EARLY STAGES OF THE BRAIN OF ACANTHIAS

BY

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY

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EARLY STAGES OF THE BRAIN OF ACANTHIAS.

INTRODUCTION.

Although considerable work has been done upon the early brain of Acanthias in connection with the subject of metamerism, there has been no consecutive study of the early stages from the single standpoint of vertebrate cephalogenesis.

The investigation of which this paper is an account, was carried on in the Zoological Laboratory of the University of Illinois under the direction of Dr. J. S. Kingsley, to whom the writer wishes to express his indebtedness for valuable advice and criticism during the course of the work.

MATERIALS AND METHODS.

The material employed was the series of prepared slides of the University, both sections and toto mounts. Camera drawings were made and the most interesting stages in the development were reconstructed by Born's wax plate method. For several reasons, study of the development of the brain was not carried beyond the 65 somite stage, or about 11 mm. total length.

HISTORICAL.

Numerous investigators have used Acanthias chiefly in solving the quesion of the segementation of the head. Balfour (78)

was the first to take up the comparative study of the head and made the discovery of the continuous extension of the primary body cavity into the head. In this he was followed by his pupils, Marshall('81) and Sedgwick ('92) but the great paper in this line was by Van Wihje ('82) who confirmed the direct morphological comparability between head and trunk and described a metameric head of nine segments, four of these being preotic and five postotic which number has been generally accepted by investigators to-day, although Miss Platt ('91) showed the existance of another somite (the "A" of later papers) anterior to the first of Van Wihje. Locy ('95) discovered segments in the early blastoderm which he traced into the formation of the neuromeres and then the later divisions of the brain. These segments appeared long before there were any segmental divisions of the middle germ layer. In Acanthias he found the neural segments extending into the germ ring and, in the chick, at times into the primitive streak. The segments were serially homologous, more definitely shown in the ectoderm, with the other layers only slightly affected. Locy's conclusion was that the brain was distinctly metameric and consisted of 14 segments, nine in the hindbrain and five in the combined forebrain and midbrain. Neal ('98) through his studies of the primitive nerve centers of the cranial nerves, the early segmentation of the embryo and the formation of the visceral arches, concluded, that there was a primitive correspondance between neuromerism, mesomerism and branchiomerism.

OBSERVATIONS.

Embryo 2 mm.

In the present study an embryo with five mesodermic

somites, about 2 mm. in total length, begins the series. At this stage, (fig. 1) the medullary plate is widely expanded anteriorly to form the anterior part of the cephalic plate and, with the rest of the embryonic part of the germ, is raised somewhat above the blastodermic area. The neural plate is nearly flat at this stage, but its edges are bent slightly ventrally, while along the sagittal line of the dorsal surface is a shallow groove, most marked behind which indicates the line of concrescence of the two halves of the embryo. From this the edges slope gradually upwards and outwards, the whole of this part of the plate forming the neural groove. In his study of Amblystoma, Griggs ('10) finds a similar median groove which persists until the neural tube is formed. But he also describes two germinal depressions, the "blastogroove" and "peripheral groove" for which I find no parallel in Acanthias embryos, and hence they need not be discussed here. It may be that study of fresh or living embryos would bring out similar markings. The notochord, lying in the axis just beneath the neural plate, causes a slight elevation in the floor of this medial groove. In this stage the notochord passes in front into a mass of tissue which later is differentiated into entoderm and mesoderm while the entodermal part of the alimentary canal extends far forward beyond the end of the notochord. Near the anterior end of the neural plate are a pair of slight depressions either side of the median line. These are the first indications of the developing optic vesicles and are fairly well indicated in the reconstruction. The edges of the cephalic plate are irregularly lobulated, the lobules being the neuromeres of Locy, who believed that they were the remnants of a primitive metamerism of the

vertebrate body; that once established in these very early stages they could be traced onward until they became the neuromeres of other investigators and showed definite relations to the spinal and cranial nerves. Hill ('00) found an early appearance of neural segments in his studies on chick embryos and claimed that they were identical with the neuromeres of later stages.

