THE DEVELOPMENT OF THE LIVER AND PANCREAS IN AMBLYSTOMA PUNCTATUM.

A THESIS

SUBMITTED TO THE FACULTY

OF THE

GRADUATE SCHOOL

OF

THE UNIVERSITY OF MINNESOTA

BY

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In partial fulfillment of the Requirements

for the Degree of

Doctor of Philosophy

May 1915.

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(A thesis submitted to the Graduate School of the University of Minnesota in partial fulfillment of the requirements for the degree of Doctor of Philosophy).

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1. Introduction.

Comparatively little work has been done on the morphology of the biliary and pancreatic duct systems in vertebrates. The arrangement of these structures has been worked out in the adult forms of a few species but no attempt has been made to correlate these scattered observations or to determine what may be considered the typical arrangement in vertebrates and the major variations which may occur in the various groups of the phylum. The development of these systems is also almost unknown. Although the formation of the anlagen of the liver and pancreas has been investigated in almost every group of vertebrates, the later history of duct systems of these structures has been quite neglected. The two exceptions to this statement are furnished by the work of Corner ('13) who investigated the development of the pancreatic ducts of the pig by means of injection methods, and Scammon's study of the biliary system of selachians.

The following study is an attempt to follow in detail the development of these duct systems in the tailed amphibia, and to point out the embryologic significance of the principal variations which are encountered in the adult and the mechanical influences which are, in part at least, responsible for them. Although we are not as yet in possession of sufficient data to formulate a statement of the typical vertebrate plan of biliary and pancreatic duct systems, it is hoped that this description of these structures in a representative amphibian may add to the material upon which such a schema must eventually be based.

The material used for this work consisted of embryos of Amblystoma punctatum from a 4 mm. to 20 cm. in length. These were sectioned serially in transverse and sagittal planes. Graphic and wax reconstructions were made of the hepatic ducts, gall bladder, liver and pancreas of different embryos and adults.

A correlation of the embryos employed in this study with those described in the Normal Plates of Necturus maculosus by Eycleshymer and Wilson, may be desirable. This correlation is based on a comparison of the digestive system, liver and pancreas, as well as partially on the external form. Probably the greatest difference between the development of the digestive tract between these two forms is in the time of union of the dorsal and ventral pancreatic anlagen which had taken place in most of the 13 mm. Amblystoma embryos which I have observed, and is described in stage 42 (29 mm.) in the Normal Plate series of Necturus. Also the limbs, particularly the caudal ones, appear comparatively later in Amblystoma. Such a table of course can be only an approximate comparison.

Table I

Correlation of Amblystoma embryos with the Normal-plate series of Necturus

Figures	Embryos	Normal-plate series	
Figure	Length in mm.	Stage No.	Length in mm.
1	4.5	21	8
2	5	22-23	9
3	7	25	12
4	9	28	15
5	9	29	16
27-30	11	30	17
6	11.5	31	18
21	12.5	34	21
31,45	13		
18	13	38	25
19	13.5	39	26
8,39,40	14	42	29
7A,9,41	13.5	43	30
10,33,42,46	15	45	32
11,20,43	20	49	39

2. Literature.

The literature of the development of the great glands of the digestive tract of Amphibia can be conveniently divided into two parts covering two fairly distinct periods. First, the work of the early investigators who determined the position of these glands in the embryo and their relation to the lower germ layer. Second, the series of contributions beginning with Goette's large monograph upon the development of Bombinator ('75) and dealing mainly with the detailed developmental anatomy of these organs.

The following table gives a list of the authors, the dates of their publications and the material upon which their work on the development of the liver and pancreas was based.

Table II.

Table of authors and the forms studied.

Author	Date	Material
Steinheim	1820	Rana
Rusconi	1826	Rana
Reichert	1840	Rana temporaria " esculenta
Rusconi	1854	Salamdra
Vogt	1842	Alytes obstetricans
Remak	1855	Rana temporaria " esculenta
Rathke	1861	"Vertebrates"
Bambecke	1868	Pelobates fuscus
Goette	1875	Bombinator igneus
Wiedersheim	1875	Salamandra perspicillata
Balfour	1881	"Amphibia"
Shore	1891	Rana
Goeppert	1891	Salamandra maculata, etc. Bufo vulgaris, etc.
Marshall	1893	Rana
Minot	1893	"Amphibia"

Author	Date	Material
Weysse	1895	Rana temporaria " esculenta
Stöhr	1895	Rana temporaria
Hertwig	1896	"Amphibia"
Brachet	1896	Review
Hammar	1897	Rana
Woit	1897	Rana temporaria Triton taeniatus, etc.
Kollmann	1898	"Amphibia"
Gianelli	1899	Triton cristatus, ~~etc.~~
Choronshitzky	1900	Rana temporaria Salamandra maculosa, etc.
Reuter	1900	Alytes obstetricans
Granelli	1901-02	Triton
Piper	1902	Review
Weber	1903	Review
Braun	1906	Alytes obstetricans
Eycleshymer and Wilson	1910	Necturus maculosus
Baumgartner	1914	Amblystoma punctatum

Steinheim published the first observations upon the development of the liver in Amphibia. In 1820 in his "Entwickelung der Frösche" he noted the liver in a young embryo and its connection to the gut. The gall bladder he observed in a later stage. Also, he observed that the liver was later divided, forming three lobes.

Rusconi ('26) made some observations of embryos probably younger than those studied by Steinheim. He stated that the liver is derived from the ventral intestinal wall.

Reichert ('40) described the liver and pancreas as developing from the large yolk mass just caudal to the heart. In the course of the development of the duodenum and pancreas the liver is crowded somewhat to the right. It divides into four lobes (lappen) of which the caudal one becomes the gall bladder. The liver remains very closely attached to the pancreas, indeed, he regarded them as part of the same organ. A common duct then develops which receives a branch from the liver and one from the pancreatic anlage.

Vogt ('42) described the liver as developing as a solid cell mass on the anterior side of the yolk mass caudal to the heart.

According to Remak ('55) the liver of the frog and salamander arises as an outpouching of the ventral intestinal wall. This soon divides into two lobes (lappen). The gall bladder develops from the right lobe.

v.Bambecke ('68) agreed in the main with the description given by Remak.

According to Goette ('75), the liver in Bombinator originates as a ventral outpouching of the foregut posterior to the heart. This diverticulum becomes separated from the gut by a gradual cranio-caudal constriction, and the narrow connection which remains forms the common hepatic duct. The outpouching then grows by the production of folds or buds from its sides which form the primary hepatic columns. The lumina remain in these columns although they may be very small. Goette regarded the early anastomoses and formation of the net-like hepatic cylinders as aided by the ingrowth of a capillary network. The gall bladder develops as an outpouching of the posterior part of the primitive hepatic duct caudal to which the ductus choledochus is formed.

Balfour ('81) made the statement that there is a single ventral diverticulum from the gut which later develops into two secondary branches and so forms the liver.

Shore ('91) in his study on the frog found that the liver takes origin as a ventral lengthening of the gut lumen into the mass of yolk cells which lies posterior to the heart. The yolk cells lining this lumen are transformed into hepatic cells and this mass becomes partially separated from the gut. This constriction is aided by the caudal growth of the sinus venosus. Later there is formed at the expense of the yolk cells and by cell division a large cell mass into which the blood vessels tunnel forming a tubular gland, whose columns divide and anastomose producing a network interlacing with that of "blood lacunae".

Marshall ('93) gave a brief account of the development of the liver in the frog in his vertebrate embryology. He described a caudo-ventral projection from the anterior part of the mesenteron. The anterior wall of this depression is thrown into folds, blood vessels penetrate between these structures and outgrowths from the hypoblast form the hepatic cylinders.

