THE NASAL ORGAN IN AMPHIBIA

BY

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY

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Table of Contents.

Introduction.

There is a considerable literature upon the development of the chondrocranium of the Amphibia, but only a little of it gives adequate details of the process of chondrification of the nasal capsules in this class of vertebrates.

Parker, in a long series of extensively illustrated papers, ('71-'73-'75-'76-'82) was the first to give any adequate account of the development of the skull in the Amphibia; but his remarks, so far as the nasal capsules are concerned, are general and no detailed descriptions of parts or processes of chondrification are given. Born ('77) gives, in considerable detail, the process of chondrification in Triton cristatus; while Stohr('79) has also described the chondrocranium of Triton, but pays but slight attention to the ethmoidal region.

Gaupp ('93) in his well known work on the chondrocranium of Rana fusca discusses four stages in the development of the skull of the frog, treating all parts with more detail than any other writer. According to Miss Platt ('97) the nasal capsule in Necturus to a great extent chondrifies independently of the trabeculae, but she gives but a slight account of the development of the fenestrated roof of the capsule. Winslow ('98) dealt with the chondrocrania of several of the Ichthyopsida, but his account of the development of the nasal capsules has but slight detail. Peter ('98) is the only one who has described any Gymnophione, while Terry ('06) who followed the history of the nasal capsule of Amblystoma through five stages, states that the process of chondrification in Amblystoma agrees closely with that of Triton.

The work covered by this paper was undertaken with the idea of

ascertaining what homologies, if any, could be drawn between the nasal capsules of the various groups of Amphibia; and to determine in how far these structures would substantiate or alter the different classifications proposed for this vertebrate group.

The work was done in the Zoological laboratory of the University of Illinois, almost entirely upon the departmental collections. It was carried on under the supervision of Professor J. S. Kingsley to whom the writer wishes to acknowledge his sincere appreciation for the many helpful suggestions and his kindly attitude during the investigation and preparation of this paper.

I wish to acknowledge my best thanks to Professor A. C. Eycles-heimer of the Illinois Medical School, for the loan of several of his series of slides of Necturus. My thanks are also extended to Professor H. W. Norris of Grinnell College, Iowa, for the loan of his slides of the Gymnophiona, which however could not be used as the stages were too far advanced for my particular purpose.

Amblystoma punctatum.

Amblystoma was selected as the basis of these studies, because of the larger number of stages available and because of its intermediate position among the Urodeles. I have studied and modelled seven stages of Amblystoma which show the successive steps in the chondrification of the nasal capsule.

A larva 11 mm. long,(fig. 1), shows but few features of a nasal capsule. In the region of the eye the trabeculae (t), with slightly developed cristae, inclined toward each other, but do not meet to form an ethmoid plate. They are triangular in section and lie along the mesal margin of the nasal sac. Anteriorly each trabecula expands into a broad plate, the cornu (c.t.), upon which the nasal sac rests. A slight process, extending toward the median line from each trabecula is to form the ethmoid plate.

In a 13 mm. larva which was studied though not modelled, a few cartilage cells appear above the mesal margin of the cornu trabeculae of the left side only, very near the anterior end. This is the anlage of the columna ethmoidalis or "Ethmoidalpfeiler" of Gaupp ('93). In this stage neither trabecular crests nor ethmoid plate have been formed. (fig. 41.)

In a 20 mm. larva chondrification is much more advanced. An antorbital process (a.p.),has formed anterior to the choana and extends laterally a distance equal to the width of the trabecula, which has become circular in section and the two trabeculae have united in the median line to form a broad planum ethmoidalis (p.e.), supporting the anterior end of the telencephalon. The lateral margins of the concave ethmoid plate are marked by thickenings, the extension forward of the trabeculae. The posterior margin is

arcuate, the anterior more nearly straight, passing into the expanding cornua, which have increased in size and form triangular plates in practically the same plane as the trabeculae. The dorsal surface of each cornu is slightly concave and supports the nasal sac and the organ and glands of Jacobson. The posterior end of each cornu reaches about the level of the middle of the ethmoid plate, where it terminates in a slight caudal process; while its antero-lateral margin is at about an angle of 45 degrees to the median axis of the skull and meets the inner margin of the cornu, extending forward from the anterior margin of the ethmoid plate, at an acute angle. (fig. 2.)

Dorsal and parallel to the trabecular extension (t.e.) of either side is an elongate rod of cartilage, the columna ethmoidalis (c.e.), the anlage of which has appeared in the 13 mm. larva. It lies between the telencephalon and the nasal sac and extends just posteriorly beyond the caudal limit of the ethmoid plate. In a similar stage Terry ('06) has described the junction of the caudal end of this rod with the trabecula,but I have not seen this condition in my material. It is not connected with the trabecula but ends in the tissue above the nasal sac just posterior to the ethmoid plate. From the caudal limit of the bar, chondrification is developing laterally, to form the anlage of the lamina cribosa. It is of especial interest that this rod, though later fusing with the trabecula arises independently of it. It is of further interest that although chondrification of this rod develops posteriorly from its cephalic anlage, yet the lateral expansion arises from the caudal limit.

In the next stage (fig. 3.), several features have been added

to the capsule, The cristae trabeculorum (cr.t.) are well developed and their cephalic margins have united to the columnae ethmoidalis, thus forming a wide trough in which the telencephalon lies. The cristae trabeculorum are curved upon their inner aspect and extend forward to the region of the choana, from which the trabecular extensions (t.e.) turn abruptly toward the center to form the ethmoid plate (p.e.). In this stage there is an almost complete separation of the dorsal from the ventral half of the capsule, the crista trabecula forming the only connection. The median processes of the ethmoidal columns have united to form the beginning of a nasal septum just dorsal to the cephalic limit of the ethmoid plate. Although chondrification is in process, as shown by the presence of procartilage cells, the septum is not complete and there is as yet no union of the columnae ethmoidalis and the ethmoid plate. Chondrification progresses toward the trabecular extensions of the ethmoid plate, and not in the opposite direction. The dorsal surface of the ethmoidal plate is concave near the trabeculae but become slightly convex upon its cephalic margin which continues laterally into the broad cornua. These cornua are roughly triangular in outline and are slightly concave dorsally to support the anterior portion of the nasal organ. The lateral margin is broadly convex, embracing an arc of about 90 degrees, as it curves laterally and ventrally from the emarginate limits of the ethmoid plate to a point in line with its median plane. It terminates posteriorly in a short process upon which the cephalic portion of the organ of Jacobson rests.

Between the cornu trabecula and the antorbital process is a wide bay in which the main nasal sac and the nasal glands lie.

The ethmoidal columns remain parallel and dorsal to the trabecular extensions, although several modifications occur. Each column develops a lateral expansion, the beginning of a nasal roof. This is especially marked posteriorly where, just anterior to its junction with the crista, a curved plate passes laterally over the caudal limit of the nasal sac and the choana. This is the further development of the lamina cribosa (l.c.) described in the earlier stage. Further anteriorly this rod is considerably flattened and covers the medial dorsal margin of the nasal sac and the glands of Jacobson. Medial processes of each rod have united to form what Terry calls an ethmoidal bridge, although it marks the beginning of the nasal septum, completed in the later stage. The fenestra ethmoidalis (fen.eth.) passes beneath this bridge and connects the internasal space (in.s.) with the brain cavity. From the antero-lateral margin of the ethmoidal bridge (e.b.) each column turns laterally in an oblique direction and ends in the tissue directly dorsal to the cephalic extension of the trabecula.

The olfactory nerve leaves the brain at right angles to the axis of the body and enters the capsule just anterior to the crista trabecula, through the large foramen beneath the columna ethmoidalis. It divides into dorsal and ventral roots.

In a larva 34 mm. long (fig. 5.), the columna ethmoidalis has fused with the trabecula, separated from it only by the small olfactory foramen (f.o.), to be described later. Anteriorly the ethmoidal columns have united to the trabecular extensions, while posteriorly they have united to the dorsal crests of the trabeculae; so that column and crista of either side appear as one continuous elevation, pierced by the olfactory foramina. Just anterior to

theseforamina the ethmoid plate, which is thin behind, becomes a-bruptly thickened, the result of the fusion of the ethmoidal bridge with the ethmoid plate of the preceding stage. The fusion of these parts and the subsequent caudal growth has produced the broad and thick septum of this stage so characteristic for the Amblystoma capsule. By reason of the antero-lateral expansions of the septum, its anterior margin becomes deeply excavate, forming a V-shaped internasal space (in.s.). Each lateral surface of the septum nasi is curved and bordered dorsally by the median nasal process which covers the medial and dorsal surface of the olfactory organ. This process continues anteriorly, and, near its cephalic margin, is pierced by a foramen (f.n.i.) through which the ramus nasalis internus of the fifth nerve passes to the internasal space.

The expanded cornua trabecula continue from the antero-lateral margins of the ethmoid plate. They do not differ greatly from the preceding stage. The lateral margin of each cornu is broadly convex and extends caudally to the level of the posterior limit of the septum nasi. From its junction to the lateral margin, the posterior margin is directed medially for a short distance when it turns abruptly cephalad and then, with a broad sweeping curve, continues posteriorly and fuses with the caudal lateral margin of the ethmoid plate ventral to the olfactory foramen. Between the caudal extension of the cornu and the cephalic portion of the lamina, yet to be described, lies the organ of Jacobson, and the glands of Jacobson extend medially from this process.

Just dorsal to the olfactory foramen a strong lamina cribosa (l.c.) extends laterally and anteriorly and, curving ventrally forms a vault over the caudal limit of the nasal sac.

Its lateral margin extends nearly to the level of the gap between the caudal extension of the cornu and the antorbital process; the posterior margin of the lamina is oblique, its lateral margin slightly arcuate, and its anterior margin continues forward as a small conical process to the level of the posterior margin of the cornu trabecula. The stages thus far described, show that the lamina cribosa is developed as a lateral outgrowth from the caudal part of the columna ethmoidalis.

The antorbital process, outlined in the preceding stage, is now more strongly developed and more closely associated with the capsule. In the earlier stage it was considerably removed from the ethmoid plate, but by forward growth its anterior margin is now in line with the posterior margin of the ethmoid. Each process extends laterally a short distance and then bends abruptly forward and terminates anteriorly in a small projection posterior to the caudal lateral angle of the lamina cribosa. The proximity of the antorbital process to the lamina is indicative of the part it is to take in the completely differentiated capsule.

In a 45 mm. larva (fig. 7), chondrification has not greatly advanced beyond that in the 34 mm. stage. The capsule has not increased in length although there is an appreciable increase in depth and in breadth. The forebrain lies within the brain case (c.c.) for about one-third the length of the capsule and, with growth and development of the olfactory lobes, there is a corresponding increase in the size of the brain case which is now approximately hemispherical. The olfactory foramina look obliquely forward and the olfactory nerves pass obliquely from the anterior margin of the olfactory lobe to the caudal region of the nasal sac.

The olfactory organ has moved forward so that it is anterior to the forebrain except for its caudal one-third; a relation which is more pronounced in the last stage to be described.

The nasal septum (s.n.) has decreased slightly in length although it is almost twice as thick as that described for the 34 mm. stage. Its posterior dorsal margin is broadly concave, although the posterior surface is almost vertical to the plane of the ethmoid plate, which curves downward and backward. The internasal space bounding the septum in front is arcuate and is occupied by the intermaxillary glands common to most Urodeles. The medial nasal processes (m.n.p.) of the ethmoidal columns have developed laterally, so that they now form a roof for the mesal half of the nasal organ. Each is pierced near its lateral margin by a foramen for the branch of the nasalis internus which innervates the anterior dorsal region of the snout. Anteriorly each process terminates abruptly and is separated from the blunt trabecular extension by a notch, the median nasal incisure of Terry ('06), which allows for the passage of the main ramus nasalis internus to the internasal space. In the 34 mm. stage the notch and the foramen were near each other, but they have become separated in this stage by growth in the intermediate region.

Anteriorly procartilage cells cover the capsule and lie around the nasal duct where it passes inward to unite to the main nasal sac. These procartilage cells suggest the vault that later forms over the entire cephalic end of the nasal capsule.

The lamina cribosa (l.c.) is more vaulted and covers the nasal organ from the choana to the well developed organ of Jacobson which lies between its ventral margin and the caudal extension of the cornu trabecula. Anteriorly the distal angle of the lamina cribosa

has fused with the cornu trabecula so that there is a complete band of cartilage around the external naris. The naso-lacrimal duct passes above this connecting bar and unites to the main nasal sac just above the cephalic limit of Jacobson's organ. The nasal canal formed by the ring of cartilage is an elongate ovoid, exposed on its dorsal surface by the broad bay, the fenestra narina (fen.n.) of Gaupp, and, on its ventral surface, by the oval gap between the antorbital process and the cornu.

In a larva approaching the end of metamorphosis (fig. 9.) many modifications of the nasal capsule add to the complexity of the structure. The length and breadth of the capsule are approximately the same, although there has been a reduction in the length of both septum nasi and ethmoid plate, so that the anterior three-fourths of the nasal sac lies cephalad to the forebrain. The nasal septum is reduced in width by one-half, to accommodate the lateral growth of the olfactory organs of the two sides, which now more closely approximate each other. It is broadly concave on its anterior surface, the dorsal margin extending more cephalad than the ventral, so that a partial roof is formed over the inter-nasal space.

The median nasal process (m.n.p.) and the lamina cribosa have expanded laterally and form a complete roof over the nasal sac. Anteriorly the cephalic part of the median nasal process and the cornu trabecula have united above the distal end of the olfactory organ to form a complete vault of cartilage. This growth has necessitated a change in the position of the external narial opening which is now lateral in contrast to the terminal position of the earlier stages. The broad deep bay of the fenestra narina has

been obliterated so that the narial opening is now an elongate oval, looking obliquely forward.

The antorbital process has united to the lamina cribosa, a condition suggested by the close association of these parts in the earlier stage, thus forming a cup-like structure, pierced posteriorly by a large orbito-nasal foramen (f.o.n.), Into this foramen the caudal portions of the nasal sac have extended and through it the nerves of the nasal region enter the capsule. The united elements of the lamina cribosa and the antorbital process bend obliquely forward and completely arch the choana and the caudal parts of the main nasal sac. This arch is pierced by two foramina near its ventral lateral margin through which the ramus profundus of the fifth nerve and two blood vessels enter the capsule. Anterior to these openings, the cribosa unites to a process which I believe to be the caudal extension of the cornu trabecula, which as in earlier stages so in this, ends blindly in a process supporting the caudal part of Jacobson's organ.

In addition to the large narial opening and separated from it by a bar of cartilage, the development of the band of the earlier stage, is a second foramen, the infra-conchalis of Gaupp, (fen.i.c.) through which the organ of Jacobson extends to the lateral enveloping tissue. Lying close to this foramen is a deep furrow in the lateral surface of the cribosa along which the naso-lacrimal duct passes to its junction with the nasal sac at the posterior margin of the narial opening.

The dorsal surface of the roof of the capsule has four foramina. The anterior three of these are smaller and conduct rami of the superficialis of the ophthalmic from the capsule.

The posterior foramen, directly opposite the nasal septum, is the larger and probably represents the beginning of the resorption of cartilage which so completely changes the capsule to the adult form. Upon the mesal surface of the capsule the foramen nasalis internus conducts the main branch of the superficialis to the internasal space which contains the well-developed intermaxillary gland. A prenasal process marks the cephalic extension of the capsule, and it extends forward from the mesal surface near the above described foramen. There is a large gap in the floor of the capsule, oval in outline, bounded by the ethmoid plate and lamina cribosa on the sides, anteriorly by the cornu trabecula, and posteriorly by the antorbital process.

The nasal capsule of the adult Amblystoma (fig.10) is the result of growth and specialization of those structures present in the stage just described. It has increased both in width and in length by one-half the original dimensions; effected by a growth of certain parts and a reduction of others. The septum nasi and the ethmoid plate are further reduced and are nearer the posterior limit of the capsule, resulting in a more cephalic extension of the olfactory organ beyond the forebrain. In contrast to the closed capsule of the earlier stages, that of the adult is decidedly open and a large five-sided gap exposes the entire dorsal surface of the nasal organ. This gap is the further result of the process of resorption of cartilage which began in the earlier stage in the foramen opposite the nasal septum. From this point the process has continued anteriorly, laterally and posteriorly until all that now remains of the complete cartilage roof is a slender bar of cartilage, the dorsal process (d.p.), running

diagonally across the nasal sac from the plate covering Jacobson's organ, to the posterior angle of the dorsal surface of the cupola (c.). The fused elements of the lamina cribosa and the antorbital process are reduced to a broad band of cartilage which, curving obliquely forward, forms a roof for the choana and the lateral aspects of the main nasal sac. This band is pierced by three foramina through which the nerve and blood vessels, mentioned in the earlier stage, pass. The fenestra infra-conchalis is more elongate and completely contains the organ of Jacobson. The further modification of the band of cartilage uniting the lamina cribosa to the cornu in the earlier stages, which now unites the dorsal process above described to the lateral margin of the cornu, is pierced by a small foramen through which the ramus profundus passes to the exterior. The cupola is more completely formed and the narial opening is more lateral and somewhat dorsal.

The final stage in the chondrification of the nasal capsule of Amblystoma is evidently a specialization of cartilage structures present in the earlier stage. The ethmoid plate, nasal septum and cristae trabeculorum become greatly reduced, while the median nasal process, lamina cribosa and antorbital process become greatly specialized. The greatest change in the adult has occurred anterior to the septum nasi where the median nasal process and the cornu trabeculae have expanded into a complete vault over the anterior parts of the olfactory sac. With a large ventral gap from external nares to choana, and a dorsal gap reaching from cupola to cribosa, the capsule is now much in contrast to the closed type of all the earlier stages.

Salamandra maculata.

In a larva of Salamandra maculata, 25 mm. long, chondrification of the nasal capsule has advanced to a stage intermediate between the 25 mm. and 34 mm. Amblystoma larvae. The trabeculae with well developed crests extend to the region of the antorbital processes where the cristae terminate abruptly. Turning toward the median line the trabeculae unite to form the broad trapezoidal ethmoid plate (p.e.), its posterior margin being parallel to and one half longer than the anterior margin. It is more conspicuously concave dorsally than that of a corresponding stage of Amblystoma and the trabecular extensions (t.e.) are more pronounced, thus forming a trough for the olfactory lobes. The anterior margin is straight between the cornua, but the posterior bears a strong process (c.p.), which Parker has called the hinder process, lacking in all other stages in all other forms of Urodeles which I have studied with the exception of a single stage of Cryptobranchus.

The broad plates of the trabecular cornua arise from the antero-lateral angles of the ethmoid plate. These are thin, slightly curved triangular cartilages which support the anterior part of the nasal sac.Their antero-lateral margins are distinctly curved in lateral posterior direction and terminate in an angle at the level of the anterior limits of the ethmoid plate. The lateral part of the posterior margin of each cornu is nearly straight; more medially it curves backward and fuses with the lateral margin of the trabecular ridge at the level of the transverse axis of the ethmoid plate.

Parallel to each trabecular ridge (t.r.) and separated from it by a distance equal to twice its width is the columna ethmoidalis (c.e.). The lack of earlier stages has prevented the determination

of the origin of this column, but I am inclined to believe that it arises from the medial margin of the cornu and then grows posteriorly along the nasal sac; because of the similarity of this structure to that in Spelerpes in which the columna arises from the medial margin of the cornu. This is in contrast, however, to the independent origin of this bar in Amblystoma. The fusion of these bars is not the same in both capsules. The ethmoidal columns in Amblystoma unite to form an ethmoidal bridge before there is a connection with plate or cornu, while in Salamandra there is no ethmoidal bridge formed. Continuing posteriorly each columna ethmoidalis rests against the dorsal mesal margin of the olfactory organ. From being circular in section at the anterior end it gradually becomes more oval, forming a partial roof for the capsule, and dorsal to the choana, a lateral process curves downward to cover completely the caudal limit of the nasal sac. This is the anlage of the lamina cribosa (l.c.) which is formed by a lateral extension of the caudal end of the ethmoidal column, so well developed in the later stage. A small groove between the anterior limit of the cornu and column allows the passage of the nasalis internus nerve to the internasal space.

Antorbital processes arise from the lateral margin of each trabecula just posterior to the cribosal anlage; they are directed latero- ventrally and then turn abruptly cephalad for a distance equal to the length of the process and terminate at the level of the caudal margin of the ethmoid plate.

In a larva 38 mm. long (fig. 12.) the nasal capsule shows many resemblances to that of the 45 mm. Amblystoma. The capsule has doubled in size and chondrification has advanced in all parts, thus

affording a much more complete protection for the olfactory organs. The crista trabeculae (cr.t.) which had appeared in the 25 mm. stage, has now united to the caudal limit of the columna ethmoidalis and forms a complete lateral wall of the cavum cranii in this region. A much younger Amblystoma shows this fusion already accomplished.

The ethmoidal plate (p.e.), though trapezoidal in outline, has completely lost the hinder process of the earlier stage, so that the posterior margin is semicircularly excavate, like that of the 45 mm. Amblystoma larva. Trabecular ridges (t.r.) still persist, although they are not as marked as in the earlier stage. Anteriorly the ethmoid plate continues into the nasal septum.

The cephalic end of the ethmoidal columns have grown toward each other and have fused in the median line to form a small nasal septum above the anterior margin of the ethmoid. The dorsal surface of the septum nasi is flat and continuous with the median nasal process (m.n.p.) of each side; its anterior margin has developed a triangular cephalic process (ce.p.) projecting into the internasal space midway to the anterior limit of the capsule covering the intermaxillary gland. The nasal septum has not completely united to the ethmoid plate, a large opening, the fenestra ethmoidalis (fen.eth.), existing between the brain cavity and the internasal space. This foramen is merely transitory for in the later stage cavum cranii and internasal space are completely separated from each other by com- plete nasal septum. The septum is triangular in sagittal section; its posterior side being vertical, the dorsal surface flat and the anterior face, curving posteriorly, together with the cephalic process forms a roof for the internasal space in which the intermaxillary glands lie.

Anterior to the olfactory lobes the united columna ethmoidalis and cornu trabecula extend forward a distance about equal to the length of the septum nasi and form a complete vault over the anterior end of the olfactory organ, a condition similar to the 55 mm. Amblystoma larva. The median nasal process (m.n.p.), whose anlage was observed in the 25 mm. stage, now forms a complete roof for the capsule and is separated from the lateral margin of the cornu by a large oval gap the external narial opening (e.n.). The olfactory organ opens laterally and a blind end of the sac extends into the cartilage vault (c.) anterior to the naris, while in a corresponding stage of Amblystoma this opening is terminal and the organ does not become associated with the capsule for several sections. Upon the medial surface of this cartilage cap (c.), just anterior to the septum nasi is a small foramen (f.n.i.) for the nasalis internus nerve which passes to the intermaxillary gland. The lamina cribosa (l.c.), which arose as a lateral process of the posterior part of the ethmoidal column has now curved down over the entire caudal area of the nasal sac and is continuous in front with the median nasal process. Laterally it has united at its anterior angle to the caudal limit of the cornu, thus forming a complete band of cartilage around the olfactory organ. The naso-lacrimal duct passes over this bar, divides into two tubes, distributed to the inner angle of the eye. The cornu continues posterior to this bar and terminates in a short caudal process supporting the organ of Jacobson.