Neal ('98) is a very severe critic as regards the neuromeres of Locy and Hill. He found no constancy in the number of segments in different individuals; nor agreement in number or position upon the two sides of the cephalic plate of a single individual. In no case were the segments symmetrical nor was he able to determine definite relations between these neural segments and the somites. Neal believed that the irregularity and inconstancy of the segments precluded a phylogenetic interpretation

In the restoration which was made, (fig. 1) the lobes on the two sides of the cephalic plate do not correspond either as to number or position. In some cases it is almost impossible to determine their boundaries. Such an irregularity of so called neural segments is totally at variance with the neuromeres of later stages.

There now arises the question of the limit of the cephalic plate. Locy ('95) has stated, that before the closure of the neural tube, head and trunk could be distinguished. Neither in the preserved embryos nor in the restoration which was made was any evidence of a line separating the expanded portion of the neural plate from that of the unexpanded portion, to be found. However near the hinder end of the expanded portion of the cephalic plate is the region of greatest ventral flexure. Neal has traced this

point into later stages where the neural tube is transformed into a closed tube and found that it corresponded exactly with the hinder boundary of encephalomere VI, the hindbrain neuromere.

Embryo 3.2 mm.

In Stage 2 (3.2 mm., fig. 2) the edges of the neural plate have begun to turn dorsally to form the medullary folds. This process begins at the anterior end, so that while the anterior part of the neural plate has become U-shaped, the posterior part is still somewhat flattened. At the anterior end the primitive groove is very shallow, growing deeper as it runs caudally, until, in the posterior brain region, it is deeply V-shaped. The optic vesicles have become deeper cup-like depressions, growing outwards as well as downwards and forming evaginations of the lateral walls. Just behind these primary optic vesicles is another pair of depressions which have pushed out the lateral walls. According to Locy ('93) who found such accessory vesicles in his study of Acanthias, and Hill ('00) who describes similar pits in his study of the chick, these depressions may be a pair of accessory optic vesicles which later develope to form the dorsal part of the walls of the diencephalon and its principal outgrowth the pinealis.

The notochord at this stage shows distinctly its origin from the entoderm of the archenteron. At its very anterior end it is a broad oval plate of cells which have been given off from the dorsal side of the archenteron. As it runs posteriorly it grows smaller and more cylindrical, still unattached to the ventral side of the brain floor until about the beginning of the hindbrain region where its cells are in close contact with those of the main trunk of the neural tube, being separated merely by a basilar membrane.

Embryo 3.5 mm.

Gradually the folding of the medullary plate increases, the lateral parts assuming a more vertical position and the margins near the anterior end begin to fuse. Next, a fusion occurs in the hind brain region which gradually extends forward towards the first until the whole is converted into a neural tube except at the anterior end where the canal remains open as the anterior neuropore, (fig.3) This opening persists until the embryo is 4 mm. long and has about 19 mesodermic somites. The primary or mesencephalic flexure has begun at this stage and has continued so far that the anterior part of the brain, including the optic vesicles, now lies in a plain at right angles to the axis of the hindbrain. The brain as yet is very simple; very slight constrictions divide it into the three typical regions, forebrain, midbrain and hindbrain. The walls are fairly uniform in thickness throughout. The forebrain is somewhat expanded and the anlagen of the optic vesicles project from it, outward and caudally. The midbrain is a simple enlargement of the neural tube, and the hindbrain, as long as the fore and midbrain together, is only a simple tube, with a slight lateral expansion anteriorly. At the anterior end of the hindbrain the roof has begun to widen a little, the result being a somewhat triangular outline in cross-section. The notochord becomes free from the basilar membrane which connects it with the neural tube at about the middle of the hindbrain; from thence it runs forward to just below the midbrain and ends a little dorsal and in front of the tip of the forebrain as the latter is bent downward.

Embryo 4 mm.

The next great change is the closing of the anterior

neuropore and with this, as seen in figure 4, is associated an increased primary flexure. The forebrain has increased markedly in length. The optic vesicles have begun to grow dorsally as well as laterally and are now separated from the forebrain in front by a shallow groove. The walls have become thinner and the cavity has become larger. There is little change in the midbrain, although its sides are dilated somewhat laterally. In the hindbrain the floor and sides are of about the same thickness while the roof is composed of only two or three layers of cells. The notochord, growing smaller as it runs forward becomes free from the basilar membrane which connects it to the neural tube, about the middle of the hindbrain and gradually bends downward as it approaches the anterior end of the forebrain.