Weysse ('95) found in the frog that the liver anlage is a dorso-ventral cleft extending into the yolk mass from the gut lumen. A caudal extension of this cleft forms the posterior hepatic duct, while the cranial hepatic duct is formed by a folding of the anterior wall of the hepatic anlage. The yolk cells are transformed into the true hepatic cells and can be early recognized by the deposit of pigment within them.

Hertwig ('96) and Kollmann ('98) gave only short descriptions, stating that in Amphibia the hepatic anlage is a single outpouching from the ventral wall of the duodenum.

Hammar ('97) who worked on the development of the frog's liver, has named the entodermal cell mass posterior to the heart the "Leberprominenz". Into this extends an early lengthening cavity which is continuous with the lumen of the gut. This he termed the "Leberbucht". By a cranio-caudal constriction this hepatic anlage is separated from the gut. The cell mass about the fundus of this anteriorly directed sac develops into trabeculae of the adult organ and the posterior part forms the ductus choledochus. The gall bladder is developed very early as a diverticulum of the ventral wall of the common bile duct, and by further growth comes to be a pedunculated organ, consisting of a cystic duct and gall bladder proper. He regarded the origin of the trabeculae as perhaps due partially to the developing capillary network tunnelling into the hepatic cell mass as suggested by Shore.

Choronshitzky ('00) showed the anlage of the liver in the salamander in a figure of a sagittal section of a 9 mm. embryo, in which there is a ventral fold in the wall of the foregut. This fold is lined with yolk laden cylindrical cells which posteriorly pass gradually over into the polygonal yolk cells which form a mass projecting into the lumen of the gut. In the anterior ventral wall of the gut is a second slight pouch which later forms the gall bladder. The two omphalo-mesenteric veins crowd in on either side of the liver outpouching, thereby aiding the constriction of the lateral walls of the gut. These veins unite anteriorly and form the ductus venosus. The liver anlage therefore first grows ventrally and then anteriorly below the horsehhoe shaped union of the omphalo-mesenteric veins and the ductus venosus. A similar sagittal section of a later stage shows the liver at the cranial end of a short ductus hepaticus which is continuous caudally with the ductus choledochus. From the ventral wall of the ductus choledochus there is now a very marked outpouching, the gall bladder, which is united with the common duct by a short cystic duct. The primitive liver anlage has thus grown cranialward and become separated from the gut. Choronshitzky believes this process to be due to the growth and differentiation of the gut. The walls of the primitive liver anlage have folded and these folds later develop into solid liver columns. The liver grows around the developing ductus venosus even to its dorsal surface and in so doing produces many folds and columns which grow through the ductus venosus and divide it into sinus-like branches.

Reuter ('00) in his studies on the development of the intestine of the Alytes obstetricans made mention of the early origin of the liver. This develops from the "Anfangsdarm" division of the mid gut. In later embryos the liver develops very rapidly and is divided into three lobes.

Gianelli ('01 and '02) described the hepatic anlage in Triton as developing in two parts, the anterior giving rise to the hepatic tissue proper and the caudal forming the hepatic duct. The gall bladder arises from a mass of cells belonging to the primitive hepatic outpouching. By the development of the intestinal folds the hepatic duct becomes attached to the dorsal side of the gut.

Weber ('03) stated that the observations made on the development of the liver in the frog and Triton differ but little. In the latter the intimate relation of the anterior end of the hepatic outpouching and the blood vessels account for the development of this part into the hepatic tissue proper.

Bates ('04) in a paper on the histology of the digestive tract of Amblystoma has described the hepatic and pancreatic ducts. He has described a bile duct which lies free in the body cavity for a short distance and then enters the pancreas which lies between the liver and the intestine. Here it is joined by two hepatic ducts and just as this enters the intestine it is joined by two other hepatic ducts.

To briefly summarize, the early investigators described the liver and pancreas as developing at the same time from the ventral wall of the gut, and also considered that they were parts or lobes of the same organ. Remak ('55) first noted that the liver is separate and distinct from the pancreas. Goette first gave a detailed account of the development of the liver in Amphibia. Most of the investigators from that time have agreed that the liver begins as a single ventral outpouching of the gut wall caudal to the heart. The question as to the origin of the gall bladder, whether from the caudal end of the ductus choledochus or from the wall of the intestine in this region may be, as Piper ('02) stated, one of interpretation rather than one of observation. Whether the hepatic cylinders divide and the blood capillaries then grow between them, or whether the capillaries grow into the solid hepatic anlage so forming hepatic cylinders seems not to have been definitely determined. Shore's ('91) observations support the latter theory. According to the observations of Weysse and others the yolk cells are transformed directly into hepatic cells. Very little has been written about the development of the hepatic ducts. The common bile duct is described as the constricted attachment of the hepatic anlage, or the posterior end of the hepatic outpouching.

3. Early development of the liver.

The liver in Amblystoma first appears in embryos about 4.5 mm. in length, which corresponds roughly to No.21 of Keibel's Normal-plate series. The digestive tract at this stage is quite simple. The pharyngeal cavity is large and extends anteriorly to the oral cavity. Caudally it opens widely into the mesenteron which is composed of a large mass of yolk cells and extends backward to the proctodaeum. The yolk mass extends dorsally to the notochord and bulges ~~ant~~ ventrally.

Posterior to the anlage of the heart a sagittal section shows a ventrally and somewhat caudally directed projection of the gut lumen (fig.1), which extends backward near the dorsal side of the yolk mass. The anterior wall of the ventrally directed extension of the gut lumen is lined by yolk laden columnar cells and its posterior wall is formed by the cells of the large yolk mass. This cavity is quite wide transversely and is connected to the gut lumen above by a wide cleft.

Weysse ('95) has described this cavity in the frog as a cleft in the ventral mass of yolk cells, and Hammar ('97) has termed it the "Leberbucht". From the study of a slightly more advanced stage Weysse concluded that the caudal and ventral end of this cleft finally formed a caudal hepatic duct. He correlated this with the caudal hepatic duct described in the chick. That the caudal projection does not form a caudal hepatic duct in Amphibia seems clear from a study of the later development. The reason for this error was probably, as Hammar has pointed out, that Weysse did not follow the development beyond a very early stage.

In an embryo approximately 5 mm. long (fig.2) the anterior wall of this early ventro-caudal projecting cavity has become more prominent. The extension of the gut lumen into this outpouching is a large cone shaped cavity somewhat flattened in transection. The columnar epithelial cells lining it are now found farther caudalward than in the preceding stage.

In a sagittal section of an embryo 7 mm. long there is shown a more advanced stage of the condition just described. From a comparison of this stage (fig.3) with the previous one and the one following, it will be seen that the hepatic anlage has become more prominent by a cranio-caudal constriction from the gut. Folds have begun to form on the outer surface of the liver. The cavity of the hepatic diverticulum is widely connected with that of the gut. In the ventral wall there is a slight median depression (GB) which is the earliest indication of the gall bladder. This depression is at the caudal end of the liver anlage in the region where the primitive ductus choledochus is forming.

The liver of another embryo 7 mm. long appears as an anterior and ventral outpouching of the gut. Figure 36 is of a plastic reconstruction of this region of the archenteron. That the constriction from the gut has proceeded caudally will be apparent by comparison with earlier and later stages. The cavity projecting into the liver anlage from the lumen of the gut is now much longer, and there are indications of further projections from it on the right side as the lumina of ducts.

Choronshitzky noted this transverse extension of the lumen in the hepatic anlage of the salamander but did not follow its further history. At the posterior end in the median ventral wall is a marked outpouching which is the gall bladder (GB, fig. 36). The opening of this outpouching into the gut is still very wide laterally and shows no differentiation into cystic duct and gall bladder. The evagination is wide transversely though not extending as far laterally as the liver. In ventral view the gall bladder appears as a wide transverse outpouching. There is a slight furrow separating it anteriorly and laterally from the liver proper, and a more pronounced one separating it from the caudally placed yolk mass.

