# The Embryology of the Chum Salmon Oncorhynchus Keta Walbaum

by

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# EMBRYOLOGY OF THE CHUM SALMON (Oncorhynchus keta).

## INTRODUCTION

The following paper, dealing with the embryology of the Chum Salmon (Oncorhynchus keta), is the result of work carried on by the writer at the University of British Columbia, during the sessions of 1920-21 and 1921-22.

This species is known under the various names of Chum Salmon, Dog Salmon and Keta. The spawning season at Harrison Lake in 1920 lasted from October 24th to December 5th. The material was obtained from the Harrison Lake Hatchery, through the kindness of Mr. Alexander Robertson, superintendent of the hatchery.

The material was collected regularly every day, from a batch of eggs that were fertilized on November 8th, until the yolk was drawn into the body, April 13th, 1921. The temperature of the water during this time varied from 5°C. to 10°C. The percentage that hatched out was large, being approximately 92%. The greater number hatched in 101 days and the remainder within the next few days. The period from the time of hatching until the yolk was drawn into the body was 55 to 60 days.

The killing and fixing solution that was used was composed of 95% alcohol, formaldehyde, glacial acetic acid and

water in the proportions of - 500 : 12½ : 5 : 200. When the material reached the University of British Columbia it was at once changed to 70% alcohol.

After trying various stains, it was found that Mayer's Alcoholic Cochineal (See Lee: The Microtomist's Vade Mecum, 7th Edition, 1913, p. 150, pp. 236) gave good differentiation, so this stain was used throughout. All embryos were stained whole and then imbeded in paraffin according to the usual methods.

The egg membrane on Chum eggs is very tough. Both this and the yolk when they were dehydrated became very brittle and rendered sectioning very difficult. This difficulty was overcome by removing the egg membrane in all cases and as much of the yolk as could be removed without damaging the embryo. Small embryos, with a small portion of the surrounding and underlying yolk, were cut from the surface of the yolk with a razor, before the imbedding was completed. Large embryos were dissected from the surface of the yolk, with needles.

All embryos were studied as whole mounts and in series of transverse sections. In cases of difficulty series of longitudinal sections were also prepared to aid in the correct interpretation.

The writer takes this opportunity of acknowledging his indebtedness to, and of thanking Mr. Alexander Robertson, Superintendent of the Harrison Lake Hatchery, Dr. A.H.Hutchin-

son, Head of the Department of Botany of the University of British Columbia, for suggestions in histological matters, and in parti ular Dr. C. McLean Fraser, Head of the Department of Zoology of the University of British Columbia, and Director of the Marine Biological Station, Nanaimo, B. C., for encouragement and many valuable suggestions.

## THE MATURE OVUM

The ovum is telolecithal, consisting of a central yolk mass and a layer of cortical protoplasm, slightly thicker at the animal pole. Closely upon the cortical protoplasm, and secreted by it, is a thin vitelline membrane perforated by pores and known as the zona radiata. Exterior to this is a thick tough chorion, secreted by the cells surrounding the egg in the ovary. There is a funnel-shaped opening, the micropyle, perforating both the chorion and zona radiata. The micropyle affords an aperture for the entrance of the sperm.

## FERTILIZATION

When the sperm enters the egg the cortical protoplasm flows to the animal pole where it forms the germinal disc. Part of the protoplasm never reaches the disc but remains as a thin layer enclosing the yolk. The disc is prominent and before cleavage shows numerous fine granules in its matrix (Fig. 1). Through expansion of the protective

membranes or shrinkage of the yolk mass a space, the perivitelline cavity, filled with a watery fluid appears between the zona radiata and the cortical protoplasm. These changes are described in detail by M'Intosh and Prince, (Transactions of the Royal Society of Edinburgh, Vol. XXXV., part III - for the Session 1887 - 88, p. 694 to 696.).

## SEGMENTATION

Cleavage is of the incomplete discoid type. The first cleavage furrow is vertical and divides the disc into two approximately equal reniform blastomeres (Fig. 2). The second cleavage furrow is at right angles to the first producing four blastomeres that are almost equal (Fig. 3). The first two cleavage furrows do not pass completely through the disc (Fig. 4). The third cleavage furrow is in the same general direction as the first and produces four unequal blastomeres. There is considerable variation in this cleavage as is well illustrated by Figures 5 and 6. This represents the development of the first day after fertilization.

Subsequently the cells divide individually and division may occur in either the vertical or horizontal plane until the whole disc is divided and the cells are several layers thick. At the end of the second day the disc contains about sixty-four cells , of which the peripheral ones are considerably larger than those at the centre (Fig. 7). The cell walls of all the cells except the lower peripheral

ones are complete. A thin layer of unnucleated protoplasm separates the lower cells in the centre of the disc from the yolk. This is the central periblast (per.). The periblast and the peripheral cells are continuous however (Fig. 8). Between the central periblast and the disc is a flattened cavity, the segmentation cavity (seg. cav.).

## BLASTULATION

As the cells continue to divide, they become smaller and approach equality in size. At the same time the outer cells begin to assume the regularity of a layer. By the end of the seventh day, all the cells are about equal in size, and the outermost form a row of rectangular cells (Fig. 9).

As was mentioned above, all the cortical protoplasm does not enter the disc. It persists as a thin layer around the yolk and is thickened at the margin of the disc, forming the periblast. The periblast is continued between the disc and the yolk as the central periblast. At first the periblast is unnucleated (Fig. 8, per.), but by the seventh day large nuclei, obtained from the peripheral blastodermal cells, appear outside the margin of the disc, forming a syncytium (Fig. 9, nu.). These rapidly extend outward to form the nuclear zone and at the same time extend inward in the central periblast.

By the end of the fifth day, the shape of the blastoderm has changed considerably and is markedly biconvex, the

lower surface resting on a depression in the surface of the yolk. The blastoderm soon extends laterally and becomes flattened and of about equal thickness throughout, though it is still several cells thick. This thining continues and by the tenth day the central part of the blastoderm is not more than two or three cells thick (Fig. 10). The periphery remains several cells thick forming the germ wall (g.w.). Due to the change of shape, the segmentation cavity (seg. cav.) becomes more elevated and the blastoderm rests on its periphery.

## GASTRULATION AND FORMATION OF THE EMBRYO

As the thining takes place, the blastoderm begins to extend over the yolk, the process being known as epiboly. The germ wall during the 12th day becomes greatly thickened along the margin that corresponds to the posterior end of the future embryo. Before the end of the day, an involution of this edge of the blastoderm takes place. The inturned edge lies between the periblast and the blastoderm. The involution soon progresses around both margins of the blastoderm forming a ring, the germ ring.

In surface view the germ ring (g.r.) appears as a darker area around the margin of the blastoderm. In transverse section the germ ring appears in the same condition as at the anterior pole (a.p.) in Fig. 13.

The outer or columnar layer of the blastoderm takes no part in the formation of the germ ring. It remains as a distinct layer to the point of contact with the periblast.

Centripetal growth of the germ ring takes place at the posterior pole, forming the endoderm of the future embryo.

During the 13th day, a denser area, the embryonic shield (emb. sh.) appears at the posterior pole of the blastoderm (Fig. 12) and marks the position of the head region when the embryo is formed. This dense area is formed by a thickening of the ectoderm and the forward growth of the endoderm. The outer edge of the endoderm coincides, or nearly so, with the edge of the thickened ectodermal area. Figure 13 shows the structure of the shield as it appears in a section along the longitudinal axis of the shield. The ectoderm (ect.) is thickened and the endoderm (end.) extends to the edge of the thickening. At no place are the endoderm or ectoderm differentiated to the margin of the blastoderm. Both merge into the thickened germ wall (g.w.).

About the 14th day an elongated thickening appears in the middle of the embryonic shield and gradually extends posteriorly. This is the medullary plate (med. pl.), the primordium of the nervous system (Fig. 14). Due to the earlier development of the anterior end of the medullary plate, the anterior end of the central nervous system, the brain, is larger than the spinal cord throughout life.

The medullary plate (med. pl.) is an elongated thickening of the ectoderm. Its appearance in transverse section shortly after it is formed is shown in various regions from the posterior to the anterior end of the embryo in Fig. 15, A to E. At the anterior end it is a small keel-like structure (15,E), which gradually enlarges (15,D) to the point where it first appeared and then becomes smaller more posteriorly (15,B).

The endoderm (end.) at this time is several cells thick at the anterior end of the medullary plate (Fig. 15 E). It extends to the posterior end of the brain region however as a two-celled layer (15,D). From this point two lateral thickenings, the mesoderm (mes.), extends to the posterior end of the embryo. At the anterior end the mesoderm is free from both ectoderm and endoderm, (15,B). Between the free bands of mesoderm is a thickened ridge of notochordal cells, connected to the endoderm except at its extreme anterior end where it is free, forming the notochord. It is free from the ectoderm farther posteriorly than it is free from the endoderm. Farther posteriorly it is not distinct from the mesoderm or the mesoderm from ectoderm. Thus at the posterior end all the structures pass into an undifferentiated cell mass (pr. s.) of considerable extent. This posterior mass is slightly elongated, and, as it corresponds to primitive streak in higher forms, this term will be used in referring to it.