The cornua trabeculorum which form the floor of the capsule are distinctly convex on their ventral aspect and extend as far as the roof of the capsule. At the anterior end of the ventral surface of each cornu is a small prenasal process (pn.p.), which extends

ventrally to the level of the floor. At this stage the olfactory foramina have not completely formed, but the olfactory nerve passes through the large fenestra extending from the anterior level of the ethmoid plate almost to the line of its posterior margin. The antorbital process (a.p.) is more slender than in the corresponding stage of Amblystoma; it extends laterally a distance equal to the width of the trabecula and then turns cephalad to end near the lateral margin of the lamina cribosa.

In a larva approaching the end of metamorphosis (fig. 15.), the nasal capsule resembles that of the adult Amblystoma in several respects. The ethmoid plate (p.e.) is shorter than in the preceding stage and the nasal septum (s.n.) unites the median parts of the capsules, so that two thirds of the nasal sacs lie anterior to the brain. The fenestra ethmoidalis (fen.eth.) has entirely disappeared so that internasal space and brain cavity are entirely separated by a cartilaginous wall, a condition described by Seydel as characteristic for the adult. From the median line of the dorsal surface of the septum nasi the cephalic process (ce.p.), more slender in this stage extends forward to the level of the base of the prenasal process (pn.p.). It covers the intermaxillary glands. I have not observed this structure in any other Urodele.

The antorbital process has united to the caudal extension of the cornu, thus outlining two large fenestrae. Of these the larger is ventral and lies between the cornu and antorbital process, while the small orbito-nasal foramen (f.o.n.) lies posterior to the caudal margin of the cribosa. There is no association between the lamina cribosa and the antorbital process. These structures approximate each other, but do not unite, so that a complete lateral covering for

the nasal organs has not yet been formed. The caudal extension of the lamina cribosa, completely covering the choana, is pierced by a small opening through which a small branch of the nasalis internus leaves the capsule.

This capsule very closely resembles that of the last larval stage of Amblystoma. Its general shape, the nasal septum, the ethmoid plate, the foramina for the rami of the fifth nerve are features shared by both these forms. Salamandra possesses no fenestra infra-conchalis, though I am inclined to believe that a later stage would show the formation of the cartilage around the organ of Jacobson. A further difference exists in the complete separation of the lamina cribosa and antorbital process so that the lateral aspect of the nasal sac is exposed in these parts. The ethmo-palatine process of Parker is the antorbital process and he says it is very likely to fuse with the anterior parts of the capsule as shown in this stage. In the adult, Parker describes the persistence of the prenasal processes and the median rostrum and says that they seem to be the non-segmented rudiments of the paired and unpaired elements of the foremost visceral arch, whose splints are the premaxillaries. This median rostrum is not present in any other Urodele, although the prenasal processes are found in other types. Parker's homologies are hardly borne out by our present knowledge.

Triton cristatus.

The nasal capsule of Triton cristatus, though bearing some resemblances to those of Salamandra and Amblystoma shows many striking contrasts. In a larva 28 mm. long (fig. 16), the capsule is somewhat rectangular in outline, the width slightly exceeding its length at its widest part, and gradually tapering toward the anterior end.

At this stage the trabecular crests(cr.t.) are well developed, being wider at their ventral than at their dorsal margins and extend in a latero-dorsal oblique direction, forming the lateral walls of the brain case in this region. At the anterior margin of the cristae the trabeculae fuse by their ventral margins to form a very small ethmoid plate (p.e.) which, strikingly in contrast to the broad ethmoid plate of Salamandra and Amblystoma, resemble somewhat that of Cryptobranchus yet to be described. It is equal in length to about the width of the trabecula and it unites the capsules of either side at a point just beneath the large olfactory foramen (f.o.).

Dorsal to and separated from the planum ethmoidalis by a considerable distance is a narrow bar, the nasal septum (s.n.), which roofs the internasal space between the capsules. This septal bar unites the cephalic extensions of the cristae at the antero-dorsal margins of the olfactory foramina and is separated from the ethmoid plate by a large fenestra ethmoidalis (fen.eth.) similar to that in the 58 mm. Salamandra.

In contrast to the larval stages of other Urodeles studied, the nasal organs of Triton are almost entirely anterior to the forebrain; so that ethmoid plate and nasal septum are near the caudal limit of the capsule. As a result of the relation of the central

nervous system to the nasal structures, the capsule appears as a segment of a elongate cone, obliquely truncate anteriorly, with its lateral wall interrupted by a very large narial opening. As is true for all Urodeles, the cartilage structures of each side are separated by an internasal space which in Triton is more elongate and extends between the walls of the anterior two thirds of the capsule. This internasal space, the intermaxillary room of Born ('77) is continuous with the cavum cranii and is separated from it by membranous structures only.

Anterior to its junction with the crista trabecula, the lamina cribosa (l.c.) forms a wide curved plate which roofs the choana and posterior parts of the nasal sac and forms a complete vault extending from the septum nasi and dorsal margin of the olfactory foramen to the plane of the ventral margin of the trabecula. Upon its lateral ventral angle this vault unites to the cephalic extension of the antorbital process (a.p.), thus forming a large orbito-nasal foramen (f.o.n.) through which the nerves of the nasal region pass to the interior of the capsule. Anteriorly the lamina cribosa unites upon its lateral angle to the caudal extension of the floor of the capsule, thus forming a complete band of cartilage around the nasal organ, a condition observed for every Urodele thus far studied. This band is also associated with the organ of Jacobson which lies upon a small extension of the floor of the capsule posterior to the union with the lamina cribosa. The naso-lacrimal duct passes over this bar as in both Amblystoma and Salamandra.

Anterior to the nasal septum the trabecular extensions have expanded into a plate which has grown ventrally to form the floor of the capsule and dorsally to form the inner wall. This inner wall

curves upward and outward and is directly continuous with the anterior margin of the lamina cribosa, so that these fused structures form a complete cartilage roof for the capsule, pierced by a single large opening, the dorso-lateral fenestra, separated from the dorsal lateral margin by a narrow bar. A small foramen in the vault near the nasal septum conducts a branch of the profundus nerve to the dorsal surface of the capsule.

Upon the ventral aspect of the capsule, the trabecular extension has expanded into a trapezoidal cornu which forms the floor of the capsule and is uninterrupted as far back as the level of the septum nasi where it unites upon its lateral margin to the lamina cribosa above described. At the anterior end the floors of the two capsules approach each other, and at the extreme medial ventral tip of each there is a small projection, the prenasal process (pn.p.), probably the homologue of that structure in both Salamandra and Amblystoma. Above this process is the foramen nasalis internus (f.n.i.) which passes the superficialis nerve to the internasal space. The tip of the capsule is not vaulted in this stage, but the anterior margin is widely curved and the olfactory sac continues beyond the limit of the capsule to open by the terminal narial opening.

The nasal capsule, although well chondrified at this stage, has several large gaps, the largest of which is the external naris for the main nasal sac and the naso-lacrimal duct. The second largest gap is ventral and lies between the caudal end of the cornu and the antorbital process where the nasal organ is separated from the mouth cavity by the epithelial lining of the mouth. The orbito-nasal, olfactory and dorsal foramina are about the same size.

The second larva of Triton cristatus studied was 35 mm. long (fig. 17.). It showed characters intermediate between those of the 28 mm. larva and the stage described by Born ('77). In his account of the structures of the adult, Born described large gaps that appear to be formed by the continuous increase of smaller openings present in my older stage. There has been a reduction in the length of the capsule, most of which occurs at the anterior end, so that the width is greater in proportion to the length than in the 28 mm. larva. The cartilage bar uniting the antorbital process to the lamina cribos has separated into two bars between which the outer branch of the profundus nerve enters the capsule to be distributed to Jacobson's organ. The brain lies lateral to the caudal fourth of the nasal sac, a condition true of the earlier larva; but Born says that in the adult, the brain lies entirely posterior to the nasal sac. The olfactory foramina (f.o.) are more ovoid in this stage and this has caused a wider separation between the septum nasi at the anterior margin of the foramina and the ethmoid plate so that there is an increase in the size of the fenestra ethmoidalis (fen.eth) connecting the large internasal space with the cavity of the forebrain, causing the olfactory lobes and the intermaxillary glands to overlap in this stage.

Anterior to the olfactory foramen, the inner wall of the capsule is pierced by a small opening for the main branch of the superficialis which passes to the intermaxillary glands while another branch of the same nerve leaves the capsule through the foramen on the dorsal surface near the septum nasi. Through the foramen in the inner wall at the base of the prenasal process of the capsule, the main branch of the profundus nerve passes to the lower parts of the upper lip.

On the floor of the capsule near the anterior end is a small gap which I believe to be the first appearance of the large opening which is the result of a further resorption of cartilage, described by Born for the adult. In contrast to the earlier stage the capsule now forms a vault (c.) over the anterior end of the nasal organ and thus the anterior naris is lateral, a condition even more marked in the adult stage.

To try to homologize the structures of Triton with those of Amblystoma is well nigh impossible without the early stages. Born ('77) has described the process of chondrification but has shown no figures of his early stages. Terry ('06) says, "The development of the cartilaginous nasal skeleton of Amblystoma is comparable in many respects with the processes in Triton as described by Born." Born says nothing of an ethmoidal column which chondrifies independently and then subsequently becomes associated with the trabecula; on the contrary he says, "Bei den Tritonen die Knorpelkapseln der Näsenhohlen durch directes auswachsen der Trabecel gebildet werden". The side wall, roof and floor of the capsule has been formed by a continuous dorso-lateral and ventro-lateral growth from the trabecular extensions. The many gaps in the structure have been formed not by fusion of parts independently chondrified, but by interruptions of a continuous growth. On the contrary the independent chondrification of parts in Amblystoma and their fusion to the main trabecula, to form the side wall of the capsule reverses the process that Born has described for Triton, and yet Terry concludes his comparison by stating, "It appears to me that there is after all not much difference in the origin of the capsule of these two animals." In my six stages of Amblystoma I have never observed a well developed

connection between the internasal space and the brain cavity. In Triton this fenestra is present in both larval stages and Born says, "Dieser Internasalraum ist bei Triton cristatus und taeniatus, niemals durch eine knorplige Wand von der Schädel höhle geschieden, sondern immer hautig gegen dieselbe abgeschlossen." I have described a similar opening in Salamandra where it exists only in the larval stage. It also occurs in the larvae of Pelobates and Rana.

Resemblances to the 38 mm. nasal capsule of Salamandra are somewhat striking. The ethmoid plate, fenestra ethmoidalis, olfactory foramen and nasal septum can be readily compared. The antorbital process and its connection to the lamina cribosa forms the palatal process of Born ('77) and later of [illegible] ('9[illegible]). Seydel ('95) called the posterior [illegible] of [illegible] vomer, "Gaumenfortsatz" even before it had united to the antorbital process. Both the floor and the roof of the capsule of Salamandra resemble those of Triton, but the absence of the large gaps in these parts preclude drawing definite homologies.

Diemictylus viridescens.

The nasal capsule of a larva 38 mm. long (fig. 14.) is well chondrified and resembles in many respects that of the 35 mm. Triton cristatus. In both animals the two capsules are united by a very narrow ethmoid plate, the only connection between them in Diemictylus, which does not possess a septum nasi as does Triton. The nasal organs are well encased in cartilage and the same gaps are well represented in both forms. In the region of the eye the cristae trabeculorum (cr.t.) are high, completely separating the optic organ from the central nervous system.

The antorbital processes (a.p.) have already united to the lamina cribosa (l.c.) so that these structures form a curved plate which completely covers the dorsal and lateral parts of the choanal region. This plate is pierced on its posterior surface by two foramina, the inner of which is the orbito-nasal opening (f.o.n.) for the nerves of the nasal region and the outer is smaller and passes a branch of the profundus nerve into the capsule to be distributed to Jacobson's organ.

Anterior to these foramina this plate continues forward to roof the nasal sac and glands and its lateral ventral margin is abruptly curved toward the median line so that a shelf is formed in which the caudal parts of Jacobson's organ lie; while the cephalic end of this organ lies in a small circular foramen in the lateral wall of the cribosa. This foramen is separated from the external narial opening by a narrow bar of cartilage which is not present in Triton where the two foramina are confluent; but Jacobson's organ bears the same relation to the deep bay in Triton as it does to the foramen in Diemictylus.

The roof of the anterior part of the capsule is interrupted by two oval foramina of which the lateral is the external narial opening which extends from about the middle nearly to the anterior end of the capsule. On the dorsal surface, separated from the naris by a cartilage bar is a small gap which marks the beginning of the process of resorption of cartilage well advanced in a later stage.

The inner wall is pierced by a small foramen for a branch of the superficialis nerve which passes to the well defined internasal space (in.s.) filled with the intermaxillary glands. Slightly anterior to this foramen is the prenasal process (pn.p.), at the base of which is the opening for the profundus nerve as in both stages of Triton. The cephalic part of the capsule (c.) is vaulted and covers the anterior extension of the nasal sac beyond the narial opening.

In contrast to all other animals studied Diemictylus has no nasal septum. I have described in Triton a very narrow septum nasi uniting the dorsal margin of the capsules, just anterior to the olfactory foramen. This structure is absent in Diemictylus so that there is no roof for the internasal space or for the fenestra ethmoidalis leading to the cavity of the forebrain. These cavities are continuous so that the intermaxillary glands extend back beneath the forebrain and rest upon the narrow ethmoid plate. In contrast to Triton the forebrain of Diemictylus extends anteriorly beyond the ethmoid plate as far as the cephalic limit of the olfactory foramen and overlaps the intermaxillary glands.

The adult shows no further chondrification of structures than those present in the earlier larva (fig. 15.). Ossification

has taken place in all parts and further resorption has increased the size of gaps present in the earlier stage. A single orbito-nasal foramen (f.o.n.) exists between the antorbital process and the lamina cribosa through which the nasalis externus and internus nerves enter the capsule. The shelf-like process on the ventral surface of the capsule has increased in size and has extended caudally as a short process supporting the posterior limit of Jacobson's organ. The anterior end of the organ extends into the foramen as in the larval stage, while the naso-lacrimal duct passes over the bar separating this foramen from the narial opening, to empty into the nasal sac.

Anteriorly, the gap in the roof of the capsule has increased so that the entire dorsal aspect of the nasal sac is exposed. It is separated from the oval narial opening by an elongate rod which forms the only roof of the capsule in this region. Anteriorly the vaulted end is pierced by three small foramina for the exit of branches of the ophthalmic branch of the fifth nerve.

The same relations exist in this stage between the internasal space and the cavity of the forebrain. The intermaxillary glands reach to the narrow ethmoid plate, but extend cephalad only to the anterior margin of the large choanal opening, while in the larva they reached to the prenasal process.

Upon resemblances of the nasal capsules, Triton and Diemictylus are very close. The entire separation of the nasal capsules except for the narrow planum ethmoidalis has not been noticed in other Urodeles. The complete connection between the brain cavity and the internasal space has not been described for any other adult although there is a transitory connection between these regions in

certain of the larvae. Born ('77) says that in Triton cristatus this relationship persists throughout life and this fact places Triton and Diemictylus alone in this respect.

There are some resemblances between the adult Amblystoma and Diemictylus. The relation of the organ of Jacobson to the foramen associated with it and the bar of cartilage separating it from the narial opening over which the naso-lacrimal duct passes to the nasal sac, are alike in both animals. Furthermore the diagonal bar of cartilage uniting the anterior margin of the cribosa to the posterior limit of the cephalic vault are alike and a further advance in the resorption of cartilage in Diemictylus would result in the conspicuous dorsal gap of Amblystoma. The orbito-nasal foramen, the choana opening, and the characteristic shelf for the organ of Jacobson are points strikingly similar in the nasal capsules of these animals. On the other hand the complete absence of a nasal septum, the reduced ethmoid plate, and the complete connection of the internasal space with the cavum cranii preclude the determination of close relationships here.

Cryptobranchus alleghaniensis.

Practically no work has been done on the larval stages of Cryptobranchus, though the adult head and nasal structures have been detailed by Parker ('76), Wiedersheim ('77) and Wilder ('92). I have been able to study four different stages in the chondrification of the nasal capsule and although certain stages have not been seen because of lack of intermediate stages, yet I am able to recognize the method of development and to note some features that may proove interesting from a phylogenetic point of view.

The early process of chondrification is similar to that in Amblystoma, and the earlier stage I have, suggests the 11 mm. larva of that animal, with certain additional features. In a larval Cryptobranchus two weeks old (fig. 22.), the nasal capsule is incomplete. In the optic region the crista trabeculae is very strong and lies between the diencephalon and the eye. The crests (cr.t.) terminate abruptly near the anterior margin of the eye, while the trabeculae continue cephalad, turning slighly toward the median line, but as yet do not meet to form the ethmoid plate. They are oval in section, curved upon the medial surface to approximate the ventral margin of the brain, while laterally they conform to the medial surface of the nasal sac. Near their cephalic end each trabecula expands laterally, forming a slight process, the beginning of the cornu trabeculae, which ends as a blunt process in the enveloping tissue.

In contrast to the 11 mm. Amblystoma larva, there are well formed crests in Cryptobranchus; while on the other hand the cornua trabeculorm which are well developed in the 11 mm. Amblystoma larva are only just forming in this stage of Cryptobranchus. The external

naris of the larval Amblystoma is terminal and opens at the cephalic end of the nasal organ which is closely associated with the capsule; in Cryptobranchus, the narial opening is ventral and the nasal sac extends behind the narial opening and the anterior end of the trabecula. An antorbital process is not formed, nor is there any evidence of the separate chondrification of an ethmoidal column as in the early stage of Amblystoma.

The next stage is a larva five weeks old (fig. [illegible].). Chondrification has advanced in all parts, but the absence of a series intermediate between this and the last stage prevents a definite conclusion as to the origin of certain structures. The nasal capsule is similar in many respects to that of the 25 mm. Salamandra larva. The columna ethmoidalis ascends from the medial margin of the trabecula, anterior to the ethmoid plate, as a broad band of cartilage which separates the nasal sac from the internasal space (in.s.). More posteriorly it becomes rodlike and lies along the dorsal medial margin of the nasal organ, and, at the level of the anterior margin of the ethmoid plate, the column fuses with the medial margin of the large rhomboidal lamina cribosa which curves over the caudal portion of the nasal sac. Behind the lamina cribosa the ethmoidal column continues backward to join the crista trabecula. Near its median plane the lamina cribosa is pierced by a small foramen through which the superficialis branch of the fifth nerve passes to the dorsal side, while its anterior margin extends obliquely forward and outward to about the level of the posterior margin of the cornu, resembling the condition in a 34 mm. larval Amblystoma.

Anterior to the lamina cribosa each ethmoidal column turns medially and, bending ventrally, unites to the medial margin of the

cornu trabeculae, just as in the 25 mm. Salamandra larva. These columns do not fuse to form an ethmoidal bridge like that which Terry ('06) described in Amblystoma, but they unite to the cornua and then subsequently become connected with each other by a small septum nasi yet to be described. Although my material does not show the method of origin of the ethmoidal columns, for reasons to be given later, I am inclined to believe that these columns arise as dorsal outgrowths from the medial margins of the cornua and then grow posteriorly over the nasal sac, uniting to the cristae trabeculorum which are formed earlier in the process of chondrification. A small notch at the anterior end of the capsule, the median nasal incisure (m.n.i.), marks the junction of column to cornu and allows for the passage of the profundus of the fifth nerve to the internasal space.

From its junction with the crista, each trabecula inclines toward the median line for a short distance and then passes straight forward until, on a level with the anterior margin of the lamina cribosa, the two fuse to form an ethmoid plate (p.e.). This planum ethmoidalis differs from that of any of the Urodeles thus far described; first, in its size, and second in the absence of the characteristic concave dorsal surface. The plate is very short and the trabecular ridges are not pronounced; and, in contrast to the other capsules, the dorsal surface, although level at its posterior margin, becomes rapidly convex and bears upon its anterior half a distinct swelling which I have called the beginning of the septum nasi. The ventral surface is decidedly concave, so that the ethmoid plate is a convex-concave cartilage whose posterior and anterior margins are parallel with each other, while the lateral

margins are confluent with the trabecular extensions. The posterior margin possesses a short caudal process similar to that of the 25 mm. Salamandra larva.

A large oval fenestra, bounded posteriorly by the crista trabecüla, dorsally by the ethmoidalis and ventrally by the trabecula, allows the passage of the olfactory nerve to the nasal organ. The fore-brain extends slightly beyond the septum, so that two-thirds of the olfactory sac is lateral to the brain. The narial opening is terminal, but is still ventral and considerably anterior to the capsular structures. In contrast to the broad curved plate of both Amblystoma and Salamandra, the cornu trabeculae of Cryptobranchus is reduced to a narrow curved bar which extends from the cephalic lateral margin of the trabecular ridge almost to the anterior limit of the cribosa to which it fuses in a later stage.

From the ventral margin of the crista trabeculae, just posterior to the large olfactory foramen, a slender process passes laterally a distance equal to the width of the trabecula and then bends abruptly and extends backward to the quadrate. The morphological relations of this bar, which must be recognized as a pterygoid, will be discussed in a later stage, which I have figured.

A larva two months old shows but a very slight advance in the chondrification of the nasal capsule. The ethmoid plate has increased in size and has lost the hinder process of the earlier stage while the septum nasi, arising as a dorsal growth from the anterior part of the ethmoid plate, has enlarged and has become continuous upon its lateral anterior angles with the ventral margins of the cephalic extensions of the ethmoidal columns.

As yet there is no median nasal process, so the entire dorsal

surface of the cephalic portion of the nasal sac is exposed. The anterior angular process of the lamina cribosa and the lateral margin of the cornu more closely approximate each other, but as yet there is no cartilage ring around the olfactory organ. The cornu trabeculae and the antorbital process compose the whole floor of the capsule. The antorbital processes now extend forward from the anterior end of the pterygoid process.

The last stage of Cryptobranchus studied, was a larva three months old,(fig.24.) ; chondrification has advanced in all parts and a better defined nasal capsule is now present. The lamina cribosa is vaulted and forms a roof over the caudal parts of the olfactory organ which extends behind the choana, which is long and narrow and reaches forward to the level of the ethmoid plate. The lamina cribosa of the earlier stage has grown forward and it now covers the posterior two thirds of the olfactory organ, and terminates abruptly at about one fourth of the length of the capsule from the anterior end.

The septum nasi (s.n.) now completely unites the capsules of both sides: it is a narrow bar continuous ventrally with the ethmoid plate upon which the olfactory lobes rest. This septum which arises as a small process from the median line of the dorsal surface of the ethmoid plate, is now level with the dorsal margins of the ethmoidal columns and presents an anterior surface perpendicular to the main axis. The posterior margin of the ethmoid plate is straight and parallel to the anterior; the ventral surface is flat, while the dorsal grades into the septum, so that in sagittal section the fused ethmoid and septum appear triangular .

Anterior to the junction of the laminar plate to the ethmoidal

column, each column has developed a strong median nasal process (m.n.p.), resembling this structures in a 45 mm. Amblystoma larva, and each is separated from the lamina cribosa by an elongate fenestra narina(fen. n.) which is confluent with the external narial opening. This process forms the roof for the medial parts of the nasal sac and the nasal glands, as in other Urodeles. It is also pierced by a small foramen for a branch of the ophthalmic superficialis nerve. Anteriorly, the extensions of the ethmoidal columns have fused to the cephalic limits of the cornua, thus forming a complete dome or vault over the anterior parts of the sensory structures. The olfactory duct continues forward from the lateral margin of this dome and opens through the external naris anterior to all capsular structures. The medial wall of the cupola is pierced by two foramina for the rami profundus and superficialis of the fifth nerve. Intermaxillary glands do not occur in this animal.