In an embryo approximately 9 mm. in length (fig. 37) the liver is distinctly farther advanced than in the preceding one. The caudal constriction from the gut has progressed rapidly (fig. 4). The original anterior convex surface of the liver has become markedly irregular showing numerous depressions or furrows between projecting masses of cells. The anteriorly directed cavity has become constricted dorso-ventrally and the division into ducts is more distinct. On the left side (fig.37) there is a ventral (vl) and a dorsal (d m) projection of the lumen. On the right side the ventro-lateral extension is prominent. The median ventral evagination(GB) has become more pronounced. There is now the beginning of a lateral constriction of this evagination representing the formation of a cystic duct. The anterior lip of the evagination has developed into quite a ridge separating the gall bladder from the developing hepatic ducts. On the ventral surface the anterior furrow separating liver and gall bladder from yolk mass is, as before, the more marked.

According to Shore ('91) in the frog the furrows found in the liver mass are caused by the "tunnelling in" of blood vessels. That it is not due only to this is apparent in Amblystoma where sections of this and other embryos show furrows in which there are no blood vessels (fig.4). It is important to note that Shore saw no vascular endothelium in these spaces which he regarded as blood vessels.

In another embryo of 9 mm. length the liver in cross section (fig.5) appears as a large oval mass with an irregular surface showing deep furrows separating the developing ducts. There is also a very marked dorso-ventral furrow separating the liver mass into two unequal lateral portions of which the left is the smaller. The right portion is marked by two lesser furrows, one quite ventral, the other lateral.

In 10 mm. embryos a beginning of the network of anastomosing trabeculae can be seen. The development of the sinusoidal capillary circulation in this network has progressed. In the 11 and 12 mm. embryos there is a confusing network of trabeculae and it is difficult to differentiate the main ducts from the hepatic columns. Shore believed that in the frog the tubules were first solid and that later a lumen developed. Goette expressed the opinion that a lumen was present from the earliest formation, though he admitted this was hard to demonstrate. The reason of the difficulty of proving this either way is apparent. However, from a study of sections of Amblystoma it would seem that a lumen is present from the earliest stages.

4. Position of the organ during development.

At a stage represented by 11.5 mm. embryos there is a shffting to the right particularly of the caudal end of the liver (fig.6). Such a shifting of the posterior part of the liver was noted at a later stage in Necturus by Eycleshymer and Wilson ('10) and others. The reason for this lateralward shifting is probably the pressure of the rapidly growing stomach and duodenum which are beginning to take a ventral and sinistral position. It is possible also that the spleen which is now a prominent organ in the left dorsal region of the body cavity has some influence on this movement. Then, too, the ventral pancreas forms quite a mass in the median ventral region. Figures 7, A, B and C show the lateral and upward shifting of the posterior portion of the liver. The first drawing in each of the series shows a section taken near the anterior end of the liver which here is median and ventral in position and occupies somewhat more than one-half of the area of a circle. Figures 7 A and B show a beginning of a depression on the left side caused largely by the change in shape and position of the stomach and duodenum as mentioned above. Figures 8 to 12 are cross sections of embryos 13.5 to 35 mm. in length showing the position of the liver at the level of the junction of gall bladder and cystic ducts. Here the lateral and dorsal growth of the liver is marked. A somewhat farther shifting is shown in the third drawing of figures 7 A and B and the second of 7 C. These sections were taken near the anterior extremity of the gall bladder. In all of these the liver is crescentic in transsection and extends upward almost to the level of the dorsal wall of the stomach. The last drawings in figure 7 shows the relation of parts at the level of the opening of the ductus choledochus in the gut. In all cases a small portion of the liver is found dorsal to the duodenum in this region of the embryo. In an embryo 45 mm. long the anterior end of the liver was median and ventral as described above. There was a marked lateral and dorsal growth of the caudal end but in this embryo there was also quite a marked ventral growth which would indicate that from now on the shifting to the right will not be so noticeable, and that there is a growth to the left also.

5. Development of the biliary apparatus.

a. Description of the hepatic ducts in the adult.

A description of the fully formed biliary apparatus may be of interest before describing the development of the hepatic ducts.

The liver in the adult Amblystoma is a large organ extending fully one-half the length of the abdominal cavity (fig.13). It has a ventral convex surface conforming to the wall of the abdomen and is divided by an indefinite median line into a right and a left part of which the left is the longer and covers the left ventral surface and a part of the lateral wall of the stomach. The right portion or lobe, though somewhat shorter, covers the ventral surface of the stomach to the right of the mid line and laterally extends well toward the dorsal wall of the stomach. There are usually one or two lesser indefinite furrows dividing the right lobe into two or three parts. The gall bladder is embedded in the caudal end of the right lobe some distance from its ventral surface. Only a small part of its rounded fundus appears beyond the hepatic tissue. From the notch in the liver caused by the gall bladder the one or two lesser furrows of the right lobe extend forward. The gall bladder is a pear shaped sac with its larger end extending laterally and somewhat posteriorly. The smaller, medial and ventral end projects forward and connects with the short cystic duct. Only the large blind end of the gall bladder receives a peritoneal covering, the remainder is embedded in hepatic tissue.

There are two main hepatic ducts. These unite to form a common bile duct of variable length which may be joined by the pancreatic duct just before opening into the gut (fig.14). Quite often, however, the pancreatic duct opend into the gut immediately beside the ostium of the common bile duct. The ductus choledochus is embedded for some distance in the long narrow pancreas lying on the anterior surface of the duodenum and finally empties into the anterior side of the gut near the ventral surface.

The right hepatic duct is divided into lateral and medial rami[1]. The lateral ramus divides into medial and lateral branches. Generally the cystic duct opens into the latter (fig.14 and 16). However, sometimes the cystic duct is one or even two divisions further removed from the common duct as shown in figures 17 and 44. In a graphic reconstruction of the biliary apparatus of a 7 cm. embryo (fig.15) the cystic duct joins the right lateral ramus as is shown also in figure 43. The hepatic radicle to which the cystic duct is attached shortly divides into trabeculae beyond this point. The right medial hepatic ramus divides and subdivides into branches as shown in figure 14. Its branches sometimes anastomose with the branches of the right lateral or left medial ramus (fig.17).

The left hepatic duct is generally shorter and of slightly smaller diameter than the right one, as well as more ventral in position. It is divided as the latter into lateral and medial rami. The left medial ramus sometimes joins the right medial ramus as shown in figure 16, and this duct then subdivides as a single one. Frequently, however, the left medial ramus runs anteriorly subdividing into smaller branches of which some may anastomose with those of the right medial (fig.17). The left lateral ramus is shortly divided into two of which the lateral either turns caudally (fig.44) or sends out branches that go to the posterior portion of the longer left lobe.

b. Development of the ductus choledochus.

The ductus choledochus in 9 mm. embryos is still very wide and short. The original caudalward projection from the gut cavity has disappeared and there is only the anterior directed common duct. In a model of an embryo 9 mm. long the ductus choledochus is wide transversely but constricted dorsoventrally (fig.37 and 38). It is attached at the anterior side of the now ventrally directed gut. At 11 mm. the duodenum has turned ventrally and folded to the right. A very much constricted and short common duct is attached to its superior anterior surface. In a 13 mm. embryo the common duct is attached to the anterior surface of the cranial fold of the duodenum. As before, the duct is small and short, soon dividing into right and left hepatic ducts. The epithelial lining of the duct still contains yolk granules and except for a quite irregular but prominent lumen is very much like the hepatic ducts. Indeed, the difference in the lining cells of this duct and those of the hepatic trabeculae is not great.