Embryo 4.5 mm.

In an embryo of 4.5 mm. (fig. 5) the cranial flexure is more pronounced, causing the posterior portion of the midbrain to form the extreme anterior part of the long axis of the embryo. As a result of the increased flexure the forebrain now extends further posteriorly, decreasing the angle between its ventral side and the ventral side of the hindbrain. The optic vesicles are larger and extend more toward the anterior end of the forebrain The midbrain has grown laterally, the roof becoming thinner as the sides expand, while the enclosed ventricle, a simple cavity, is scarcely distinguishable from that of the hindbrain. At this stage the first indications of the division of the hindbrain into cerebellum and medulla are recognizable. The roof of the hindbrain becomes thinner toward the posterior end. Just in front

of the thickened epithelium, which marks the very early formation of the otocysts, the roof is composed of several layers of cells, from which has grown out the anlage of the acustico-facialis nerve. Posterior to this thickened epithelium the roof is only a single layer of cells. The lateral walls of the hindbrain are so thickened that the ventricle is hour-glass shaped in transverse section, thus dividing the central canal into two enlargements, dorsal and ventral, almost equal in size, connected by a narrower portion. Gradually, passing back from the hindbrain into the medulla, the ventricle becomes a simple cavity ovoid in transverse section, with the broader portion near the floor. The notochord remains in contact with the floor of the brain until just in front of the beginning of the acustico-facialis anlage. Its origin from the entoderm of the mesenteron is clearly seen, and, as it extends dorsally from the ventral side of the forebrain, it makes almost a right angle in relation with the primary flexure. At its anterior end the notochord is laterally compressed, gradually becoming cylindrical and at the same time increasing in diameter as it proceeds caudally.

Embryo 5 mm.

The conditions in an embryo of 5 mm. (fig. 6) are not essentially different from those in the stage just described. Forebrain, midbrain and hindbrain are separated by very faint dorsal constrictions. The forebrain has been pushed a little more caudally, thus decreasing the angle at the flexure. The optic vesicles have pushed out laterally and become extended more dorsally. The midbrain is only slightly dilated, but is somewhat

broader on the ventral surface than on the dorsal. There is only a single layer of columnar cells in the roof of the hindbrain while the lateral walls have become greatly thickened. The ventricle in the anterior portion of the hindbrain is kite-shaped in transverse section, while in the posterior portion it has the shape of an hour-glass. The notochord only extends as far forward as the anterior edge of the acusticus-facialis anlage and is attached to the neural tube throughout its length except for a short space at the anterior end.

Embryo 6.2 mm.

In a 6.2 mm. embryo (fig. 7) some very decided changes occur. The forebrain is greatly enlarged, with the vertical and horizantal axes approximately the same. A well defined dorsal groove separates it from the midbrain. The optic vesicles stand out prominently from the brain wall on a well defined optic stalk. The outer wall of the vesicle has invaginated to form the optic cup in which lies a spherical lens. At this stage the infundibulum appears as a slight evagination from the floor of the forebrain and lies directly beneath the upper end of the hypophysis. The hypophysis has arisen from the ectoderm of the mouth cavity and in a 5.2 mm. embryo, Scammon ('11) describes it as a thickened hypophyseal plate of epithelium in contact with the ventral surface of the forebrain. In a 5.8mm. embryo he describes it as an evagination of the oral cavity which has extended inward so far as to be in contact with the brain at the median line, from the recessus praeopticus nearly to the tuberculum posterius. In the restoration which was made (fig. 7) the posterior (upper) end of the hypophysis is separated from the surface of the

forebrain and is slightly notched on the upper side to form a shallow pocket into which the tip of the notochord has extended. This may be the beginning of the inferior sacs as described by Baumgartner ('15) although he finds no such constriction until the 22 mm. embryo.