It is at once apparent that all the structures post-

erior to the brain region are being differentiated from the primitive streak and that the differentiation travels from before backward.

There has been much discussion as to the origin of the mesoderm. In this case there is every reason to believe that the mesoderm of the body is derived directly from the region of the primitive streak.

## DEVELOPMENT OF THE PRIMITIVE STREAK AND THE CLOSURE OF THE BLASTOPORE

Epiboly, which was mentioned above, continues throughout the entire margin of the blastoderm but much more rapidly at its anterior pole. At the posterior pole due to the thick mass of cells, the germ wall progresses posteriorly very slowly. As it does so, the primitive streak is formed by the concrescence of the extra-embryonic portion of the germ wall and germ ring. Thus the primitive streak is continually receiving portions of the germ wall and germ ring at its posterior end. The primitive streak in turn loses cellular material at its anterior end by the progressive posterior differentiation of tissues, as was explained above. In the Chum Salmon the primitive streak is never very long, (Fig. 16 - pr.st.).

The blastopore may be said to exist from the moment epiboly begins. It coincides with the margin of the germ ring and may be regarded as a spacious mouth from which the yolk projects. The extension of the blastoderm over the yolk increases the size of the blastopore (b.p.) until the equator is

reached, but from that time its radius narrows until finally about the 22nd day it is a small round opening at the posterior end of theembryo with the yolk-plug (y.p.) projecting into it (Fig. 17). As mentioned above the posterior pole advances more slowly than the anterior one. Thus in the Chum the blastopore closes less than one-quarter of the circumference of the egg, posterior to the point where the embryonic shield first appears.

About the 22nd day, the blastopore closes the lateral edges come close together making it elongated in the line of the primitive streak. This would seem to agree very well with the idea that the primitive streak is formed by the concresence of the extra-embryonic germ walls. Finally the walls fuse and form a solid caudal mass which supplies the cells for the backward growth of the various layers found in the caudal region.

About the 18th day, before the blastopore closes, a small vesicle appears slightly anterior to the edge of the blastopore. This is Kupffer's vesicle, a vestige of the archenteron (Fig.18-A, k.v.). It lies ventral to the endoderm (end.). Below it there is no trace of cellular division so it must be bounded ventrally by the periblast (per.). Before the blastopore closes the vesicle is cut off from the periblast by the ingrowth of the endoderm around its lateral margin. In this condition the vesicle appears as a dorsoventrally compressed lumen surrounded by endodermal cells (Fig. 18-B , k.v.).

Posteriorly the lumen is in some cases continued as a minute opening, for some little distance. This may be a vestige of the neurenteric canal which, if it were present, would open into Kupffer's vesicle, the posterior part of the archenteron. This is plausible as the lumen is much longer than the area of endoderm that arches the cavity before it is cut off from the periblast.

## DEVELOPMENT OF THE BRAIN

During the 16th day, the enlarged anterior end of the keel-like neural plate, the brain (br.), begins to be constricted from the epidermic layer of ectoderm, at its anterior end. At the same time two lateral optic areas (opt.) appear as protruberances near the anterior end (Fig. 19). By the 18th day the brain is entirely constricted from the ectoderm, leaving its dorsal surface rounded. In the optic vesicles (opt. ves.) a fissure appears forming a narrow lumen (Fig.20). In the region of the future midbrain there is a median fissure, the neurocoele, not yet continuous with the lumina of the vesicles. The neurocoele develops anteriorly and posteriorly and at the same time the connection is established with each optic vesicle by separation of the intervening cells (Fig. 21). Its posterior development in the brain is completed before the 20th day at which time it extends into the neurochord to the region anterior to the primitive streak.

As it first appears the neurocoele is a vertical

fissure with thick lateral walls but thin dorsal and ventral walls. This structure remains for a few days though the neurocoele may become slightly broader (Fig. 21).

A notable change now takes place giving distinction to certain regions of the brain. As early as the 20th day, lateral development takes place in the regions of the mid-brain (m. br.) or mesencephalon and hindbrain (h. br.), establishing a definite mesocoele and metacoele (Fig. 22). The intervening region does not develop appreciably and by the 25th day appears as a deep construction, the isthmus (Fig. 23- isth.). Before this time, the anterior end of the brain begins its lateral development, forming the telencephalon (telen.), which is separated from the midbrain by a narrower part, the diencephalon (dien.) The lumina of these two parts are the prosocoele and diacoele respectively.

There are fairly definite limits to the different parts of the brain though they pass gradually into the adjacent regions (Fig. 23). In transverse section there is considerable difference in structure of the various regions.

The prosocoele is almost square at its widest point (Fig. 24), but narrows anteriorly and posteriorly. The diacoele is narrower (Fig. 25) and is produced ventrally into a small diverticulum, the infundibulum (inf.), which appears first at this time. The walls of these regions are of about the same relative thickness as those of the earlier embryos. At its greatest extent the large mesocoele (Fig. 26) is

rather cruciform in shape. The latero-ventral walls are becoming thick in the region of the crura cerebri. The dorsal wall is thin medianly but thickens laterally. The lumen of the isthmus, the iter, is narrow and considerably depressed. Its walls, with the exception of the ventral, are thick. The hindbrain (Fig. 27) is triangular with its apex placed ventrally. The latero-ventral walls are very thick and are separated by a fissure. The dorsal wall is a single layer of non-nervous tissue, the choroid plexus, (chor.pl.), except at the extreme anterior end where it is several cells thick. This anterior thickening is the metencephalon or cerebellum and the remainder of the hindbrain, the melencephalon or medulla oblongata.

From this stage the development of the parts of the brain already described may well be taken separately. The important changes are not so much in the relative sizes of the parts but in the distribution of the nervous matter and hence the thickness of the walls.

The myelencephalon during its development increases in size. This increase is due to a greater thickening of the nervous part. Thus the metacoele becomes relatively smaller as the ventral and ventro-lateral walls become thickened. At the time of hatching (Fig. 28) the medulla (med.) consists of two thick latero-ventral bands of nervous tissue with the metacoele dorsal to them, and the dorsal non-nervous choroid plexus (chor. pl.). By the time the yolk is absorbed the floor of

the metacoele has become even thicker. Anteriorly the choroid plexus ends at the posterior basal edge of the cerebellum. Posteriorly the medulla passes gradually into the spinal cord by a thinning of the floor and a thickening of the roof of the lumen.

The cerebellum until shortly before the 80th day consists of a thickened mass of cells at the anterior end of the choroid plexus. At this time however an evagination takes place. The walls remain several cells thick and enclose the cerebellar lumen or epicoele. The cerebellum develops posteriorly dorsal to the choroid plexus of the medulla and is as broad as the medulla. By the time of hatching, it extends well over the medulla (Figures 28 and 29, cblm.), which it completely covers by the time the yolk is absorbed. The epicoele persists for some time after hatching, but is obliterated by a thickening of the walls, before the yolk is absorbed.

The midbrain develops greatly on the dorsal surface. Due to this development it gradually extends anteriorly over the diencephalon (Fig. 34, m.br.), and posteriorly over the cerebellum (Fig. 29, m.br.). By the time of hatching the diencephalon proper is completely covered. As the midbrain develops the mesocoele is reduced by the development of two longitudinal masses, the crura cerebri (cr. cer.), on its floor. The dorsal part by a median constriction becomes divided into the optic lobes (opt.l.) whose ventricles or optocoeles extend laterally (Fig. 30). The walls of the optic lobes remain thin in the mid-dorsal line where the

lobes are divided.

The diencephalon develops considerably laterally with and increase in the extent of the diacoele and a thinning of the dorsal wall. As early as 60 days it shows two large lateral swellings, the optic thalami (opt. th.), on the ventral wall. By the 80th day these thalami fill most of the space of the diacoele, which is a narrow vertical lumen with lateral extensions above the thalami. By this time the roof is a thin layer of epithelial cells, the choroid plexus. These characters are retained and the optic thalami show a slight thickening by the time the yolk is absorbed (Fig. 31).

In the telencephalon the dorsal wall thins and the latero-ventral walls become thickened about the same time as in the diencephalon. At the time of hatching the lateral thickenings, the corpora striata (corp. st.), almost meet in the middle line, and the dorsal wall, the pallium, has been a thin epithelial layer for some time. The prosocoele is reduced to a T-shaped cavity much the same as the diacoele (Fig. 35). The place of division of the forebrain is very indistinct up to the time the yolk is absorbed.