In another embryo of approximately 13 mm. length, which is somewhat more advanced, the ductus choledochus is longer and of larger calibre (figs.18 and 19). It is, however, still attached to the cranial surface of the anterior fold of the duodenum. The epithelium here is now definitely columnar in type, though yolk granules are still present. In this case the pancreatic duct is attached near the gut to the common duct(2). In an embryo 13.5 mm. long the ductus choledochus (fig.7-A) is attached in a fold to the left side of the gut. The duct here is large but shortly divides into the right and left hepatic ducts. The attachment of the duct to the left wall of the gut is to be seen in a less completely developed embryo 14 mm. long. From now on the common duct is attached to the left side of the gut which is faced somewhat cranialward, due to its growth anteriorly and to the right. The length of the common bile duct before its division varies. In a 35 mm. embryo modelled the common duct is quite long and had a distinct turn shortly before it entered the gut. Here again the pancreatic duct opened into the common duct. There has been a continual change of position of the two ducts from the earliest stage to the fully developed one. In an embryo 13 mm. long a distinct pancreatic duct is seen ventral to the common duct. In the further development, with the gradual rotation of the liver to the right, there has been a change in position of the common duct until, in the 35 mm. embryo, it lies to the left of the pancreatic duct which is the condition found in the adult (fig.44).

c. Development of the major hepatic ducts.

The earliest indication of the hepatic ducts was pointed out in the description of the formation of the liver. In a model of an embryo approximately 5 mm. long, as previously stated, the cavity of the early hepatic anlage extends far laterally. On either side the cavity is constricted dorso-ventrally. From the drawings shown by Choronshitzky it is probable his lateral cylindrical extensions are the early hepatic ducts. In Amblystoma these lateral extensions form only the lateral rami of the hepatic ducts. The medial rami are shown in the model of an embryo about 7 mm. long (fig.36). On the right side in this model there is a lateral extension of the hepatic lumen. A longitudinal ridge in the floor of this side shows a beginning constriction into lateral and medial rami. The medial ramus is more dorsal in position and appears as a swelling on the outer surface. On the left side there is a wide cavity. On the external surface there is a slight dorso-ventral furrow, an indication of the beginning division into lateral and medial rami.

In an embryo approximately 9 mm. long the right side shows a more marked lateral ramus. The medial still somewhat dorsal ramus is to be seen (fig.37). Here the left side shows a marked dorso-medial and a ventro-lateral prolongation. The outer surface of both sides of the organ shows many projections, the beginning of tubules from these main rami. The cystic duct though slightly to the right shows more of a constriction from that side. The anterior lip of the cystic evagination also is very prominent.

The rami are formed from the early hepatic ducts by a caudalward constriction and by elongation. Mitotic figures are to be seen at this stage but are more numerous in later ones. As Scammon ('13) has pointed out in fishes, there is a reduction both relative and actual, in the size of the ducts.

In another 9 mm. embryo the development of the ducts is seen to have progressed rapidly (fig.38). Numerous mitotic figures are to be seen in different sections indicating a rapid growth of the ducts. There are distinct right and left hepatic ducts which show a marked growth. There is a medial longitudinal ridge in the ventral wall of the ductus choledochus indicating a caudalward progressing constriction and division (fig.38). The cystic duct (D.cy.) is distinctly differentiated and attaches to the right of the beginning constriction in the common duct. It extends ventrally and somewhat towards the right. The right hepatic duct as seen in figure 38, and in a figure of a model of the cavity of ducts (fig.20) is divided into a lateral and a dorso-medial ramus. The lateral ramus is further divided into lateral dorsal and medial ventral branches. The left ramus also has medial and lateral divisions.

In embryos from 10 to 12 mm. in length, the ducts and trabecula present a confusing network. The epithelium of both are heavily laden with yolk granules, and that of the ducts is not yet differentiated into a distinct columnar type. However, the right and left hepatic ducts are clear. In an 11 mm. embryo the right duct is distinctly divided into lateral and medial rami. A short cystic duct is attached to the caudal end of the lateral ramus and on its ventral side. In an embryo somewhat less than 13 mm. long the same arrangement of a short common duct and right and left hepatic ducts is present. The right duct is divided into the medial and lateral rami. The cystic duct here projects somewhat to the left and dorsalward connecting as before with the right lateral ramus.

In a graphic reconstruction of a 13 mm. embryo (fig.18) the right hepatic duct is divided into lateral and dorso-medial rami. The short cystic duct extends upward and opens into the right lateral ramus. A short lateral branch is the only other division of the right lateral ramus. The dorso-medial branch shortly breaks up into trabeculae. The left duct is also divided into rami. The differentiation of hepatic ducts from trabeculae is now clearer as the epithelium of the former is columnar in type.

In figure 19 from an embryo less than one mm. longer than the above, the formation of ducts is seen to have continued. The right hepatic duct is divided into lateral and medial rami, each of which is further divided into dorsal and ventral branches. The same holds true in a general way for the left hepatic duct and its divisions.

In the ventral view of the model of a 14 mm. embryo (fig.39) the relation of pancreatic duct to the common duct is shown. The short thick common duct divides into right and left hepatic ducts (figs. 39 and 40). They lie in almost the same horizontal plane and are of about the same diameter, but the right is the shorter, dividing almost immediately into its lateral and medial rami. In a 13.5 mm. embryo (fig.41) the right hepatic duct is of larger diameter than the left. In a 15 mm. embryo the common duct is very short (fig.42). The right and left hepatic ducts here are very long as compared with those in other embryos. The left duct has come to lie in a more ventral plane due to the shifting of the whole posterior part of the liver and gall bladder to the right. The same is true to a greater extent for the left ducts in the 20 and 35 mm. embryos (figs. 43 and 44). In a 20 mm. embryo the right hepatic duct is the shorter as it is in a 35 mm. embryo. In a 35 mm. stage the left hepatic duct is almost ventral to the right. The same holds true for a 45 mm. embryo. In the adult, however, the left duct is again more lateral to the right, but still somewhat more ventral.

d. Development of the minor hepatic ducts.

Right lateral ramus.

The right hepatic duct in a 14 mm. stage is divided into lateral and medial rami and the right lateral ramus is subdivided into lateral and medial branches (fig.39). The short cystic duct is attached to the lateral branch. The medial branch (fig.40) gives off several tubules in an oblique dorso-ventral plane. In a 13.5 mm. embryo the right lateral ramus is quite ventral to the medial one (fig.41). As in the earlier stage it is divided into lateral and medial branches. The cystic duct which is now directed almost horizontally, is attached to the right side of the lateral branch. The anterior portion of the lateral branch anastomoses with a duct from the right medial ramus. In a 15 mm. embryo (fig.42) the right lateral ramus is shorter than in the preceding specimen. The right hepatic duct is, however, longer so that the cystic duct is attached to the lateral branch farther from the gut. The lateral branch here divides into dorsal and ventral branches. In a 20 mm. embryo the right lateral ramus is very short (fig.43). In position it is now somewhat dorsal to the right medial ramus. It soon breaks up into dorso-lateral and ventro-medial branches. Both of these branches are very long. At the attachment of the cystic duct to the lateral branch there is a further division of the lateral again into medial and lateral radicles. The medial branch has anastomoses with the right medial hepatic ramus. Its further division is in a dorso-ventral plane. In a 35 mm. embryo the right lateral ramus divides into dorsal and ventral branches (fig.44). There is another division of the dorsal branch and the cystic duct is attached to the dorsal one of this last division. Frequent anastomoses are formed between the tubules of the dorsal and ventral branches, and between those of the dorsal branch and those from the right medial hepatic ramus, as also of the left medial ramus.

Right medial ramus.