The cornu trabeculae of each side curves backward and unites distally to the anterior limits of the lamina cribosa, so that now a complete ring of cartilage is developed around the nasal organ. Although as yet very small, the organ of Jacobson rests upon the caudal extension of the cornu beyond its junction with the lamina cribosa. I have not observed the naso-lacrimal duct and its relation to this bar in Cryptobranchus. The cephalic extension of the antorbital process has increased, but no connection between it and the lamina cribosa has yet been established, although I am inclined to believe that a later stage would show one, as in Amblystoma and Salamandra.

This bar of cartilage, mentioned in connection with the five

weeks stage, which extends back from the antorbital process to the quadrate, is undoubtedly the pterygoid which does not exist, so far as I know, in such complete form, in any Urodele with the single exception of the Siberian genus Ranodon (Wiedersheim '76, fig. 69), although the junction of the bar with the anterior region of the cranium is the normal condition in the Anura. This condition throws some light upon the nature of the antorbital process in the Urodeles. Some years ago Gaupp questioned a statement by Kingsley ('92,, p. 672), who said:"the lower process may retain the name, antorbital, usually applied to it, for Amphiuma presents no evidence that it is the palatine cartilage as Gaupp interprets it." Gaupp ('93, foot-note p.430) says: " Hierzu mochte ich bemerken, dass ich die beiden Namen "Antorbital-forsatz" und"Cartilago palatina" durchaus fur dasselbe Gebilde gebraucht habe(17, p. 115: "die Cartilago palatina" oder wie die englischen Autoren HUXLEY und PARKER den Knorpel nennen, den "Processus antorbitalis"). Als "Processus palatinus" wird der Knorpel aber z. B. von FRIEDRICH und GEGENBAUR bezeichnet auch HERTWIG nennt ihn auf den Figuren "Cartilago palatina", und Wiedersheim spricht von einem Antorbitalfortsatz oder "Gaumenfortsatz" der deutschen Autoren. Da ich beide Bezeichnungen in der Literatur vorfand, so erwahnte ich sie auch beide, habe aber nicht etwa einem bekannten Gebilde eine neue Deutung geben wollen. KINGSLEY scheint unter "Palatine cartilage" hier etwas Besonderes zu verstehen; was das ist, kann ich aus seinen Angaben nicht ersehen". Winslow ('99) discussed the question and concluded that until it was shown that the process in Urodeles arising from the trabeculae in front of the orbit was actually a part of the pterygoquadrate, the name antorbital should be continued

in use. With the evidence now presented by Cryptobranchus it would seem as if the basal part of the process in all Urodeles is really an anterior portion of the pterygoquadrate. But the anterior prolongation of the process is something additional and cannot be regarded in any way as pterygoidal in character but may retain the name antorbital process. Then in all other genera where the posterior connection is lost, the whole outgrowth is best known as the antorbital. Of course its retention in both Cryptobranchus and Ranodon larvae is an ancestral feature lost elsewhere in the Urodeles. In the adult of both the American and Japanese species of Cryptobranchus the connection of the pterygoid with the side of the cranial wall is lost, and in both the direction of the posterior part of the cartilage would not suggest that in the larva there was any such connection with the trabecula or any relation with a palatine bone.

Of the Urodeles thus far described, Cryptobranchus stands alone in the origin of the septum nasi. In both Amblystoma and Salamandra, this structure arises by the fusion of the medial processes from the cephalic ends of the columnae ethmoidalis. On the other hand in Cryptobranchus it arises as a dorsal growth from the middle line of the planum ethmoidalis and subsequently becomes united to the ethmoidal column. The later chondrification of the capsule presents structures which are probably homologous to those in Amblystoma, such as the median nasal process, the anterior cupola and the lamina cribosa; but on the other hand, the large ethmoid plate and the nasal septum in the 45 mm. Amblystoma larva do not exist at any time in Cryptobranchus, both of these structures being greatly reduced.

Spelerpes bilineatus.

In a larva of Spelerpes 15 mm. long (fig. 18.) no nasal capsule is developed. The trabeculae (t.) extend forward to the limit of the forebrain, but do not meet to form an ethmoid plate. In the region of the choana the trabecular bars are approximately circular in section and lie along the ventral lateral margin of the forebrain, while anterior to the choana they become oval in section and nearer their cephalic limit each bar expands into a small curved cornu trabecula (c.t.) which extends toward the nasal sac but does not reach it. At no time is either trabecula close to the nasal sac, but each lies nearer the brain throughout its entire length.

The early stages of all the Urodelan capsules are strikingly similar and, although later development produces capsules widely divergent, yet the earlier stages of Cryptobranchus, Spelerpes, Desmognathus and Amblystoma are essentially similar with their simple trabeculae and cornual extensions.

In a larva 37 mm. long(fig. 19.) several parts of the nasal capsule are formed, and fundamental structures can be readily homologized with those of other Urodeles. In the region of the eye chondrification of the trabeculae has progressed dorsally so that well developed crests are formed which extend forward to the level of the antorbital processes (a.p.), where they terminate abruptly, although their dorsal margins continue cephalad a short distance to end in small processes. The trabeculae,approximately circular in section, lie along the medial margin of the nasal sac at the choana. From this point they turn toward the median line and fuse to form a small ethmoid plate (p.e.). At the point of fusion the trabeculae have expanded dorsally, the ethmoid plate on either side

being as thick as the trabecula, so that it is high and long and resembles that of Cryptobranchus. Dorsal processes from the medial margins of the trabeculae, just anterior to the planum ethmoidalis, are beginning to develop at this stage (fig. 60.), so that the lateral trabecular margin is concave, thus forming a groove in which lie the superficialis and profundus branches of the fifth nerve. The cephalic extensions of the trabeculae expand into broad flat triangular cornua whose caudal lateral angles are in a line with the anterior margin of the ethmoid plate. Anteriorly they extend to the level of the external narial opening and are separated from each other by a deep intra-trabecular notch (i.t.n.), as wide as the length of the ethmoid plate.

The antorbital processes have developed from the ventro-lateral margins of the trabeculae at the level of the anterior margin of the crista, and extend laterally a distance equal to the trabecular width, when they bend anteriorly a short distance to end near the choanal opening.

The last stage of Spelerpes studied, was a larva 46 mm. long (fig. 20.). Some additional structures are present, but this stage is not sufficiently developed to homologize the complete nasal capsule with those of the other Urodeles. In the region of the eye the cristae trabeculorm (cr.t.) are low, but slightly anterior to the antorbital process the crest has extended considerably upwards, its anterior end being free from the lower trabecula. This anterior end of the crest is possibly the posterior beginning of the ethmoidal column. The trabeculae, in front of the anterior end of the cristae, turn obliquely inwards and then run parallel to each other a short distance to unite into a narrow ethmoid plate.

The ethmoid plate itself is decidedly smaller (through resorption) than in the earlier stage, both in thickness and in length. Anterior to the planum ethmoidalis the trabeculae continue forward, separated from each other by a narrow intra-trabeculae notch, and then each, at a point the width of this notch anterior to the ethmoid plate, gives rise to a small process from its dorsal medial margin which is directed caudally above the trabeculae (fig. 61.). From its origin and relation to the trabecula I believe this to be the anterior portion of the ethmoidal column. These processes were observed in the 37 mm. stage where the dorsal development of each trabecula indicated the early stage of this rudimentary column. Anterior to this columnar process the trabecula expandes into a cornu similar to that in the 37 mm. stage.

I regret that I have no older stages showing the further chondrification of parts already laid down hence I am not able to make a careful comparison with the other capsules, but in general Spelerpes seems to indicate a retarded growth of all parts. In corresponding ages of Amblystoma, and Cryptobranchus a more complete nasal capsule is developed than in Spelerpes. In the 15 mm. larva and even in a 21 mm. larva the trabeculae alone are chondrified while in the above mentioned genera many additional structures are already formed. In all forms studied the trabecular rods and the cornua trabeculorum are first laid down, but the later chondrification presents difficulties of homologies. In no other Urodele have I observed the cephalic extension of the crista trabecula, although Amphiuma has a structure which I believe to be the homologue of this process, and, judging from their relation to the nasal organ and trabecula, I believe it to be the posterior limiting

of the columna ethmoidalis. In the 19 mm. Amblystoma larva the columna ethmoidalis arises independently, and grows subsequently back to the crista trabecula; but the dorsal process from the trabecula anterior to the planum ethmoidalis in Spelerpes is very evidently the beginning of the column in this animal. I am not able to say whether an older stage would show the connection of this anterior process to the crista or not; but the five weeks Cryptobranchus larva shows such a relationship established. The 25 mm. Salamandra larva shows a connection between the ethmoidal column and the cornu but no connection between that column and the crista. The absence of earlier stages of both Cryptobranchus and Salamandra preclude the determination of the origin of these columns so that definite relationships cannot be established. The small ethmoidal plate is similar to that of Cryptobranchus, but the broad triangular cornu is an Amblystomal character. The ethmoidal plate is narrower than in the other types, the result of the abrupt turning toward the median line of the trabeculae anterior to the crests. This close approximation of the trabeculae is possible because the anterior end of the telencephalon reaches only to the cristae. Thus the ethmoid plate and the trabeculae in front of the cristae are entirely anterior to the forebrain which does not hold for any of the higher Urodeles. The complete absence of intermaxillary glands as well as the small ethmoid plate and undifferentiated nasal structures are points of similarity to Cryptobranchus, to which I believe Spelerpes is closely related.

Plethodon erythronotus.

Winslow ('98) has described the nasal capsules of a 20 mm. larva of Plethodon glutinosus, and he compares it to a 45 mm. Amblystoma larva with which he homologizes the various parts. I have not been able to study any larval form of the genus, but have examined and modelled the capsule of the adult and find many resemblances to the capsule of the adult Amblystoma. In the adult, ossification is extensive and in certain parts all traces of a chondrocranium have disappeared. In the region of the eye the trabecular crests have been lost and the resorption process has continued up to the olfactory foramina so that these openings are confluent with the orbito-nasal foramina. The sensory structures are exposed both dorsally and ventrally by large gaps in the capsule similar to those in the adult Amblystoma.

Choanal glands and parts of the olfactory sac posterior to the choana extend back into the orbito-nasal foramen through which the profundus and superficialis of the fifth nerve enter the capsule. The olfactory nerve leaves the anterior end of the forebrain and, entering the capsule, divides into two branches which pass to the dorsal and ventral parts of the nasal organ respectively. From this region forward, a lamina cribosa (fig. 63, l.c.) covers only the lateral aspect of the nasal sac and the choana. This plate is curved and extending laterally it covers the organ of Jacobson (j.o.) which opens into the mouth cavity together with the main olfactory duct (fig. 62). A branch of the profundus nerve enters the capsule through the small foramen in the cribosa and lies along the dorsal surface of the organ of Jacobson. Anterior to this foramen the cribosa is flat, restricted in width and forms a roof for Jacobson's

organ only, and is continuous upon its anterior medial angle to the cephalic vault by a dorsal process (d.p.), similar in every respect to the structures in Amblystoma. The cephalic margin of the cribosa is pierced by a small foramen through which the profundus nerve passes from the capsule to the anterior region of the snout. From its cephalo-lateral angle the cribosa continues into the lateral margin of the cornu trabeculae which has expanded to form the floor for the entire anterior parts of the capsule. The anterior limit of the lamina cribosa is marked by a small process which is separated from the dorsal process by a deep groove along which the naso-lacrimal duct passes to empty into the nasal organ.

The vaulted tip of the capsule (c.) is formed by the expanded cornu trabeculae and trabecular extensions. Its posterior lateral angle continues as an elongate process which forms a floor for the organ of Jacobson, which comes to lie closely applied between the laminar plate and the cornu. This relationship is true for Amblystoma as well, although here the organ is completely surrounded by cartilage.

The ethmoid plate (p.e.) and septum nasi are small, separating the capsules only in the region of the choana. They are similar in all respects to those structures in Amblystoma as also are the trabeculae in front of the septum, which are narrow and bandlike forming the medial wall of the capsule (fig. 28). This wall is pierced by two foramina, through the dorsal of which the main branch of the profundus passes to the internasal space (in.s.), while blood vessel passes through the ventral. The internasal space is deep and narrow and well filled with intermaxillary glands which extend back beneath the ethmoid plate to its posterior margin. In

this we note a similarity to Salamandra and Amblystoma, as well as a difference from Cryptobranchus and Spelerpes.

In all essentials Plethodon possesses many of the structures of Amblystoma. The absence of earlier stages has not enabled me to follow the development of the nasal capsule, but, comparing the single larval stage described by Winslow with my larval stages of Amblystoma, coupled with the many resemblances between the adult capsules, I am inclined to place Plethodon very near to Amblystoma. The position and size of the nasal septum and ethmoid plate, the lamina cribosa and its relation to the organ of Jacobson, the large dorsal and ventral gaps, together with the deep internasal space indicate a very close relationship between these animals.

Amphiuma means.

The basis of my study upon the nasal capsule of Amphiuma means was the larva described by Kingsley, ('92) and figured by Winslow ('98, fig.18). Chondrification of the nasal capsule is not yet complete, although many structures are present which resemble the larval capsules of other Urodeles.

The trabecular crests are already well developed and, anterior to the eye, each crest continues cephalad as a small process which rests against the dorsal medial margin of the nasal sac. This process then bends laterally and, curving over the dorsal surface of the olfactory organ, inclines in an antero-ventral direction, ending at the level of the caudal margin of the ethmoid plate. This bar is the early stage of both ethmoidal column and lamina cribosa, which, in contrast to Amblystoma, arises in Amphiuma from the cephalic extension of the crests. Development of these structures then takes place from behind forwards in contrast to the reverse direction in the other groups. The significance of this method of development and its relation and bearing on interrelationships will be discussed later. Kay speaks of this bar as the rudimentary nasal capsule.

Anterior to its junction with the lamina cribosa, the slender trabeculae incline toward the median line and unite to form a rectangular ethmoid plate, which is concave dorsally and supports the olfactory lobes which extend almost to the cephalic end of the capsule. The posterior margin of the plate is concave, while in front the plate passes into the cornua which have a deep and narrow intertrabecular notch between them. The cornu trabecula (c.t.) is broadly triangular, its lateral angle being acute. The anterior part of the nasal sac rests upon the cornu, but the external

narial opening and cephalic end of the nasal sac are anterior to all cartilage structures. There is no olfactory foramen and the olfactory nerve passes over the trabecula anterior to the crista where nasal organ and olfactory lobe are closely approximate. A small antorbital process (a.p.) extends anteriorly from the ventral margin of the trabecula, opposite the origin of the lamina cribosa; and the caudal part of the nasal sac lies between it and the trabecula.

In an older Amphiuma larva, a complete nasal capsule(fig.30.) has been formed, which is similar in some respects to that of Amblystoma. It is somewhat ovoid in outline, its greatest width being about a fifth its length. From the anterior end of the crista, each trabecula inclines medially, and, passing along the lower margin of the forebrain, the two unite at about the level of the middle of the capsule, to form the ethmoid plate. This plate is roughly hexagonal; the posterior margin is straight, while each lateral caudal margin is curved and is directed latero-anteriorly to a point, corresponding to the lateral angle of the cornu of the earlier stage, where it fuses with another cartilage yet to be described. Each lateral cephalic margin is also curved and passes into a process directed forward, the anterior end of the cornu; the two cornua being separated by an intertrabecular notch, wider than in the earlier stage. Thus the ethmoid plate is united upon its posterior margin to the trabeculae, on each lateral aspect to a cartilage bar yet to be described, and on its anterior margin, it is continuous into a pair of small expanded processes, the cornua trabeculorum. The dorsal surface of the planum ethmoidalis is concave, either side of the middle line, the middle of the olfactory sac resting in the concavity.

From the median dorsal aspect of the planum ethmoidalis just posterior to the deep intra-trabecular notch, the short nasal septum (s.n.) extends dorsally, and then divides into two broad bars which are directed from the line of the septum at about an angle of 30 degrees, to form a partial roof over the medial surface of the nasal sac. These processes extend anteriorly and terminate bluntly in a line continuous with the anterior end of the cornua, while behind they unite with the ethmoidal columns.

The ethmoidal column now extends as a slender bar from the crista to the septum, bending strongly toward the middle line in its course. The anterior part of this column is apparently the tectal cartilage of authors. At about its middle point it gives off laterally a reduced lamina cribosa which bends ventrally and laterally from the columna ethmoidalis; this part is broader than the columna and forms the only lateral covering for the olfactory sac in this region. It then continues forward as a more slender bar, which lies closely associated with a longitudinal groove in the outer wall of the nasal sac. About the level of the nasal septum it unites ventrally to a bar of cartilage mentioned above, which arises from the lateral margin of the planum ethmoidalis, thus forming a broad plate which covers the lateral surface of the olfactory sac in this region. The cartilage resulting from the fusion of the lamina cribosa and the bar from the ethmoid extends anteriorly and, at its distal end, expands into a ring of cartilage which entirely surrounds the olfactory duct where it passes to the naris. External nasal glands which lie beside the nasal sac open into it by a duct which passes lateral to the anterior end of the cribosa and the posterior side of the circumnarial ring.

The antorbital process (a.p.), in contrast to all other Urodeles studied, is not directed at right angles or caudally, but from its junction with the trabecula it extends outward and forward at about an angle of 30 degrees to the main axis of the body.

The nasal capsule of Amphiuma resembles in many ways those of the other Urodeles above described. The large vacuity in the dorsal and lateral walls of the capsule and the consequent lack of skeletal protection of the nasal epithelium is in contrast to both Amblystoma and Salamandra and may be the result of a reduction of parts. The septum nasi is reduced, but is comparable in its origin to that of Cryptobranchus. The six-sided ethmoid plate is a fused ethmoid and cornua, and the junction of the anterior end of the elongate lamina cribosa with the lateral process of the ethmoid is readily compared to the bar of cartilage uniting the cephalic end of the lamina and the caudal end of the cornu in Amblystoma. Further, this bar holds the same relation to a ventro-lateral diverticulum of the nasal sac, which occurs between that structure and the organ of Jacobson in both Amblystoma and Salamandra.

There is a small median nasal process in the lateral growth of each columna ethmoidalis dorsal to its fusion to its mate to form the dorsal part of the septum nasi. The anterior ring of cartilage cannot be homologized with any similar structure of the higher Urodeles, but the terminal position of the external naris in Amphiuma, in contrast to its lateral position in the adult Amblystoma, would occasion this modification.

In a larva 82 mm. long appear many of the features that Wilder ('92) has described in the adult. The nasal capsule has doubled in size and there is more chondrification in the anterior

parts. The crista trabeculae, antorbital process, ethmoidal column and lamina cribosa are similar in all respects, except size, to the earlier stage. The extension of the columna ethmoidalis beyond the nasal septum has grown forward and is now united in front to the circumnarial cartilage ring and to the anterior dorsal margin of the lamina cribosa. Thus a broad band of cartilage is formed by the fusion of ethmoidal column, lamina cribosa and the circumnarial cartilage which completely encloses the anterior third of the olfactory sac, except on the ventral side, Together with the median nasal process and the ethmoidal column, it forms the roof of the capsule. A large foramen in this plate conducts the ramus superficialis from the capsule to the dorsal region of the snout, while a small foramen in the lamina cribosa near its fusion with the lateral process of the ethmoid plate allows the ramus glandularis nerve to pass through the capsule to be distributed to the external nasal glands.

In the chondrification of the anterior parts of the capsule a large fontanelle has formed between the ethmoidal column and the lamina cribosa, which resembles in many ways the large gap on the dorsal surface of the capsule of the adult Amblystoma, inclosed by similar structures. No olfactory foramina has been formed, nor does Wilder show one; but the olfactory nerve passes underneath the ethmoidal column just posterior to the septum nasi. The antorbital process extends anteriorly and is closely associated with the nasal organ, but it has not united to any capsular structure, nor do I know of its association with the lamina cribosa in the later stages which is so characteristic for all other Urodeles.

Necturus maculatus.

In the larval stages of Necturus, the process of chondrification is greatly retarded, so that there is no evidence of a nasal capsule, beyond the mere extension of the trabeculae into the head region, up to the 25 mm. stage. This is in marked contrast to the condition in both Salamandra and Amblystoma, in which a more or less well-defined nasal capsule is already laid down at that size. On the other hand it resembles Spelerpes in which the differentiated capsule appears very late.

In a 24 mm. larva, the trabecular crests are not developed and the cylindrical trabeculae incline toward each other, but the ethmoid plate is not yet formed. There is no evidence of a cornu at the anterior end of these bars, nor has the antorbital process formed, but the presence of procartilage cells near the trabeculae indicate its later development. The forebrain lies lateral to the nasal sac throughout its entire length and reaches beyond the anterior end of the trabeculae.

In a slightly older stage (fig. 25), the cephalic ends of the trabeculae are closer to each other and have expanded dorso-laterally, so that a cross section of the trabecula in this region is reniform, similar to the same bar in Spelerpes. Miss Platt ('97) has described the independent chondrification of the ethmoid plate, and its subsequent connection with the trabeculae. I have no stage showing this condition, but I have observed a few small cartilage cells lying in the tissue between the trabeculae, near their anterior ends. This may be the beginning of the ethmoid plate as described by Miss Platt. The forebrain still extends anterior to all cartilages, and nearly reaches the anterior end of the olfact-

ory organ.

In a 30 mm. larva (fig. 26), chondrification has advanced, and some structures of the characteristic Necturan capsule are now laid down. The ethmoid plate(p.e.) now unites the trabeculae; it is roughly trapezoidal in outline, its posterior margin being one and one-half times the length of the anterior. Its lateral margins are thicker, the result of the trabecular swellings, and these thickenings together with a strong median ridge give the ethmoid a double concavity. The nasal septum (s.n.), although slightly evident at the posterior margin, is more prominent in front and thus gives the anterior half of the plate a decidedly convex surface. Anterior to the planum ethmoidalis, the trabeculae extend forward as cornua,a distance equal to one-half the length of the plate, when each terminates abruptly without the lateral expansion, which is so characteristic of the trabeculae of even the younger Amblystoma larvae.

The beginning of the well-known fenestrated nasal capsule covering the nasal organs, mentioned and figured in the adult by Wiedersheim ('76), is formed in this stage. Directly over the nasal sac and some distance from the trabecula, is a narrow bar of cartilage, the columna ethmoidalis (c.e.), which is not united to the other parts of the capsule. This bar chondrifies independently just as in Amblystoma, but in contrast, there is, as yet, no caudal capsular structures. Starting at a level slightly caudal to the ethmoid plate, it runs forward and medially passing along the dorsal medial border of the nasal sac. It terminates at a point a little in front of the cornua. I regard this bar as the homologue of the columna ethmoidalis of the other Urodeles, although I have

not seen its origin. In 31 and 32 mm. larvae, its increased caudal extension leads me to conclude that it develops from in front backward, just as the ethmoidal column develops in Spelerpes and other Urodeles.

In the same stages I have observed chondrification and cartilage cells along the lateral margin of the nasal sac, some of which lie between the folds of the nasal epithelium. These several areas do not seem to arise as a continuum, but chondrify independently and subsequently become connected to form the roof of the fenestrated capsule.

The last stage of Necturus studied, was a larva 45 mm. long (fig. 27.), in which the fenestrated nasal capsule (fen. pr.) has chondrified to an extent comparable to that of the adult. The trabeculae (t.),ethmoid plate(p.e.), septum nasi(s.n.), and the trabecular extensions are similar to those of the preceding stage, differing from them only in size. The septum nasi, however, has suffered a reduction and hence the anterior margin of the ethmoid plate does not have the convex outline of the 30 mm. larva. The entire dorsal surface of the simple nasal sac and part of its lateral aspect is covered by a curved and fenestrated cartilage plate, the further development of the bar and cartilage cells of the 30 and 33 mm. larvae. Small lateral processes have developed from the dorsal bar, and these have united, leaving a series of small openings over the entire dorsal surface of the nasal sac. In front the lateral parts of the capsular roof are smaller or lacking, so that the roof over the tip of the nasal sac is formed by the extension of the ethmoidal column alone. This rather complete development of the fenestrated capsule over the posterior parts of the nasal

sac and the reduction at the anterior end, indicates a development here from behind forwards. This is in accord with the direction of growth in the chondrification of the lamina cribosa and the median nasal process of the higher Urodeles, and, although these parts are wholly separated from the trabeculae, yet the fenestrated capsule of Necturus is the probable homologue of the lamina cribosa and the ethmoidal column of the typical Urodelan capsule.