The infundibulum, mentioned above, develops posteriorly. About the 40th day a thickening appears in the ectoderm, slightly anterior to the mouth and immediately ventral to the posterior end of the infundibulum. It at once becomes invaginated and remains connected to the exterior for several days (Fig. 32). About the 45th day it loses its connection

becoming the pituitary body, in close contact with the infundibulum (Fig. 33). At first the cells are epithelial in character, but shortly after it loses its connection with the ectoderm the cells become loosely arranged and the whole mass glandular in appearance. It persists in close contact with the ventral wall of the infundibulum which is thin in this region (Fig. 30, pit.).

The infundibulum until about the 80th day has a single cavity and extends scarcely to the posterior end of the pituitary body. At this time however it gives off two lateral diverticula, the lobi inferiores, which grow posteriorly. At the time of hatching these do not extend beyond the end of the infundibulum and pituitary body which lie below the midbrain but by the time the yolk is absorbed they extend beyond these to the anterior end of the hindbrain. At this time the lobes (l.inf.) are distinct from the infundibulum (inf.) except at their anterior ends where their walls are continuous and their cavities join (Fig. 30).

About the time that the lobi interiores begin to develop the posterior end of the infundibulum begins to develop posteriorly forming the saccus vasculosus. At the time of hatching this extends slightly beyond the end of the pituitary body and by the 156th day slightly beyond the end of the lobi inferiores. The cavity of the saccus vasculosus is irregular and is connected by a narrower portion with the cavity of the infundibulum.

About the 45th day, at the time the pituitary body is separated from the ectoderm, a narrow evagination shows on the dorsal surface of the diencephalon near its posterior margin. This is the pineal body (Fig. 34, pin.). At first its walls are one cell thick and the cavity is flattened, but as it develops anteriorly its walls become thicker and it assumes an ovoid form. Its lumen at first flattened assumes the same shape. As it lengthens, it becomes broader and more flattened due to the limited space except at the posterior extremity which retains its original form. By the time the yolk is absorbed the anterior end of the pineal organ is glandular (Fig. 31, pin.) in appearance and much larger than the posterior region where the lumen is a mere fissure though the cells retain a columnar arrangement.

Before the 70th day another outgrowth appears on the dorsal surface of the diencephalon anterior to the pineal organ. This outgrowth, the paraphysis, is large and thin walled. Soon it begins to extend anteriorly beneath the pineal organ. By the 156th day it is a thin walled chamber almost as broad as the forebrain (Fig. 31, par.) and extending well forward dorsal to it beyond the anterior end of the pineal organ. The cavity of paraphysis retains its broad opening into the diacoele.

The telencephalon persists as an undivided body (Fig. 35). Its posterior limit is indefinite as no transverse fissure is indicated between it and the diencephalon.

Prior to the time of hatching two antero-ventral thickenings appear, one on each side of the median line. These develop anteriorly to form the olfactory lobes. By the time the yolk is absorbed they project considerably beyond the end of the prosencephalon to which they are attached by short olfactory tracts (Fig. 33, olf. t.) and touch in the median line. At this time there is no indication of lumina in them.

## THE EYES

By the 16th day, as mentioned under the development of the brain, two solid proliferations of cells arise near the anterior end of the brain, the future forebrain. The place of origin is the mid-lateral part of the brain and the protruberances develop laterally (Fig. 19). Before two days have passed a lumen appears in the outgrowths forming the optic vesicles. Due to the restricted space for development the lumen appears as a flattened cavity (Fig. 20). At the lumen appears the cells of the walls, which are several cells thick, assume a radial arrangement. At this time the lumen does not continue into the optic stalk. About this time a thickening, the lens, appears as a thickening in the ectodermal layer and pushes against the dorsal edge of the vesicle, forcing the corresponding edge inward till it lies closely against the remaining part of the wall. This makes the lumen of the vesicle a mere fissure (Fig. 21). About the same time the lumen becomes continuous with the brain by a separation of

the cells of the optic stalk (opt. st.). The proximal layer by this time is thin and the distal layer thick.

The position of the eye changes gradually and by the 25th day it lies opposite the narrow part of the brain anterior to mid-brain (Fig. 23). This is somewhat posterior to the position in which it originally lay. As a result the optic stalk joins the brain in front of the anterior margin of the eye. The optic stalk at this time joins the brain at the ventro-lateral margin, considerably ventral to its original position. The lumen of the stalk persists for some time.

By the 21st day the thickened lower layer of ectoderm that forms the lens is definitely invaginated. Soon the external margins of the lumen grow together and the opening is almost closed. In the interior of the lens, the lumen is almost filled by a loose mass of cells proliferated from the proximal part of the outer columnar layer (Fig. 24,l.). The lumina is always separated from the exterior by the outer or epidermal layer of the ectoderm.

The margin of the optic cup becomes thinner and grows around the lens, which has assumed a spherical form, except in one place where lack of growth on the ventral margin leaves the choroid fissure. The choroid fissure extends from the rim of the cup to the optic stalk which closes and folds to form a groove along its ventral margin. The lumina of the lens is closed by the 30th day and the lens itself is almost separated from the ectoderm.

By the 35th day the lens is separated from the ectoderm and the margin of the optic cup overlaps the lens except at the choroid fissure (ch.fis.) through which mesodermal cells are at this time entering the cup. In no case were more than a few free mesodermal cells (mes.) observed in the cavity of the optic cup, and these were all close to the choroid fissure (Fig. 36). The choroidal fissure at this time is oblique and somewhat posterior to the lens. It extends from the distal edge of the optic cup to the point where the optic stalk is attached to the cup. At the time of hatching the edges of the cup at the fissure are definitely fused (Fig. 29).

As mentioned above the distal wall of the double walled cup becomes noticeably thick and the proximal wall very thin as early as the 20th day. The former layer is the retina (ret.) and the latter the pigmented epithelium (pig.). By the 25th day the mesoderm (mes.) extends into the region of the eye where it rapidly proliferates (Fig.24). Part of this mesoderm enters the eye by the choroid fissure and part becomes differentiated to form the choroid and sclerotic layers.

The retina becomes thicker as development advances and differentiates into the characteristic teleostean layers. By the 45th day nerve fibres from the distal surface of the retina pass through the choroid fissure (to the diencephalon) along the ventral side of the small flattened optic stalk which by this time has no lumen.

The pigmented epithelium by the 40th day becomes very thin and lies against the retina, obliterating the lumen of the primary optic vesicle. Shortly after this its distal surface becomes pigmented.

From the surrounding mesoderm, two other layers are formed. The inner of these is the choroid (chor.), a vascular layer and the outer, the sclerotic (scl.). These are distinct by the 80th day and by the time of hatching are separated by a pigmented layer, the argentea (Fig. 29, arg.).

By the time of hatching the choroid overlaps the lens (with the pigmented epithelium) while a thin continuation of retina extends to its margin. The pigmented layer lies closely against the lens. By the time the yolk is absorbed the pigmented layer and the choroid have developed farther forming the iris. At this time the lens is suspended in a thin membrane attached to a very small ciliary process on the inner side of the iris.

The sclerotic or external mesodermal layer encloses the eye except at the point where the optic nerve enters. On the distal surface it becomes attached to a single epidermic layer of cells, the conjunctive. This region, the cornea, corresponds to the outer margin of the iris from which it is separated by a cavity. Proximally, the sclerotic covers the optic nerve and is continuous with the dura mater of the brain.

## OLFACTORY ORGANS

Before the 25th day, a slight thickening appears in the inner layer of ectoderm on each side of the median line at the anterior end (Fig. 22, olf.). At first they are slightly dorsal but as the ectoderm becomes enfolded and separates the head region from the yolk, they become ventral in position. Within a few days the cells become proliferated to form thick hemispherical masses. At this time, they occupy a ventral position in front of the anterior margin of the optic cups. By the 40th day, the cells of these olfactory areas become elongated, and the areas themselves become more extensive and relatively thinner (Fig. 37, A.).

Shortly after the hypophysis is invaginated and separated from the ectoderm, the epidermic layer of the ectoderm (epi.) disappears toward the centre of the olfactory areas and these become invaginated, forming the olfactory sacs (Fig. 37, B. olf. s.). The lumina extend dorsally and posteriorly into the masses of cells, which are free from the epidermic layer at their posterior extremities.

Before the 60th day, the olfactory sacs are connected to the ventral surface of the telencephalon, near its extremity by strands of nervous tissue, the olfactory nerves. If this is merely a secondary position, as M'Intosh and Prince state, (Transactions of the Royal Society of Edinburgh, Vol. XXXV., part III - for the 1887 - 88, p. 763.) there is no indication of it.

Within the next two or three weeks the sacs become considerably deeper and the cells of the part away from the aperture are ciliated.