The right medial hepatic ramus of a 14 mm. embryo as shown by model is very simple (fig.39). It joins with the left medial ramus, the further division of this common ramus is into right and left branches. The division of the medial ramus is very short and its lateral and medial branches long. Caudally directed tubules are given off from the lateral branch. The medial branch here is connected with the right lateral ramus. The medial branch divides dorso-ventrally into tubules. In a 15 mm. embryo (fig.42) the medial hepatic ramus is again very simple. It is short and divides into lateral and medial branches of which the latter is given off almost at right angles and from its anterior surface are given off several tubules. The medial hepatic ramus in a 20 mm. embryo as in a 14 mm. one is joined with the left medial ramus (fig.43). The resulting common ramus divides into a right dorsal (R.Br.) and a left ventral branch (L.Br.). From the right dorsal branch, dorso-lateral tubules are given off some of which are directed caudally. In a 35 mm. embryo (fig.44) the right medial ramus is on the same horizontal plane as the right lateral. Its divisions are also into dorsal and ventral branches. Many anastomoses are found between the tubules of this ramus. Tubules from this ramus join those from the right lateral and from the left medial ramus.

Left medial ramus.

The left medial ramus is joined to the right medial in a 14 mm. embryo (fig.39). In a 13.5 mm. embryo the left medial is long and divides into dorsal and ventral branches (fig.41). Also in a 15 mm. embryo is the left medial ramus quite long (fig.42). It divides into medial and lateral branches both of which have dorsal and ventral tubules. The left medial ramus in a 20 mm. embryo (fig.43) is joined to the right. The left ventral branch of this combined duct divides shortly into dorsal and ventral radicles. In a 35 mm. embryo (fig.44) the left hepatic ramus is quite long. Its anastomoses with the other rami have been noted. There are also several anastomoses with the left lateral ramus.

Left lateral ramus.

In a 14 mm. embryo the left lateral ramus is very simple, dividing into medial and lateral branches (fig.40). The left lateral ramus in the next stage shows further development and growth (fig.41). In a 15 mm. embryo this ramus has lateral branches given off at quite an angle (fig.42). It is shorter than the left medial ramus and divides into medial and lateral branches, the latter sending tubules far out to the side. The left lateral ramus in a 20 mm. stage is given off nearly at right angles to the left hepatic duct (fig.43). It divides into dorso-medial and ventro-lateral branches. In this case the lateral branch is the longer. Several tubules go out laterally almost at right angles and from these tubules hepatic columns go posteriorly as well as anteriorly. In a 35 mm. embryo (fig.44) the left lateral ramus forms quite a network of ducts. The ventral branch makes an arch forward and is then divided into anterior and posterior branches. In an embryo 45 mm. long the main hepatic ducts are more nearly on the same horizontal plane. Of these ducts the left hepatic has extended farther to the left.

e. Development of the gall bladder and cystic duct.

The gall bladder appears somewhat later than the liver, as noted by Hammar ('97). It arises as a median ventral outpouching caudal to or in the posterior end of the hepatic anlage. Choronshitzky has figured the anlage of the bladder in a median sagittal section. The structure is shown as a slight depression developing from the gut, at the entrance of the common duct, and a definite fold is shown between this and the ventrally extending lumen of the hepatic anlage. In an embryo approximately 7 mm. long, which is undoubtedly an earlier stage in Amblystoma (fig.3), there is no distinct fold between the gall bladder and liver anlage. Only a slight median depression of the floor at the posterior end of the hepatic diverticulum is present. No difference is shown by ordinary stains in the epithelium lining this early cystic evagination and that of the liver. Not until later does the epithelium change into the low cuboidal type characteristic of the adult gall bladder.

A little later the depression in the floor of the hepatic diverticulum is considerably increased (fig.36). The position of the gall bladder with reference to the opening of the hepatic anlage has not changed. In a model of liver and gall bladder of a 9 mm. embryo (fig.37) the evagination is quite deep. There is a distinct lateral constriction of the dorsal opening of the gall bladder and distinct anterior and posterior lips to the evagination indicating the formation of a cystic duct (fig.4). There is also a deep furrow anterior to the evagination separating the gall bladder from the hepatic anlage. The posterior furrow is even more marked. The gall bladder is, however, still very wide laterally.

In another embryo approximately 9 mm. long the gall bladder has a long cranio-caudal diameter. The furrow marking off the gall bladder from the hepatic tissue laterally is distinct. The cystic duct is short and of large diameter and it as well as the gall bladder, lies to the right of the mid line. The cystic duct projects upward and to the left (fig.21).

A section of the gall bladder of an embryo 11.5 mm. long shows there has been a continual shifting to the right (fig.6). The cystic duct has become longer but is still of wide diameter. It projects more to the left and upward. The gall bladder, though embedded between hepatic tissue and caudal yolk mass, is completely separated from both (fig.22). In figure 23 is shown an increased cranio-caudal diameter, although the transverse is still the greater. The cystic duct here projects more to the left, still somewhat dorsally and slightly backward. The cranio-caudal diameter increases rapidly from now on, and the position of the cystic duct would indicate that there is a more rapid caudal growth. Figure 23 shows the model of a gall bladder of an embryo almost 14 mm. long. The cystic duct attached near the anterior end, projects to the left and dorsally.

In two graphic reconstructions of embryos 13 and 13.5 mm. in length respectively (figs. 18 and 19), the gall bladder is attached by a short and constricted cystic duct to a radicle of the right hepatic duct. In figure 18 the cystic duct leads from the anterior dorsal end of the gall bladder to the left, caudally and somewhat dorsally, the gall bladder being distinctly to the right of the mid line. In figure 19 the larger of these two embryos the cystic duct is not quite at the anterior end, but the cranio-caudal length of the gall bladder is distinctly greater. The general direction of the cystic duct is the same. The gall bladder is relatively as far caudally here as the one shown in figure 18. From the connection of the cystic duct to the gall bladder, it appears that there has been a marked growth cranialward.

In an embryo almost 14 mm. (fig.39) long the gall bladder has decidedly increased in its cranio-caudal diameter. In transverse section it is almost circular. The cystic duct is of very small diameter as compared with its earlier size. It projects now somewhat upward but almost directly to the left, due to the increased lateral shifting of the liver and the gall bladder. In this embryo the cystic duct is attached to the extreme anterior dorsal end of the gall bladder.

Figure 41 is of a model of a 13.5 mm. embryo. In this the general shape of the gall bladder is the same as of the one just described, except that there is a slight increase in the vertical diameter (fig.9). The cystic duct, however, is not attached at the extreme anterior end but to the left upper side. It extends towards the left as before but is now almost horizontal.

In a 15 mm. embryo the attachment of cystic duct to the gall bladder is farther caudalward than the previous one (fig.42). This seems to mark the limit in its caudal attachment for all sizes examined. It would be difficult to say whether this shifting in attachment of the gall bladder to the duct were due to a difference in the anterio posterior growth of the gall bladder or to the rapidity of differentiation and growth of hepatic ducts. The cystic duct in this embryo extended toward the left, but now slightly ventrally, which can be taken as evidence of continued rotation to the right and dorsalward of the entire biliary apparatus (fig.10).

Marshall ('93) has described the gall bladder of amphibians developing as a lateral outgrowth from the bile ducts. From its position at this stage one could easily be led to such a conclusion.

The gall bladder of a 20 mm. embryo shows a very distinct dorso-ventral increase in diameter (fig.11). With this there has been a marked cranio-caudal lengthening (fig.43). The relative size of the gall bladder is now greater. As before indicated, the cystic duct is here again nearer the anterior end, it extends towards the left and now distinctly ventralward (fig.11). A right lateral and slightly ventral view of the gall bladder is shown in figure 43.

In a 35 mm. embryo (fig.44) the vertical diameter of the gall bladder has greatly increased. The cystic duct is now in the left anterior ventral end extending ventrally and to the left. In a 45 mm. embryo the gall bladder has the same general shape as in the preceding, and the cystic duct has not changed in position (fig.12).