The axis of the midbrain is almost at right angles to that of the hindbrain. In the anterior part the walls and floor of the midbrain are composed of five or six layers of cells and as it extends posteriorly the roof becomes gradually thinner until it is only made up of a single layer of cells. In cross-section the ventricle is rectangular. The thickness of the walls has increased with the lengthening, A shallow dorso-ventral groove, which is in line with the anterior end of the hypophysis, marks the beginning of this hindbrain region. Just behind it the roof ofthe brain is composed of several layers of cells which is the beginning of the cerebellum. This thickened portion extends just posterior to the end of the trigeminus anlage, at which point the roof becomes thinner, until it is composed of only a single layer of cells. This thin portion is the beginning of the tela chorioidea of the fourth ventricle which extends throughout the rest of the brain region.

Embryo 10.2 mm.

Between the 6.2 mm. embryo and the last stage to be described, an embryo of 10.2 mm. (fig. 8) the anterior brain region has undergone considerable changes. In the dorsal portion of the forebrain two expansions have appeared, causing a division into a large anterior and a small posterior portion. The anterior

expansion is the telencephalon which is to develop into the cerebral hemispheres and olfactory lobes. The roof of this anterior portion is composed of ten to twelve layers of cells and grows thinner as it approaches the epiphysial structures roofing in the third ventricle. At the point where the velar fold begins, the roof is only three or four layers of cells in thickness, increasing as it proceeds caudally. The velum transversum is in a line almost parallel with the lower border of the optic cup and extends a little posteriorly into the brain cavity for a distance of about 150 μ. This fold separates the telencephalon from the posterior portion, which is to form the thalamencephalon. The walls and roof of the posterior expansion are about of the same thickness and enclose a simple cavity except at the anterior end, where there is a slight trace of another invagination, in front of which is to form the parancephalon (the "Zirbelpolster" , of the Germans) behind which the pinealis develops. The midbrain is separated from the thalamencephalon by another fold which extends into the brain cavity about 100 μ.

The optic cup is now connected with the twixtbrain by a slender optic stalk, on the ventral side of which is the first indication of a groove, the later chorioid fissure. The two walls of the lens of the eye have become differentiated into a thin exterior and a thick interior and the lens now lies about in the aperature of the optic cup. From being but an inconspicuous invagination in the 6.2 mm. stage, the infundibulum has greatly increased and now forms a sac-like projection, extending somewhat backward from the floor of the forebrain in a curve; higher in front and sloping downward till it blends with the floor of the forebrain

having its cavity in a broad open connection with the ventricle. The hypophysis has increased in size. The groove which was so marked in the previous stage has completely disappeared, leaving a single tube with its closed dorsal end in contact with the infundibulum. The notochord is in contact with the central nervous system throughout its length; the anterior end curving slightly downwards towards the dorsal end of the hypophysis. It increases in diameter backward as far as the brain extends.

In the midbrain the roof is becoming progressively thinner and the sides thicker. Dorsally the midbrain is only one simple expansion, while ventrally and laterally three slight expansions are found. These are probably the three segments of the primary midbrain, described by Zimmermann ('91) and Neal ('98). The anterior expansion is bounded in front by the primary constriction between the forebrain and the midbrain and behind by a lateral constriction extending ventrally from the point of origin of the oculomotor nerve. The second expansion has for its posterior boundary a ventral constriction beginning half way up the side of the midbrain and extending a little postero-ventrally into the primary flexure. Behind this a third expansion which extends back to the beginning of the hindbrain. The boundary between the midbrain and the hindbrain is a marked dorso-ventral constriction which lies just in front of the trigeminus anlage. The hindbrain is still a fairly uniform structure with a simple cavity. At the anterior end the roof is composed of several layers of cells which indicates the rudiment of the cerebellum, which has extended posteriorly so that, just in front of the origin of the acustico-facialis anlage the roof becomes thinner, marking the beginning of

the medulla.

DEVELOPMENT OF THE CRANIAL NERVES.

In direct relation to the formation of the brain comes the formation of the cranial nerves and the reconstructions which were made have included these structures. The remainder of this paper deals with the early stages of the nerve development from the time of their first appearance up to about the 65 somite stage.