Subsequently, the epidermic layer (epi.) seems to become invaginated. Thus at the time of hatching the sensory part (cil. epith.) of the sacs are sunk below the surface and the lumina are connected with the exterior by narrower cavities, whose walls are non-nervous. At this time the external apertures, the nares, are lateral and slightly dorsal in position.

The only notable change that takes place after hatching is in the nares. Soon after hatching, an outgrowth arises from the ventral margin of the lumen at the exterior. This extends dorsally as it develops, and finally reaches the mid-dorsal margin, with which it fuses. Thus two external nares are formed and open separately into each olfactory sac, prior to the total absorption of the yolk.

Considerable difference in the rate of development of the right and left olfactory sacs is apparent, when the embryo lies more on one side than on the other. In this case, the one that lies more below the embryo develops more slowly.

## AUDITORY ORGANS

About the 18th day, at the time the lens of the eye begins to develop, two thickenings appear in the deeper layer of the ectoderm, posterior to the eyes. These thickenings soon become invaginated (Fig. 39), and the cavity formed is

separated from the exterior by the thin epidermic layer (epi.). By the 20th day, distinct auditory sacs are formed (Figures 22 and 27, ot.).

Very soon the auditory sacs are enclosed by the ingrowth and fusion of the lips of the sacs. Each auditory vesicle at this time is spherical except on the mid-dorsal surface, where the endolymphatic cavity is continued into a narrow process, the primitive endolymphatic duct (Fig. 27, end. d.). By the 25th day the vesicle is more compressed laterally due to the limited space between the nerve cord and the lateral epidermal layer (Fig. 27).

The walls of the vesicles become thinner as the vesicles increase in size, except mid-ventrally. This is the ganglionic part of the vesicle and by the 40th day it receives the auditory nerve.

As the vesicles become larger, the dorsal wall, external to the base of the endolymphatic duct, develop dorsally. By the 40th day, due to this growth, the endolymphatic duct is attached to the mid-lateral wall of the vesicle and its distal end does not reach to the dorsal surface of the vesicle.

About this time, pairs of ridges grow into the lumen in the positions of the future canals (Fig. 40). The couples meet and fuse, so that the cavity cut off by each pair is continuous at each end with the lumen of the vesicle. The post-

erior canal develops later than the anterior and horizontal canals. Each rudimentary canal then begins to enlarge and in the middle becomes raised from the surface of the vesicle.

At this time the endolymphatic cavity first shows some indication of division into utriculus and sacculus. A ridge appears along the external lateral and posterior walls, imperfectly dividing the cavity. The posterior wall at the same time becomes infolded along the ridges. From the posterior wall of the sacculus, a small hollow outgrowth, the lagena, first appears about the 60th day.

By the 80th day, the septum, growing in from the posterior wall, reaches to the point where the endolymphatic duct opens into the endolymphatic cavity, and it is slightly dorsal to the opening of the duct, placing the opening in the wall of the sacculus. The sacculo-utricular canal is at this time very wide, but soon an antero-ventral constriction narrows it. By the time of hatching the canal is greatly reduced.

About the same time as the antero-ventral wall becomes constricted, the ampullae are formed by constrictions of the wall of the sacculus around the anterior apertures of the anterior and horizontal canals and around the posterior aperture of the posterior canal. These are definitely formed by the time of hatching.

The parts described constitute part of the membranous labyrinth. The walls of the labyrinth become truly sensory in certain regions, with which fibres of the auditory nerve are

related. By the 60th day thickenings of the floor of the labyrinth appears in the regions where the ampullae later develop, on the floor at the anterior end of the imperfectly differentiated utriculus and on the inner ventro-lateral wall of the sacculus and lagena. When the ampullae and anterior septum between the sacculus and utriculus develop, these thickenings are limited to definite regions, one to each ampulla; one to the floor of the utriculus, anterior to the sacculus and lagena. The sensory areas in the ampullae (Fig. 30, amp.) that in the utriculus, and that in the sacculus and lagena become respectively the aristae acusticae (Fig. 30, ar. ac.), the macula acustica neglecta, and the macula acustica. By the 90th day the sensory areas are ciliated. At the time the yolk is absorbed, the aristae and maculae are characterized by long and short stout cilia, respectively.

Two otoliths develop in the membranous labyrinth. As early as the 50th day, they are quite distinct - a very small one at the anterior end and a larger one at the posterior end of the sacculo-utricular cavity. The antero-ventral constriction, that divides the cavity, places the smaller one in the anterior end of the utriculus and the larger one in the sacculus. By the time that the yolk is absorbed, the utricular otolith is still small and rests on the macula acustica neglecta. The saccular otolith (Fig.41, oto.) becomes so large that it occupies most of the cavity. It lies just external to the macula acustica (mac. ac.).

Shortly after the semicircular canals are formed, cartilage begins to develop on all except the inner side of the membranous labyrinth (Fig. 41, m.lab.). By the time the yolk is absorbed, the membranous labyrinth is enclosed by the cartilaginous labyrinth (Fig. 41, cart.), except on the inner side where the perilymphatic cavity (p.ly.cav.) is separated from the cranial cavity by a fibrous partition.

## THE SPINAL CORD AND SPINAL NERVES

The spinal part of the solid, keel-like plate, whose origin is described above, becomes separated from the ectoderm after the brain is completely separated. The separation is first apparent at the anterior end of the cord and it progresses posteriorly. By the 20th day, it extends to the region of the primitive streak. The neurocoele, which also progresses posteriorly from the brain, by separation of the cells of the neural cord, appears in each region as soon as the cord is separated from the ectoderm.

The neurocoele, as it first appears, is a mere vertical fissure, whose dorsal and ventral walls are not more than two or three cells in thickness and lateral walls several cells thick. The inner lateral layers of cells divide rapidly increasing the thickness of the lateral walls (Fig. 46, sp.c.). At the same time the fissure becomes open to form a vertical ovoid lumen.

The walls at this time are composed of germinal cells. These divide rapidly in the lateral walls, increasing their thickness. As this division takes place, the germinal layer or dividing layer becomes thinner, and a layer of cells, the neuroblasts and neuroglia cells, is left external to it.

The neuroblasts develop nerve fibres that run longitudinally outside the nerve cells, forming the white matter of the cord. By the 40th day, the white matter (w.mat.) consists of two lateral bands of fibres. These become thicker as other neuroblasts develop fibres. From the ventro-lateral surface of these fibre tracts, the ventral roots (v.root) of the spinal nerves are given off, before the 50th day (Fig.49). The more central mass of cells may at this time be considered the gray matter (g.mat.).

About the 60th day, the ependyma or inner layer of germinal cells begins to obliterate the dorsal part of the central canal, by fusion of the oposing walls. This fusion continues and at the time of hatching the neurocoele (c.can.) is reduced to an almost circular opening, somewhat ventral to the middle of the cord. The dorsal fissure (d.fis.) persists as a non-nervous septum between the dorso-lateral bands of nervous tissue.

The lateral layers of white matter increase in thickness and extend gradually to the dorsal and ventral surface of the cord. By the 80th day, the fibres of the dorsal roots

can be seen entering the white matter near the mid-dorsal line. This completes the division of the white matter into the three characteristic pairs of funiculi - dorsal, lateral and ventral.

The gray matter becomes more differentiated into neuroblasts and neuroglia. At the time of hatching, it consists of a thick layer on each side of the neurocoele and dorsal fissure to the dorsal surface. Ventrally it is considerably thinner. By the time the yolk is absorbed there is no indication of true dorsal and ventral columns.

After hatching, ventral swellings are formed on either side of the median line. These project so far that they form a groove, the ventral fissure (Fig. 52, v.fis.). At the time that the yolk is absorbed, the two edges have come together and the fissure appears as a vertical line.

The dorsal roots of the spinal nerves are formed by the growth of fibres to the dorsal surface of the cord near the median line, from the spinal ganglia. These ganglia are formed from cells, that become separated from the dorso-lateral surface of the cord about the 25th day. These grow down segmentally around the side of the cord to the region immediately above the ventral roots, where the cells form the spinal ganglia (Fig. 52, sp.gang.). Each cell develops a fibre at each end. One of these fibres grows to the dorsal root while the other grows to the ventral root and peripherally with the fibres of that root. By the 80th day fibres from the ganglia reach the spinal cord, forming the dorsal roots (d.root.).

At first the spinal cord is thicker dorso-ventrally than laterally. Due to the lateral thickening of the walls, it is about round at the 50th day (Fig. 45). The lateral thickening continues, making it much thicker laterally than dorso-ventrally. When the thickening of the ventral wall takes place, the form becomes again approximately round (Fig. 49).

## THE DIGESTIVE SYSTEM

The first indication of the enteric canal is the formation of Kupffer's vesicle. About the 18th day, in the posterior region of the embryo, where the endoderm and notochord are fused, the endoderm becomes columnar and raised off the periblast, forming a shallow cavity, the vesicle (Fig. 18-A, k.v.). This marks the extreme posterior limit of the digestive system, when it develops.

