THE NASAL SKELETON OF AMBLYSTOMA PUNCTATUM (Linn.)

WITH PLATES II, III, IV, V.

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THE NASAL SKELETON OF AMBLYSTOMA PUNCTATUM (Linn.)

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The nasal skeleton of the Urodela presents itself in a number of forms which differ more or less widely from each other as well as from the types met with in the Anura; that is to say, comparisons of the fully formed skeletons have shown apparently no common order of structure.

One object of this work was to study the early stages in the chondrification of the nasal skeleton of an Amphibian and to compare them with the developing nasal skeletons in others in the hope of finding resemblances which in the adults are not marked. For this purpose Amblystoma was selected because it is a typical form and because a certain part of the work has already been accomplished. A second object concerned the plan of chondrocranial formation and perfection in the ethmoidal region for which Amblystoma seemed suitable in the vigorous development of its cartilaginous head-skeleton. The bony framework of the nose has not been included in the present investigation.

Winslow ('98) used Amblystoma as the basis of his work on the chondrocranium describing five stages, viz., in the body-lengths of 10, 11, 12, 39 and 69 mm., and though he does not deal specially with the nasal skeleton, his discriptions of this region are full. I have selected and described stages between the total lengths of 12 and 39 mm., but was unable to obtain animals between 45 and 69 mm., the want of which was much felt.

The excellent series of young larval heads which were at my disposal were kindly loaned by my friends Professor and Mrs. Simon H. Gage, to whom I offer my best thanks. This material from the Cornell Embryological

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Laboratory, consisted in eight heads of Amblystoma punctatum, serial sectioned.

The animals were of the following total lengths:

No. 57	12mm.
" 58	13mm.
" 59a	17mm.
" 59	19mm.
" 60a	21–24mm.
" 61	24–27mm.
" 62	27–30mm.
" 63	30–33mm.

All of these heads were transected, except the last one in the list which was cut in the frontal plane; all sections were 10μ thick.

Besides this full series of small larval heads the nasal region in Amblystoma of 40–45mm. in length was studied by means of serial sections and dissection. These animals were obtained at Woods Hole, and I take this opportunity to express my appreciation of the courtesies shown me while finishing the work at the Marine Biological Laboratory. Dissections of adult heads also were made, and frontal sections of an adult right nasal capsule were prepared and studied. For this material I am indebted to my friend, Mr. Julius Hurter.

The ethmoidal region of Nos. 58, 59a and 60a, and the left nasal sac and skeleton of head No. 62 were modeled in wax after the method of Born with Bardeen's ('01) modifications. These are referred to in the description as stages I, II, III and IV. Amblystoma of 40–45mm. is my stage V.

The olfactory organs of Amblystoma have been described by Bawden ('94) in his work on the nose and Jacobson's organ. It will be necessary here to make only a brief statement regarding the anatomy of the olfactory bulb, nerve and nasal sac.

The caudal limit of the olfactory bulb in young larvae of Amblystoma is indicated on the surface by a slight groove on the lateral aspect of the cephalic end of the brain (Fig. 2, Olf.). Stieda ('75) describes a limiting furrow for the Tuberculum olfactorium in Axolotl; Gaupp ('99) has shown one to be present in Rana; and Kingsbury ('95) finds the area of olfactory glomerules in Necturus outlined by a furrow, better marked on the lateral surface of the brain. Corresponding closely to the position of this groove is the limit of the terminations of the olfactory nerve fibers which make a conspicuous field in the sections; the glomerulary arrangement itself, however, is hardly discernible. The direction of the olfactory nerve is laterad in the younger animals in conformity with the position of the nasal sac. This is at first lateral of the brain and projects further ventrad, while the cephalic extremities of the two organs reach about the same level. These relations are considerably changed while the animals are still very small. The nasal sac presents thick walls except laterally where the narrow lumen lies near the surface. The general cavity of the nose in the younger animals is a simple tunnel running between the external and internal nares. Midway between these openings is the mouth of a diverticulum from the main nasal sac, the Jacobson's organ of Bawden's account (J. O. in the figures). The position of Jacobson's organ in young larvae is at the ventral side of the main-sac; in older ones lateral and beneath it. This organ presents a small surface toward the median plane where the duct of Jacobson's gland opens. The latter lies between the ventral wall of the main nasal sac and the floor of the nasal capsule, extending mesad to the olfactory foramen. In older animals a small protrusion from the side of the general cavity near its cephalic end receives the nasolacrimal duct (Fig. 4, N. L. P.).

Winslow's stage III. is a larva of 12mm. in which the trabeculae terminate in the plates known as Cornua and present crests which have grown dorsally serving in this and later stages as cranial side-walls. Each Crista trabeculae, highest caudally, gradually descends toward the snout. There is no union between the trabeculae in front; antorbital processes are not present and with the exception of the Cornua trabecularum no mention is made by Winslow of a cartilaginous nasal skeleton.

These conditions were found as described, in the larva of 12 mm. which I studied.

Stage I.

Amblystoma 13mm. Fig. 1.

The simple, somewhat oval, nasal sac lies laterad of the brain, extending beyond its level ventrally. A groove on its lateral surface separates Jacobson's organ from a dorsal prominence. The narial passage is simple; everywhere, except laterally, its walls are thick. A narrow off-shoot from the general cavity close to the internal naris leads into Jacobson's organ.

The trabeculae (Tr.) are unconnected anteriorly and lie ventrad of the brain beyond which they project to the level of the cephalic ends of the olfactory organs. The Crista trabeculae (C. tr.) reaches forward, almost to the level of the nasal sac and olfactory bulb where it ends in an abruptly descending edge. The trabecula is triangular in section from the crest as far as the horn. Opposite the latter it sends a blunt process (Medial Process of the trabecula; Pr. med.) mesad toward its fellow, and also dorsad a little way. The trabecular horn (Co. tr.) lies beneath and supports the olfactory sac; in this function the neighboring part of the trabecula also shares.

The left "Processus" antorbitalis is present in the form of a slender stick of cartilage between the olfactory organ and eye-ball. It is just behind the internal naris and is continued as a prochondral rod medialwards to the trabecula, joining it at the level of the cephalic end of the Crista.

Ossification of the roof of the cranium is already well advanced at this stage but there is no bone in the olfactory region of the cranial wall. Here a thin membrane extends dorsad from the trabecula to the roof bones and from the cephalic edge of one crista forward and across the middle line in front of the brain to become continuous with the same sheet of the opposite side. In the dorsal part of this membrane there is present a small rod of cartilage (Col. eth.) running in the long axis of the head and therefore parallel with the trabecula, its anterior end just dorsad of the above mentioned medial process, its caudal extremity over the olfactory nerve. The little column of cartilage projects laterally among the loosely disposed cells of the perirhinal tissue, and faces medially the olfactory bulb.

The anlage of this independent cartilage appears in the 12mm. embryo as a group of closely arranged, oval cells (Fig. 5, Anl.) between which and the end of the trabecula, and connecting the two, is a column of large cells of irregular forms. This column reaches the anterior end of the anlage of the rod passing in front of the olfactory nerve (Fig. 5, C.).

Stage II.

Amblystoma 17mm. Figs. 2, 6 and 7.

The nasal sacs now project about one-fourth of their length in front of the brain so that an Internasal Space can be spoken of; brain and sac reach the same level ventrally. The groove on the side of the main nasal sac is wide and deep and is limited below by the now prominent Jacobson's organ.