The antorbital processes (a.p.) are well-developed but have not united to the lattice-work capsule, nor is this relationship ever established; although the approximation of the lateral roof of the capsule and the antorbital process is close.

The early stages of the nasal capsule of Necturus resemble in many ways those for other Urodelan larvae, to this certain extent: the trabeculae with their antorbital processes, the ethmoid plate and the columnae ethmoidalis all recall these structures in the other Urodeles; but there are considerable differences in the method of origin of these parts. The independent chondrification of the ethmoid plate and the absence of lateral expansions of the tips of the trabeculae are features not found in the other groups; on the other hand the direction of the chondrification of the ethmoidal column and the fenestrated capsule, resembles this process in Amblystoma.

The fenestration of the nasal capsule and the absence in the later stages of a septum nasi, together with the very unspecialized nasal organs suggest either ancestral conditions or a degeneration of parts. To regard Necturus, with its fenestrated nasal capsule which has no counterpart throughout the entire Urodelan order,

as primitive, would be unjustified; but, its very belated process of chondrification, the absence of cristae and cornua, together with the entire separation of the roof of the nasal capsule from the ethmoid plate and the trabeculae, may be explained in either of two ways: Necturus has either descended from some more specialized Urodele,like Spelerpes, or may represent a neotenic condition.

Epicrium glutinosus.

Considerable diversity of opinion has existed in the past in regard to the phylogenetic position of the Gymnophiona, or blind footless Amphibia of the tropics. Cope('89) classed them as a family of the Urodeles, the Caecilidae, related to the higher Urodeles through Amphiuma. The cousins Sarasin ('90), following Cope, also regarded them as Urodeles and believed them to be a neotenic condition of Amphiuma. Kingsley ('02) reviewed the evidence as to the position of the group, showing that many of the points supposed to indicate relationships, were based upon erroneous statements or misconceptions and that the Caecilians are a distinct group without any close relations to any other existing Amphibians.

To determine to what extent if any, the nasal capsules of this order would shed light on their relationships to the Urodeles,two larvae of Epicrium glutinosus were studied, in which chondrification is well advanced and the nasal structure formed.

Peter ('98) has described the chondrification of the skull of a Caecilian embryo, and Winslow ('98) has described a stage in which the embryo is still spirally coiled within the egg, and which is considerably younger than my earliest material. In contrast to all other Amphibia studied, the trabeculae of each side are double, each consisting of a dorsal and a ventral bar in the position of trabecular crest and trabecula of other forms, the dorsal doubtless being the homologue of the alisphenoid cartilage of Sewertzow. In the region of the eye these bars are united by postorbital and preorbital band, between which is the foramen for the optic nerve. The preorbital band is a broad plate forming a lateral wall for the anterior part of the brain case; just behind the choana it divides,

the ventral bar, the true trabecula, turning abruptly toward the median line to unite with the trabecula of the opposite side to form the ethmoid plate (p.e.), while the upper portion extends forward for a short distance as a lateral wall to the nasal sac. Just anterior to the preorbital band, this wall has a slight groove on its lateral surface for the superficialis and the profundus rami of the fifth nerve; and through the large foramen at the end of this groove the superficialis enters the capsule, while the profundus turns dorsally and passes along the upper surface of the nasal organ.

Continuing forward from this region, the lateral wall widens and extends dorsally over the dorsal surface of the nasal sac, where its dorsal angle terminating in a short process, is separated from the more anterior parts of the lateral wall by a notch for the superficialis of the fifth nerve. Lateral to this notch and piercing the lateral wall is a foramen through which another branch of the superficialis passes to the epithelium lateral to the capsule. Ventral to this superficialis foramen, the lateral wall passes ventrally and medially into a bar, the solum nasale (so.na.) of Peter ('98) which joins the ethmoid plate.

The upper surface of the ethmoid plate, formed by the fusion of the trabeculae is slightly convex, there being no trabecular ridges along the margin. Its posterior and lateral margins are straight, the lateral margin receiving the solum nasi, in front of which it turns toward the median line and then outwards as the margin of the alinasal process, the processes of the two sides being separated by a broad rectangular groove. These alinasal processes may be the reduced cornua. The septum nasi arises from the

median line of the anterior half of the dorsal surface of the ethmoid plate. It is a thin plate which, extending dorsally, separates the olfactory organs from each other. Its base is rather wide but more dorsally it narrows to a thin plate. Anteriorly it continues forward beyond the anterior end of the planum ethmoidalis, at first somewhat deep, farther in front as a short and slender rod, the rostrum (r.). At the junction of septum and rostrum are the procartilage cells which are to give rise to lateral outgrowths, the alary processes of Peter.

Winslow ('98) has described in his early stage a small antorbital process which extends from the trabecula outward and forward towards the lamina cribosa. I do not find an antorbital process as such in my material. There is however, a small and short bar of cartilage lateral to the trabecula and just posterior to the preorbital band. It is not in connection with the trabecular rods at any time, but is probably the rudiment of the anterior part of the pterygoid process which reaches as far forward as the postorbital band in this stage. I am not able to say whether these parts were in continuity at an earlier stage, but the complete absence of either pterygoid or this cartilage in the older larva leads me to conclude that they now are in the process of resorption and that they may have been connected at an earlier stage.

In a 90 mm. larva (fig. 35.), the nasal capsule is completely formed and additional features are present. The greatest modification has occured in the anterior part of the capsule, while the posterior region is composed largely of those structures present in the earlier stage. The capsule is somewhat ovoid in outline, its greatest width being about one third its length; and in contrast

to all other capsules, with the exception of Amphiuma, it is decidedly incomplete, exposing the nasal organs dorsally and ventrally.

Anterior to the preorbital band the lateral wall is very oblique, the ventral margin being much farther from the median line than is the dorsal. The ramus profundus enters the capsule, while the superficialis passes to its interior through the large notch described in the earlier stage. The lateral wall is broad, and a little in front of the orbito-nasal foramen it extends abruptly downward, this expansion being produced backwards in a short blunt process. In the dorsal part of this expanded portion is the foramen through which the profundus nerve leaves the capsule while medial to it is the process and the notch for the superficialis described in the younger stage. The solum nasi is much as in the earlier embryo.

The trabeculae which reached the ethmoid plate in the earlier stage have now lost all connection with that structure and have been resorbed anterior to the preorbital band; their only remnants are a pair of small caudal processes from the posterior margin of the ethmoid plate, the intermediate parts having become ossified.

In front of the level of the solum nasi two long and parallel bars extend forward and slightly toward the median line, continuing the lateral wall of the capsule forward, and inclosing the nasal sac and Jacobson's organ. In front, the dorsal of these bars joins the now fully developed alary process (al.p.) forming a hood, the anterior cupola, for the nasal sac. The anterior wall of this cupola bends abruptly downward, its ventral margin fusing with the lower of the two bars, while the lateral part of this vertical portion extends laterally as a short broad process, posterior to which is the external naris. There is no floor to the cupola. There is a small foramen

in the ventral surface of the anterior cupola, through which the ramus profundus passes from the capsule to the anterior parts of the snout.

The ethmoid plate is relatively smaller and is connected with the other parts of the capsule only by the solum nasi and the roof of the cupola. Its differences from the earlier stage are of little importance. The cornua are somewhat larger and wider apart. The septum has now a prominent posterior prolongation which is above and entirely free from the ethmoid plate, and which reaches a little farther back than does the ethmoid plate. This bar separates the olfactory nerves of the two sides. The rostral rod is now longer and slenderer than before.

To homologize the parts of the nasal capsule of the Caecilian with that of the Urodeles is almost impossible. In a few points it resembles the Urodelan type, but these are so few that a satisfactory comparison cannot be made. The distinctness of the trabecula and the alisphenoid and their independent chondrification has no parallel among the Urodeles where trabecular crests and trabeculae contribute to form the lateral wall of the cavum cranii. The points of resemblance between the capsules of Amphiuma and Epicrium are as follows: The six-sided ethmoid plate with its processes and angles is strikingly similar. The origin of the septum nasi from the dorsal surface of the ethmoid plate and its subsequent division into antero-lateral processus alares, which form the anterior cupola, possibly indicate a common ancestry. Epicrium has no circumnarial cartilage ring, but in its vaulted tip there is some resemblance to Amblystoma and Salamandra, although these structures do not arise in the same way in both animals. The anterior process of the septum nasi of

Salamandra recalls the rostrum of Epicrium and yet I am inclined to believe that this resemblance is one of convergence rather then of inheritance.

In general the capsules of Amphiuma and Epicrium are similar in the following respects. The absence of olfactory foramina, the shape of the ethmoid plate, the nasal septum and the slight extent to which the nasal capsule is roofed by cartilage structures, cannot be overlooked. The cupola of the capsule may be the result of the burrowing habit and habitat of this blind animal.

Urodelan Comparisons.

Upon the basis of the nasal capsules of several families of Urodeles, this order may be divided into four groups, based upon similarity of larval structures and the progressive method of chondrification. The largest group comprises Cryptobranchus, Spelerpes, Plethodon and Amblystoma. The second includes Salamandra, Triton and Diemictylus, while Amphiuma is placed alone in the third and Necturus forms the fourth group.

This classification is based almost entirely upon similarities of nasal structures during the larval development. In some forms where larval stages could not be secured, adult characters were employed; while in others the early method of chondrification was the only criterion available.

To recognize in the nasal capsules of the Urodeles a complete phylogenetic development or gradual transition from one animal to another is impossible, for many large gaps exist, concerning which evidences of structural relationships are wanting. On the other hand many resemblances in the development of certain structures of the nasal capsules may throw some light upon the interrelationships of this Amphibian order.

I have studied the young of the American species of Cryptobranchus. It would seem as if the capsule of this animal possesses characters that appear most ancestral and which show relationships to both the Urodeles and the Anura. The youngest larva of Cryptobranchus, which I have studied, has a well developed trabecular crest which is not present in the corresponding stages of either Spelerpes or Amblystoma; the development of the crest of Amblystoma being apparently correlated with the development backward of the

ethmoidal column. It would appear that in Cryptobranchus the crest is developed before the column is laid down, while in Amblystoma the column is begun before the crest is developed and the crest only begins to appear when the column has extended back to the cristal region. In the only early available stage of Spelerpes, the crest is developed while but a small part of the column is laid down. I have no material which shows the early stage of the ethmoidal column in Cryptobranchus, but, judging from its relation to the cornu and the complete separation of the columns of either side, Cryptobranchus and Spelerpes are closely related. It is evident in Spelerpes that the columna ethmoidalis arises from a medial margin of the cornu and grows posteriorly along the dorsal medial surface of the nasal sac. My oldest larva does not show the formation of the complete column, but the anterior projection of the dorsal margin of the crista trabecula suggests that the ethmoidal column in Spelerpes may arise from anterior and posterior rudiments. The crista of the earliest Cryptobranchus larva shows no such projection, and yet I am inclined to believe that the ethmoidal column in this form may develop the same way. In the 25 mm. Salamandra larva the beginning of the column is connected to the cornu much as in Cryptobranchus, and yet the early lamina cribosa, appearing in Salamandra prior to any relation to the crista, suggests an independence of the ethmoidal column like that characteristic of Amblystoma. The crista trabeculae is well developed in the 25mm. Salamandra larva, but they do not become connected with the ethmoidal column until the 58 mm. stage, in contrast to the early association of these parts in Cryptobranchus.

The separation of the ethmoidal column and the cornu is complete in Amblystoma. In a 15 mm. larva I have described the presence of

a few cartilage cells lying above the medial margin of the cornu of the left trabecula. This is the first appearance of the ethmoidal column. The fact that I have observed these cells appearing first on only one side has no special significance; but in the independent chondrification and the complete development of the ethmoidal column from in front backwards, prior to any association with the trabeculae, Amblystoma differs from any other Urodele.

The trabecular crests which appear so early in Cryptobranchus are retarded in Amblystoma, and do no appear until both ethmoidal column and ethmoid plate have chondrified; so that the 19 mm. larva possesses an ethmoid plate and cornu trabeculae already well developed, while the columna ethmoidalis, entirely separate from all other structures, extends along the medial margin of the nasal organ. In my youngest larva of Amphiuma there is no evidence of an ethmoidal column in the anterior parts of the capsule, but posteriorly the trabecular crest is already well developed and from its anterior end a small rod passes anteriorly and laterally around the nasal organ. This is the beginning of the lamina cribosa and, in a later stage, the ethmoidal column has been formed by a growth forward of parts present in the earlier stage. Accordingly, this method of chondrification of the crest and lamina cribosa recalls Cryptobranchus with which I have associated Amphiuma.

In all Urodeles studied the ethmoid plate is formed by the fusion of the trabeculae in the middle line, and in some forms this plate is the only connection between the two nasal capsules. In Necturus and Cryptobranchus the upper surface of the plate is convex, since the reduced nasal septum arises from the median line of the ethmoid plate as a small ridge. In contrast to this convex type of planum ethmoid-

alis, Salamandra and Amblystoma have a concave ethmoid. The size of the plate is variable in the different species, being very small in Cryptobranchus and Spelerpes, somewhat larger in Salamandra and reaching its greatest development in the larvae of Amblystoma, where the fused septum nasi and planum ethmoidalis form a thick anterior wall to the cavum cranii. Larvae approaching the end of metamorphosis and adults show a reduction in the size of the ethmoid plate, correlated with the increase in the growth of the accessory parts of the capsule. The ethmoid plates of Triton and Diemictylus are greatly reduced in both larva and adult and are unique in their posterior position in relation to the other capsular structures.

The nasal septum arises in different ways throughout the order. In Cryptobranchus the septum nasi arises from the median line of the dorsal surface of the ethmoid plate. It increases in height and in the larva three months old, it has united to the columns of either side so that a complete wall is formed between the capsules, separating the internasal space from the cavum cranii. Further, in the larvae of Necturus, although there is a slight ridge on the dorsal surface of the ethmoid plate, a complete septum nasi is not developed. The lack of a later stage of Spelerpes does not allow me to determine the origin of the septum nasi in this genus and yet the early column and its relation to the flat ethmoid plate suggests a development of the septum similar to that in Salamandra and Amblystoma.

In the 25mm. Amblystoma larva the medial margins of the ethmoidal columns, just above the anterior margin of the ethmoid plate, have grown toward the middle line and have united to form an ethmoidal bridge or septum nasi which for a while is wholly distinct from the ethmoid plate. Gradually a connection is established between them,

chondrification beginning at the junction of the septum nasi to the column and proceeding toward the median line, completely closing off the internasal space from the brain cavity. The process of chondrification then continues posteriorly until in the 34 mm. larva a solid thick plate has formed, just anterior to the olfactory foramina.

In Salamandra this process varies slightly. Cornu and column are connected in front and then the nasal septum is formed by a growth medially of the two columnae, this taking place in front of the anterior margin of the ethmoid plate, leaving a gap, the fenestra ethmoidalis, between septum and plate. This foramen is only temporary in Salamandra, closing in the later larva, but in Triton cristatus and Diemictylus viridescens, the internasal space and the cavity of the brain case are never separated from each other except by membranous structures. Born ('76) describes the early process of chondrification of the whole capsule in Triton cristatus as a continuous growth of cartilage from the trabeculae. He says nothing of the independent chondrification of parts, so that the septum nasi has probably been formed in a manner similar to that of Salamandra, by a lateral growth of the dorsal margin of the inner wall of the capsule. Because of the continuous development of the cartilage capsule of Triton and the persistance of the fenestra ethmoidalis, together with the greatly reduced septum nasi, I have placed Salamandra close to Triton. In Diemictylus, in which a septum is entirely lacking, there is a further reduction from the condition in Triton. This complete absence of a septum nasi in both larva and adult separates Diemictylus from Triton and Salamandra, yet the many resemblances between the capsules of these animals would indicate a close relationship

between them. In Amphiuma the septum nasi develops from the median line of the planum ethmoidalis as in both Cryptobranchus and Necturus; but the highly specialized septum of Amphiuma with its relation to the ethmoidal columns preclude exact homologies here.

The antorbital process is present in all Urodeles and in all except Cryptobranchus, it develops from the ventral margins of the trabecula just back of the choana. This process is directed anteriorly and although connected with the cranial wall back of the nasal region it becomes definitely connected with the capsular structures. In all of the adults and in some of the late larval forms, that I have studied, the connection between the antorbital process and the lateral margin of the lamina cribosa has been established, forming a large orbito-nasal foramen through which the nerves of the nasal region enter the capsule. In Necturus the antorbital process, although its tip reaches nearly to the fenestrated capsule, the two never unite.

Gaupp ('91,'93) held that the antorbital process of Urodeles is homologous with the pterygo-quadrate arch of the Anura. If we regard Cryptobranchus as ancestral, or at least more primitive, a conclusion I believe both the nasal capsule and olfactory organs justify, then the relations and development of the antorbital process in this animal may throw some light upon the homology of these structures. In the youngest larva studied, in which the trabecular crests are already well developed, there is no appearance of an antorbital process. But slightly posterior to the place where it should develop, there are procartilage cells near the lateral ventral margin of the trabecula. Posteriorly these cells pass into a cartilage rod which is the anterior end of the pterygoid process ex-

tending back to the quadrate.It is very evident that this cartilage bar is the anterior end of the pterygoid process which is growing forward into the nasal region. In the later stage it unites to the trabecula in the region where the antorbital process occurs in the Anura and the other vertebrates, just posterior to the choana. In this stage there is no extension forward of this bar beyond its junction with the trabecula, but in the two months larva a short process extends forward into the nasal region, just as does the antorbital process in other Urodeles. I have no stage later than the three months larva to determine whether a connection is established between the lamina cribosa and the antorbital process. Nor can I say at what time a process of resorption takes place in the pterygoid bar to separate this structure from the functional antorbital process as it occurs in the adult of this and other Urodeles, Ranodon excepted.

Regarding Cryptobranchus as ancestral or primitive, then the Urodelan antorbital process is in reality composed of the anterior end of the pterygoid plus an anterior extension which secondarily becomes associated with the nasal region. In the Anura the pterygoid bar extends forward from the quadrate and unites to the trabecula in the same way as in the larval Cryptobranchus; an inheritance from a common ancestor. The relation of these structures in Cryptobranchus and the Anuran capsules tend to support the original conclusion of Gaupp that the basal part of the antorbital process of Urodeles and the "palatine cartilage" of the Anura are homologous structures. But the anterior portion of the process is a structure not a part of the original pterygo-quadrate arch.

Winslow ('98) has described in his second stage of Epicrium,

two isolated cartilages in front of the anterior end of the pterygoid process of the quadrate, which may well be parts of a former pterygoid extending well towards the capsular region. In addition he figures and describes an antorbital process, the relationships of which are not clear, but apparently it is not the homologue of the antorbital of other Urodeles. My reconstructions differ from his in several respects.

Wiedersheim ('77) has described the nasal capsule of Ranodon and has figured the relation of the antorbital process to the pterygoid much as it occurs in Cryptobranchus, as has been referred to on a previous page. This as well as other structures suggest a close relationship of these genera. An older larva of Spelerpes also described by Wiedersheim, possesses a caudal extension of the antorbital process which he calls the maxillary process. It does not join the posterior pterygoid process of the quadrate, and yet the proximity of the two is suggestive of an earlier union, a further evidence of a close relationship of Spelerpes to Cryptobranchus.

A strong pterygoid process extends forward from the quadrate in several Urodeles, as is shown in the figures of Parker ('75, '76) and Wiedersheim ('77), but it does not appear in the larvae which I have of Triton, although present in Diemictylus larvae, but present in the adult. In the youngest known stage of Amphiuma (Winslow,'98 fig. 18), there is no pterygoid process, although the epipterygoid is present as in all Urodeles. In a later stage, the process is well developed, persisting as cartilage in the adult. In many Urodeles, the antorbital process is developed, but, as stated above, no where except in Cryptobranchus and Ranodon is there any connection between pterygoid and antorbital. I hesitate to base any

statement of relationships on the relative extent of development of this structure. Further it is apart from my main subject and, in any case could only be invoked as affording confirmatory evidence.

The complexity of the nasal capsule of Amphiuma renders it difficult to draw definite homologies with other Urodeles; and yet in the early method of chondrification there are some resemblances to Cryptobranchus. The early development of the crista trabecula, ethmoidal column and the septum nasi are identical in these genera. If the lamina cribosa which is associated with the cornu trabecula and the columna ethmoidalis be homologized with that structure in Cryptobranchus, then Amphiuma can be regarded as related to Cryptobranchus, and the more anterior structures secondarily acquired.

Salamandra differs from Amblystoma primarily in the size of the septum nasi and the persistence of the fenestra ethmoidalis as well as the method of origin of the ethmoidal columns. Salamandra has retained one larval character of Cryptobranchus in the presence of a caudal process from the ethmoid plate, but this genus more closely resembles Spelerpes in the origin of the columna ethmoidalis. On the other hand the length of the ethmoid plate is an Amblystomal character, while the absence of the strong septum nasi and ethmoid plate in Salamandra preclude close relationships, but it would seem that Salamandra and Amblystoma have descended from some common ancestor.

Triton and Diemictylus are far removed from the larger group just discussed, and are probably related to it through Salamandra. The complete development of the inner walls of the capsule, with a deep internasal space between them, and the fact that the nasal organs lie entirely in front of the tip of the brain, are characters

not found among the other Urodeles. The fenestra ethmoidalis, between the internasal space and the cavum cranii, which persists so long in the larva of Salamandra is permanent in the adults of Triton and Diemictylus, forming a large fontanelle between the septum and the ethmoid plate. In Diemictylus, the complete loss of the septum nasi converts this fenestra into a gap, only a membranous partition separating the internasal space and the cavum cranii. It would follow that Diemictylus has descended from a Triton-like form, and both genera are related to Salamandra which has developed along a line parallel to that of Amblystoma, and it is through some form like Spelerpes, so far as the nasal capsules are concerned, that this group is connected with Amblystoma by a line running back through an intermediate form like Salamandra.

Necturus and Proteus have usually been regarded as primitive, and united into a group apart from the Urodeles, as the Proteida of Cope ('89). I have been unable to study Proteus, but Necturus possesses a nasal capsule readily compared to that of any other Urodele. Pinkus ('94) has called attention to the similarity of the nasal capsules of Necturus and Protopterus. The fenestration of both capsules is similar and yet the fusion of the parts of the nasal covering to the septum and the ethmoid plate in Protopterus find no counterpart in Necturus. Miss Platt ('97) has described the chondrification of certain structures of the nasal capsule of Necturus, such as the trabecular crests, ethmoidal plate, and columna ethmoidalis. These parts chondrify independently and subsequently unite to each other, with the exception of the ethmoidal column, which never becomes connected to the other structures. I have observed the development of the column which chondrifies

from in front backwards as in Amblystoma. From this rod lateral processes grow out, which become fenestrated to produce the adult capsule. The capsular structures of Necturus are late in developing. In a 25 mm. larva there is only a pair of trab cular rods, and no sign of either ethmoidal column or ethmoid plate. This retardation in the chondrification is explicable on the hypothesis that Necturus is a persistent larva.