Neal ('98) states that in an early stage, when the cephalic plate is still widely expanded, there is a disassociation of the neural crest cells, the fundament of the trigeminus, which is clearly differentiated from that portion of the neural plate which is destined to form the neural tube. However not until the stage when the cephalic plate is closed except in the region of the forebrain did I find any differentiation in the neural crest. As shown in figure 3.,the neural crest is very distinct, extending close along the upper side of the brain, from a point a little behind the closed portion of the neuropore to the middle part of the hindbrain. The cells which compose it have already extended half way down the side of the neural tube.

In an embryo of about 19 somites, figure 4., there are two of these regions of cell proliferation, the beginnings of the fifth and seventh-eighth nerves. The fifth arises as an outgrowth from the extreme dorsal summit of the posterior part of the midbrain It extends ventrally, covering the entire side of the neural tube and is in close contact with its walls. At this time only one

continuous plate of cells has developed and the two later branches, namely the ophthalmic and the mandibular are not yet differentiated. The seventh and eighth nerve is outlined shortly after the fifth as is shown by the fact that in this stage the cells have only just begun their descent. These facial-acustic ganglion cells are located a little distance behind and independent of the fifth and like the trigeminal, they arise from the extreme dorsal summit of the neural axis. It is only later that the seventh and eighth nerves are differentiated from this common anlage.

In the next stage, (fig. 5) the trigeminal anlage is a continuous neural ridge, lying dorsal to the optic vesicle, but subdivided ventrally into two somewhat distinct portions. Of these the anterior is the smaller; it passes in front of the midbrain vesicle toward the optic evagination. The larger posterior portion is quite elongate and extends ventrally into the region of the mandibular arch. The acustico-facialis anlage extends ventrally over half of the neural tube in the direction of the hyoid arch. It is now only a thin sheet of cells, somewhat triangular in shape as viewed from the side.

From the dorsal and posterior part of the hindbrain now comes a third proliferation of cells, the first indication of the ninth and tenth nerves. They arise, like the others, from the very summit of the neural axis. They have just begun their latero-ventral extension and now appear only as a small ridge, no differentiation into separate nerves having taken place.

Some important changes occur in an embryo of 30 somites, (fig. 6). Owingto a further flexure of the head the trigeminal

crest does not extend so far forward. There is a slight thickening of the anlage and the first indication of a division into two branches. The anterior portion or ophthalmic branch is in close contact with the walls of the midbrain and only extends a short distance ventrally along its side. The posterior portion of the nerve, lying almost in the constriction between mid and hindbrain, now extends into the mandibular arch. A slight differentiation has begun in the acustico-facialis anlage together with a decided thickening of the cells, which have grown out to meet the thickening of the auditory epithelium. In the vagus anlage a differentiation has likewise taken place. Two distinct portions are visible, the anterior, the early stage of the glossopharyngeus, the posterior, the vagus proper. In this figure they extend ventrally only half way down over the side of the neural tube. Only the beginning of the tenth nerve has been shown and at this stage there is no evidence of the four branches which later arise from it.

In an embryo of 50 somites, (fig. 7) the trigeminus anlage has become very much shortened and is now connected to the neural tube by a root of about 75 μ in length. The cells have increased until the nerve is about three times as thick as in the previous stage. The single rudiment of the seven and eight is also somewhat enlarged and it has begun to divide into two distinct parts. Leaving the side of the neural tube the main trunk runs ventrally and a little posteriorly, dividing into the branch which is to form the seventh nerve and a posterior acusticus. The facialis continues to extend ventrally. The auditory nerve begins to widen and at the same time expands, like a cup, around the ventral side

of the auditory vesicle with the epithelium of which it is fused. Behind the ear capsule the glossopharyngeus anlage forms a long thin strand which arises from the midlateral portion of the neural tube. Immediately behind this come the cells of the vagus, now completely separated from the former. Anteriorly the anlage is only a faint ridge projecting from the side of the neural tube. Posterior it becomes a broad sheet of cells extending ventrally between the ectoderm and the mesoderm in the region of the pharynx where the latter begins to be divided by the formation of the visceral clefts.