The trabeculae (Tr.) are connected by a narrow Anterior Trabecular Plate (Ant. tr. pl.), the ethmoid plate of Winslow's description, beyond which they extend to the level of the ends of the nasal sac, separated by an intertrabecular notch. The Crista trabeculae (C. tr.) is high, reaching half way up the side of the brain and presenting a straight cephalic margin; it is still caudad of the olfactory bulb. The trabecular horn (Co. tr.), broad at its origin at the trabecula, is directed laterad and caudad and is hollowed dorsally to receive the nasal sac; the narrow end of the horn is in contact with the organ of Jacobson. An antorbital process (Pr. ao.) is present on each side and is chondrified throughout and connected by cartilage with the trabecula. The line of union is easily distinguishable by the presence of young cartilage, and is just opposite the cephalic free margin of the trabecular crest. The little rod of cartilage (Col. eth.) present in the 13mm. larva dorsad of the olfactory nerve, has lengthened considerably and reaches nearly to the trabecular crest. It extends along the caudal two-thirds of the nasal sac between it and the brain, inclining cephalo-ventrad to join by a broad base the trabecula in front of the level of the anterior trabecular plate. While the rod follows the dorso-mesal edge of the nasal sac it, on the other hand, crosses the surface of the olfactory bulb. Its ending is noteworthy: it bends ventrally in a small but distinct hook (Pr. unc.) just behind the olfactory bulb and a very short distance in front of the corner of the Crista. Where the rod expands to join the trabecula two processes arise; one of these, the Ethmoidal Process, (Pr. eth.) points dorso-mesad in front of the olfactory bulb and approaches its fellow; the other the Medial Nasal Process, (Pr. n. med.) grows cephalo-ventrad along the internasal surface of the olfactory sac. The latter process is separated from the end of the trabecula and the horn by a notch, the Medial incisure (Inc. med.) which allows the passage of the third main branch of the ophthalmic V (Fig. 4, Oph. V_3). Another little spur of cartilage on the rod in question, the Lateral Process (Pr. lat.), is present near the hinder end and reaches out into the perirhinal membrane of the dorsal side of the nasal sac. No separate centers of chondrification in this membrane were discovered either in this or in subsequent stages.

Reviewing the cartilaginous rod (Col. eth.) at this stage, it is seen to arise from the trabecula just in front of the anterior trabecular plate by a thick base from which two processes spring, then to arch backward across the olfactory bulb and over the olfactory nerve to end free in a ventrally turned hook a little way in front of the dorsal corner of the trabecular crest.

The anterior trabecular plate (Ant. tr. pl.) underlies the cephalic end of the brain and connects the trabeculae some distance caudad of their extremities; its cephalic margin is a little behind the level of the junction of the trabecula and the base of the rod (Col. eth.). I could not discover that this plate chondrifies independently of the trabeculae.

Stage III.

Amblystoma 21–24mm. Figs. 3 and 8.

The nasal sac, which has a cephalo-caudal direction in the 13 and 17mm. larvae, now holds an oblique position, the caudal end being farther from the middle line than the cephalic extremity. About one-third of the nasal sac is cephalad of the brain and the internasal space is correspondingly increased. The organ of Jacobson (J. O.) is quite prominent, projecting laterally as well as ventrally. The groove dorsad of it is relatively wider than in the younger animals and its floor now shows a slight convexity, best marked in front.

A narrow cartilaginous cranial floor is formed by the anterior trabecular plate and by a ledge extending from the medial side of the trabecula. The broad horn of the latter (Co. tr.) sends its upturned end around the under surface of Jacobson's organ. The blunt end of the trabecula projects a little way beyond the cephalic margin of the Cornu. The anterior part of the main nasal sac does not rest directly upon the upper concave surface of the Cornu, as does Jacobson's organ, but is separated by a narrow but well defined Subnasal Space (Sub. s.) which is occupied by a loose web of mesenchymal tissue and by some of the branches of Jacobson's gland.

The antorbital process (Pr. ao.) juts out from the trabecula just caudad of the Olfactory Window (Fen. ol.); between it and the Cornu trabeculae there is a wide notch, or bay, in which lie the caudal part of the main nasal sac with the posterior naris and also the caudal part of the organ of Jacobson.

The olfactory window (Fen. ol.) has resulted from the union of the rod (Col. eth.) with the dorsal corner of the Crista trabeculae; its ventral boundary is the trabecula while the cephalic limit is made by the union of the latter and the rod. The distance between the middle of the rod and the trabecula, (i. e., the height of the olfactory window) has increased relatively, the rod suffering a bend, convex dorso-laterally. This appears to be due to the growth dorsally of the nasal sac to which the rod is now indirectly fixed through the lamina cribrosa to be described presently. Through the window passes the olfactory nerve; in its ventral and cephalic corner is the end of Jacobson's gland. This does not enter the cranial cavity but presses against a membrane which fills the window and which is traversed by the olfactory nerve. The caudal boundary of the window is the anterior free edge of the trabecular crest and also to some extent, the ventrally turned end of the rod (Pr.unc.) which has grown behind the olfactory nerve. Just as the nasal sac itself, so the olfactory window has an oblique position and forms an obtuse angle with the sagittally directed Crista trabeculae.

The rod (Col. eth.) is now considerably flattened and sends an irregular edge over the nasal sac into the perirhinal membrane. The rods of opposite sides are in this stage connected across the middle line by a bridge of cartilage which I shall call the Ethmoidal Bridge (Eth. br.). This is formed, in part at least, by extension and fusion of the ethmoidal processes (Pr. eth.) of Stage II. The bridge passes in front of the brain, partially separating the cranial cavity and internasal space, and lies in a transverse plane cephalad of the anterior margin of the anterior trabecular plate. Between these parts and the bases of the rods (Col. eth.) laterally is the ethmoidal window (Fen. eth.) filled with membrane; part of it is beginning to chondrify.

The medial nasal process (Pr. n. med.) has grown forward and widened in the dorso-ventral direction in the perirhinal tissue. It makes the medial wall of the nasal capsule in its anterior part; ventrally it is still separated from the extremity of the trabecula by the notch (Inc. med.) described for the 17mm. larva.

The Lamina cribrosa (Winslow), (L.), is a broad plate of cartilage, connected medially with the dorsal arch over the olfactory window, and bent outward to cover the caudal part of the main nasal sac above and at the side. It occupies part of the perirhinal membrane, and while it consists of but one piece it is fenestrated and irregular along its margins. The pointed extremity of the Lamina is just dorsad of Jacobson's organ; a wide gap separates its caudal edge from the antorbital process.

The anterior trabecular plate (Ant. tr. pl.) is no longer in a frontal plane but is inclined cephalo-dorsad so that it now enters into both the floor and cephalic wall of the cranium. The ethmoidal bridge, window and anterior trabecular plate form a curved partition in front of and below the olfactory bulbs.

Stage IV.

Amblystoma, 27–30mm. Fig. 4.

The nasal sac of this larva is only in its posterior half alongside of the brain. Its contour is less regular than in preceding stages, due mainly to the increase in the size of the organ of Jacobson and to the further separation of this part from the main-sac. The latter presents a great thickening of its dorso-lateral wall appearing on the surface as a rounded eminence sharply marked off from the middle lateral region by a groove. The floor of this sulcus had already, in the 21–24 mm. larva, lifted itself into a convexity and in the present stage a small diverticulum of the main nasal cavity bulges the floor into a little eminence (N. L. P.) which connects with the end of the Nasolacrimal Duct (D. nl).

Jacobson's organ lies ventrad of the lateral region of the main-sac and has pushed its way mesad between the latter and the trabecular horn. Into its medial side opens the long, branched, tubular Jacobson's gland with wide lumen and rather thick walls. The end of this gland occupies a position close to the ventral cephalic corner of the olfactory window, and in the rest of its extent is situated between the main-sac and the upper surface of the Cornu trabeculae in the space (Sub. s) already mentioned.

The differences that are noticed in the cartilaginous framework over the preceding stage are due chiefly to growth of existing parts; there are no new centers of chondrification.

The cranial floor in the olfactory region is broader, the part made by the anterior trabecular plate giving support to the bulbs. The olfactory window is of the same size as it was in the third stage; the opening is therefore relatively smaller and begins to assume the appearance of the adult olfactory foramen. The part of the capsular wall occupied by the olfactory foramen is obliquely placed and faces forward and outward. Since the nasal sac has increased in length very much, extending in half its length beyond the cranial cavity and ending behind the olfactory foramen, it happens now, for the first time, that a part of the cartilaginous cranial side wall, made by the Crista trabeculae, stands between the brain and the sac.