Of the early larval forms of all the Urodeles, which I have studied, the nasal capsular structures of Necturus bears the closest resemblance to that of both Spelerpes and Desmognathus. In these larvae the trabeculae are cylindrical and have slight cornual expansions while trabecular crests have not appeared. In the later stage, further resemblance is lost, for Spelerpes has gained true Urodelan characters, while Necturus still possesses larval relations.

As stated above, Cope placed Proteus and Necturus in the Proteida, regarding them as primitive or ancestral forms, connected with the Stegocephala by the presence of an intercalary bone. Kingsbury ('04) rejects Cope's thesis, affirming the absence of the os intercalare in Necturus, and believing that Cope confused this with the posterior process of the opisthotic, and further that the intercalary of the Stegocephala is a membrane bone.

Further evidence that Necturus is not primitive is submitted by Norris ('11). Norris, working upon the cranial nerves of Necturus, concludes that this animal is not primitive. The distribution of the cranial nerves agrees in detail with that of the higher Urodeles, a condition which would not be expected in a primitive

form. Kingsbury has regarded Necturus as a neotenic larva, and would place it near Spelerpes. His conclusion is based largely upon the absence of certain cranial bones, such as the nasals, prefrontals, and maxillaries, which are present in other Urodeles.

Rudimentary nasal capsules are characteristic of the larvae of both Spelerpes and Necturus, although the fenestrated nasal capsule of the latter, is a further development in Necturus. The larvae of Spelerpes frequently retain their larval characters indefinitely, and sometimes do not transform for even two or three years after hatching, having attained at this time a length of 60 mm. The absence of certain bones of the skull may not be proof of larval conditions, but may indicate degeneration.

I am inclined to regard Necturus as a neotenic larva, possibly related to the other Urodeles through a Spelerpes-like ancestor. The retention of the larval characters of the trabeculae and the ethmoid plate can certainly not be regarded as ancestral; nor can degeneration alone explain the present structure of Necturus.

Considerable diversity of opinion has existed regarding the phylogenetic position of the Gymnophiona. Huxley ('78) stated that there was not the slightest indication of any approximation to either the Anura or the Urodeles. On the other hand, Cope ('89) even placed the Caecilians in a family of the Urodeles, regarding them as degenerate and related to the main line through Amphiuma. The Sarasins ('90) have come to regard Amphiuma as a permanent larval form of Gymnophione. Kingsley ('02) has discussed the views of both Cope and the Sarasins and presents conclusive evidence that the Caecilians are to be regarded as distinct from both Urodeles and Anura and placed in a separate order, the Gymnophiona.

The nasal capsules of Epicrium presents little of classificatory value, except that there are practically no resemblances to the characteristic Urodelan capsule. I have not been able to study the early method of chondrification in Ichthyophis, and the earliest stage described by Peter ('98) is a larva in which chondrification is already well advanced. In this stage the trabecular cornua so characteristic of all Urodelan capsules, are absent. The ethmoid plate has formed and the nasal septum arises from its dorsal surface, recalling the origin of that structure in both Cryptobranchus and especially Amphiuma, a condition which may be correlated with the very elongate body, although reasons for the correlation are not evident.

In both Amphiuma and Epicrium, the nasal septum is high; it arises from the anterior half of the dorsal surface of the ethmoid plate and divides into lateral processes which pass over the medial and dorsal sides of the nasal sac to unite with the lateral structures of the capsules. The anterior margin of the ethmoid bears a pair of processes which project anteriorly on either side of the septum, these being in Amphiuma and possibly in the Caecilian, the vestigial cornua. The two bars in the side wall of the capsule of Epicrium do not occur in Amphiuma, and yet the shape of the ethmoid plate together with the origin and the relations of the septum nasi are points of comparison that suggest a possible relationship.

Although there are thus some resemblances between the nasal capsules of Epicrium and Amphiuma, yet the many contrasts between the Caecilian and the typical Urodelan capsules supports the idea of the long separation of the Caecilian from the Urodelan groups.

The burrowing habits of the blind worms have probably caused some degeneration, and although there are some resemblances between the nasal capsules of Amphiuma and Epicrium, I do not believe that Cope's view of the interrelationships can be maintained.

Pipa americana.

The Surinam toad, a representative of the Aglossate Anura, is unique among the Amphibia in its quiescent larval period during which the entire process of metamorphosis takes place; so that the characters of the adult are well laid down before the animal takes up its free existence, a contrast to the long, free larval life of the Phaneroglossal Anura.

As described by Parker('76), and using largely his terminology, the early chondrification of Pipa lacks the large hypophysial fenestra so common in other Amphibian skulls; so that the fusion of the trabeculae into a broad basal plate has completely obliterated this opening, except for an imperfect chondrification in the middle line. The coalesced trabeculae form a broad, slightly emarginate internasal plate which is continuous with the anterior margin of the skull, and from its lateral cephalic margins the "recurrent trabeculae" suddenly bend laterally and passing caudally beneath the nasal sac terminate in rounded projections near the narial lamina. At this stage the recurrent trabeculae are not continuous with the narial laminae, which are the cephalic projections from the ethmo-palatine cartilage and which later form the prepalatine spurs, the probable homologues of the lamina cribosa of the Urodelous capsule.

In the later stage, before the young Pipa has assumed active life, although it has assumed the adult form and is nearly two thirds of an inch long, much of the cartilage of the early stage has been resorbed. The broad trabecular and intertrabecular floor has been reduced to a pair of well developed trabeculae, the crests of which terminate opposite the optic organ.(fig.34,35). In the nasal region

the cartilage structures have been reduced to an ethmoid plate, a median ventral keel and a pair of side wings, the olfactory organs, dorsally and ventrally, being without skeletal coverings, a marked contrast to the protection afforded the sensory structures in the Phaneroglossa described below.

Just anterior to the crests the trabeculae are oval in section, slightly concave on their inner surface to accommodate the forebrain. They parallel each other for a short distance and then, without bending toward the median line they join the broad ethmoid plate which is concave on its dorsal surface, forming a wide trough for the olfactory lobes (fig. 73). The posterior margin of the ethmoid plate (p.e.) is straight with the exception of a slight triangular posterior process similar to that in the larvae of both Cryptobranchus and Salamandra. The anterior lateral angle of the ethmoid plate is continuous with a broad triangular plate, the ethmo-palatine of Parker, the lamina cribosa (l.c.) which sends a triangular process (Parker's prepalatine spur) forward almost to the level of the base of the alinasal cartilage. Posteriorly this plate is continuous with the pterygo-quadrate arch. At the junction of the lamina cribosal cartilage and ethmoid plate the orbito-nasal foramen (f.o.n.) conducts the nasalis internus branch of the fifth nerve into the capsule. A branch of this nerve passes along the dorsal surface of the ethmoid plate, then through the foramen in this plate just lateral to the larger olfactory opening to become associated with the olfactory nerve, which leaves the brain from the ventral surface of the olfactory lobe.

From the median line of its anterior margin, the ethmoid plate gives rise to the median keel or nasal septum which continues forward

to the anterior end of the capsule. Where the septum nasi (s.n.) joins the ethmoid plate it is triangular in cross section and its dorsal margins partially overhang the medial portions of the nasal sacs. Further anterior the septum forms a vertical plate which reaches forward to the end of the capsule. At its tip this plate gives off on either side a plate which bounds the naris on the medial side and above and which passes at its lateral posterior angle into a cartilage bar, the dorsal process of Winslow, (d.p.),(the recurrent trabecula of Parker), although it has no trabecular characters, which runs backwards and slightly outwards to join the ventral process and the ventral side of the lamina cribosa as described below.

A little behind the tip of the septum nasi an alinasal cartilage (an.c.) arises from either side of the trabecula. It extends outwards and forwards, its anterior margin bounding the lateral side of the naris; its dorsal margin is separated by a narrow slit from the anterior end of the dorsal process, while behind it gives off the ventral process (v.p.) which runs obliquely backwards and outwards and joins the dorsal process a little lateral to the choana, the dorsal process bending at right angles to make the union, and then the united structure continues into the ventral surface of the lamina cribosa.

As I interpret Parker's account of the early stage, it would appear that in Pipa this septum nasi is trabecular in origin, the alinasal cartilages being the vestigial cornua. According to Parker there is no connection between the dorsal process and the lamina cribosa either in the early or later stages; but both Winslow ('98) and I find such a connection as described above. In this union of the dorsal process and the lamina cribosa there is a remote

similarity to the fusion of the cornua with the laminae cribosa of the Urodeles.

Bufo americana.

In contrast to the nasal organs of Pipa and Dactylethra, the Phaneroglossa are characterized by a more complex capsule, which completely incloses the sensory structures. Relationships to the Urodelan type of capsule are very remote and it is impossible to establish definite homologies between certain structures of the nasal capsules of these two Amphibian orders.

I have studied a single stage of Bufo, 9 mm. long, just after metamorphosis;and I find that the nasal capsule closely resembles that of the 13 mm. Rana fusca larva, described by Gaupp ('93), while in other respects the whole chondrocranium is more like his 50 mm. stage.

In this stage the nasal capsule is well chondrified(fig. 36.). The alisphenoid cartilages (alis.) are high and the floor of the cavum cranii(c.c.) is well developed, forming a trough for the olfactory lobes, which are completely shut off from the nasal region by a vertical ethmoid plate. This planum ethmoidalis (p.e.) forms the posterior boundary of the nasal capsule, and is pierced by two foramina for the olfactory nerves which leave the brain from its antero-ventral margin, as in Pipa. Laterally the planum ethmoidalis is continued beyond the alisphenoid cartilages, into broad plates which form the side walls of the capsule in the posterior region, the pars plana of Parker ('79). At the junction of pars plana and alisphenoid cartilage, the nerves of the nasal region enter the capsule through the orbito-nasal foramen(f.o.n.). From the middle line of the planum ethmoidalis a strong nasal septum (s.n.) continues forward completely separating the nasal organs of each side and uniting the floor and the roof of the capsule. The nasal tectum(t.n.) nar-

rower than the planum ethmoidalis, extends forward from the dorsal margin of the ethmoid plate to the anterior end of the capsule, nearly covering the dorsal margin of the nasal sacs. Its ventral surface is continuous with the strong nasal septum, while anteriorly it broadens at the junction of the oblique cartilages, described below, and then turns abruptly ventrad to form the anterior wall of the capsule, and then bends backward to form the floor of the superior cavity,(c.s.) in which the anterior end of the nasal sac is situated. This floor or solum anterius extends back, joining the septum at about its middle, to the naso-basalis fenestra. From the anterior lateral margin of this floor the alinasal process (an.p.) extends laterally forming a floor and a lateral wall to the naris. At the junction of the alinasal process and the solum anterius, a short superior prenasal cartilage(s.p.c.) extends downward and ends in the midst of the intermaxillary glands. The vertical anterior wall above this process is pierced by a foramen for the superficialis nerve.

The floor of the capsule proper, the solum nasale(so.na.), is a broad thick plate, equal in width to the nasal tectum and connecting by its dorsal surface with the nasal septum. It extends forward from the ventral margin of the ethmoid plate, supporting the main nasal sac, as far forward as the naso-basalis openings. At its anterior lateral angle, the solum nasale extends anteriorly and laterally to form the floor and anterior wall(paries inferius) of Gaupp's cavum inferius(c.i.). Where this wall bends upward it gives off from its medial margin an inferior prenasal cartilage(i.p.c.). From the posterior lateral angle of the paries inferius a short pro-

cess extends backward and forms the floor of the cavum medium(c.m.), in which a small diverticulum of the nasal sac rests. The lacrimal ducts arise from the eye by two branches, then pass forward over the oblique cartilage, down through a groove where the planum terminale (p.t.) joins the anterior wall, then back over the process just mentioned to open into the dorsal side of the nasal diverticulum.

The lateral wall of the capsule is formed by the oblique cartilage which passes outwards, downwards, and slightly backwards from the middle of the lateral margin of the nasal tectum over the nasal organ. At its ventral end it unites with a triangular process, the planum terminale of Gaupp, itself an anterior continuation of the pars plana, which unites in front with the antero-dorsal wall of the cavum inferius.

Internally, a bar passes in the floor of the capsule forward from the solum nasale to join the solum anterius(s,a.), bounding the large fenestra naso-basalis(fen.n.b.), through which the frontalis branch of the nasalis internus passes to the intermaxillary gland, and separating it from the cavum inferius in which the organ of Jacobson lies. Beneath this bar the cavum inferius opens broadly into the fenestra naso-basalis. The cavum medium is small and inconspicuous, it lies beneath and just outside the planum terminale and is practically, in this animal, a lateral continuation of the cavum inferius. From the anterior margin of the solum anterius, adjacent to the large fenestra naso-basalis, is an elongate inferior prenasal process.

Hyla pickeringii.

I have studied only the capsule of the adult Hyla. Ossification has therefore replaced many cartilage structures in the nasal region by bone. In general the nasal capsule of Hyla resembles somewhat closely that of its Arciferan relative Bufo. The characteristic compactness of the capsule and the reduction in sagittal direction of the anterior parts of the nasal capsule are common to both, although the extent to which resorption of cartilage in the posterior region of the capsule of Hyla has gone, has made the determination of homologies with Bufo less certain.

Ossification in the choanal region has reduced the floor of the capsule to flat cartilage plates which support the caudal parts of the olfactory sacs. These plates, the vestiges of the solum nasale, unite in the middle line at the caudal limit of the septum nasi, while in front the solum continues uninterruptedly forward to the cephalic end of the capsule. The ethmoid plate and a large part of the nasal tectum have been replaced by bone, the posterior region of the tectum being reduced to a rod on either side which lies diagonally across the nasal organs, separated from the oblique cartilage (o.c.) by an elongate fenestra, both being connected by the pars plana. Thus the cartilage structures of the posterior part of the nasal capsule in this adult stage are reduced to a pars plana, a small solum nasale, and a bar, the remnant of the tectum nasale.

The anterior end of the capsule is more complete; the oblique cartilage and the bar which represents the tectum behind, unite with the tectum nasale(t.n.), to form a roof somewhat concave on its upper surface. The anterior wall is nearly vertical, and is pierced on either side for the passage of the superficialis nerve.

The lateral wall is largely formed by the oblique bar which passes behind into the pars plana, and sends downwards from its ventral margin a bar, which I interpret as the planum terminale(p.t.). Behind this terminal plate and the pars plana is a gap, possibly the result of resorption, as no nervous or sensory structures pass through it.

In front of the planum terminale and ventral to the oblique bar is the external naris, the olfactory duct resting upon a short laterally directed alinasal process(an.c.). A posterior extension of this narial fenestra lies below the anterior part of the planum terminale and accommodates the lacrimal duct, which is supported below by a lateral expansion of the planum terminale. The duct after passing this point enters the cavum inferius.

Ventrally, the alinasal cartilage passes into a downwardly directed superior prenasal process(s.p.c.), and a little behind this the planum terminale bends ventrally and then backwards, passing into the solum nasale(so.na.), and forming the anterior and lateral walls of the cavum medium.

The ventral surface of the solum nasale calls for little description. At its posterior lateral angle it sends a process backward as in Bufo, while medial to the floor of the cavum medium is a rather long inferior prenasal process(i.p.c.). The fenestra naso-basalis is much smaller than in Bufo and it opens almost directly downwards. Internally the bar, which in Bufo separates the fenestra naso-basalis from the cavum inferius is incomplete in Hyla, being represented by a short backwardly directed process from the floor of the cavum superius.

Rana viridescens.

The nasal capsules of the Arcifera and the Firmisternia are essentially alike and although I have not had a complete series of stages showing the chondrification of the nasal capsule in Rana, yet the work of Gaupp ('93) has made it possible for me to study the method of growth of the nasal capsule in connection with the two stages that I have.

I have studied the chondrification of the nasal capsule of a larva 28 mm. long, total length, in which the characteristic Anuran structures are just beginning to chondrify. In this stage the nasal capsule (fig. 40.) is restricted to an elongate internasal plate (i.p.) with its cephalic prolongations of the trabeculae which extend forward to the labial cartilages (la.c.). At the junction of the internasal plate and the muscularis process of the quadrate (m.p.q.) a dorsal process arises which is to become the side wall of the capsule. This process is the 'Ethmoidalpfeiler' of Gaupp which differs from the ethmoidal column of Amblystoma where chondrification progresses toward the trabeculae rather than from it. At its summit this dorsal process sends a horizontal plate toward the median line, the plates of the two sides fusing to form the ethmoid plate (p.e.). This does not differ greatly from the formation of the ethmoidal bridge in the 25 mm. Amblystoma larva, a large fenestra ethmoidalis (fen.eth.) persisting for some time connecting the nasal region with the cravum cranii. This opening is only temporary. Chondrification extends from the beginning of the ethmoid plate ventrally to the internasal plate forming the vertical planum ethmoidalis, which in the later stages except for the olfactory foramina, completely separates the nasal structures from the olfactory lobes.

From the lateral dorsal margin of the 'Ethmoidalpfeiler', upon a level with the dorsal surface of the ethmoid plate, a small process extends laterally toward the muscularis process of the quadrate. This process which is pierced by an orbito-nasal foramen (f.o.n.) for the nasalis internus nerve is the beginning of the ethmo-palatine of the Anura; it may be the homologue of the Urodelan antorbital process which has been forced dorsally by the connection of the muscularis process of the quadrate with the side of the trabecula. This is the more probable as in a later stage, with the posterior migration of the quadrate, this palatal process has extended ventrally to the side of the trabecula.

Just in front of the choana a longitudinal constriction partially divides the nasal sac into two chambers, one medial and dorsal lying on the trabecula, the other lateral and more ventral (it is the beginning of Jacobson's organ) which lies to the side of and to some extent ventral to the trabecula.

The olfactory nerves of the two sides now pass through the large opening between the internasal plate and the roof of the planum ethmoidalis. They pass over the margin of the internasal plate just anterior to the'Ethmoidalpfeiler' to connect with the nasal sac. Later, a chondrification medial to this nerve will give rise to the complete planum ethmoidalis and will result in the limitation of the foramen around the olfactory nerve, while the lateral process will give rise to the pars plana of the later stage. That part of the internasal plate in front of the planum ethmoidalis will, in later stages become the solum nasale.

The trabeculae widen as they extend forward, and just in front of the level of the naris they bend abruptly downward, approaching

the inferior labial cartilage. This vertical portion is apparently what Gaupp calls the superior labial cartilage and which he figures as a discrete element in both earlier and later stages. In my material I am unable to find any line of demarcation between the trabecula and superior labial cartilage.

I have not had any material between the larval stage just described and a young frog soon after metamorphosis, but it is easy to see that the changes that have been undergone are about as follows, this account agreeing substantially with that of Gaupp.

As in the young Bufo, the tadpole of Rana approaching the end of metamorphosis, according to Gaupp, shows a decided reduction in the sagittal direction of the anterior nasal cartilages, occasioned by a partial resorption of structures of the younger stages, so that the definitive nasal capsule is formed by developments from the posterior half of each trabecular rod, while the anterior half and labial cartilages are entirely resorbed. The frame work of the capsule of this stage is formed partly from structures already chondrified at an earlier stage and partly from independent chondrifications.

Subsequent to the closure of the fenestra ethmoidalis by the formation of the complete ethmoid plate, the septum nasi extends anteriorly from the median line of the planum ethmoidalis. It separates the nasal organs of the two sides and unites ventrally to the solum nasale and dorsally to the nasal tectum which has grown forward from the anterior dorsal margin of the ethmoid plate. Chondrification of the septum nasi and the nasal tectum thus takes place from behind forwards. The side walls of the capsule and the planum terminale, as well as the oblique cartilages chondrify independently and unite to the nasal tectum and the solum nasale, bounding the

lateral gaps in the capsule.

In the anterior part of the capsule the greatest modification takes place. The loss of the labial cartilages and the anterior parts of the trabeculae, results in a fore and aft condensation of parts. The anterior half of the internasal plate becomes the solum nasale, while in front the trabeculae give rise to the alinasal cartilages which support the anterior parts of the nasal sacs. The large naso-basalis fenestra between the solum nasale and the alinasal cartilage opens from the main cavity of the capsule to the anterior space filled with the large intermaxillary gland. From the base of the alinasal cartilage a small superior pre-nasal process extends medially and ventrally over the large opening above described, while just beneath this fenestra the inferior pre-nasal process extends ventrally forward into the intermaxillary glands. The nasal tectum, just anterior to its connection with the oblique cartilages, is pierced by a pair of small foramina for the exit of the nasalis internus nerves.

In this stage the articulation of the lower jaw has moved back so that the deeply curved muscularis process of the quadrate is more posterior than earlier. The small ethmo-palatine of the early stage has broadened and passes over the posterior parts of the nasal sac, and then divides into two processes. Of these, an anterior maxillary process extends forward to the level of the posterior end of the oblique cartilage, while the posterior is the direct continuation of the pterygoid arch. This relation is similar to that in Bufo, although I have not seen any anterior maxillary process in the capsule of the latter form.

In a young adult of Rana viridescens, there has been a reduction in the depth of the nasal capsule by one half, although the relative breadth and length are approximately unchanged. Chondrification has extended back over the anterior part of the forebrain, reducing the large dorsal fontanelle and enclosing the olfactory lobes within the cavum cranii. Olfactory foramina open from the antero-lateral angle of the brain cavity and enter the nasal region just beneath the opening of the nasalis internus nerve which enters the capsule just lateral to the cranial wall. Just anterior to the orbito-nasal foramen the broad nasal tectum continues laterally into the pars plana which covers the choanal region just as in the earlier stage.

The nasal sac is completely covered dorsally by the lateral parts of the nasal tectum, which extends forward from the pterygoid, its width in front being about half that in the choanal region. At about the middle of the tectum, the oblique cartilage bar extends backwards and slightly outwards, ending at the level of the tip of the anterior maxillary process, the anterior continuation of the pars plana. On the ventral side the oblique cartilage is connected by a narrow bar to the base of the alinasal cartilage, the olfactory duct from the external naris passing between them. The solum nasale is much as in the earlier stage but the foramen naso-basalis is reduced to a small opening for the ramus frontalis between the superior and inferior prenasal cartilages which bear the same relation to the capsular structures as before. Between the bases of superior and inferior prenasal processes is a short, stout, process, directed downward. This is the crista subnasalis of Gaupp, the morphology of which is not certain.

Anuran Comparisons.

Upon the basis of the nasal capsule, the Anura are readily separated into two groups, the first includes Pipa, while Bufo, Hyla and Rana belong to the second. This distinction is in keeping with the suborders Aglossa and Phaneroglossa of the generally accepted classification. The capsule of Pipa with its large vacuities is very different from the compact one of Bufo, and at first sight bears a closer resemblance to the typical Urodelan capsule.

There are some marked resemblances between the capsules of these Anuran groups. In both, the pterygo-quadrate arch is complete and joins the cranial wall at the posterior region of the nasal capsule. In Pipa, the pars plana(in part, a portion of the pterygoid) fuses to the entire height of the trabecula, while in Bufo and adult Rana, where the trabecular crest is high, the pars plana has also extended dorsally. In the tadpole of Rana, the attachment to the rudimentary pars plana is to the dorsal part of the crista, this position being probably the result of the attachment of the muscularis process of the quadrate to the trabecula. In all Anura the orbito-nasal foramen pierces the capsule where the pterygoid unites to the trabecula.