In the next stage, an embryo of 10.2 mm. (fig. 8) the first appearance of the oculomotor nerve is seen. At first it is a thin process extending from the base of the midbrain ventrally to join the ophthalmic profundus branch of the fifth just before the latter enters the optic cup. The trigeminus crest has constricted and four branches are recognizable. Anteriorly there is a slight projection which is to form the ophthalmicus superficialis. Just below this is a short ganglionic commissure which connects the mesocephalic and the main ganglion. From the mesocephalic ganglion the ophthalmicus profundus branch passes anteriorly and ventrally into the optic cup. Just back of the mesocephalic ganglion is the larger branch of the fifth, which breaks up to form the maxillaris in front and the mandibularis posteriorly, as it runs ventrally and a little caudally.

In the acustico-facialis anlage four branches are now developed. Anteriorly in close connection with the skin, the ophthalmicus superficialis has begun to send out its sensory fibers which lie almost parallel with the notochord. Directly below this

the buccalis branch has just begun to develop. Posterior to the buccalis branch, extending further ventrally and curving a little posteriorly, is the mixed hyoid branch of the facialis which goes to the developing muscles and skin of the second visceral arch. Somewhat dorsal and behind the hyoid branch is the acusticus branch which is connected with the median and ventral side of the otic capsule. The glossopharyngeus is practically unchanged and is still a slender strand arising from the mid-lateral portion of the neural tube. The anlage of the vagus is connected to the ninth nerve by a thin ridge of cells. Ventrally the vagus divides into four branches (only the anterior two are shown in the figure) each of which goes to the skin and muscles of the visceral arches. Posteriorly two other branches are given off, an upper one which continues as the lateralis along the lateral line and a lower one, the visceralis, which extends a little ventrally as it proceeds caudally. Its posterior extent was not traced.

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ABBREVIATIONS.

ac.	acusticus nerve
ac. fac.	acustico-facialis anlage
ac. op. v.	accessory optic vesicle
bc.	buccalis nerve
cb.	cerbellum
crs. n.	neural crest
fac.	facialis nerve
fb.	forebrain
fl.	primary flexure
gn. mes.	mesocephalic ganglion
gph.	glossopharyngeus nerve
hb.	hindbrain
hyo.	hyoid nerve
hyp.	hypophysis
in.	infunbibulum
ls.	lens.
mb.	midbrain
md.	mandibularis nerve
med. pl.	medullary plate
m.f.	medullary folds
m.o.	medulla oblongata
mx.	maxillaris nerve
n.g.	neural groove
no.	notochord
np. a.	anterior neuropore
oc.	oculomotor nerve

op. c.	optic cup
op.v.	optic vesicle
oph. f.	ophthalmicus profundus (Vth)
oph. s.	ophthalmicus superficialis (Vth)
oph. s".	ophthalmicus superficialis (VIIth)
o. s.	optic stalk
tel.	telencephalon
thal.	thalmencephalon
trig.	trigeminus anlage
vg.	vagus anlage
v. t.	velum transversum

PLATE 1.

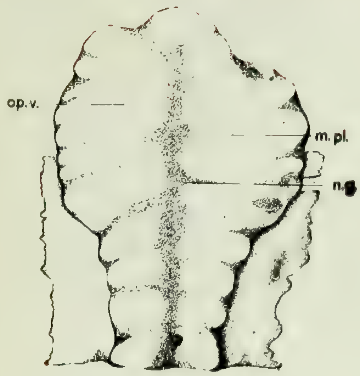
Explanation of Figures

1. Wax reconstruction of a 2 mm. embryo. Dorsal view. (x 1/3)
3. Wax reconstruction of a 3.5 mm. embryo. Side view. (x 1/3)
4. Wax reconstruction of a 4 mm. embryo. Side view. (x 1/3)
5. Wax reconstruction of a 4.5 mm. embryo. Side view. (x 1/3)
6. Wax reconstruction of a 5 mm. embryo. Side view. (x 1/3)

PLATE 2.