There is a complete cartilaginous wall separating the cranial cavity and internasal space, stretching from side to side at the level of the anterior margins of the olfactory foramina. Although it is thin in its middle part, this partition, which I have called the Ethmoidal Plate (Eth. pl.) in the same sense that Gaupp* uses the term, is chondrified throughout. Its caudal surface slopes gently into the dorsal surface of the anterior trabecular plate without interruption. The cephalic surface of the ethmoidal plate is thickened along its dorsal and lateral margins corresponding to the positions of the ethmoidal bridge and base of the rod (Col. eth.) in the earlier stages of development. At these places the growth of cartilage in the mesenchymal tissue of the internasal space appears to be most active. In later stages (30-33mm.) as a

* Morph. Arbeit. 2, p. 313.

result of the growth of the ethmoidal plate in these regions the nasal capsules are connected by a broad commissure which has the form of an arch covering dorsally and laterally the hinder part of the internasal space. The Fenestra ethmoidalis has been obliterated through chondrification, but the cartilage here is thin as compared with the dorsal and lateral parts of the plate. This manner of growth of the ethmoidal plate explains, then, the adult form of the nasal septum and its relation to the internasal space. Intermaxillary glands were not present in this or preceding stages, the space being filled with mesenchyma.

The medial nasal process (Pr. n. med.) has begun to take part in forming a roof over the anterior part of the nasal sac, its dorsal edge bending laterally and presenting several irregular projections. The ventral margin inclines laterally also toward the ventral surface of the main nasal sac; it is separated from the conical end of the trabecula and horn by the medial incisure (Inc. med.) the width of which is greater than in Stage III. The medial incisure leads from the internasal space into the narrow cave (Sub. s.) between the under surface of the nasal sac and the upper concave side of the Cornu trabeculae. Into the lateral part of this space the medial portion of the organ of Jacobson (J. O.) has grown, and through the space from the latter organ to the olfactory foramen stretches the large branched Jacobson's gland already mentioned. The end of the trabecular horn supports Jacobson's organ, around the side of which it is bent.

The antorbital process at this stage is turned forward toward the internal naris; its free end presents two little tubercles, one pointing forward, the other laterally. The caudal end of the nasal sac overhangs the antorbital process and the curve of the latter appears to be in adaptation to the adjacent posterior naris.

The Lamina cribrosa (L.) covers the caudal half of the main sac. It is connected with the side wall of the cranium opposite the whole length of the olfactory foramen and a little way caudad of this. As it stretches outward it becomes narrower, terminating opposite the groove which separates the dorsal enlargement of the main nasal sac from the lateral diverticulum in which the nasolacrimal duct ends. The latter is supported by a little process of cartilage which grows forward from the Lamina cribrosa and turns ventrad toward the trabecular horn.

The cartilaginous nasal skeleton of Stage IV. is far from completion; dorsally the nasal organ is only partly covered by the Lamina cribrosa and the edge of the medial nasal process; the future anterior and posterior cupolas are only suggested by these processes of cartilage which are inclining in their growth toward the antorbital process and the trabecular horn respectively.

The conditions present in the ethmoidal region of a 39mm. larva of Amblystoma jeffersonianum have been described by Winslow. The nasal capsule of my Stage IV seems to be less advanced.

Stage V.

Amblystoma of 40–45 mm. Gills partly atrophied.

The nasal sac is in front of the brain except for its caudal one-third; the olfactory foramen looks more forward than outward.

The nasal capsule is provided with a broad, continuous roof extending over nearly the whole dorsal aspect of the main-sac. Its caudal part is the Lamina cribrosa; its cephalic part the medial nasal process which now reaches beyond the external naris and forms the anterior cupola. Between these parts is a broad bay within which are the external naris and the cephalic end of the nasolacrimal duct. This bay becomes the Fenestra narina (Gaupp '05. 2, foot-note, p. 280).

The ventral edge of the medial nasal process turns under the main-sac a little way and is still separated from the trabecular horn by the now widely extended medial incisure. The extreme lateral end of the process is, however, very near the trabecular horn. The latter sends dorso-caudad a cylindrical process the end of which is connected by precartilage with the tip of the little cartilaginous support afforded the nasolacrimal duct by the Lamina cribrosa. The nasolacrimal duct crosses this little bridge to end in the nasal sac. Followed in the opposite direction, the duct runs back in a slight groove on the side of the nasal capsule (original Lamina cribrosa). A little elongate (in section) mass of densely packed cells is applied to the medial side of the bridge near the trabecular horn. I suspect that this is the anlage of the dilator naris muscle.

The cartilaginous nasal capsules of the 69mm. Amblystoma described by Winslow ('98) present conditions which are, in the main, probably the results of continued growth and readjustment of the parts present in the stage just described. The capsules are mostly anterior to the brain-case and the olfactory foramina look forward and a little outward. There is no longer a medial incisure, only a small foramen (Fig. 12, ni.), the Foramen apicale (Gaupp '05.1), transmitting a branch of the Nasalis internus. The Lamina and antorbital process are united in a posterior wall or cupola, a foramen (orbito-nasal) being enclosed. Three windows are shown (fig. 12) in the capsular wall. The largest is situated dorsally and is separated by a strip of cartilage called "dorsal process" from the other two foramina. These openings are placed laterally, separated from each other by a "short connecting rod." The hinder of the two is at about the middle of the capsule in its cephalo-caudal extent. In the explanation of the figures (p. 199) "nl.", which points to this foramen, refers to "nostril;" and in the text (p. 159) the short connecting rod (the anterior boundary of the foramen) is said to be in front of the nasal duct.

In the nasal capsule of the adult studied by means of frontal sections I find these windows. Jacobson's organ appears in the posterior of the lateral openings, the Fenestra infraconchalis (Gaupp, '05.1) while the external naris and the termination of the nasolacrimal duct were found in the anterior one, the Fenestra narina.

The nerves were reconstructed in my stage IV in order to to observe their relations to the nasal skeleton; the reference letters will be found in figs. 4, 6 and 8. My results in the main agree with Herrick's ('94).

The olfactory nerve, consisting at its origin of two parts as described by Locy, ('99) Coghill ('02) and others, runs through the olfactory foramen and divides into four large branches. One of these passes ventro-laterad among the tubules of Jacobson's gland; a second goes dorso-laterad, a third ventrad, the fourth caudad. They were not followed to their ends.

The Ramus frontalis V (F.) runs forward above the Lamina cribrosa and then upon the laterally turned edge of the medial nasal process. A twig communicates with a branch of the third division of the ophthalmic (C. F.).

The Ramus maxillaris V (Max.) breaks up into twigs laterad of Jacobson's organ and among the external nasal glands in this region. Its relation to the maxillary bone has been mentioned by Herrick.

The first of the three main branches into which the Ramus ophthalmicus trigemini divides at the fore part of the orbit (Oph. V_1.) turns around the caudal end of the nasal sac in the wide interval between the antorbital process and the Lamina cribrosa. In older animals this nerve enters the nasal capsule by the orbito-nasal foramen in the posterior cupola. Further forward it passes under the tip of the Lamina and then runs close to the side of Jacobson's organ.

The second main branch of the ophthalmic (Oph. V_2) enters the space between the nasal sac and the Crista trabeculae and turning ventrad passes over the antorbital process to anastomose with the Ramus palatinus of the VII (P).

The third main branch of the trigeminal in the orbit (Oph. V_3) enters the nasal capsule beneath the caudal margin of the Lamina cribrosa close to the cranial side wall. It passes forward dorsal to the olfactory nerve and comes out of the nasal capsule at the medial incisure (later a foramen). The communicating branch to the Ramus frontalis (C. F.) and the branch accompanying the nasolacrimal duct (R. nl.) run under the Lamina cribrosa and emerge through slight notches in its cephalic edge.

The Ramus palatinus of the VII (P.) appears to consist of two bundles which run together along the lateral edge of the trabecula and then under the trabecular horn. The medial bundle is joined by the second branch of the ophthalmic.

SUMMARY OF OBSERVATIONS.

1. The nasal sac is at first laterad of the brain. In the last stage it is laterad of the brain in its caudal third only; in their cephalic two-thirds the sacs are in front of the brain, separated from each other by the nasal septum and the internasal space. Jacobson's organ, at first ventrad of the main-sac, later lies in a ventro-lateral position. Between the main-sac and the trabecular horn is a narrow space occupied in part by Jacobson's organ and glands.

2. The Crista trabeculae, in the early stages, reaches forward only as far as the olfactory bulb.

3. The trabeculae in the ethmoidal region are at first separate and end in medially directed processes.

4. The Cornu trabeculae extends beneath the cephalic end of the olfactory sac; its extremity is always near Jacobson's organ which it supports in the older stages.

5. The antorbital process chondrifies independently in Amblystoma. Its union with the trabecula is at the level of the anterior edge of the trabecular crest.