Those parts of the system, that persist throughout life, are formed by a folding of the endoderm subsequent to a thickening of the same. As in the case of the other systems, the anterior region develops first.

Very shortly after the vesicle is formed, the endoderm along the middle line becomes thickened to the branchial region, where two lateral thickenings converge to meet it. The thickenings are more pronounced at the anterior end, where folding is about to commence.

The two thickenings at the anterior end become more

pronounced and form two folds (Fig. 39, end.) which grow towards the middle line, gradually enclosing the branchial cavity (Fig. 42, end.). Folding begins at the extreme anterior end of the thickenings, ventral to the otocysts (ot.), and progresses posteriorly. In this way, the anterior end of the branchial cavity is enclosed first by the fusion of the folds along the mid-ventral line. The point of fusion of the folds gradually moves posteriorly.

By the 20th day, the branchial cavity is completly enclosed. It is broad at its anterior end (Fig. 27, br.cav.) and narrows posteriorly. Throughout it is flattened dorso-ventrally, making it slit-like. Posteriorly the folding is continued on each side of the thickened median endoderm. More posteriorly, folds gradually merge with the flattened endoderm.

By this time, the endoderm around the margin of Kupffer's vesicle is sharply marked, preparatory to ingrowth. Within the next day, the vesicle is cut off from the periblast, by the ingrowth and fusion of the endoderm. In this condition, it is a narrow elongated opening, completely enclosed by endoderm (Fig. 18-B, k.v.). Anterior to the vesicle, the endoderm is thickened to form the rudimentary post-anal gut, which does not develop farther.

By the 21st day, the oesophageal region of the canal is completely formed and the folds extend well back in the intestinal region. In the anal region the cells show a decided

columnar arrangement. This shows the anterior limit of the post-anal gut.

At this time the lateral walls of the branchial cavity (br.cav.) at its broad anterior end are fused with the ectoderm, and a pair of narrow openings, the first branchial clefts (br. cl.1.), open to the perivitelline cavity. The oesophagus is narrow and flattened dorso-ventrally, making its lumen slit-like.

During the day, the folds in the stomach region fuse and a narrow diverticulum of the ventral wall posterior to this appears. This is the primordium of the liver (Fig. 44, lr.).

By the 24th day, Kupffer's vesicle is obliterated by the surrounding endoderm and the caudal knob, which is separated from the periblast by the tail-fold, renews its posterior development. The post-anal gut is still distinguishable, but its posterior end is separated from the periblast by the tail-fold. At this time, the intestine is partly formed and the endodermal folds extend almost to the anal region. The liver at this time is still very small and no part of it is distinctly separated from the enteric canal. It extends farther ventrally and posteriorly. Its lumen throughout is distinctly joined to that of the enteric canal.

The branchial cavity shows some development at its anterior end as it extends to the posterior margin of the mid-brain. As far as could be determined, this anterior portion

is formed by a splitting of the endoderm.

Before the 26th day, the endodermal folds meet and fuse in the anal region of the intestine. Posterior to the anal region, the endoderm of the degenerated post-anal gut (p.a.g.) is continued as a rod of loosely arranged cells immediately ventral to the notochord. It is separated from the periblast by the tail fold (t.f.) which, at this time, reaches to the end of the intestine (an.). Its posterior end cannot be distinguished as it is undifferentiated from the surrounding mesoderm.

It is notable, that the endodermal folds seem to draw the endoderm away from the lateral margins of the embryo (Fig. 39), though the folds do not appear at the margins. At any rate, when the folds form, no endoderm can be found at the margin (Fig. 42) and, when the folds meet in any region, no endoderm can be found in the region except that contained in the enteric canal (Figures 43 and 44). As this is the case, it would seem that the endoderm is, with the exception of that which forms the post-anal gut, entirely contained in the enteric canal. The endoderm of the post-anal gut disappears, apparently absorbed by the surrounding tissue.

By the 30th day the liver is considerably larger and extends posteriorly, ventral to the enteric canal. The distal portion is greatly expanded and contains a single large lumen with thick walls. The whole is dorso-ventrally compressed and extends laterally on each side of the canal.

About this time, the splanchnic mesoderm (sp.mes.), which completely encloses the tract (ent.), begins to assume a regular arrangement of its cells. These form at least a double layer around the endodermic enteric canal (Fig. 46). This is the primordium of the outer layers of the digestive tract.

The branchial region shows considerable development. The ectoderm and endoderm are fused on the ventral side of the cavity, forming the oral plate. This area is of small size and ventral to the anterior margin of the otocysts. There is no true invagination of the ectoderm at this point to form a stomodaeum, even when the oral plate breaks through as it does by the 35th day (Fig. 47, mth.).

Posterior to the first gill clefts, three pairs of pouches have begun to develop by the 30th day. These are formed by a thinning of the mesoderm and hollow outgrowth of the endoderm to meet the ectoderm. As in other systems, development progresses posteriorly from the anterior end. Thus at the time the endoderm of the first pair of pouches is fused with the ectoderm, the third pair of pouches is slightly indicated by a pair of furrows.

By the 35th day these three pouches have broken through, forming the second, third and fourth gill clefts (br. cl.2,3,4), and the first, second and third interbranchial septa, and another pair of pouches are partly formed. Each inter branchial septum is covered externally with ectoderm, internally with

endoderm, and has a central axis of mesoderm. In the next few days the fourth visceral pouch breaks through, forming the fifth gill cleft, and the fourth interbranchial septum. This cleft is immediately anterior to the developing pectoral fin buds and slightly dorsal to them.

In observing the appearance of the gill clefts from the exterior, it is noticeable that each cleft forms immediately after the head fold extends to that particular region.

About the 40th day another diverticulum is given off from the same region as the liver but slightly dorsal to it. The distal end of this becomes enlarged. This is the ventral pancreas (pn.) and the tube joining it to the intestine is the pancreatic duct which persists throughout life (Fig. 48).

By the 40th day, the diverticulum that forms the liver is much enlarged distally, forming the liver proper. Its anterior or proximal portion is constricted in a narrow tube, the bile duct (Fig. 48, b.d.), which is enlarged, where it joins the liver, to form the sac-like gall bladder. The gall bladder is enclosed by the liver except on its ventral surface which touches the periblast. The cells of the proximal portion of the liver are arranged in definite tubules, which connect with the gall bladder. More distally the tubules are rudimentary and at the extreme posterior extremity are totally undifferentiated.

At this time, there is a slight enlargement of the

digestive tract just anterior to the point where the bile duct opens into the intestine. This is the primordium of the stomach.

By the 45th day, a small diverticulum appears in the dorsal wall of the intestine, slightly posterior to the bile-duct. This is the dorsal pancreas (d.pn.) and its distal end develops as the ventral pancreas and fuses with it. Its duct disappears within a few days. The posterior end of the intestine is curved ventrally and lies against the ectoderm with which it fuses to form the anal plate. There is no sign of invagination of the ectoderm (proctodaeum) either at this time or a few days later, when the anal opening (an) is formed by the separation of the cells of the anal plate (Fig. 50.).

The stomach, at the time the anal opening is formed, is slightly larger than the remainder of the tract. The endodermal portion of the walls is beginning to show longitudinal ridges, which very soon become definite villi. The splanchnic mesoderm in this region is very much thicker than elsewhere.

The primordium of the swim bladder (s.b.) appears, before the 60th day, as a thick walled endodermal diverticulum at the anterior end of the stomach (Fig. 51). At the time of its appearance, its relation to the stomach and intestine is indefinite but it later appears to be more closely related to the anterior or cardiac end of the stomach. As it develops, it extends dorsally and posteriorly. At the time of hatching it becomes short, not extending beyond the posterior end of the stomach. By the time the yolk is absorbed, it extends well

back in the abdominal cavity immediately ventral to the kidney, and is divisible in two distinct parts. The anterior portion, the pneumatic duct is thick walled and has a narrow lumen. The posterior portion, the swim-bladder proper, is thin-walled and has a large lumen.

The pancreas, whose double origin has been given above, develops considerably in size and at the time of hatching lies along the intestine close to the muscular layer. Its duct is short and opens into the intestine slightly dorsal to the bile-duct. This position is retained.

The liver develops greatly in size and extends over the surface of the yolk. At the time of hatching very little of it is anterior to the point where the bile-duct enters the intestine and this part contains the gall-bladder. Later however its position changes and most of it is anterior to the stomach.

About two weeks before the time of hatching the gill filaments (g.f.) appear as two rows of finger like processes on the external surface of the interbranchial septa (Fig. 29). On the internal surface of the operculum a smaller row, the hemi-branch, develops. Due to the presence of the operculum, the gill arches which show the curve characteristic of the adult and the gill filaments are bent posteriorly. Thus each row of filaments overlaps and lies exterior to the one posterior to it (Fig. 28).