Explanation of Figures

2. Wax reconstruction of a 3.2 mm. embryo. Dorsal view. (x 1/3)
7. Wax reconstruction of a 6.2 mm. embryo. Side view. (x 1/3)
8. Wax reconstruction of a 10.2 mm. embryo. Side view. (x 1/3)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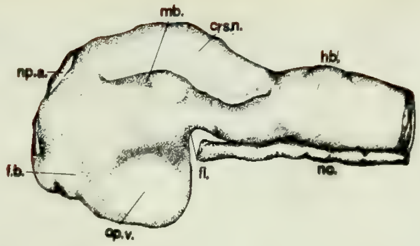
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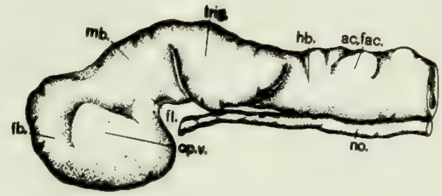
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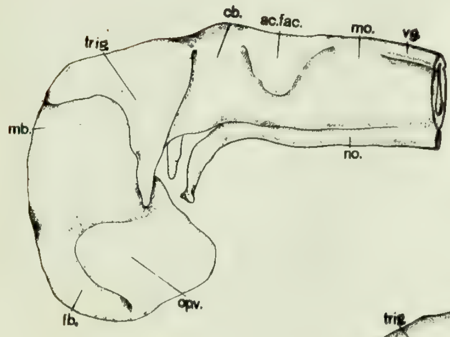
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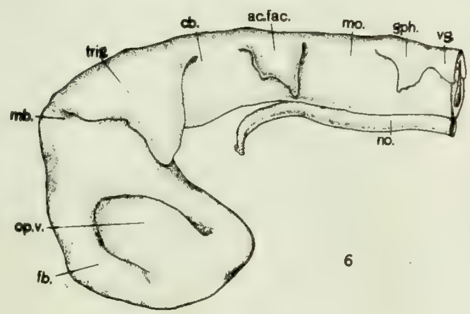
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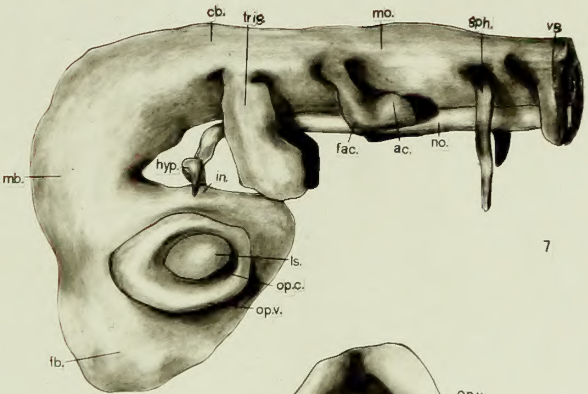
6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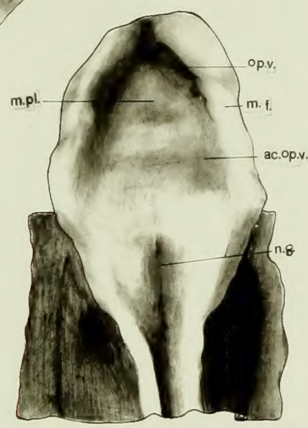
7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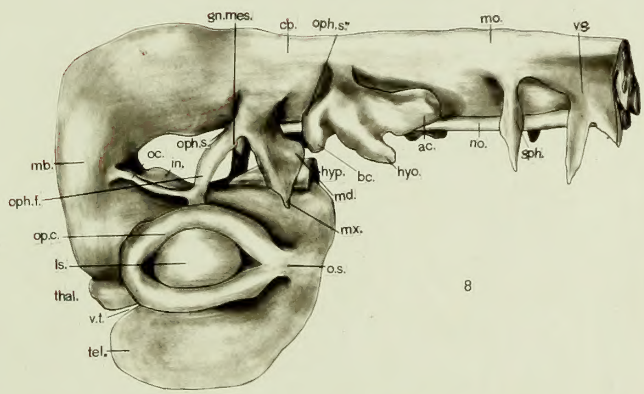
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8