6. The rod (Col. eth.) chondrifies independently in the membranous cranial wall of the ethmoidal region. Its position is opposite the dorso-cephalic part of the olfactory bulb and dorsad of the olfactory nerve; the rod is in the same sagittal plane as the trabecula and alongside of the dorso-mesal angle of the nasal sac.

7. The rod (Col. eth.) becomes connected secondarily with the trabecula and with the trabecular crest completing the boundaries of the olfactory foramen.

8. Growth of cartilage takes place actively at certain regions along the rod and spreads, a) into the membranous cranial wall of the ethmoidal region and b) into the perirhinal tissue.

9. Thus there appear: a Processus uncinatus turning back of the olfactory bulb and entering into the cranial side wall; a Processus ethmoidalis, the first piece in the formation of the anterior cranial wall, the later ethmoidal plate; a Processus nasalis medialis which builds the anterior cupola and the medial wall of the nasal capsule in its anterior part; a Processus lateralis which gives rise, in part to the Lamina cribrosa.

10. The anterior trabecular plate was formed in connection with the trabeculae; it supports the olfactory bulbs, participates in the ventral boundary of the ethmoidal window, and is secondarily connected with the bases of the rods (Col. eth.) and their ethmoidal processes through the chondrification in the ethmoidal window.

11. A nasal septum begins by growth along the dorsal and lateral regions of the cephalic surface of the ethmoidal plate, extending forward through the mesenchymal tissue of the internasal space.

12. The capsular wall about the olfactory foramen is at first medial, but later caudal and medial of the nasal sac.

13. The nasal capsule in the 40–45 mm. Amblystoma possesses a continuous roof.

14. The Fenestra narina begins as a bay between the anterior cupola and the Lamina cribrosa. It includes the external naris and the end of the nasolacrimal duct.

15. A bridge of cartilage and precartilage connects the trabecular horn and Lamina cribrosa. It is crossed superficially by the nasolacrimal duct.

(A) The primary position of the rod (Col. eth.) of the 13 mm. larva (a) in the membranous cranial wall of the ethmoidal region, (b) over the olfactory nerve and (c) in close relation to both the olfactory bulb and nasal sac; (B) its secondary connections and changes through growth in adaptation to the olfactory organs, —these things indicate, I believe, a direct relationship between the rod and the latter structures.

In its further development it has been noticed how the cartilage spreads in two directions: toward the central olfactory organ on the one hand and about the peripheral organ on the other. The ethmoidal processes, bridge and finally the ethmoidal plate are adapted to the fore part of central olfactory region, while the rod itself with its hooked end is applied to the olfactory bulb laterally and caudally. The rod also covers the olfactory nerve in its short course between the nasal sac and the brain. Through the formation of cartilage growing laterally into the perirhinal membrane (lateral process and medial nasal process) a roof and side wall are given to the nasal capsule.

The relations of the Crista trabeculae to the nasal organs I regard as wholly secondary since they are brought about in the ontogeny of Amblystoma by disproportion in the rate of growth of these parts. In the youngest stage the crest took no part in the skeleton of the ethmoidal region and it is only in later stages of development when the nasal sac and olfactory bulb have increased in size that it affords a protection for them.

The antorbital process, it was noticed, occupied a position between the eye-ball and the internal naris in the first stage described. The anlage of this process is in connection with the trabecula to which the independently forming cartilage later extends. The process projects from the trabecula at the level of the anterior edge of the Crista and therefore behind the level of the olfactory organs. In the early stage I cannot determine that the process is adapted more to the nose than to the eye. In later stages, however, it curves forward and comes in contact with the nasal sac; and finally, entering into the formation of the posterior cupola, it becomes an integral part of the nasal capsule. In considering this participation in the nasal skeleton, it must be remembered that the nasal sac has grown backward into the region of the antorbital process. Special relations of the antorbital process to the nasal skeleton of Amblystoma are developed rather late.

The trabecular horn is, from the first stage on placed ventrad of the anterior end of the nasal sac and Jacobson's organ. To the latter, the tip of the horn seems specially adapted, conforming closely to the curves of its inferior surface. The relation which this broad plate of cartilage holds to the roof of the mouth must, of course, be thought of in studying its development.

The anterior trabecular plate supports the cephalic end of the brain, mainly the olfactory bulbs. It appears to have its origin in the medial processes of the trabecula and from its earliest appearance through all stages studied holds a position beneath the olfactory bulbs. It acquires connection with the ethmoidal plate secondarily. The latter, it will be remembered, has its beginning in the ethmoidal processes of the rods (Col. eth.) The association of the trabecular plate with the olfactory region of the brain may be taken to indicate a special relationship between them, a view which is supported by its secondary connection with the ethmoidal plate, resulting in the perfection of the ethmoidal skeleton in front of and below the olfactory bulbs. I am inclined to regard the anterior trabecular plate as the floor for the olfactory region of the brain and look upon it as a special part of the ethmoidal skeleton but without denying its adaptation also to the mouth. That it does form a solid roof for the mouth in front and brace the trabeculae is of great importance, especially in some forms (such as Rana with its long larval period as Gaupp ('93) has said, but I look upon these funtions as subordinate to the ethmoidal skeleton function in Amblystoma.

The anterior trabecular plate has nothing to do with the origin or subsequent development of the so-called nasal septum of Amblystoma; this develops in connection with the ethmoidal plate as already pointed out. In no stage except the adult were intermaxillary glands present. It is easy to observe how, in Amblystoma, the disproportion in the longitudinal growth of the brain and ethmoidal skeleton results in the final relations of these organs. Concerning the formation of an internasal space, Gaupp ('05.1) has suggested the influence of cover bones in this region.

In the four stages modeled the trabeculae have a constant relation to the nasal organs. The trabecular plate, and so far as I am able to determine from my material and from the literature, the Cornua are developed in connection with the trabeculae, as is also the anlage of the rod (Col. eth.). The Crista, as has been shown, gains its relation to the nasal sac secondarily. The relations of the trabecula to the mouth do not concern us in the present work.

The development of the cartilaginous nasal skeleton of Amblystoma is comparable in many respects with the processes in Triton as described by Born ('76). The changes in the position of the nasal sacs and the formation of an internasal space are very similar in the two. The origin of a cartilaginous mesal nasal wall from the trabecula and the subsequent growth of the nasal capsule from the same are conditions not actually met with in Amblystoma. The anlage of the rod (Col. eth.), it is true, is in connection with the trabecula and it is in connection with the rod that a large part of the capsule arises, including a medial nasal wall. The cartilaginous rod does not chondrify from the trabecula out, but spreads toward it. However, this independent chondrification of the rod does not mean that genetically it has nothing to do with the trabecula; the anlage indicates a close relation between the two and so it appears to me that there is after all not much difference in the origin of the capsule in these two animals. In larval Amblystoma a proper medial nasal wall is present only for the anterior part of the olfactory sac; it is formed in the perirhinal tissue in connection with the rod through chondrification of the medial nasal process and it is separated in all the larval stages studied by a notch (Incisura medialis) from the trabecula.

Parker ('77) has described under the name of "foremost paraneural cartilage," a term used by Huxley ('74), a shell-like cartilage over the nasal sac of Siredon. The cartilage is concave forward, one limb directed laterad over the nasal sac, the other cephalad along the mesal margin of the sac. It is at first independent but later joins with the trabecular plate. This appears much like the rod (Col. eth.) and the Lamina cribrosa.

Wilders's ('92) figure of the ethmoidal region of Salamandra larva shows very much the same conditions which I have described in Stage III. A rod arches over the olfactory nerve and extends cephalad at the side of the internasal space; a process goes laterad in front of the level of the antorbital process; a bridge connects the cartilages of opposite sides at the level of the anterior margins of the olfactory foramina, forming the dorsal boundary of an ethmoidal window. The origin of these cartilages is not given in the description.

Gaupp ('93) in his well known splendid work on the primordial cranium of Rana, has, after Born, given the name *Ethmoidalpfeiler*, Columna ethmoidalis, to a little pillar of cartilage which grows upon each side from the dorsal surface of the already formed anterior trabecular plate. These two pillars grow caudad and laterad over the olfactory nerves around which they help to form a cartilaginous ring by uniting with the side walls of the cranium (the trabecular crests). Thus the olfactory foramen is formed. An ethmoidal window, filled with mucous tissue, is made through an inclination of the ethmoidal columns toward each other. In Fig. 12, Taf. XIV, there is a little salient angle on each column directed dorso-medially and helping to bound the window.