The inner or endodermal portion of the stomach and

intestine becomes raised into villi. The splanchnic mesoderm forms an inner layer of circular muscles and an outer layer of longitudinal muscles from the anterior end of the oesophagus to the anal opening. Subsequent to the time of hatching a double flexure appears in the stomach making it S-shaped. The first flexure between the cardiac and pyloric stomachs places the pylorus beside the cardia. At the point where the flexure takes place the stomach is continued posteriorly into the median caecum. The second flexure is between the pylorus and intestine. From that point the intestine passes as a straight tube to the anal opening. Before the yolk is completely drawn into the body cavity numerous small diverticula from the pylorus form the pyloric caecae.

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## ABBREVIATIONS USED IN THE FIGURES

| | |
|---|---|
| amp. | Ampulla |
| an. | Anus or anal region |
| a.p. | Anterior pole |
| ar.ac. | Arista acustica |
| arg. | Argentia |
| b.d. | Bile duct |
| b.p. | Blastopore |
| br. | Brain |
| br.cav. | Branchial cavity |
| br.cl.1-4. | Branchial clefts 1 - 4 |
| cart. | Cartilage |
| cblm. | Cerebellum |
| c.can. | Neurocoele |
| ch.fis. | Choroid fissure |
| chor. | Choroid |
| chor.pl. | Choroid plexus |
| cil.epith. | Ciliated epithelium |
| cl.1 - 3. | Cleavage furrows1- 3 |
| corp.st. | Corpora striata |
| cr.cer. | Crura cerebri |
| d.fis. | Dorsal fissure |
| dien. | Diencephalon |
| d.pn. | Dorsal pancreas |
| d.root | Dorsal root |
| emb.sh. | Embryonic shield |
| end. | Endoderm |
| end.d. | Endolymphatic duct |
| ent. | Enteron |
| epi. | Epidermal layer of the ectoderm |
| g.f. | Gill filaments |
| g.mat. | Gray matter |
| g.r. | Germ ring |
| g.w. | Germ wall |
| h.br. | Hind brain |
| inf. | Infundibulum |
| isth. | Isthmus |
| k.v. | Kupffer's vesicle |
| l. | Lens |
| l.inf. | Lobi inferiores |
| lr. | Liver |
| mac.ac. | Macula acustica |
| m.br. | Mid-brain |
| med. | Medulla |
| med.pl. | Medullary plate |
| mes. | Mesoderm |
| m.lab. | Membranous labyrinth |

| | | | |
|---|---|---|---|
| mth. | Mouth | pit. | Pituitary body or hypophysis |
| nu. | Nucleus | p.ly.cav. | Perilymphatic cavity |
| olf. | Olfactory area | pn. | Pancreas |
| olf.s. | Olfactory sac | pr.st. | Primitive streak |
| olf.t. | Olfactory tract | ret. | Retina |
| opt.l. | Optic lobe | seg.cav. | Segmentation cavity |
| opt.st. | Optic stalk | scl. | Sclerotic |
| opt.th. | Optic thalami | sp.c. | Spinal cord |
| opt.ves. | Optic vesicle | sp.gang. | Spinal ganglion |
| p.a.g. | Post-anal gut | telen. | Telencephalon |
| pal. | Pallium | t.f. | Tail fold |
| par. | Paraphysis | v.fis. | Ventral fissure |
| per. | Periblast | v.root | Ventral root |
| pig. | Pigmented epithelium | w.mat. | White matter |
| pin. | Pineal body or epithysis | y.p. | Yolk plug |

## EXPLANATION OF PLATES

### PLATE I

Fig. 1 Section through unsegmented blastodisc, x 28.

Fig. 2 Surface view of blastodisc after first cleavage, 1st day, x 28.

Fig. 3 Surface view of blastodisc after second cleavage, 1st day, x 28.

Fig. 4 Trans. section through blastodisc of four blastomeres, 1st day, x28.

Fig. 5 Surface view of blastodisc of eight cells, 1st day, x 28.

Fig. 6 Surface view of blastodisc of eight cells, 1st day, x 28.

Fig. 7 Surface view of multicellular blastodisc, 2nd day, x 28.

Fig. 8 Trans. section of multicellular blastodisc, 2nd day, x 28.

Fig. 9 Trans. section through blastoderm, 7th day, x 110.

Fig. 10 Trans. section through blastoderm, 10th day, x 28.

### PLATE II

Fig. 11 Surface view of blastoderm, 11th day, x 14.

Fig. 12 Surface view of embryonic shield, 13th day, x 8.

Fig. 13 Long. section through embryonic shield and blastoderm, 12th day, x 50.

Fig. 14 Surface view of medullary plate, 14th day, x 14.

Fig. 15 Series of trans. sections (A - E) from the posterior to the anterior ends, 16th day, x 80.

Fig. 16 Surface view of tail region, 18th day, x 32.

PLATE III

Fig. 17 Surface view of embryo, 22nd day, x 15.

Fig. 18 A. Trans. section through the region of Kupffer's vesicle, 18th day, x 80.

Fig. 18 B. Trans section through the region of Kupffer's vesicle, 21st day, x 80.

Fig. 19 Trans. section through the forebrain, 16th day, x 150.

Fig. 20 Trans. section through the forebrain and optic vesicles, 18th day, x 95.

Fig. 21 Trans. section through the diencephalon and one optic vesicle, 20th day, x 80.

Fig. 22 Surface view of the head region, 20th day, x 35.

Fig. 23 Surface view of the head region, 25th day, x 35.

Fig. 24 Trans. section through the diencephalon and one optic vesicle, 25th day, x 55.

PLATE IV

Fig. 25 Trans. section through the posterior part of the diencephalon, showing infundibulum, 25th day, x 55.

Fig. 26 Trans. section through the mesencephalon, 25th day, x 55.

Fig. 27 Trans. section through the medulla and otocysts, 25th day, x 55.

Fig. 28 Trans. section through region of the medulla, 101st day, x 20.

Fig. 29 Long. section of the head region near the median line, 101st day, x 15.

Fig. 30 Trans. section through the region of the midbrain, 156th day, x 15.

Fig. 31 Trans. section through diencephalon, paraphysis and pineal body, 156th day, x 21.

Fig. 32 Trans. section through infundibulum showing the origin of the pituitary body, 40th day, x 60.

Fig. 33 Trans. section through the posterior end of the infundibulum and the pituitary body, 45th day, x 60.

PLATE V

Fig. 34 Trans. section through diencephalon showing the origin of the pineal body, and the forward projection of the midbrain, 45th day, x 55.

Fig. 35 Trans. section of telencephalon showing olfactory tracts, 156th day, x 32.

Fig. 36 Long. section through the eye showing the choroid fissure and mesoderm entering the eye, 35th day, x 60.

Fig. 37 A. Trans. section of olfactory area, 45th day, x 150.

Fig. 37 B. Trans. section through olfactory sac, 50th day, x 150.

Fig. 38 Trans. section through olfactory organ at the exterior, 101st day, x 60.

Fig. 39 Trans. section through the hindbrain showing invagination of otocyst and beginning of the endodermal branchial folds, 18th day, x 150.

Fig. 40 Trans. section of auditory vesicle, 50th day, x 60.

PLATE VI

Fig. 41 Trans. section through ear, 156th day, x 30.

Fig. 42 Trans. section through hindbrain and partly formed branchial cavity, 19th day, x 80.

Fig. 43 Trans. section through the region of the hindbrain showing the first branchial cleft on one side, 21st day, x 60.

Fig. 44 Trans. section through region of the liver, 21st day, x 60.

Fig. 45 Median sagittal section of tail region, 25th day, x 60.

Fig. 46 Trans. section near anterior end of the body cavity, 30th day, x 60.

Fig. 47 Long. section (oblique) of the branchial cavity and clefts, 35th day, x 60.

PLATE VII

Fig. 48 Trans. section of intestine and bile duct showing the diverticulum of the ventral pancreas, 40th day, x 165.

Fig. 49 Trans. section through the region of the diverticulum of the dorsal pancreas, 45th day, x 60.

Fig. 50 Trans. section of intestine and anal opening, 50th day, x 160.

Fig. 51 Trans. section of the cardiac stomach and diverticulum of the swim bladder, 60th day, x 60.

Fig. 52 Trans. section of spinal cord, 101st day, x 150.