In a graphic reconstruction of the biliary apparatus of a 10 cm. Amblystoma the cystic duct extends to the left, somewhat ventrally and anteriorly (fig.16). The gall bladder is pear shaped (fig.13) with its large blind end projecting slightly dorsal and to the right but mainly caudalward.

f. Summary of the development of the biliary apparatus.

In summarizing the development of the hepatic ducts probably a table of the ducts as found in the various models will bring out more clearly their relations to the main duct. Such a table is here given:

Table III

Ductus choledochus

Left hepatic duct   Right hepatic duct

Lt. lat. ramus, Lt. med. ramus   Rt. med. ramus, Rt. lat. ramus

Branches,-Lat., Med.   Lat., Med.,   Med.,Lat.,   Med.,Lat.

Cystic duct

Or, in case of anastomoses of the medial rami, as was found in two embryos of 14 and 20 mm. length and two older Amblystoma of 7 and 10 cm. length respectively, the following table is given:

Table IIIa

Ductus choledochus

Left hepatic duct   Right hepatic duct

Lt. lateral ramus   Common medial ramus   Rt. lateral ramus

Branches, - Lat.,Med.   Left   Right   Med.,Lat.

Cystic duct

From these tables it will be seen that sometimes the right and left medial rami are joined. The division of the common medial ramus is into right and left branches. In their position and final division these branches are the same as the right medial and left medial rami. As will be seen in figures of the different models, the smaller embryos did not have all of the divisions and subdivisions marked in the tables. In figure 39, for instance, the right branch of the common medial ramus shows no further division, the left branch only one. Further division of both is seen in the 20 mm. stage (fig.43). The division here, however, is more into dorsal and ventral radicles, due to the more marked lateralward shifting of the liver and the ducts. The extreme of this lateral shifting is seen in figure 44, where the left hepatic duct is almost ventral to the right. The left lateral ramus in a 45 mm. embryo does not hold such a ventral position with reference to the left medial.

The variation in the connection of the cystic duct to the hepatic is shown in the following tables:

Table IV

Right lateral ramus

Medial branch Lateral branch

Cystic duct

or as found in ~~the~~ a 35 mm. embryo and one of the larger Amblystoma,

Table IV a

Right lateral ramus

Medial branch Lateral branch

Medial radicle Lateral radicle

Cystic duct

There seems to be no definite rule in regard to the anastomosing of ducts. In a 35 mm. embryo they are the most frequent and here apparently because the ducts were crowded so close together. That the right and left median rami sometimes join and form one duct is seen in the models of a 14 and a 20 mm. embryo, also in the graphic reconstruction of a 7 cm. and 10 cm. Amblystoma. It would seem this fusion of the ducts is quite probably due to crowding.

The definite position of the hepatic ducts with reference to the portal vein is seen for all embryos (figs. 8-12). The same relation is also found in the adult. As a rule there is a branching of the hepatic ducts.corresponding to the division of this vessel. In the developing embryo the ducts are found usually to the right and ventral to the portal vein.

From the usual description of the biliary apparatus in frog it would seem that there is a fairly close correlation in the main features between these two amphibians. The figures of Ecker, Wiedersheim and others show a gall bladder connected to a right hepatic duct. There is also a left hepatic duct, the two uniting in the pancreas and forming a ductus choledochus which, as usually described, is joined by the pancreatic duct. In no case in Amblystoma were two cystic ducts found as is shown for the frog. The division into rami in the frog as far as the ducts have been figured, seems to be somewhat different from that found in Amblystoma. The more marked divisions of the liver into several lobes may partially explain this. The duct system as found in Necturus is quite different. Kingsbury here described three hepatic ducts opening into the gut. These anastomosed with each other -- and two were joined by the ventral pancreatic ducts. The third is a duct direct from the gall bladder which, however, anastomoses with the other hepatic ducts. Gronberg ('94) described three hepatic ducts which unite with the cystic duct and form a ductus choledochus in Pipa americana.

Bates ('04) has described the hepatic ducts in Amblystoma. According to his description there are four hepatic ducts, two of which join the bile duct in its course through the pancreas and the other two just as it opens into the intestine. It is possible that the two he found joining the bile ducts are the right medial and lateral rami, and the other two, the left medial and lateral rami. In that case the ductus choledochus and the right and left hepatic ducts were very short as was found in some of the material used in this work. Or it may be that the two ducts which joined the bile duct as it opened into the intestine are the two pancreatic ducts which have not fused until just at the ostium of the hepatic duct. The first two ducts then would be the right and the left hepatic ducts. I have never seen the cystic duct (bile duct as Bates terms it) open directly into the common hepatic duct.

From the models and drawings it will be seen that the gall bladder at first has a wide dorsal communication just caudal to the hepatic lumen. As this communication constricts there is formed a short large cystic duct extending dorsally into the right hepatic duct. With further growth and division the cystic duct extends more and more to the left until at the 15 mm. stage it is almost horizontal and at the 20 mm. stage projecting ventrally and somewhat anteriorly. Its earliest attachment is to the ventral surface of the common bile duct, but in the lateralward shifting of the whole liver its attachment goes to the left side of a right hepatic radicle. The connection of the cystic duct to the gall bladder in early stages is to its dorsal surface about midway between cranial and caudal pole. Somewhat later the connection is nearer the cranial end and usually reaches the extreme anterior end. The cranio-caudal growth of the gall bladder has kept pace with the lengthening and differentiation of ducts in the 13 to 14 mm. stage. From the relations in a 15 mm. embryo it appears that the gall bladder has shifted anteriorly. In this case the hepatic ducts have lengthened more than the gall bladder. At 20 mm., however, there has been a marked increase in cranio-caudal growth of the gall bladder so that it is almost as long as the ducts.

Beginning about at this stage the cystic duct is again attached nearer the anterior end of the gall bladder. This may be taken as evidence that the cystic duct really shifts in its attachment to the gall bladder. This seems to be borne out in some cases by the fact that its attachment to the hepatic ducts is to a division of the lateral branch of the right lateral ramus instead of to the lateral branch proper. In some cases where the lateral branch is quite long the attachment may have remained to it.

Whether the gall bladder originates from the early hepatic anlage or from the gut has caused much discussion. As said before Piper ('02) thought this a matter of interpretation. The more marked furrow caudal to the gall bladder might be taken as evidence of its belonging to the hepatic anlage, also the fact that the same type of yolk laden cells form hepatic tissue and gall bladder. That it, at least, is directly caudal to the hepatic anlage is proven by the early connection of its duct to the common bile duct.

The connection of the cystic duct probably depends to some extent on the extent of growth and division of the hepatic ducts. It will be remembered that in the earlier stages the cystic duct opens into the common duct, then into the early right hepatic. In the further growth and division of the right hepatic duct the cystic duct becomes attached to one of its radicles. As noted above, the cystic duct opens into the lateral branch of the right lateral ramus in all of the embryos studied except one, which was 35 mm. long.

That there is considerable variation in the relative dorso-ventral position of these main hepatic ducts is to be expected. However, in general, a study of the models shows a close similarity in their positions. There is a constant rotation of the liver towards the right and with this is a similar one of the hepatic ducts. In this rotation the right ducts come to be more dorsal in position, the left more ventral. The right lateral divisions would thus be dorsal to the right medial and the reverse should be true for the left. In general such an arrangement is found. A variation in the length of the different ducts is present. However, there is quite a definite relation in the total lengths of ducts in the different embryos. In a 15 mm. embryo the common duct is quite short but the greater length of the hepatic ducts compensates for this reduction. In a 35 mm. embryo the common duct is long, the hepatic ducts and their radicles divide shortly.

II. The development of the pancreas and pancreatic ducts.

1. Literature

The literature concerning the development of the amphibian pancreas like that regarding the liver is divisible into two periods, and Goette's work ('75) may again be said to mark the beginning of the newer one. The older observers mainly considered the pancreas as a part of the liver, or a modified lobe of that organ.