The roof of the hinder division of the nasal skeleton in Rana arises in connection with the anterior part of the cranial side wall as far forward as the level of the ethmoidal plate which has formed at the site of the ethmoidal window as in

Amblystoma. This roof cartilage then arises in connection with what was originally ethmoidal column and Crista trabeculae. Subsequently it spreads over the caudal end of the nasal sac to fuse with the antorbital process, leaving a passage way for the Ramus nasalis trigemini.

The early relations and form, and the later secondary connections and development of the ethmoidal column of Rana are the same as obtained for the rod (Col. eth.) in Amblystoma and even the origins of the two are not essentially different: the one growing in connection with the anterior trabecular plate (itself a development of the trabecula), the other chondrifying in a mass of cells streaming up from the end of the trabecula at the spot where the trabecular plate is growing.

The nasal skeleton in Necturus and in Proteus remains unconnected with the brain-case throughout life and in both consists of a lattice-work of cartilage as described by Wiedersheim ('77 and '02 Fig. 200) and Wilder ('03). In Necturus this incomplete capsule covers the simple nasal sac dorsally and in part medially; also to a considerable extent at the poles.

My own studies have shown that the position of the nasal sac of Necturus is laterad of the brain in young animals and latero-cephalad in older ones, the bony wall of the cranium intervening and the branches of the olfactory nerve running an extra-cranial course to the nasal sac.

Miss Platt ('97) and Winslow ('98) have described the independent origin of the nasal skeleton in Necturus and in the work of the former writer we learn that the internasal (anterior trabecular) plate and the dorsal part of the Crista trabeculae chondrify independently. The latter is never high in Necturus as it is in Amblystoma and Rana and its cephalic ending is gradual, not abrupt. In the 45mm. larva described by Winslow a curved bar of cartilage appears on the dorso-mesal surface of the olfactory organ running about parallel with the anterior end of the trabecula, dorsad of which it lies. From this bar a number of shorter processes extend laterally over the nasal sac and there are also some separate pieces of cartilage in the neighborhood of the processes as shown in Winslow's fig. 16. The same figure shows the dorso-mesal pillar ending caudally at the level of the antorbital process.

An examination of the larvae of Necturus from 28mm. to 49mm. in length has proved that the olfactory lobe as described by Kingsbury ('95) and the nasal skeleton reach the same level caudally and that the antorbital process is connected with the trabecula where this bar is changing from the prismatic shape of the Crista region to the cylindrical form in the nasal region. The bar of cartilage described by Miss Platt and Winslow I have found in a 28mm. larva lying in the perirhinal membrane of the dorso-mesal side of the nasal sac, opposite the olfactory lobe and dorsad of the olfactory nerve branches. The lattice work of cartilage first described in the adult nasal capsule by Wiedersheim ('77) arises, as Winslow has it, as processes of the bar and as separate chondrifications. All of these I find to be located in the perirhinal membrane.

The foregoing facts respecting the origin and relations of the dorso-mesal bar in Necturus recall some of the early conditions of the nasal skeleton in Amblystoma and Rana. In the former, an ethmoidal column (Col. eth.) developed independently in the membranous wall of the olfactory region of the cranium where a cartilaginous wall was wanting, the Crista trabeculae ending caudad of the olfactory bulb. The column lies opposite the olfactory bulb and along the dorso-mesal edge of the nasal sac; in connection with it there grows a cribriform roof for the sac in its enveloping membrane. The column arches over the olfactory nerve and secondarily joins the trabecula and its crest to complete the olfactory foramen. In Necturus there is no cartilaginous wall in the olfactory region and the Crista trabeculae slopes gradually to end behind the olfactory lobe. A rod of cartilage is developed along the dorso-mesal angle of the nasal sac opposite the olfactory lobe in the perirhinal membrane, parallel to the trabecula and over the olfactory nerve. From the bar a part of the lattice-like roof of the nasal sac extends. The trabecular crest never grows high and the dorso-mesal bar joins neither it nor the trabecula to form the boundaries of an olfactory foramen; still the nerve passes between the bar and the trabecula and in front of the crest. The formation of the nasal capsule in Rana up to the point so far considered seems to me not fundamentally different from that of Amblystoma. The specialized nasal sac of Rana is provided with a highly specialized and complicated nasal capsule such as is not encountered at any time of life in Amblystoma. There are however some features in these capsules which I believe can be drawn into comparison but first it will be necessary to compare the parts about which the capsule in each case is adapted.

As stated in the beginning of this paper the nasal sac of Amblystoma is at first a simple ovoid body with a narrow lumen, becoming later complicated by the development of diverticula, one of which is Jacobson's organ. Another much smaller pouch grows out of the lateral side of the main-sac and receives the nasolacrimal duct. The main-sac and its diverticula are shown in figure 4.

The main-sac of the Urodela is in all essential respects comparable with the upper blind-sack of the Anura. The lateral pouch of Amblystoma is indicated as the possible homology of the lateral diverticle of the tadpole by Bawden while Seydel compares only that part in each group which receives the tear-duct, regarding the anterior blind end in Anura as a special development. Seydel homologizes the inferior blind-sac of the frog with the Jacobson's organ of the Urodeles, and points out the absence of this organ in fishes and the Dipnoi, as well as in Proteus and Menobranchus and its primitive state in Amphiuma and Menopoma.

Besides the roof cartilage of the hinder division of the main-sac which is described on P. 414 of Gaupp's work ('93) and which has already been mentioned in the comparison with Amblystoma, a separate chondrification of the perirhinal tissue anterior to this is described which later joins with the first roof cartilage and also grows around the medial side of the upper blind-sac to form its mesal wall. Roof and mesal wall are continuous in the anterior half of the nasal capsule of my 40–45mm. Amblystoma. Winslow's Fig. 12 shows that in an Amblystoma of 69mm. the roof of the anterior part of the nasal capsule is very slight but that it is continued into the medial wall without interruption. This roof and medial wall I found to be formed in connection with the Columna ethmoidalis, beginning as the medial nasal process. As in Rana it is in relation to the main-sac only. In Rana this medial wall turns under the upper blind-sac to form the Crista intermedia, a partition between the cavities for the upper and lower blind-sacs. There is no such partition in the stages of Amblystoma which I studied but the ventral edge of the medial wall is free and turns laterally a little way under the main-sac (Fig. 4). The ventral edge of the anterior cupola forms a little shelf beneath the main-sac, while the medial incisure exists.

In Amblystoma the caudal part of the medial surface of the main-sac faces an obliquely placed olfactory window; in Rana a corresponding part looks toward a transversely placed olfactory foramen; the middle part is opposite the ethmoidal plate (beginning septum); in Rana the same is opposite the nasal septum; the anterior part of this surface is covered by a proper medial wall, as it is in the frog. Thus the main-sac of Amblystoma agrees with the upper blind-sac of Rana in its relations to the medial wall of the nasal capsule. A proper medial wall for the inferior room of the nasal capsule does not exist in Rana and the same is true in larval Amblystoma for that space which contains the the medial portion of Jacobson's organ and glands. This subnasal space (Sub. s.) is limited medially only by the nasal septum; in the larvae it opens into the internasal room through the Incisura medialis while back of the ethmoidal plate it is limited by the membrane of the olfactory window against which the glands are pressed. The Incisura medialis transmits the septal branch of the ophthalmic V and is later converted into the apical foramen.*

* There is an analogy between this foramen and the Fenestra naso-basale of Rana in its use as the passage way of a branch of a nasal nerve; but while the adult relations are somewhat similar their development appears to be different.

The ethmoidal bridge of Amblystoma is a transitional structure in the building up of the ethmoidal plate as is the case in Salamandra; in Triton the bridge is permanent. The formation of the nasal septum of Rana bears no resemblance to the process in Amblystoma where an arch is at first made over the internasal room and later a strong commissure is formed between the nasal capsules.