Anterior to the junction of the pterygoid to the cranial wall, a process extends anteriorly, partially covering the nasal organs. This is the ethmo-palatine of Parker or the planum terminale of Gaupp. Further, this process gives rise to two bars which bear similar relations to the nasal organs throughout the order. Winslow calls these bars, the ventral and dorsal processes, and they may be readily compared to the oblique cartilage and the solum anterius of both Bufo and Rana, although they are much shorter in the latter forms. In both Pipa and Bufo, the oblique cartilage(the dorsal process in Pipa)

passes dorsally and anteriorly over the main nasal sac to connect with the nasal tectum or lateral expansion of the septum nasi; while the ventral process passes beneath the organ of Jacobson to connect with the alinasal process which supports the anterior end of the nasal sac. The ventral process is the recurrent trabecula of Parker which develops from the internasal plate much as the cornu trabeculae of the Urodeles, so that the solum anterius of Bufo may be the homologue of the Urodelan cornu.

In my last stage of Rana, the planum terminale of Gaupp's younger stage, becomes the anterior maxillary process. It has now separated from the oblique cartilage which terminates bluntly near the lateral margin of the tectum. Further, the ventral process is not connected with the more posterior structures, but persists as a small cartilage just ventral to the superior prenasal process, and is now termed the crista subnasalis.

Superior and inferior prenasal cartilages as such are not present in Pipa, and yet the free tip of the alinasal cartilage which is separated from the anterior end of the dorsal process by a crescent-shaped groove(naris), may be the homologue of a superior prenasal process which is directed ventrally in Bufo. Further, it does not violate probability to assume that the pre-palatine spur (Parker) in Pipa may be the homologue of the inferior prenasal cartilage of the Phaneroglossa.

The nasal tectum and solum nasale are evidently an additional growth in the Phaneroglossa. In Pipa there is a slight evidence of a tectum in the posterior parts and since the tectum nasale of Rana develops anteriorly from the ethmoid plate, it is possible that the lateral expansions from the dorsal margin of the septum nasi in Pipa

may be the beginning of a capsular roof.

The planum ethmoidalis in Pipa is horizontal, and as in Urodeles very slightly concave dorsally for the olfactory lobes. In the Phaneroglossa, the ethmoid plate of authors, is a vertical partition completely separating the nasal region from the cavum cranii. It is pierced by the olfactory nerves which leave the brain from its anterior margin in Bufo and Rana, but more ventrally in Pipa. From its lateral margin, the ethmoid plate unites with the pars plana, which in all Anura has fused to the pterygoquadrate arch.

Although the nasal capsules of the Aglossa appear at first sight very different from those of the Phaneroglossa, yet many homologies exist. The pterygoquadrate arch, planum terminale, oblique cartilage solum anterius and alinasal process are common to all Anura; but the complete nasal tectum and solum nasale are additional characters of the Phaneroglossa.

Discussion.

The cartilaginous nasal capsule of the Amphibia must have been derived from that of some lower vertebrate, be it Dipnoan or be it Crossopterygian, and that in turn from the Elasmobranch. So far as our knowledge goes, the Elasmobranch capsule is a continuous cartilaginous structure with no gaps or openings except that for the naris and the small foramina for the passage of nerves. The Amphibian capsule, on the other hand, has interruptions in its walls. Some of these are due to the fact that in the adult, bones appear in the nasal region and thus do away with the necessity of the persistence of protecting cartilages in certain places. Some are caused by the development of a complete olfactory duct with its choana in addition to the naris.

Within the class of Amphibia there are many differences between the capsules, caused by differences in the size and shapes of the covering bones, by the changes in development and shape of the organ of Jacobson, the modifications of the lacrimal duct, as well as by the differences in the size and shape of the olfactory sac. It follows therefore that in the history of the Amphibian capsule two stages should be recognized, one a progressive process in which the capsule is built up, a repetition of the ancestral (piscine) history; the second in which this capsule is reduced and changed into the definitive form.

In following these two stages we are hampered in our conclusions by the fact that we have no accurate and detailed account of the development of the capsule in any fish and especially in those groups universally recognized as ancestral. Neither Parker nor Sewertzow give any details of the development of the Elasmobranch capsule

which can be used in this connection. [illegible] in this laboratory of the development of the capsule in Acanthias only go far enough to show that it consists, when it first is recognizable, of a rudimentary floor and an even more incomplete roof, and that these arise independently of the trabeculae or other cranial elements.

The foregoing studies show that in those forms where the development has been followed with any detail from one stage to another that there is first a progressive development, apparently tending toward the formation of a complete capsule like that of the adult Elasmobranch. Then alterations occur, largely degenerative in character which result in the partial reduction of floor and roof. These progressive changes are well exemplified in Necturus where, even in the adult, the capsule is more nearly entire than in any other genus, a condition which can be explained on the supposition that Necturus is to be regarded, not as more primitive than other genera of Urodeles, but as a permanent larva, a view which has had considerable support in recent years.

In Amblystoma, as detailed in the foregoing pages, this history is carried further. There is first a progressive development tending toward a complete capsule, but never approaching completeness as nearly as does Necturus. Then comes a resorption of parts and a modification of those which persist (Fig. 10.), resulting in large vacuities in floor and roof of the capsule. These steps are detailed above and the final result is an envelope for the olfactory organ in which parts are recognizable [illegible] with those of the capsules of the [illegible].

In the history of the capsules in all of the Amphibia the following parts are concerned. The two trabeculae are united in the

'ethmoid' region by what Gaupp and others have called an internasal plate. This lies below the tip of the brain and is the 'ethmoid plate' of Winslow and of the foregoing description of the Urodele capsule. In front of this internasal plate the trabeculae continue, as the trabecular cornua, to the tip of the olfactory organ. In several Urodeles (the history has not been followed in the Anura with sufficient detail to say whether the same holds for them) a bar of cartilage, the columna ethmoidalis, arises on the upper medial side of the olfactory sac and lies parallel to the (lower) trabecula. By lateral growth this extends over the dorsal surface of the nasal sac, forming the lamina cribosa of Winslow and Terry. Although I have used this name it is hardly necessary to say that it cannot be homologous with the structure bearing the same name in the Mammals, as it lies wholly dorsal to the olfactory nerve. Tectum nasalis might be a better name for it, or even ectethmoidal cartilage.

In many forms, both Urodele and Anuran, the columnae of the two sides are connected by a plate which roofs the fenestra ethmoidalis. This may be connected to the floor or internasal cartilage by a vertical septum nasi, thus closing the fenestra ethmoidalis. This roof and septum form the plate in the Anura which Gaupp has called the planum ethmoidalis.

The last special element entering into the formation of the capsule is the antorbital process which needs a somewhat longer discussion. In the Urodeles a process is given off from the lateral side of each trabecula; it extends forward and forms a part of the lateral wall and floor of the capsule. This has almost universally been called the antorbital process. The larva of Cryptobranchus shows what it really is. In my second stage of this animal the

pterygoquadrate bar extends forward from the hinge of the lower jaw and joins the trabecula at the same point from which the antorbital projects in other Urodeles. In Ranodon, judging from Wiedersheim's figures ('76)(fig.69) there is a similar connection of the pterygo-quadrate with the anterior part of the skull. Elsewhere in all described Urodeles, so far as I have been able to discover, there is only an extension of a pterygoid process forward from the quadrate towards the capsular region, and even in the adult Cryptobranchus (and this holds also for the Japanese species as figured by Parker) the connection between the pterygoid and the structures further forward is lost.

In all of the Anura, on the other hand, the pterygoid cartilage is connected through life with the nasal capsule. In this respect Ranodon and to a less degree Cryptobranchus approach the Anura more closely than any of the other Urodeles. It is usual to regard this arch as the homologue of the upper jaw of the Elasmobranchs which, with the development of the Osseous upper jaw of the Teleostomes and higher groups, has lost its original function as a part of the feeding apparatus and has fused with the side of the cranium, its distal portion dropping out in the process. It may be remarked parenthetically that the name palato-quadrate commonly given this arch is decidedly a misnomer, as it contains no palatal element and no part of the palatine bone is developed from it.

In no Elasmobranch is there any extension of the pterygoquadrate as a distinct process beyond the curve of the arch of the upper jaw. On the other hand, in all of the Amphibia with a few exceptions there is such a forwardly directed process, the antorbital process already referred to. It would then apparently follow that the

antorbital process of the Urodele is in its basal part, the anterior end of the pterygoquadrate, while its anterior portion is a new formation. That this interpretation is correct is supported by all of the Anura that I have studied.

In my earlier stages of Salamandra (in which there is no connection at any stage between the tip of the pterygoid process and the structures farther forward) the antorbital process is developed and extends forward beneath the nasal capsule, but as yet it is unconnected distally with any other cartilage. Just dorsal to the base of the process both the ophthalmic profundus and superficialis nerves pass forward into the capsular region. Thus the antorbital is ventral to these nerves. In the oldest stage which I have of this genus the roof of the capsule (lamina [illegible]) has extended back so that its posterior margin overlies the [illegible] antorbital while between the lamina and the antorbital there is a very large gap. In other genera, both Urodele and Anuran, the same nerves pass through a small foramen in the region which, in the Anura, is the lateral part of Gaupp's pars plana. Clearly it follows that this part of the plana is a composite of a ventral antorbital and the roof of the capsule.

In Pipa, Bufo and Rana the pterygoid joins the side of the anterior part of the cranium, this distal portion being nearly at right angles with the axis of the skull. At the anterior side, at the bend of the pterygoid a process extends forward, forming the postero-lateral wall of the olfactory structures. This is the anterior maxillary process of Gaupp, the antero-lateral angle of the ethmo-palatine of Parker. In Pipa, Bufo, and (according to Gaupp) in Rana about the time of the end of metamorphosis, this process,

which can be no other than the end of the antorbital, is joined, either in front (Rana, Bufo) or on its ventral surface (Pipa) by the posterior end of the oblique cartilage, the region of the junction forming a plate which Gaupp has called by the rather inappropriate name of planum terminale, a part of the external wall of the capsule.

In front this planum terminale fuses with another bar, the ventral process of Winslow, the recurrent trabecula of Parker. This bar extends forward to the tip of the snout, giving off the alinasal process from its upper anterior surface while in front it bears the superior prenasal process like a spur. Both the oblique cartilage and this ventral bar are very short in Bufo, their length and slenderness progressing in Pipa. I have nothing decisive as to my belief that either the alinasal process or the ventral bar are to be regarded as a derivative of the cornu trabeculae.

Comparisons between Urodela and Anura.

The grouping of the recent Amphibia into three orders, by Muller ('32), the Gymnophiona, Urodela, and Anura is borne out by a study of the nasal capsules; and although homologies can be drawn between the structures, yet the capsules of these three orders are considerably different.

Among the Urodeles, with one or two exceptions, all larvae develop a compact nasal capsule well enclosing the nasal structures; but in the adult, as shown by both Plethodon and Amblystoma (fig 28,and10) and according to Born in the adult Triton, large vacuities occur in the roof and floor of the capsule. On the other hand the Anura possess no such regressive development. In Bufo and Rana there is a progressive chondrification which results in a compact nasal capsule of the adult devoid of any large vacuities, such as occur in the Urodeles. In other words, the Anura have retained the ancestral piscine character even into the adult stage; while the Urodeles, only in the larval period, reveal that ancestral condition. The Gymnophione is neither Urodelan nor Anuran in this respect. In both of my stages of Epicrium,(and in this I agree with Peter) the nasal capsule has several large gaps exposing the sensory structures upon all sides. In this respect, the Gymnophiona resemble the larvae of the Urodeles and more especially Amphiuma in which the nasal organs are greatly exposed, even in my oldest stage.

In both Urodeles and Anura, the development of the capsule up to a certain point is identical. In both, the trabeculae fuse in the median line to form the internasal or ethmoid plate, and then continue anterior to it as the cornua. Also, the ethmoidal columns develop

in connection with this median plate, and by medial growths form the septum nasi. The further development of the Urodelan capsule is a growth of structures already formed; while in Rana, Gaupp has described several independent chondrifications. According to Parker, the ventral process in Pipa is the recurrent trabecula or the cornu trabeculae of Urodeles; so that the solum anterius of Bufo, with which we have homologized the ventral process in Pipa, may be compared to the Urodelan cornu trabecula.

In the Gymnophiona, I have no evidence of an ethmoidal column, neither does the development of the capsule agree with that of the Urodele or Anuran. In the presence of dorsal and ventral trabecular bars, they differ from any other Amphibian, a further evidence that this order must be widely removed from the other groups.

As stated above, all Anura have retained the primitive condition of the pterygoquadrate arch. With the exception of Ranodon and the larval Cryptobranchus, the pterygoquadrate bar in the Urodeles does not reach the nasal region, although in Amphiuma, and some others it closely approaches it. At the place in the Anura, where the pterygoid process joins the trabecula, all Urodeles have an antorbital process, which, as shown by Cryptobranchus, is partially pterygoidal in character. The anterior part of the antorbital process is an additional growth, and is the probable homologue of the Anuran planum terminale or anterior maxillary process. The lamina cribosa of Urodeles is the pars plana of Anura, and both arise by a lateral growth of the ethmoidal column. This homology appears the more exact when we consider that the nerves of the nasal region enter the capsules of both groups through an orbito-nasal foramen which lies be-

tween the antorbital(pterygoid) and lamina cribosa(pars plana).

In Epicrium, the forward extension of the pterygoid reaches a condition almost Anuran. There is no functional antorbital process but in its stead is a small bar of cartilage lying parallel to the ventral trabecula. Just posterior to this bar is the anterior end of the pterygoid process, and I am inclined to believe that these structures are in the process of resorption, and are gradually departing from ancestral conditions.

Gymnophiona and Urodela have neither a nasal tectum nor a solum nasale, so that in the adult stages the sensory organs rest upon membranous structures. On the other hand, the Phaneroglossal capsule has a well chondrified roof and floor, and adequate protection for the nasal sacs.

The relation of the central nervous system to the nasal organs is quite different in these groups. Among the Urodela, and especially the larval stages, the brain extends well forward between the olfactory organs and lies lateral to the posterior three fourths of the nasal sac. In the adult Urodeles, with the development of the sensory parts, the forebrain lies lateral to the choanal region only. On the other hand, in the Anura, cartilage completely separate the sensory parts from the forebrain, which lies entirely posterior to the nasal sacs.

Classification.

The earliest classification of Amphibia did not include extinct with recent forms, largely because of the uncertainty of the systematic position of the fossils, which were regarded by some as reptiles. It was not until 1854 that Vogt stated that Archeosaurus and all Labyrinthodonts are Amphibians, and not reptiles. Both Owen ('60) and Haeckel ('66) were among the first to propose a classification to include both extinct and recent Amphibia.

Since these earlier days most zoologists divide the class into four orders: the Anura, Urodela, Gymnophiona, and Stegocephala. There have been few variations in the subdivisions in the Anura and the Gymnophiona, but with regard to the Urodeles ideas have differed greatly. Some would recognize only Salamandrina and Ichthyoidia, while more commonly the tendency has been to subdivide the group into Perennibranchs, Derotremes and Salamandrina, accordingly as external gills persist through life, as gill clefts remain permanently open or, in Salamandrina, as the animals undergo a complete metamorphosis, losing external gills and gill clefts.

Strauch ('70) divided the Urodeles into two suborders, the Salamandrida and the Iththyoidea. The bases of his classification were the presence or absence of eyes and eyelids, the arrangement of the palatal teeth and the permanence of gills and gill clefts.

The Salamandrida were subdivided into two groups according to the arrangement of the palatal teeth. Those Urodeles in which these teeth formed diverging rows upon the inner margin of the palatine were grouped into the Mecodonta; while the Lechriodonta included those animals in which the palatal teeth form converging rows along the

posterior margin of the palatine.

The Mecodonta embraces six genera, of which Salamandra, Triton and Diemictylus include those species I have studied; while in the Lechriodonta are thirteen genera represented in this study by Amblystoma, Plethodon and Spelerpes.

The Ichthyoidea are divided into two groups, the Cryptobranchiata and the Phanerobranchiata, according to the persistence of gill clefts or gills. Cryptobranchus, Menopoma, and Amphiuma belong to the first group; while Necturus, Proteus and Siren are included in the second.

The nasal capsules, would support a classification of the Urodeles similar to that of Strauch. In the foregoing pages, I have included Spelerpes, Plethodon and Amblystoma(part of the Lechriodonta of Strauch) in a group descended from the primitive Cryptobranchus; while Salamandra, Triton and Diemictylus (the Mecodonta of Strauch) are included in a group connected with the main line of Urodeles through some form like Spelerpes. I have regarded Cryptobranchus as primitive, and Amphiuma as closely related to it, although not in the main line of descent. Strauch has grouped Necturus and Proteus as the Phanerobranchiata, and more distantly related to Cryptobranchus; while I have regarded Necturus as a permanent larva of some Spelerpes-like form. I have not studied Proteus, but have placed Necturus in a separate group in keeping with the later Perennibranchiata classification.

Accordingly, on the basis of the nasal capsules, I would adhere to the classification of Urodeles into three suborders, the Perennibranchiata, Derotrema, and Salamandrina. The Salamandrina may be divided into two groups, and, following Strauch, the terms Mecodonta

and Lechriodonta may be retained.

Cope('85) misled by a supposed ethmoid bone in Amphiuma placed the Gymnophiona into a family of the Urodela; in which he was later supported by the Sarasins('90). Kingsley('02) definitely determined the position of the Caecilians, which are now regarded as a distinct order and which probably separated from the other Amphibia back in the early Carboniferous period. The nasal capsule of Epicrium fully bears out this conclusion.

The Anuran capsules are readily separated into two groups which agree with the established classification into the suborders Aglossa and Phaneroglossa. Cope's subdivision of the latter into Arcifera and Firmisternia is not so readily recognized in the nasal capsules of my material, although there are more resemblances between the capsules of Bufo and Hyla, than of either with that of Rana.

Amphibian Ancestry.

The Amphibians appear, as Stegocephals, in the Carboniferous period, and although at first they are considerably diversified, there is not known a single trace of any Tetrapodous vertebrate in the Devonian with the sole exception of a single footprint from Pennsylvania. In the Devonian and somewhat earlier fishes belonging both to the Dipnoi and to the Crossopterygian ganoids occur and both of these piscine groups have been invoked by various zoologists as the ancestors of the Amphibia, possibly the tendency of the evidence at present favoring the Crossopterygians.

All of the amphibians of the carboniferous, with the possible exception of Pelion, were caudate. Moodie, the latest to study these ancient forms, is inclined to regard Micrerpeton, a small Salamandra-like form, as representing the ancestors of the modern groups with Necturus as an annectant genus. He bases this conclusion upon the resemblances of the skull, the form of vertebrae and ribs, the peculiarities of the lateral line system, and the presence in both of "ventral scutellations", a view which closely resembles the earlier ideas of Cope.

But it would seem as if Moodie was leaning upon a weak reed in invoking ventral scutellations as an argument, no matter what view one may take with regard to the other points of resemblance. It is well known that many of the Stegocephals had ventral scutes, plates or bars upon the ventral surface of the body, but the universal view is that these structures were purely dermal, belonging like scales of fishes, to the skin. Moodie cites Wilder as stating that Necturus had small cartilages in the ventral region, and apparently he regards these as the homologues of the ventral armor of Stegoceph-

als. But there are very important differences between the two.

Most students have regarded the gastralia of Sphenodon and the Crocodilia as derivatives from the plates and bars of the Stegocephals. These latter are also suggested as forming the elements from which the clavicles of the higher vertebrates are derived. In Sphenodon, Osawa on the one hand, and Howes and Swinnerton on the other, the gastralia are stated to develop without any cartilage basis, and, with the single exception of Schneider, no one has ascribed any cartilage stage for the gastralia of the alligators and crocodiles. In short, the great bulk of the evidence goes to show that these so-called abdominal ribs are dermal elements without any cartilage stage.

Wilder explicitly states that the cartilages he describes in the ventral surface of Necturus lie in the myocommata; that is, entirely deeper than the skin. He compares them to sternal elements. Hence it would appear that other evidence than these intermuscular cartilages must be brought forward to support his thesis.

According to Moodie, Micrerpeton has well developed nasals, prefrontals and elongate maxillaries, all of which are lacking in Necturus. Now if Necturus is to represent the ancestors of the modern Urodeles in which these same elements are present, we have the difficulty of explaining how these bones disappeared from the line of descent and then were reformed in the later generations,

Cope regarded Necturus as primitive because it possessed what he called an intercalary bone in the skull, an element which he also recognized in the Stegocephals. But Kingsbury('05) says, that at least in Necturus, Cope's intercalary was the caudal extension of the opisthotic.

Nothing is known of the cartilaginous nasal capsules of the Stegocephala so that no comparison can be made between those of Necturus and Micrerpeton. However the complete isolation of the Necturan capsule and its wide separation from that of other Urodeles is certainly one argument against an ancestral position of this Urodele. Furthermore the absence of maxillaries, nasals, and prefrontals in Necturus is one of the arguments of Kingsbury ('05) in regarding Necturus as a permanent larva, a concluson which a study of the nasal capsule suggests.

Moodie ('16, p.24) says, "The condition found in the skull of Cryptobranchus alleghaniensis will represent pretty accurately the condition of most of the Coal Measures Amphibia." Further than this no emphasis is laid upon the primitive condition of Cryptobranchus. However, because of the simplicity of the nasal capsule, the persistance of the pterygoquardate arch, and also because of the manner and time of the ossification of the skull, I am inclined to regard Crytobranchus as more primitive. In the derotrematous condition of the gill clefts, Cryptobranchus and Amphiuma both resemble Stegocephalon conditions.

As a study of the nasal capsules suggests, the Urodeles and Anura are widely separated from each other. Fossil Anura occur in an excellent state of preservation as far back as the Tertiary. Earlier than this all fossil forms are caudate in character with the exception of a single specimen, Pelion lyelli, found in the Carboniferous, which closely resembles recent Salientia. Should Pelion be regarded as a primitive Anuran, then the Urodeles and the Anura have probably separated from the Stegocephalon ancester as far back as the late Devonian or early Carboniferous period.

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Abbreviations Used.

al.p., alary process.

a.m.p., anterior maxillary process.

a.n.c., alinasal cartilage.

a,p., antorbital process.

c., cupola.

c.c., cavum cranii.

c.e., columna ethmoidalis.

ce.p., cephalic process.

ch., choana.

c.i., cavum inferius.

c.m., cavum medium.

c.p., caudal process.

c.r., circumnarial ring.

cr.s., crista subnasalis.

cr.t., crista trabecula.

c.s., cavum superius.

c.t., cornu trabecula.

d.p., dorsal process.

e. ethmoid bone.

e.b., ethmoidal bridge.

e.n., external naris.

e.n.g., external nasal glands.

fen.eth., fenestra ethmoidalis.

fen.i.c., " infra-conchalis.

fen.n., " narina.

fen.n.b., " naso-basalis.

fen. pr. fenestrated process.

f.n.e.,	foramen nasalis externus.
f.n.i.,	foramen nasalis internus.
f.o.,	foramen olfactorius.
f.o.n.,	foramen orbito-nasalis.
fr.,	frontal bone.
f.r.f.,	foramen ramus frontalis.
f.s.,	frontal branch of superficialis.
i.g.,	intermaxillary gland.
i.n.g.,	internal nasal gland.
i.n.s.,	internasal space.
i.p.,	internasal plate.
i.p.c.,	inferior prenasal cartilage.
i.t.n.,	intra-trabecular notch.
j.g.,	Jacobson's glands.
j.o.,	Jacobson's organ.
l.c.,	lamina cribosa.
la.,	labial cartilage.
l.d.,	lacrimal duct.
m.,	maxillary bone.
m.n.i.,	median nasal incisure.
m.n.p.,	median nasal process.
m.p.q.,	muscularis process of the quadrate.
n.,	nasal bone.
n.o.,	nasal organ.
o.c.,	oblique cartilage.
o.l.,	olfactory lobe.
o.n.,	olfactory nerve.
o.n.d.,	dorsal root of olfactory nerve.

o.n.v.,	ventral root of olfactory nerve.
o.o.,	optic organ.
p.,	profundus nerve of the Fifth.
p.e.,	planum ethmoidalis.
p.f.,	prefrontal bone.
p.m.,	premaxillary bone.
p.n.p.,	prenasal process.
p.o.b.,	preorbital band.
p.p.,	pterygoid process.
p.pl.,	pars plana.
ps.,	parasphenoid.
p.t.,	planum terminale.
q.,	quadrate.
q.e.,	quadrato-ethmoidalis process.
r.,	rostrum.
s.a.,	solum anterius.
s.,	superficialis nerve of the Fifth.
s.l.c.,	superior labial cartilage.
s.n.,	septum nasi.
so.n.,	solum nasale.
s.p.c.,	superior prenasal cartilage.
t.,	trabecula.
t.e.,	trabecular extension.
t.n.,	tectum nasale.
t.r.,	trabecular ridge.
v.,	vomer.
v.p.,	ventral process.