A list of the investigators describing the development of the pancreas will be found included in the tabular classification of the literature on the development of the liver (table II).

Rusconi ('26) in describing the frog stated that the pancreas develops at the same time as the liver, and considered the two as parts of the same organ.

In 1840 Reichert described the liver and pancreas as developing from the same large yolk mass. He said that a part of the yolk mass formed the liver, and a part formed the pancreas. He, too, considered the pancreas as a partly separated lobe of the liver.

Remak ('55) described the dorsal pancreatic anlage as arising from the gut at the same level as the liver. He noted that this later came into close relation with the liver. He could not explain the origin of a second pancreatic duct, but thought it might be an outgrowth which extended from the pancreas to the gut.

Rathke ('61) described the pancreas as developing directly caudal to the liver. First there is a groove on the inner side of this region of the wall of the enteron, which later forms an external prominence. The evagination becomes more and more pronounced by a thickening of the wall and an increase in the size of the lumen. The outpouching constricts near its attachment to the gut, this constricted portion developing into the pancreatic duct. Sprouts and buds in the fundus of the evagination develop and form cylinders at the end of which oval swellings appear.

v. Bambecke ('68) confirmed Remak's description of the development of the dorsal pancreatic evagination.

Goette ('75) in his studies on the development of the Bombinator recognized three distinct pancreatic anlagen, two ventral and one dorsal. The dorsal one he describes as placed just caudal to the gastroduodenal loop. The two symmetrical ventral anlagen develop from the primitive hepatic duct. Of these the right grows dorsalward to join the ventral growing dorsal anlage. The right duct changes in position until it opens into the left side of the hepatic duct. The united right and left duct then separates from the common bile duct. Apparently Goette considered the left outpouching as a rudimentary one. Later the dorsal duct disappears, thus leaving but one permanent pancreatic duct.

Balfour ('81) and Hertwig ('88) described a dorsal outpouching of the gut wall caudal to the level of the common bile duct.

The development of the pancreas in both Urodela and Anura was described by Goeppert ('91). In both he found as Goette had described, one dorsal and two symmetrical ventral outpouchings. A constriction of the early dorsal outgrowth forms a duct, while folds and ridges developing on the blind end give rise to the glandular tissue. The right and left ventral ducts unite on the right side of the common bile duct. However, he found two pancreatic ducts opening into the common bile duct in an adult, also three pancreatic ducts that fused immediately before opening into the common bile duct. The numerous dorsal ducts which he found in the adult urodeles he explained are of secondary origin. He, too, found only one pancreatic duct persisting in adult Anura.

Marshall ('93) stated that in the frog the pancreas developed as a pair of hollow outgrowths caudal to the liver. Later the ducts shift and open into the bile duct instead of, as at first, into the intestine.

Minot ('93) in his text book of embryology, mentioned that in urodeles the dorsal duct persists, and in Anura only the ventral duct.

Weysse ('95) and Stöhr ('95) both agreed with the description of Goette and Goeppert. Stöhr was especially interested in the dorsal pancreatic anlage. He did not find a double dorsal pancreas as had v.Kupffer ('92) in one of the ganoids. He believed that the caudal dorsal pancreatic anlage described by v.Kupffer is part of the hind gut. Brachet ('96) reviewed the descriptions of earlier investigators.

Woit ('97), a student of v.Kupffer, and probably influenced by his views, in his work on the development of the spleen stated that the dorsal pancreas gave rise to the spleen as well as to a part of the adult pancreas in urodeles. He described two persisting ducts in urodeles.

Gianelli ('99) described an "intrahepatic pancreas" in Triton, the tubules of which are in intimate relation with the liver tubules, and it is stated by him are continuous with them.

Reuter ('00) made mention also of the early appearance of the dorsal and ventral pancreas. Both arise from the anterior part of the mid gut region (Anfangsdarm) from the yolk cells. The pancreas, as well as the liver, is found in the gastro-duodenal loop as soon as this is formed, and both are at first to the right and dorsal to the intestinal spiral.

Choronshitzky ('00) described in Necturus and the frog two lateral outpouchings from the early hepatic duct. These two lateral outpouchings form the ventral ducts, later they unite posterior (ventral) to the common duct. He described two ducts in the adult urodeles.

Gianelli ('02) described three distinct pancreatic anlagen in Triton. The dorsal anlage develops first. The ventral anlagen develop from the posterior end of the hepatic outpouching as two masses of vitelline cells into which the lumen of the hepatic evagination later extends. The right and left outpouchings both fuse with the dorsal pancreas. The ventral pancreatic duct formed from both pancreatic anlagen opens into the hepatic duct. The left pancreas remains in intimate relation with the liver.

Braun ('06) described the early development of the pancreas in Alytes obstetricans. He found a dorsal and two ventral pancreatic anlagen, which are first to be recognized as swellings of the yolk gut wall and by the more numerous nuclei. The ventral anlagen are caudal to the anlage of the hepatic duct. The right ventral pancreas is somewhat more caudal than the left, joins the dorsal pancreatic outpouching and later joins with the left ventral pancreas. The dorsal outpouching looses its connection with the yolk gut soon after coming in contact with the right ventral pancreas. The cells forming the pancreas are at this time still undifferentiated yolk cells. Differentiation of the cells and glandular development take place at the same time. The early ventral outpouchings develop into the pancreatic ducts which unite just before opening into the gut to the right of the hepatic duct. The pancreas in the adult lies in the gastroduodenal loop.

Eycleshymer and Wilson ('10) described the two ventral anlage as dorso-lateral to the ductus choledochus. These appear some time after the single dorsal anlage, and union with the dorsal pancreas does not take place until the embryo reaches a length of about 29 mm. They found that the dorsal duct opens into the duodenum just caudal to the stomach, and also mentioned two ventral ducts.

It is generally agreed by those who have described the duct system in the adult urodeles that at least two ducts persist. Hyrtl ('65) by means of injection in adult Cryptobranchus found two pancreatic ducts, one of which joined the hepatic duct. Oppel ('89) in Proteus has described an anterior and a posterior set of ducts, the latter emptying into the ductus choledochus. Kingsbury ('94) found one anterior duct opening just behind the pylorus, and two caudal ducts which open separately into the ductus choledochus. One pancreatic duct has been described as persisting in adult Anura. Bates ('04) stated that the pancreatic ducts join the hepatic ducts as they pass through the pancreas.

2. Early development of the pancreas and pancreatic ducts.

As stated in the description of the liver, the pancreas develops later than that organ. A well marked dorsal pancreas is to be found in embryos 8 mm. long. A mass of cells in the dorsal wall of the enteron is separated by a distinct transverse furrow from the anlage of the stomach in front and from the yolk mass behind. Mitotic figures are to be found in this mass of cells.

In embryos about 9 mm. long there are three pancreatic anlagen, two ventral and one dorsal, as has been described for other amphibia. The two ventral anlagen appear as evaginations posterior to the hepatic outpouching and caudal to the ventral lying gall bladder. The evaginations of the pancreas on the ventral wall of the gut extend in a longitudinal direction for some distance. Anteriorly there is quite a distinct furrow between the liver and the pancreas. A model of this stage (fig.24) shows the outpouchings of the pancreas and of the gall bladder and liver anteriorly, Posteriorly there is no sharp demarcation of the pancreas from the yolk mass and gut. A model of the lumina of the pancreatic evagination and of the gall bladder and hepatic ducts makes the position of the different parts with reference to the anterio-posterior plane more clear (fig.25). At this stage the pancreatic anlagen are caudal to the gall bladder which is directly anterior to the right pancreatic evagination. The pancreatic evaginations extend farther ventrally than do the hepatic ducts and the gall bladder.