The Cornu trabeculae of Amblystoma supports at its end the organ of Jacobson. (Compare Seydel, '95 p. 478, and fig. 7). In Rana the horn takes part in the posterior division of the floor of the inferior room; in the anterior part the floor is formed by new chondrification. A floor for the anterior part of the nasal capsule seems to be the rule for Amphibia; what part the trabecular horn plays in its formation is known in but a few cases. In Necturus and Proteus which do not possess a Jacobson's organ a nasal capsular floor is not present. On the other hand a Jacobson's organ is described by Seydel for Siren but according to Wilder's ('91) description of the capsule there appears to be no floor; yet there is to be found in Wilder's figure on the ventral side of the anterior end of the nasal skeleton a peculiar "inferior process" which is described on P. 35 where it is also stated that the R. ophthalmicus profundus is ensheathed by cartilage. The foramen of exit for this nerve is at the medial, ventral corner of the nasal capsule at its cephalic end. The meaning of the trabecular horn cannot be told until more is known of its early development and its later history.

Among the later developments, the slender bridge connecting the trabecular horn and Lamina cribrosa is interesting. The nasal capsule of my stage V, closely resembles that of the 12 cm. Siredon described and shown in fig. 7 of Seydel's work ('95). In its connections with roof and floor and in its relations to the Fenestra narina and nasal duct the little bridge is comparable with that marked "d" in Seydel's figure. Through further chondrification a fenestrated side-wall is formed for the nasal capsule as Winslow has shown (fig. 12), and in the partition between the two lateral windows I see the little bridge of my stage V. Bruner ('02) has found in Triton alpestris that the dilator naris muscle takes origin from a similar process, which he calls the anterior end of the Planum terminale. The dorsal part of this bridge in Amblystoma, begins as a process of the Lamina cribrosa, supporting the nasolacrimal duct and later coming to limit the Fenestra narina behind.

The dorsal window of Winslow's fifth stage cannot be explained through my material. There is a continuous cartilaginous roof for the nasal capsule in the 40–45 mm. animal; but whether the dorsal foramen is due to reduction, as I am inclined to think, or is circumscribed by the primary formation of the dorsal process, I cannot say. The dorsal process appears to be a common feature in the nasal capsule of Urodeles. Bruner ('02) calls it the Cartilago obliqua, a term used by Gaupp also for an oblique process of the nasal capsule of Rana.

Huxley* on theoretical grounds believed that the chondrocranium was formed phylogenetically by continuous growth and conceived that separate cartilages could have no significance in the perfection of the continuous-walled brain case. Separate pieces are regarded by the supporters of this theory as the results of reduction of the chondrocranium through the appearance of bones. It was Goette * who first brought forward the view that the chondrocranium was made by the fusion of primitively separate elements.

Regarding the significance of the independent chondrification of the ethmoidal column in Amblystoma, the claim can hardly be maintained that this piece is morphologically a separate element. Its anlage is in a mass of cells continuous with the incompletely differentiated cartilage of the trabecula. Through the mass, chondrification takes place, beginning in a spot away from the trabecula and then spreading toward it. In Rana, which possesses a much more complete chondrocranium than Amblystoma, in accordance with its long larval life (Born, Gaupp,) the ethmoidal column develops in direct connection with the basal skeleton. I am therefore inclined

* See Gaupp. ('00.)

to regard the independent chondrification of the ethmoidal column of Amblystoma as evidence of a phylogenetic reduction process in its nasal skeleton.

In Amblystoma the cartilaginous nasal capsule does not arise independently of the brain-case. It is from the beginning a part of the ethmoidal skeleton which is built in connection with the trabeculae, ethmoidal columns and antorbital processes. In the development of the cartilaginous ethmoidal skeleton there are formed *pari passu*, a capsular covering for the epithelium of the nasal sac and protecting walls for the olfactory bulb.

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DESCRIPTION OF FIGURES.

The drawings of the wax-models have been made by Dr. R. W. Mills of the Washington University Medical Department. The tracings of the transections were made with the camera lucida.

Fig. 1. Model of Stage I, showing the anterior part of the brain, left eyeball and nasal sac, the trabecular horns and ethmoidal columns. About $\frac{40}{1}$.

Fig. 2. Model of Stage II, showing the right half of the anterior end of the brain, the left eye-ball and nasal sac; the changes in the ethmoidal column and other parts of the ethmoidal skeleton appear. About $\frac{40}{1}$.

Fig. 3. Model of Stage III. The ethmoidal skeleton and the left nasal sac are shown. The latter, as in Fig. 2, is sectioned caudad of the external naris. The olfactory and ethmoidal windows are present. About $\frac{25}{1}$.

Fig. 4. Model of Stage IV. Left nasal sac and left half of the ethmoidal skeleton. The nasolacrimal duct and the nerves of this region are shown. About $\frac{40}{1}$.

Fig. 5. Transection passing through the anlage of the ethmoidal column, showing also the column of cells between it and the trabecula. Amblystoma 12 mm.

Fig. 6. Transection at the level of the base of the antorbital process and cephalic end of the trabecular crest. Stage II. $\times \frac{40}{1}$.

Fig. 7. Transection at the level of the middle of the ethmoidal column and olfactory bulb. Stage II. $\times \frac{40}{1}$.

Fig. 8. Transection passing through Jacobson's organ and gland at the level of the caudal edge of the trabecular horn. Stage III. $\times \frac{40}{1}$.

ABBREVIATIONS.

Anl. Anlage of ethmoidal column.
Ant. tr. pl. Anterior trabecular plate.
C. Cell column between anlage and trabecula.
C. F. Communicating branch from Ramus frontalis to the third main division of the Ophthalmic V.
Col. eth. Columna ethmoidalis.
Co. tr. Cornu trabeculae.
C. tr. Crista trabeculae.
D. nl. Ductus nasolacrimalis.
E. Eye-ball.
Eth. br. Ethmoidal bridge.
Eth. pl. Ethmoidal plate.
F. Ramus frontalis trigemini.
Fen. eth. Fenestra ethmoidalis.
Fen. ol. Fenestra olfactoria.
F. olf. Foramen olfactorium.
I. N. Branch of olfactory nerve.
Inc. med. Incisura medialis.
J. gl. Jacobson's gland.
J. O. Jacobson's organ.
L. Lamina cribrosa.
Max. Ramus maxillaris trigemini.
M. D. Main division of nasal sac.
N. L. P. Nasolacrimal pouch.
N. S. Nasal sac.
O. F. Olfactory nerve fibers.
Olf. Olfactory bulb.
Oph. $V_{1, 2, 3}$. First, second and third main divisions of the Ophthalmic V nerve in the orbit.
P. Ramus palatinus VII.
Pr. ao. Processus antorbitalis.
Pr. eth. Processus ethmoidalis.
Pr. lat. Processus lateralis (of the ethmoidal column).
Pr. med. Processus medialis (of the trabecula).
Pr. n. med. Processus nasalis medialis.
Pr. unc. Processus uncinatus (of the ethmoidal column).
R. nl. Branch of the third main division of the Ophthalmic V nerve, following the nasolacrimal duct.
Sub. s. Subnasal space.
Tr. Trabecula.

Issued Dec. 1, 1906.