Explanation of Plates.

The following listed figures are drawings of wax reconstructions of the nasal capsules of the different animals studied.

Fig.	1 --	Amblystoma punctatum;	11 mm. long,	dorsal view.
"	2 --	" "	; 19 " " ,	" " .
"	3 --	" "	; 25 " " ,	" " .
"	4 --	" "	; 25 " " ,	side view .
"	5 --	" "	; 34 " " ,	dorsal view.
"	6---	" "	; 34 " " ,	ventral " .
"	7 --	" "	; 45 " " ,	dorsal " .
"	8 --	" "	; 45 " " ,	ventral " .
"	9 --	" "	; 55 " " ,	dorsal " .
"	10 --	" "	; at the end of metamorphosis.	
"	11 --	Salamandra maculata	; 25 mm. long,	dorsal view.
"	12 --	" "	; 58 " " ,	" " .
"	13 --	" "	; at the end of metamorphosis.	
"	14 --	Diemictylus viridescens;	58 mm. long,	dorsal view.
"	15 --	" "	; adult stage,	" " .
"	16 --	Triton cristatus;	28 mm. long,	dorsal view.
"	17 --	" "	; 55 " " ,	" " .
"	18 --	Spelerpes bilineatus;	15 mm. long,	dorsal view.
"	19 --	" "	; 37 " " ,	" " .
"	20 --	" "	; 46 " " ,	" " .
"	21 --	" "	; 46 " " ,	side view .
"	22 --	Cryptobranchus alleghaniensis;	two weeks old,	sideview
"	23 --	" "	; two months old,	dorsal view.
"	24 --	" "	; three " " ,	ventral view.

Fig. 25 -- Necturus maculatus; 25 mm. long, dorsal view.

" 26 -- " " ; 30 " " , " " .

" 27 -- " " ; 45 " " , " " .

" 28 -- Plethodon erythronotus; young adult, dorsal view.

" 29 -- Amphiuma means; younger larva, dorsal view.

" 30 -- " " ; older " , ventral " .

" 31 -- " " ; 82 mm. long, dorsal view .

" 32 -- Epicrium glutinosus; younger larva, dorsal view.

" 33 -- " " ; 90 mm. long, " " .

" 34 -- Pipa americana; dorsal view.

" 35 -- " " ; ventral view.

" 36 -- Bufo americana; 9 mm. body length, dorsal view.

" 37 -- " " ; posterior view of anterior half of capsule.

" 38 -- Hyla pickeringii; adult, dorsal view.

" 39 -- " " ; " , side view .

" 40 -- Rana viridescens; 28 mm. total length, dorsal view.

" 85 -- " " ; adult, dorsal view.

" 86 -- " " ; " , side view .

The following listed figures are drawings of sections in the ethmoidal region of the different animals studied.

Fig. 41 -- Section through the anterior part of the nasal organ of Amblystoma punctatum, 13 mm. long.

" 42 -- Section through the middle region of the nasal organ of the same animal.

Fig. 43 -- Section through the choanal region of the 19 mm Amblystoma punctatum.

" 44 -- Section through the anterior part of the 25 mm. Amblystoma punctatum.

" 45 -- Section just anterior to the septum nasi of the 55mm. Amblystoma punctatum.

" 46 -- Section through the septum nasi of the 55 mm. Amblystoma punctatum.

" 47 -- Section through the septum nasi of an Amblystomal larva at the end of metamorphosis.

" 48 -- Section just anterior to the septum nasi of the same animal, through the fenestra infra-conchalis.

" 49 -- Section through the anterior part of the nasal capsule of Salamandra maculata, 25 mm. long.

" 50 -- Section through the choanal region of a 25 mm. Salamandra maculata.

" 51 -- Section through the septum nasi of a 38 mm. Salamandra maculata; passing through the fenestra ethmoidalis

" 52 -- Section through the posterior region of the nasal capsule of Salamandra maculata, at the end of metamorphosis.

" 53 -- Section just anterior to the ethmoid plate of Diemictylus viridescens, 38 mm. long.

" 54 -- Section through the anterior region of the nasal capsules of Diemictylus viridescens, 38 mm. long.

" 55 -- Section just anterior to the planum ethmoidalis of the adult Diemictylus viridescens.

Fig. 56 -- Section through the septum nasi of Triton cristatus 28 mm. long.

" 57 -- Section through the planum ethmoidalis of Triton cristatus, 35 mm. long.

" 58 -- Section through the planum ethmoidalis of Cryptobranchus alleghaniensis, two months old.

" 59 -- Section through the anterior end of Spelerpes bilineatus, 15 mm. long.

" 60 -- Section just anterior to planum ethmoidalis of Spelerpes bilineatus, 37 mm. long.

" 61 -- Section in the same region as above of Spelerpes bilineatus 46 mm. long.

" 62 -- Section through the choanal region of Plethodon erythronotus.

" 63 -- Section just anterior to the planum ethmoidalis of Plethodon erythronotus.

" 64 -- Section through the anterior part of the planum ethmoidalis of Necturus maculatus, 30 mm. long.

" 65 -- Section through the posterior part of the fenestrated capsule of Necturus maculatus, 45 mm. long.

" 66 -- Section through the nasal septum of younger Epicrium.

" 67 -- " " " " " " Epicrium glutinosus, 90 mm. long.

" 68 -- Section through the planum ethmoidalis of Epicrium glutinosus, 90 mm. long.

" 69 -- Section through the septum nasi of the older Amphiuma means.

Fig. 70 -- Section just anterior to the septum nasi of the 82 mm. Amphiuma means.

" 71 -- Section through the planum ethmoidalis of Amphiuma means 82 mm. long.

" 72 -- Section through the posterior part of the planum ethmoidalis of Pipa americana.

" 73 -- Section through the anterior part of the planum ethmoidalis of Pipa americana.

" 74 -- Section through the middle region of the organ of Jacobson of Pipa americana.

" 75 -- Section through the choanal region of Pipa americana.

" 76 -- Section through the external naris of the adult Hyla pickeringii.

" 77 -- Section just posterior to the external naris of the adult Hyla pickeringii.

" 78 -- Section through the planum terminale of Hyla.

" 79 -- Section through the choanal region of Bufo americana 9 mm. long, body length.

" 80 -- Section through the planum terminale of Bufo.

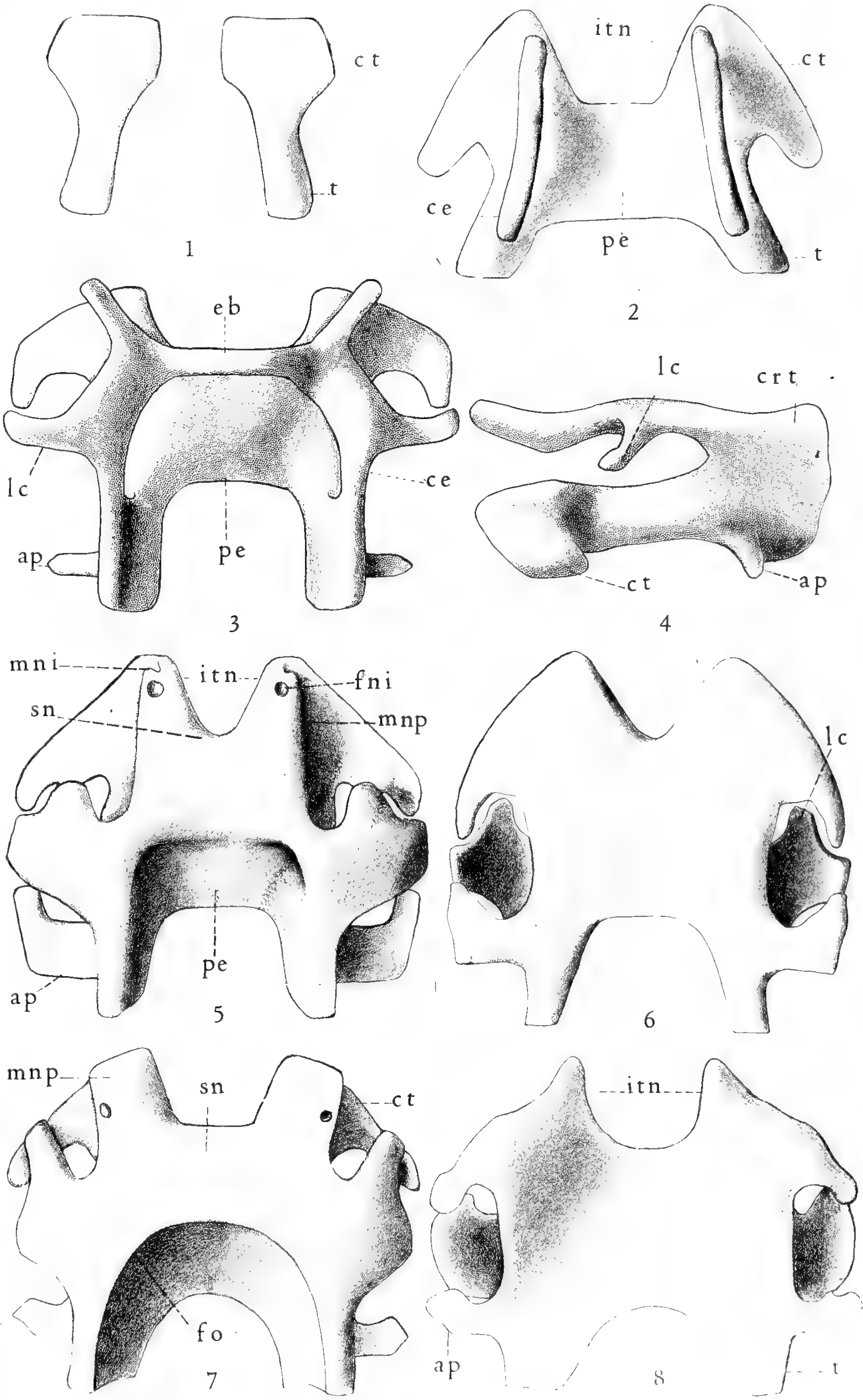
" 81 -- Section through the fenestra naso-basalis of Bufo.

" 82 -- " " " external naris of Bufo.

" 83 -- " " " muscularis process of the quadrate of Rana viridescens, 28 mm. long.

" 84 -- Section through the anterior part of the choanal region of Rana viridescens, 28 mm. long.

PLATE I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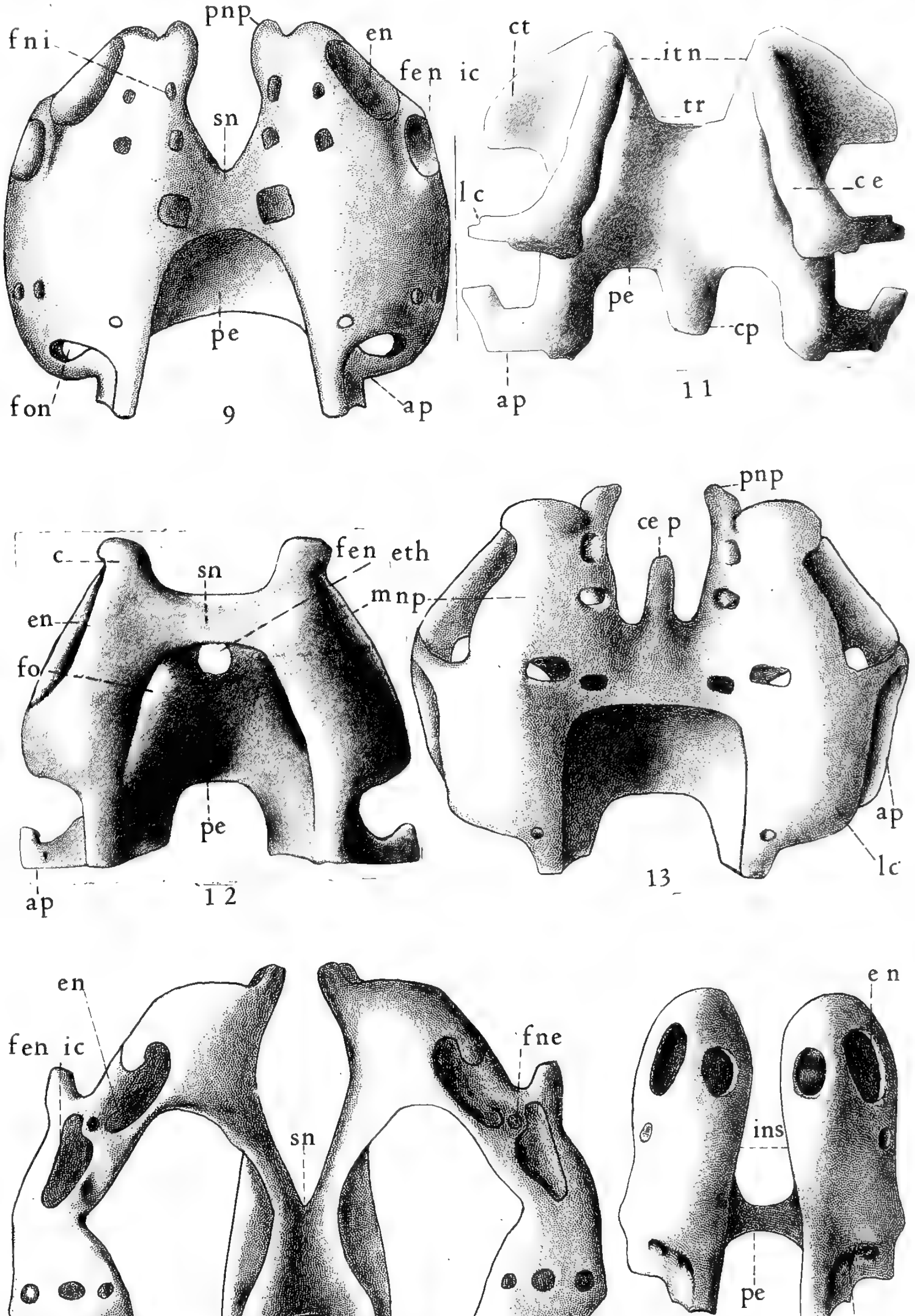
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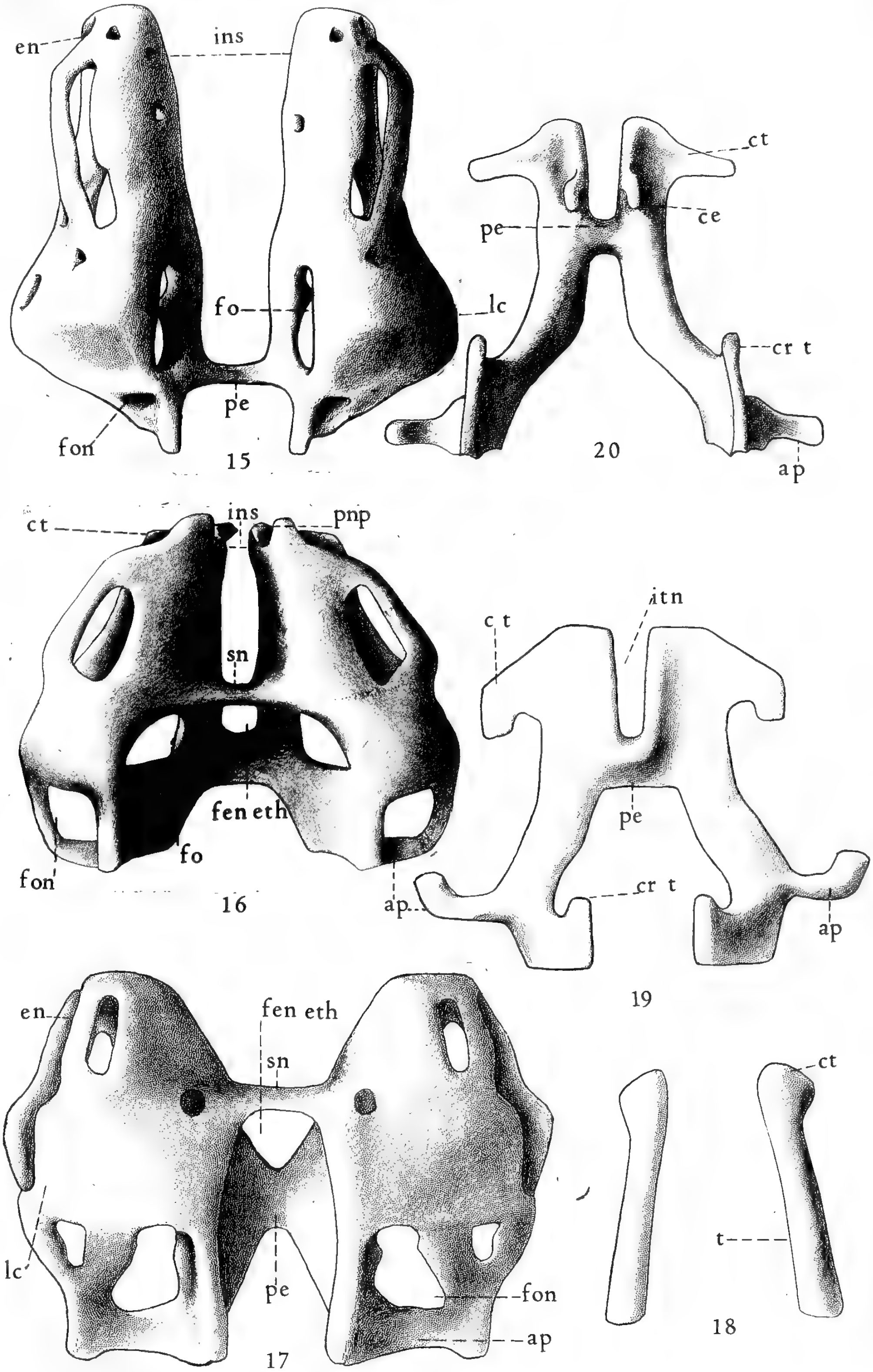
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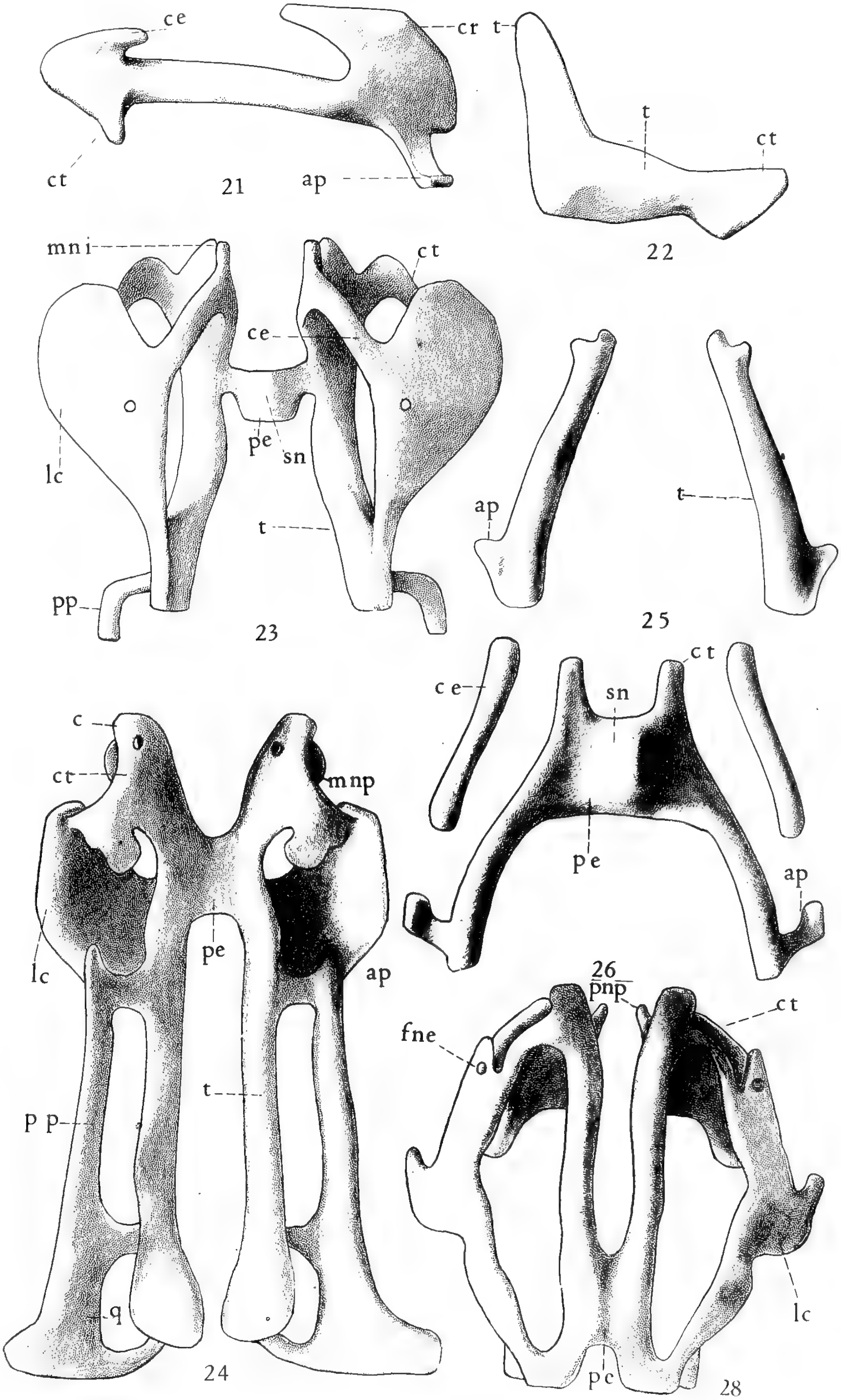
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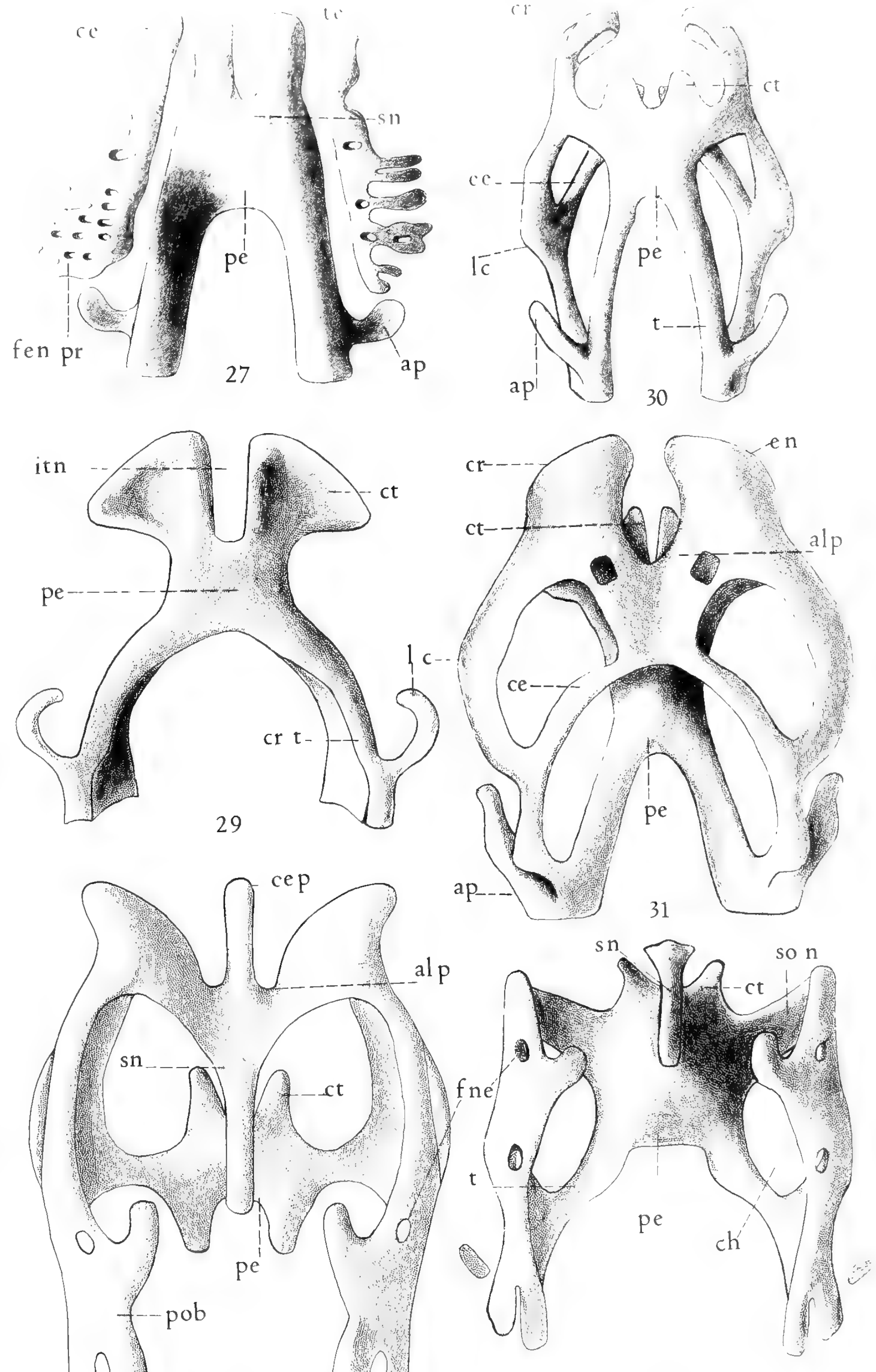
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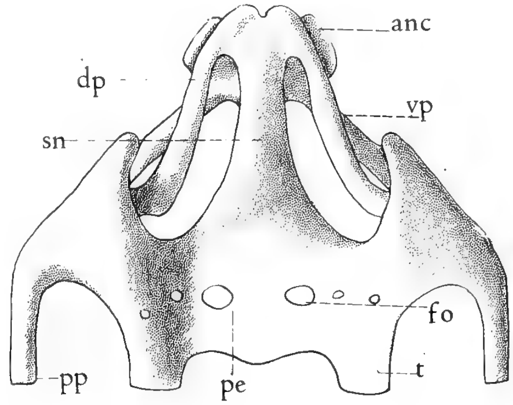