# Plate I.

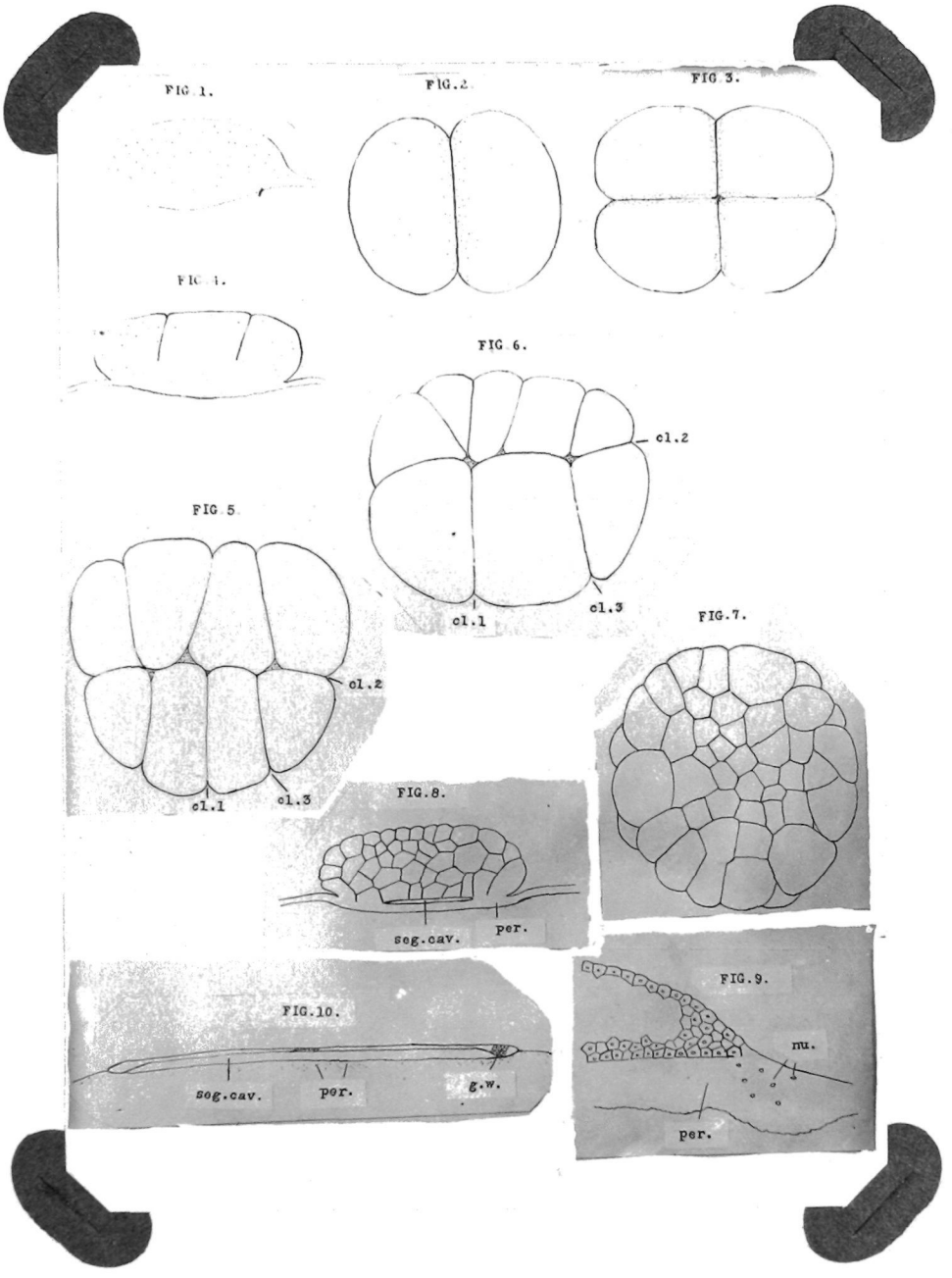
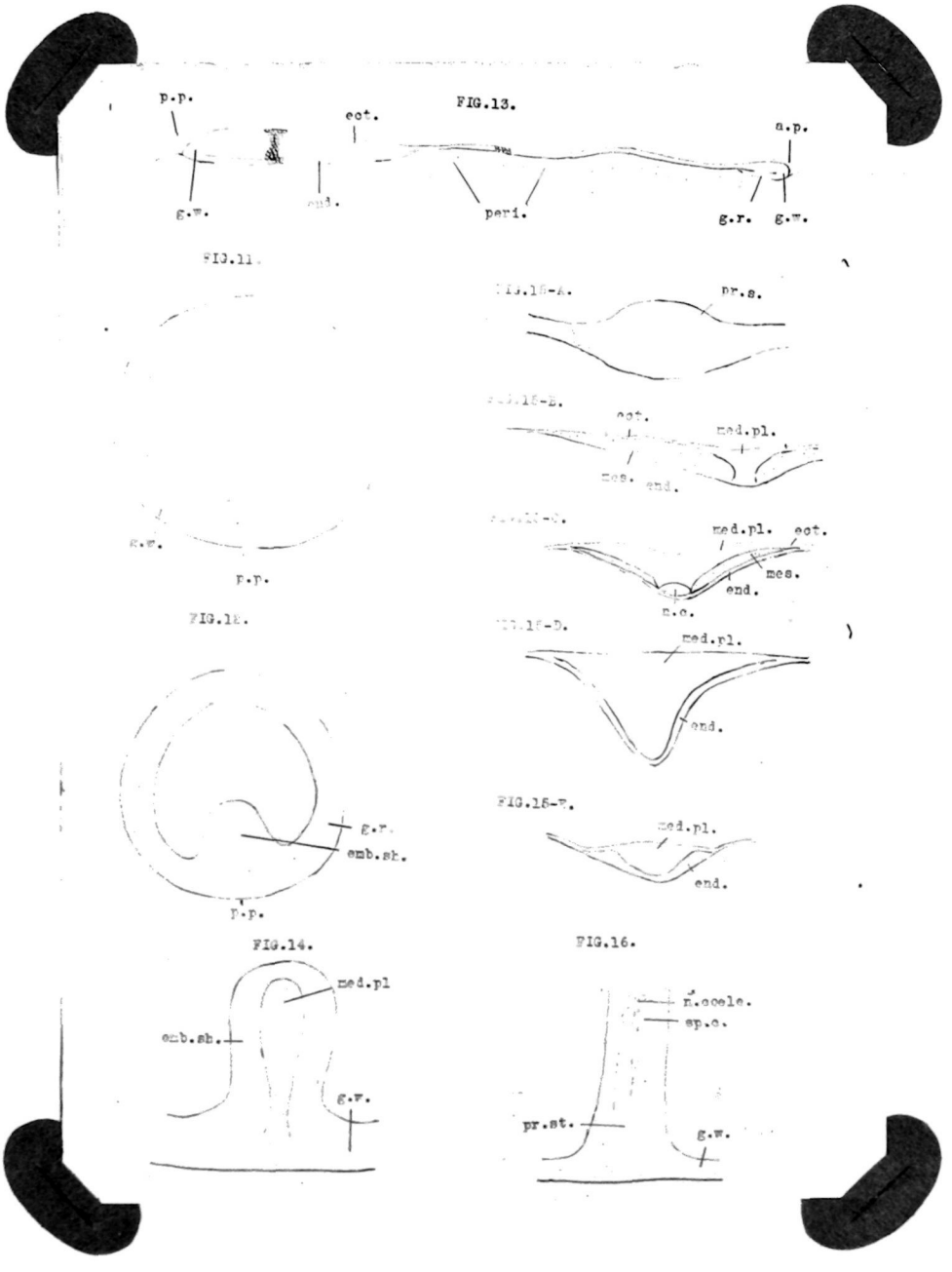
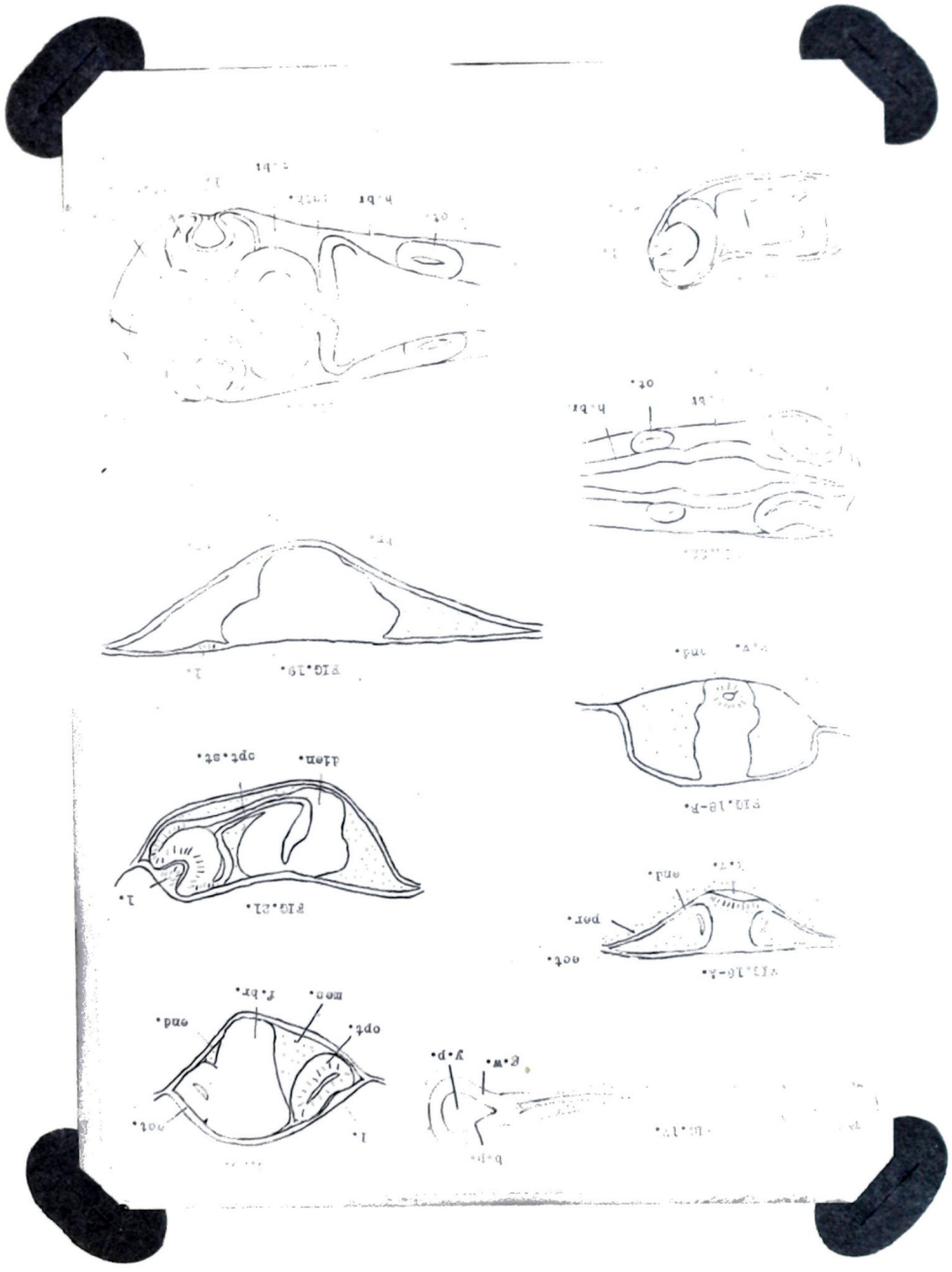