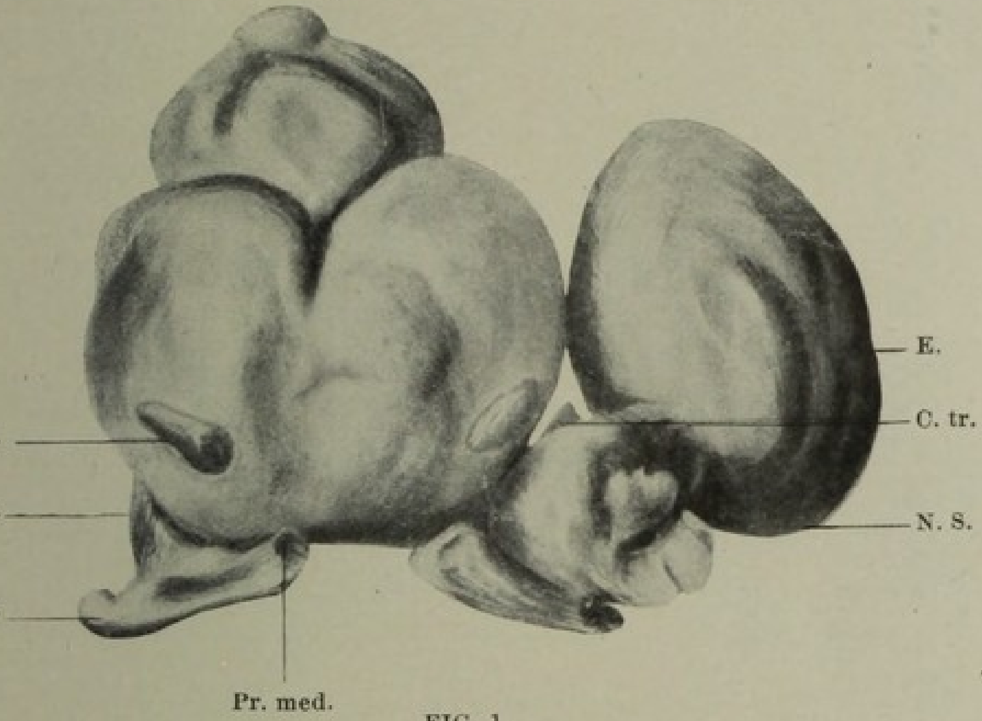
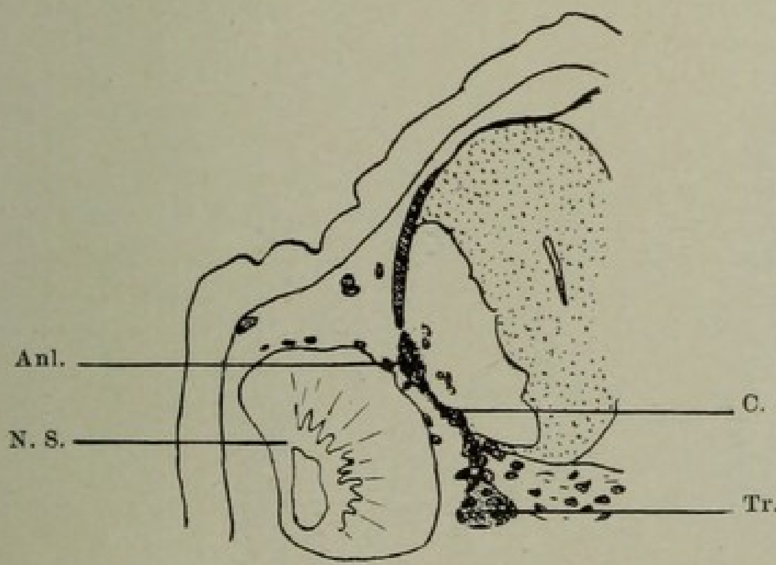


FIG. 1.



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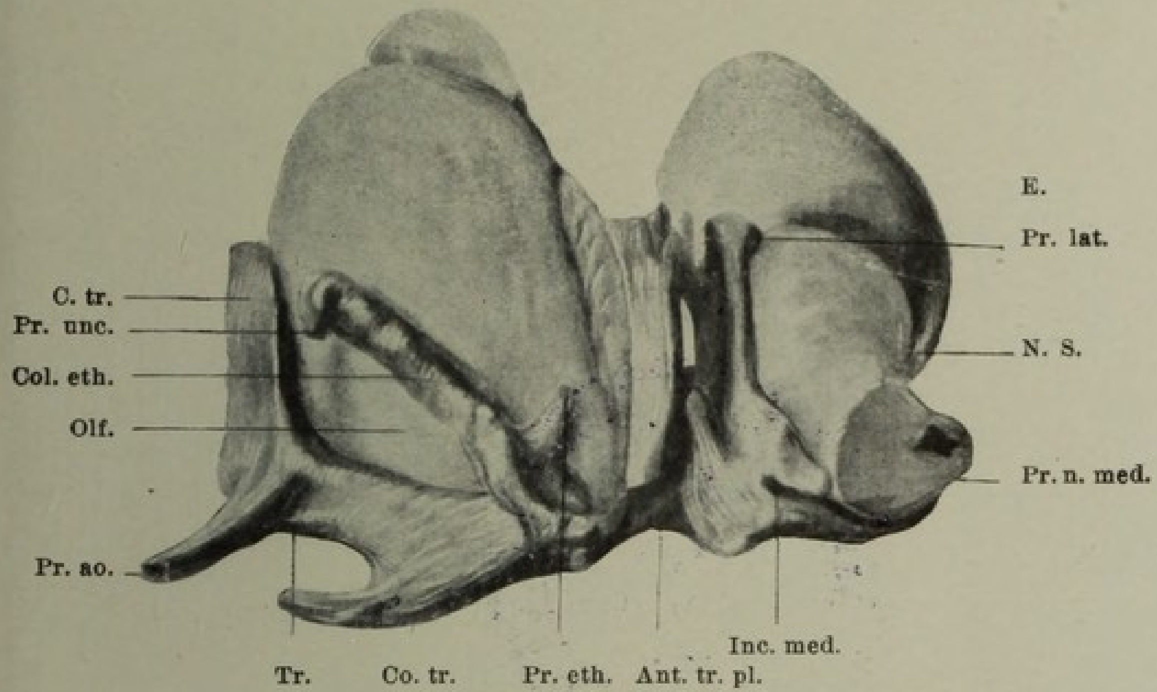

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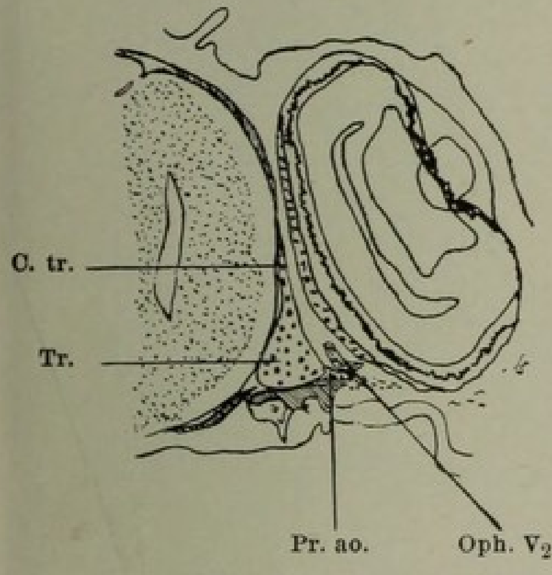

FIG. 6.

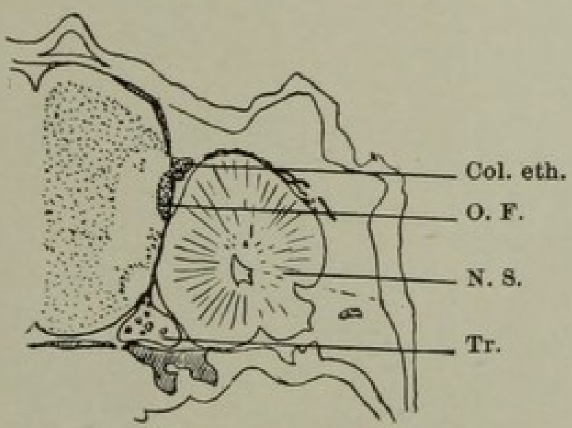

FIG. 7.