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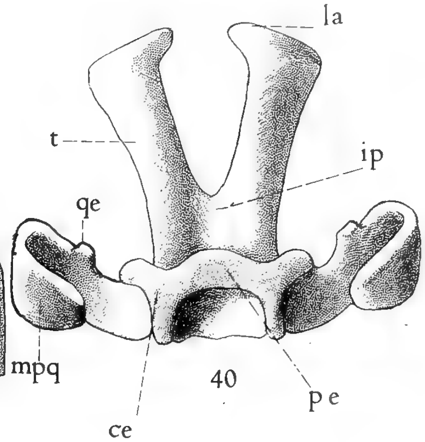

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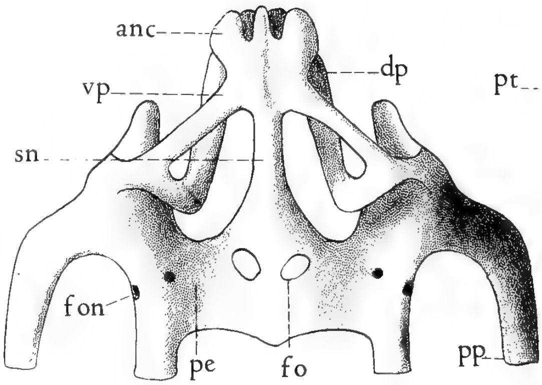

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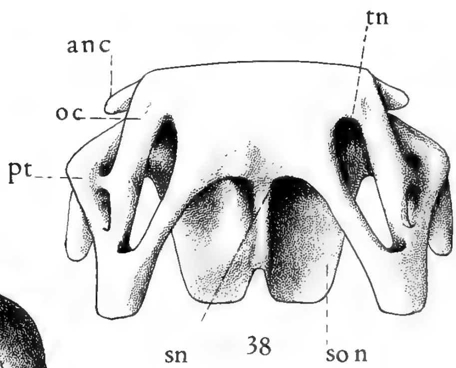

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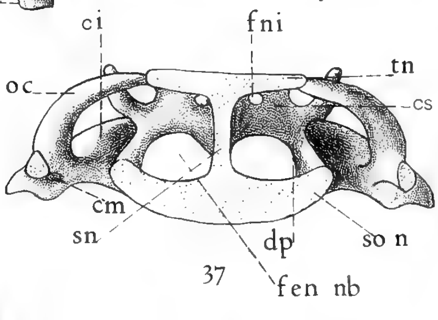

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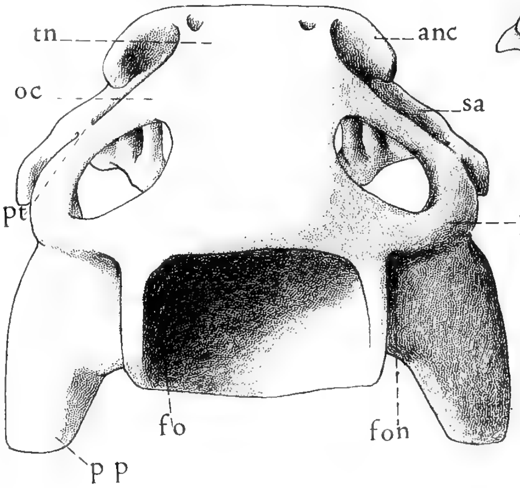

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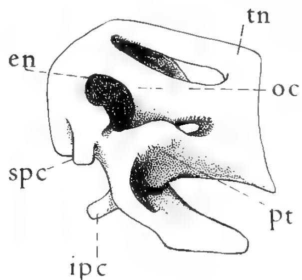

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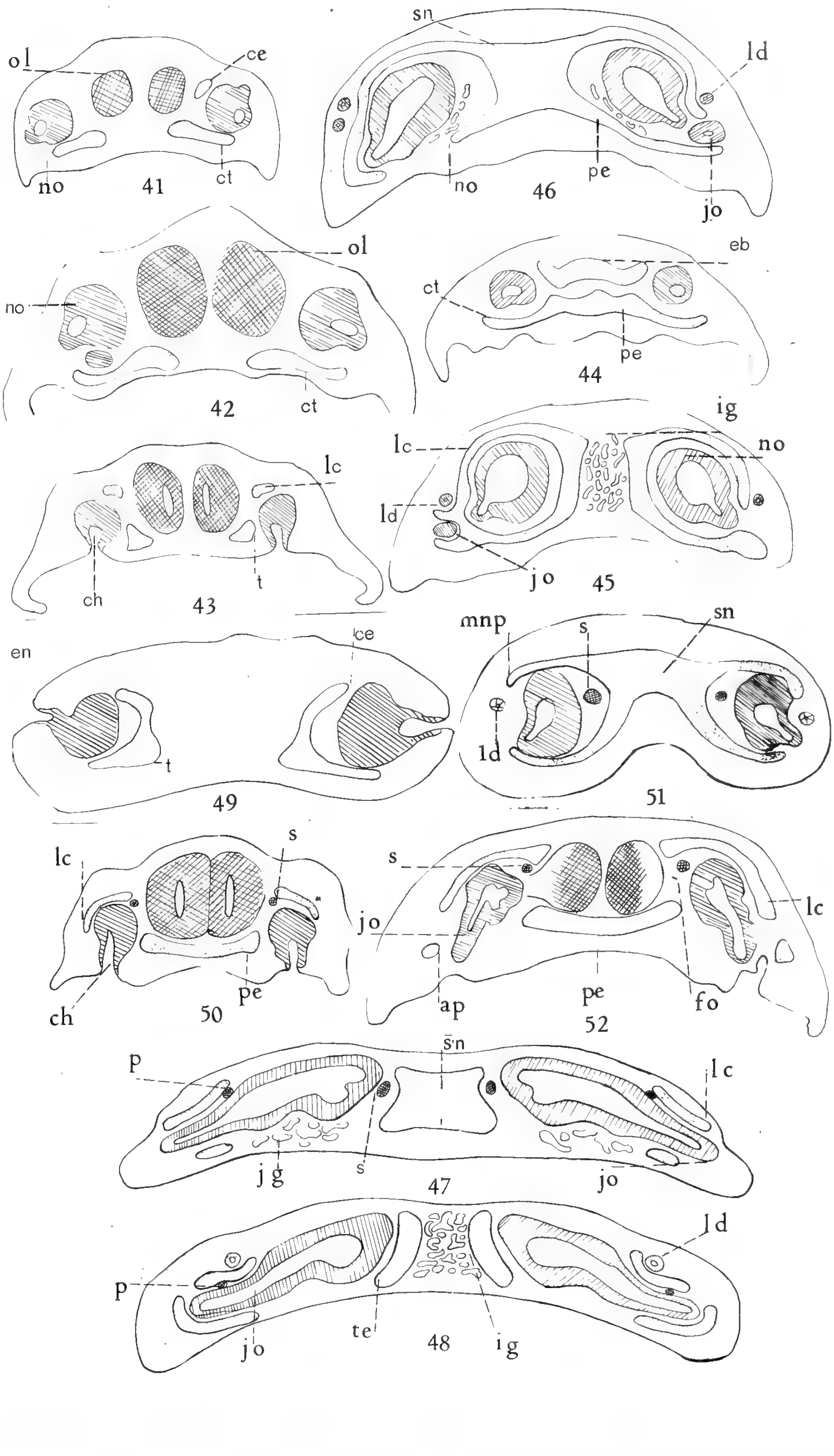
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PLATE VIII

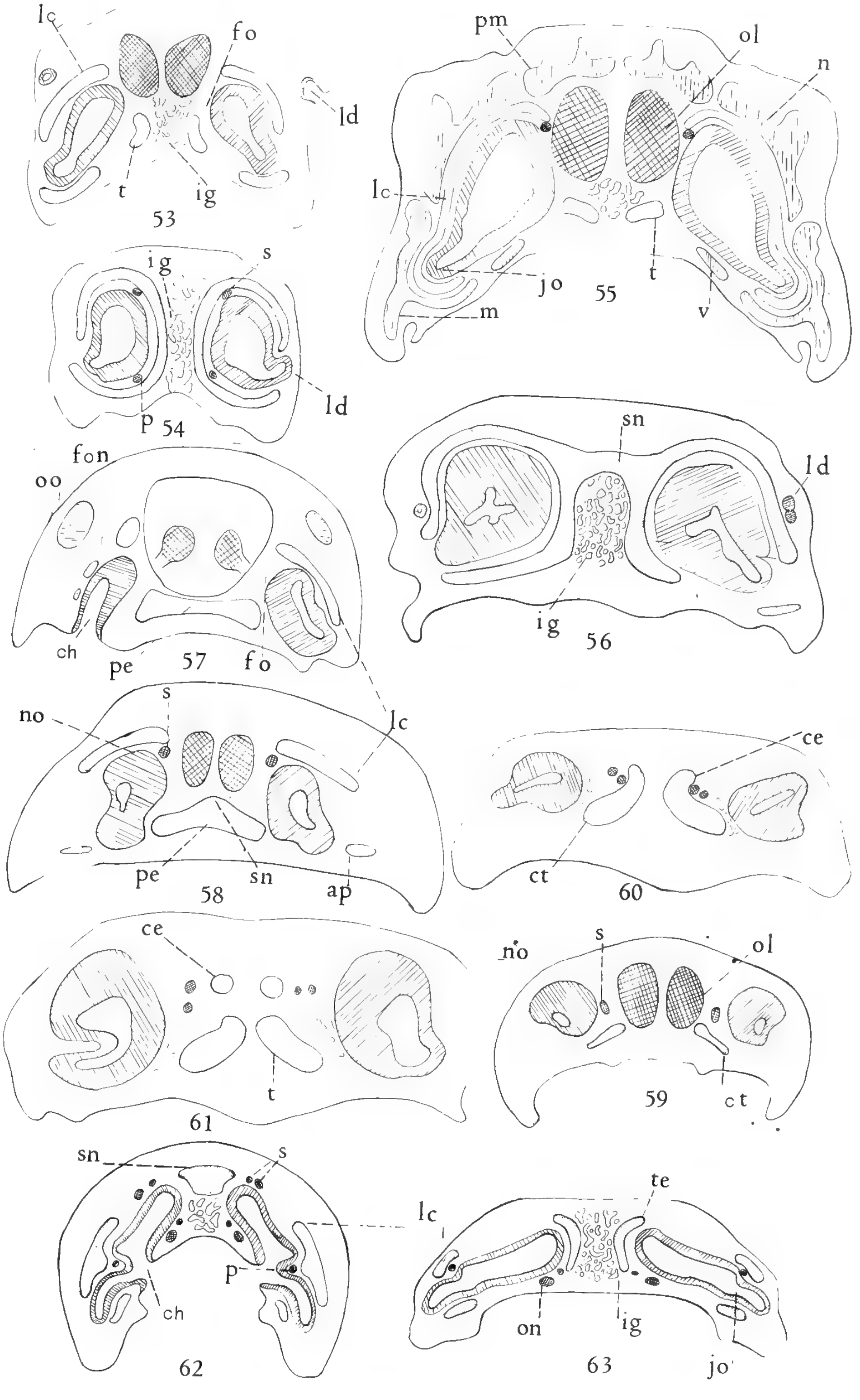

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PLATE IX

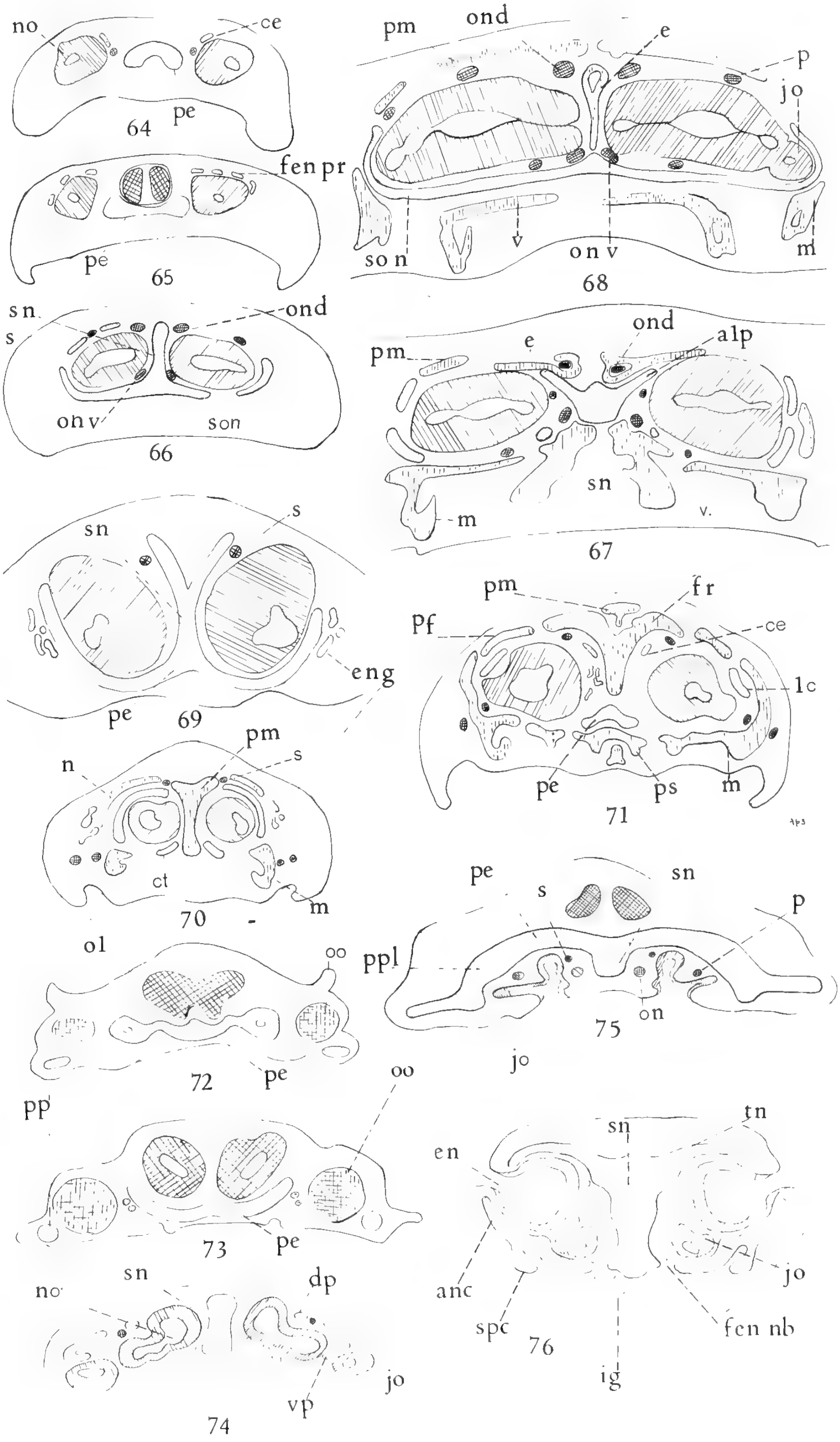
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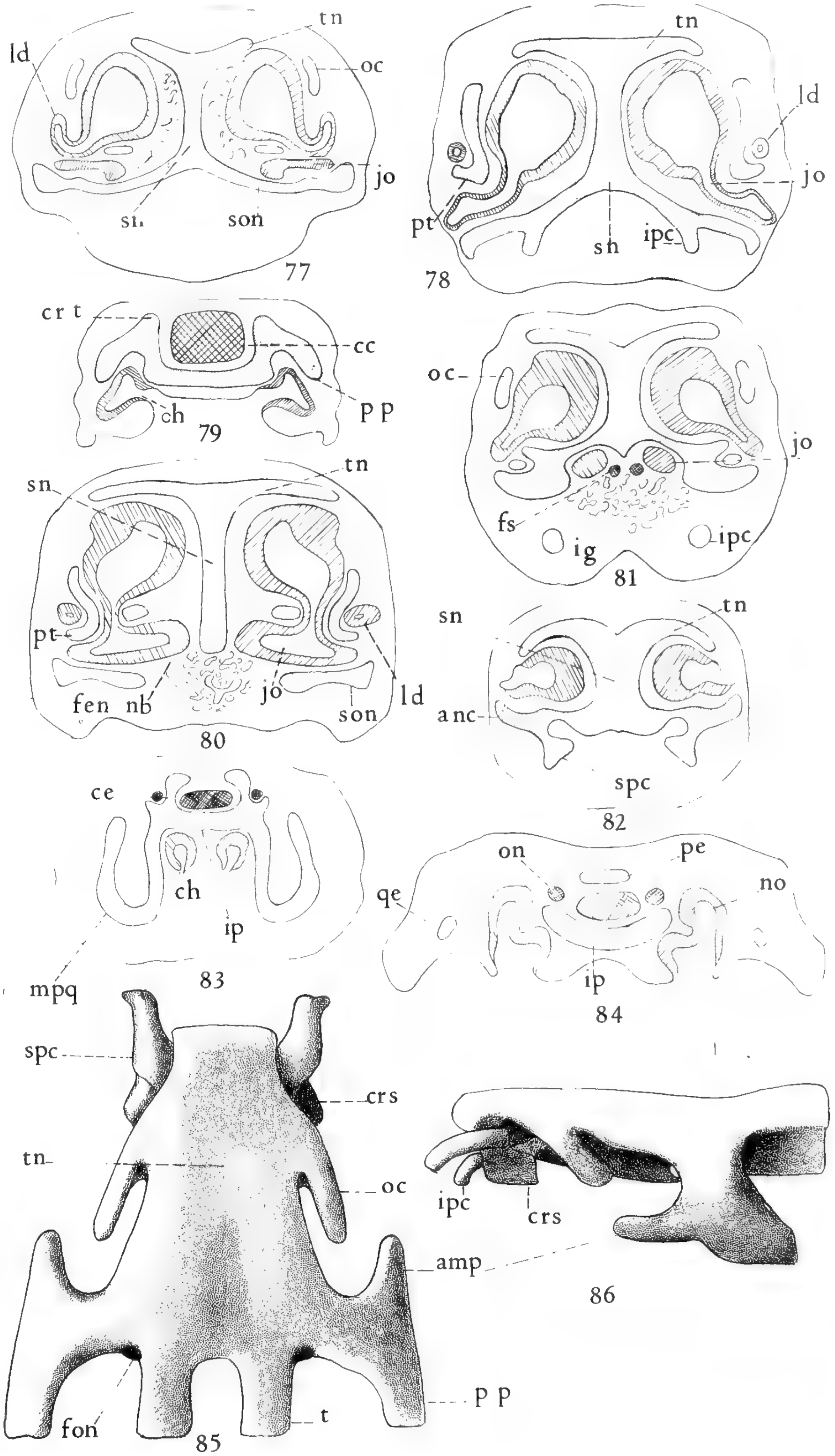
PLATE X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George Marsh Higgins

Born December 19, 1890; Elk Grove, Illinois.

Graduated from Main Township High School, Des Plaines, Ill., June, '08

Entered Knox College, Galesburg, Ill., September, 1908.

Honor Student, Knox College, 1912-1913.

Bachelor of Science degree, Knox College, June, 1914.

Graduate Assistant; Dept. of Zoology, University of Illinois, September, 1914 to June, 1915.

Master of Arts degree, University of Illinois, June, 1915.

Student and Collector, Puget Sound Marine Biological Station, Friday Harbor, Washington; summer of 1915.

Assistant; Dept. of Zoology, University of Illinois, 1915-1917.

Elected to membership in Sigma Xi; April, 1917.

In charge of Zoology, Eastern Illinois State Normal School, Charleston, Illinois; summer of 1917.

Appointed Fellow in Zoology, University of Illinois for 1917-1918.

Entered the National Service in September, 1917.

Entered the Third Officers' Training School, Camp Dodge, Ia., Jan. '18

Commissioned 2nd Lt. of Infantry, June 1, 1918.

Assigned as instructor in Central Officers' Training School, Camp Pike, Ark.

Commissioned 1st Lt. of Infantry, Aug. 20, 1918.

Discharged from the National Service, December 18, 1918.

Fellow in Zoology, University of Illinois, Jan. 1, 1919 - June 30, 1919