FIG.1.
FIG.2.
FIG.3.
FIG.4.
FIG.5.
FIG.6.
cl.2
cl.1
cl.3
cl.2
cl.1
cl.3
FIG.7.
FIG.8.
seg.cav.
per.
FIG.9.
nu.
per.
FIG.10.
seg.cav.
per.
g.w.

# Plate II.


p.p.
ect.
FIG.13.
a.p.
g.w.
emb.
peri.
g.r.
g.w.
FIG.11.
FIG.15-A.
pr.s.
FIG.15-B.
ect.
med.pl.
mes.
end.
FIG.15-C.
med.pl.
ect.
mes.
end.
n.c.
g.w.
F.P.
FIG.12.
FIG.15-D.
med.pl.
end.
g.r.
emb.sh.
F.P.
FIG.15-E.
med.pl.
end.
FIG.14.
FIG.16.
med.pl
emb.sh.
g.w.
n.ocele.
sp.c.
pr.st.
g.w.

# Plate III.



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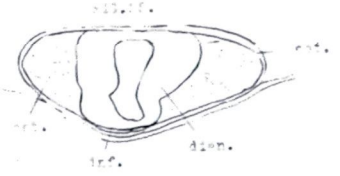




FIG.28.

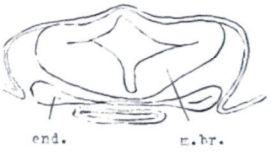




FIG.30.

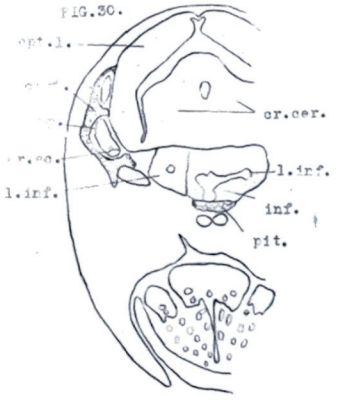



FIG.29.

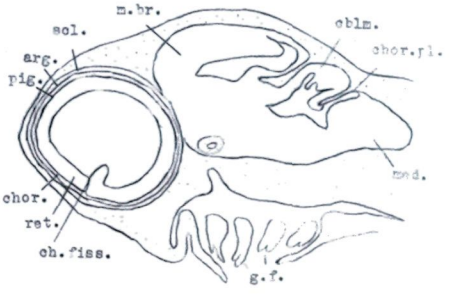



FIG.31.

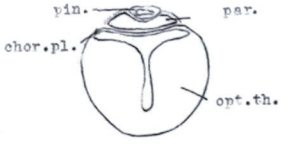



FIG.33.

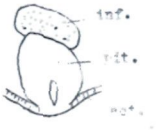
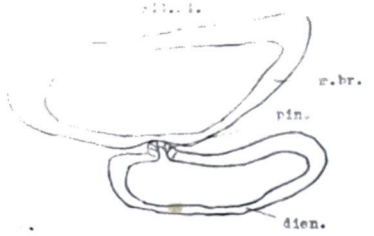



FIG.32.

# Plate V.



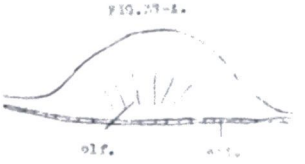




FIG.35.

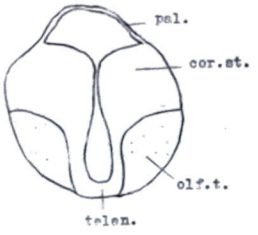



FIG.37-P.

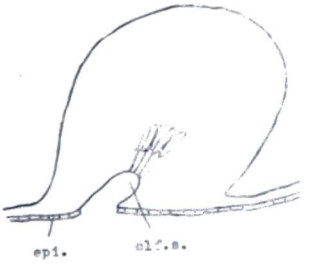



FIG.36.

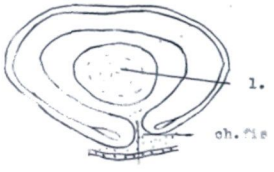



FIG.38.

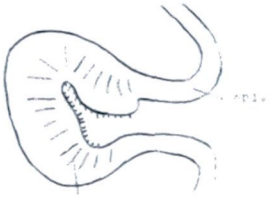
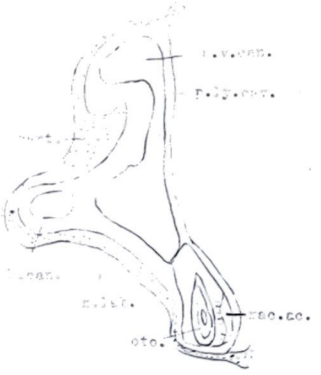



FIG.39.


FIG.40.

# Plate VI.



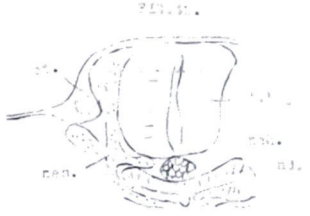




FIG.43.

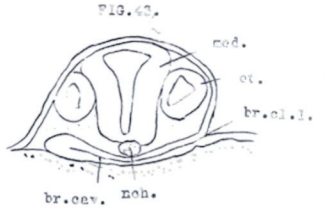



FIG.44.

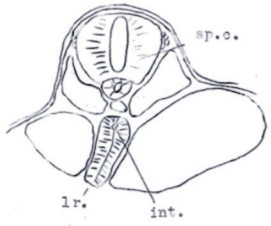



FIG.45.

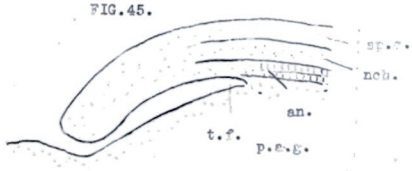



FIG.46.

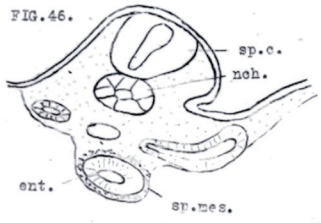
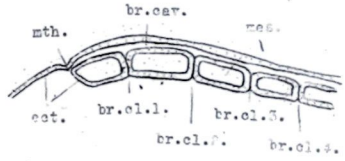



FIG.47.



# Plate VII.

FIG.48.

FIG.49.


FIG.50.

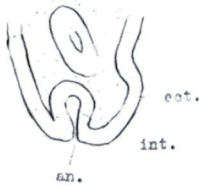



FIG.51.


FIG.52.