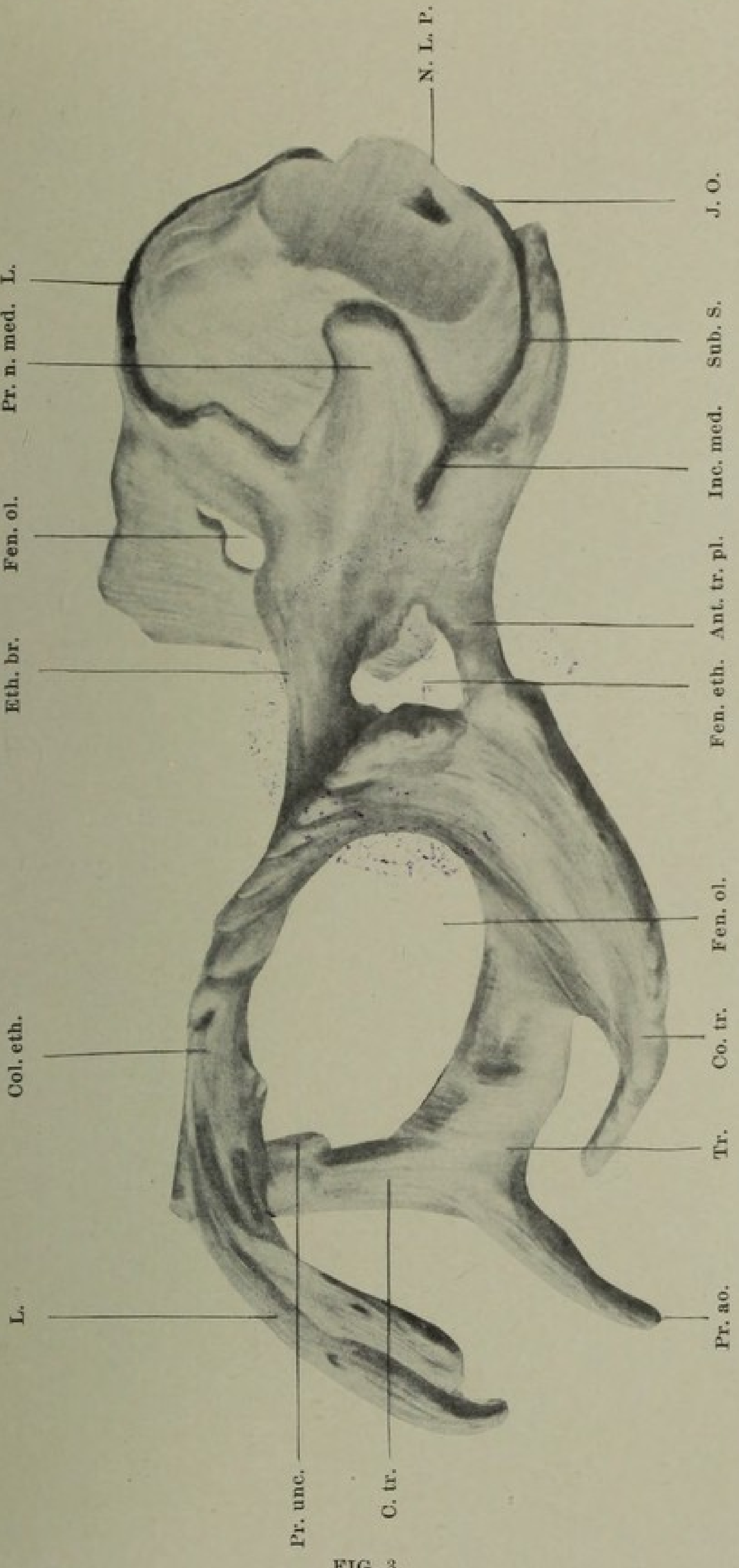
N. L. P.
J. O.
Sub. S.
Inc. med.
Ant. tr. pl.
Fen. eth.
Fen. ol.
Co. tr.
Tr.
Pr. ao.
L.
Pr. n. med.
Fen. ol.
Eth. br.
Col. eth.
L.
Pr. unc.
C. tr.

FIG. 3.

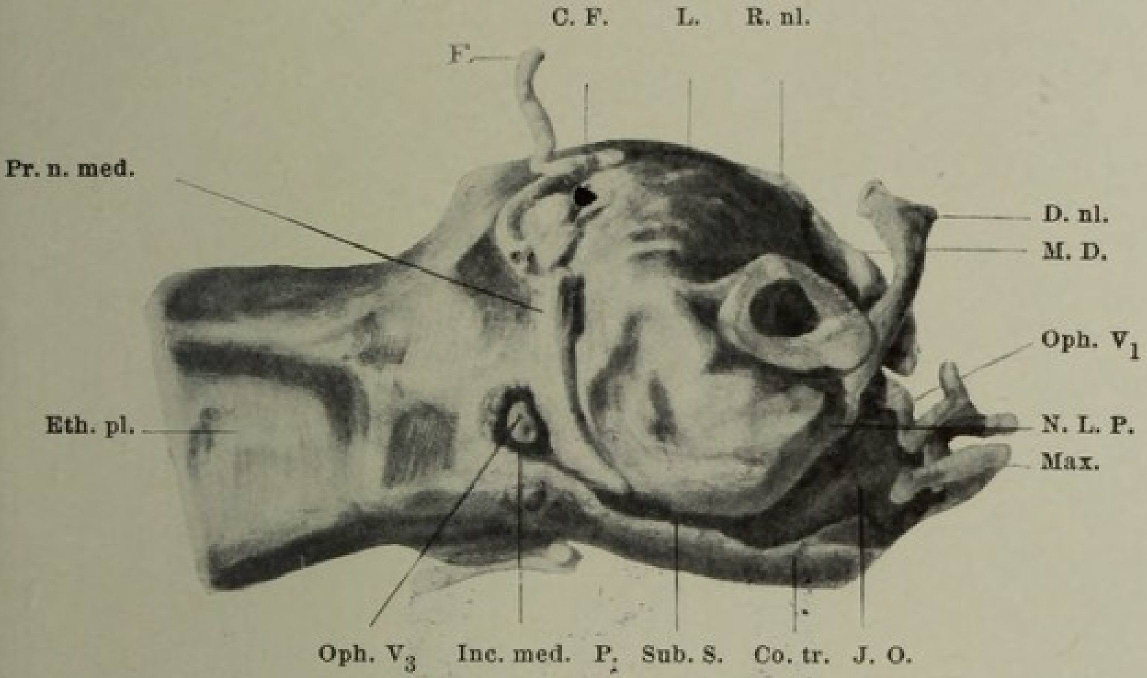
C. F.
L.
R. nl.
F.
Pr. n. med.
D. nl.
M. D.
Oph. V1
Eth. pl.
N. L. P.
Max.
Oph. V3
Inc. med.
P.
Sub. S.
Co. tr.
J. O.

FIG. 4.

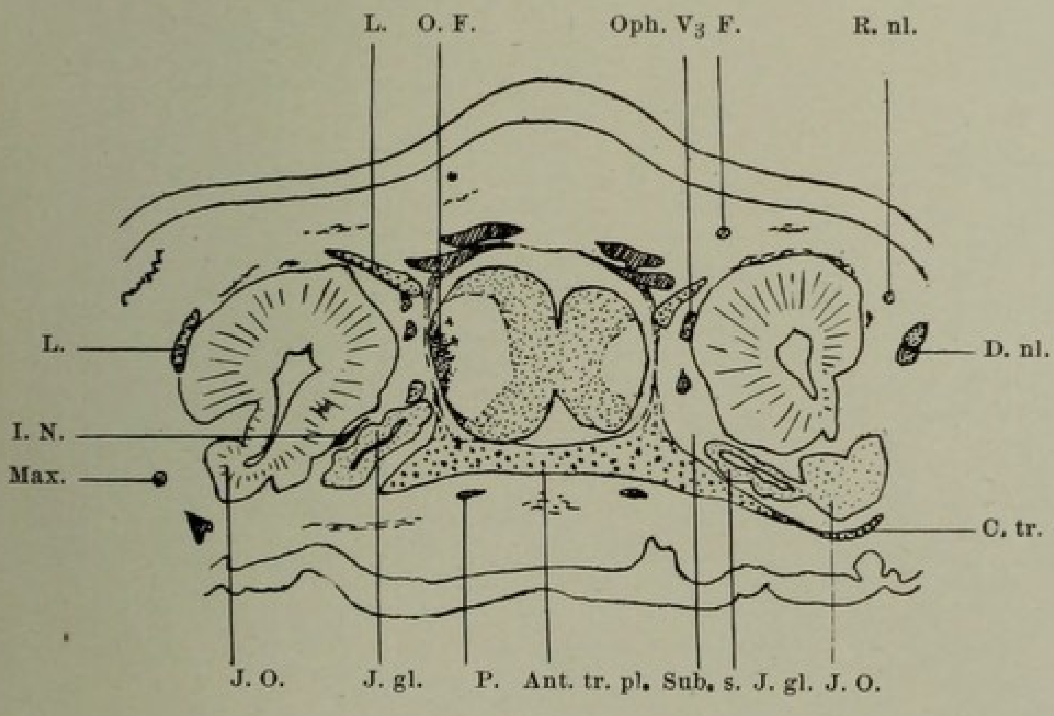
L.
O. F.
Oph. V3
F.
R. nl.
L.
D. nl.
I. N.
Max.
C. tr.
J. O.
J. gl.
P.
Ant. tr. pl.
Sub. s.
J. gl.
J. O.

FIG. 8.