The right and left pancreatic anlagen are separated anteriorly by a slight ventral furrow. Caudally the two evaginations are apparently fused as the area between them is bulged ventrally. The evidence of a division into two evaginations is much more clear in a view of the model of the lumina of the pancreatic anlagen (fig.25). This is also brought out clearly by the figure of a section taken about 80 u caudal to the gall bladder (fig.26). In this figure one sees the two very definite evaginations, and that they are separated as far as the transverse width of the gut will permit. On the lateral side there is an indefinite furrow at about the level of the dorsal margin of the liver extending caudalward in the wall of the gut and yolk mass. This marks the upper limit of the ventral pancreatic anlagen (fig.24). In figure 26 the lumina of the two ventro-lateral pancreatic diverticula open widely into a common lumen which connects dorsally with the gut cavity. Anteriorly at about the caudal end of the gall bladder this lower common lumen is separated from the lumen of the intestinal anlage as shown by the model of the lumina of the ducts (fig.25) as well as by the figure of a model of the hepatic ducts (fig.20). In the section figured (fig.26) the lower part of the right evagination is separated from the main lumen by cells. The next section anteriorly shows the left lumen also cut off. The pancreatic lumina thus very early extend somewhat forward.

The dorsal pancreatic anlage, as shown by both models (figs.24 and 25), is median and farther caudalward than the ventral. As seen in figure 24 it seems to be an elevated portion of the wall of yolk gut. The anterior and posterior furrows separating the anlage from the stomach and gut are not so prominent in this specimen. A model of the lumen shows it to be directed forward (fig.25). I can confirm Stöhr's statement that there are no evidences of double dorsal pancreatic anlagen in any stages as has been described in the ganoids by v.Kupffer. The dorsal anlage at this time is short in its cranio-caudal diameter. It is, however, farther developed than the ventral anlagen. Its ventral margin is limited by a slight groove at the anterior end. Caudally this groove is not present. Figure 24 as well as figure 25 shows that there has been quite an increase in the dorso-ventral diameter of the intestine. That the ventral part is becoming constricted from the dorsal is shown by both models and was pointed out in the description of the development of the liver. From the anterior end of the ventral part of the gut is the hepatic outpouching, caudal to this and on the right side the gall bladder, and still farther posteriorly the ventral pancreatic anlagen. Caudal to these evaginations again the gut lumen takes a more dorsal position.

In 10 mm. embryos the dorsal pancreas is much more prominent. The furrow separating it from the stomach is quite deep. Also the caudal furrow is well marked. Mitotic figures are more numerous than before. The cells lining the evagination are columnar in type but still contain considerable yolk. The lumen extends a very short distance forward.

In an 11 mm. embryo there has been considerable further development of the mid gut region. The stomach has differentiated to some extent. It has flattened dorso-ventrally, and its posterior end is constricted and shifted to the left. The duodenum extends ventrally to the left and has an anteriorly directed portion which forms, with the stomach, the gastro-duodenal loop. At its anterior end the duodenum turns to the right and is continuous with the caudal extending yolk mass. Here at the cranial end is the ventral pancreas. The pancreatic area appears at this stage as a narrow zone of the gut marked off by furrows, anteriorly from the hepatic area and posteriorly from the duodenum and yolk(fig.30). The pancreatic ducts are short and extend ventro-laterally from either side of the common duct. These ducts are caudal to that part of the common bile duct which gives off towards the right ventral side the cystic duct and anterior and somewhat dorsally two lateral hepatic ducts. The groove separating the anterior end of the pancreas from the hepatic tissue is well marked. The gall bladder extends downward and to the right of the mid line between pancreas and liver. A drawing of a section near the anterior end of the duodenal loop shows what appears to be a constricted forward projection of the gut (fig.27). Somewhat anteriorly the cells lining this constricted gut are of a tall columnar type heavily laden with yolk as are the cells lining the duodenum (fig.28). This is the caudal end of the common duct. Posterior to the section figured one can see the two lateral parts of the pancreas distinctly separated from the constricting anterior end of the gut and the beginning common duct (fig.27). About fifteen sections of 10 u anterior to this are the ventro-laterally projecting pancreatic ducts. The pancreas has grown both anterior and posterior to the ducts, but the greater growth has been forward (120 u caudalward and 140 u anterior). The left pancreas grows anteriorly sending a small projection to the left of the gall bladder. A model of the pancreas of this stage shows it as a cap placed over the anterior end of the gut, distinctly separated from it by a groove and closely united to the liver which lies in front of it. The right side shows only slight indication of its later dorsal and caudal growth (fig.30).

The dorsal pancreas forms an irregular elongated mass to the right of the gastro duodenal loop, but extends somewhat caudal to it. To the right of the pancreas and ventrally lies the large yolk mass (fig.30). The dorsal pancreas is now relatively and actually nearer the ventral pancreas than in earlier stages. There is as yet little evidence of any ventral growth of the anterior end. The duct as in the younger stages lies mainly in the cranial part of the mass forming the dorsal pancreas. Tt extends to the right and dorsalward and is nothing more than a constricted part of the evagination. As seen in figure 29, it is attached to the archenteron near the large yolk gut. The segment of the gut to which the dorsal pancreatic duct is attached is the caudal end of the duodenal loop which posteriorly is completely constricted from the ventral yolk mass. Its attachment here, then as is shown by later stages, is to the dorsal wall of the duodenum.

The dorsal and ventral pancreatic anlagen at this stage are composed of masses of cells still containing many yolk granules. The ducts of both appear as constricted portions of the outpouching connecting them with the duodenum and the common bile duct.

The development of the duodenum and the gastro-duodenal loop has been described by Goette and others who described the changes which bring the opening of the dorsal pancreatic duct nearer to the pylorus than the ventral ducts. Goeppert ('91, p. 113) stated concerning this: "-- so erhält mann in den Schnitten die dorsale Anlage später als die ventralen Anlagen. Wenn mann aber die schräg absteigende Richtung des vorderen Schenkels der gastroduodenalschlinge berücksichtigt, sieht mann leicht, dass das dorsale Pankreas trotzdem einem noch etwas vor der Mündung des Leberstieles gelegenen Theil der Darmwand angehört."

During the 12 and 13 mm. stages the dorsal pancreas comes in contact with the ventral one. The dorsal pancreas forms an irregular mass lying to the right of the duodenum and dorsal to the caudal yolk mass. A small part extends anteriorly and somewhat ventrally and comes in contact with the right pancreas. In a 13 mm. embryo the two masses are fused (fig. 31). The acini of the two actually fuse as is shown by figure 32. The ventral pancreas is the smaller. A small part of the left ventral pancreas lies along the left side of the gall bladder and anterior to the duodenum (fig.45). The hepatic ducts extend through the ventral pancreas anteriorly to the liver but have no connection with the former. The right ventral pancreas in figure 31 has not grown dorsalward to any extent to join the dorsal pancreas. The dorsal pancreas in this case has grown ventrally and to the right to join the ventral pancreas.

The dorsal duct is now well developed. It extends dorsally and slightly to the right from the right dorsal side of the duodenum near its caudal turn. The duct divides shortly sending out branches in all directions.

The ventral ducts in a model of a 13 mm. embryo come off laterally from the hepatic ducts and immediately divide into smaller rami. As a rule the ventral ducts at this stage fuse into one tube ventral to the common duct. The ducts may join the ventral wall of the common duct or the anterior end of the gut, where the common bile duct opens into the duodenum (fig.45).

In a 15 mm. embryo as well as in later stages the dorsal pancreas forms the larger part of the whole organ. It joins the right ventral pancreas by a neck of tissue, which is larger than in the preceding stages (fig.33). The ventral mass is crescentic in transsection and lies just below the stomach, and anterior and somewhat dorsal to the anterior end of the duodenum (fig.45). A part of the ventral pancreas extends anteriorly along the left side of the gall bladder. The pancreatic duct opens into the gut ventrally and slightly to the left of the common bile duct (figs. 42 and 46). The pancreatic duct directly divides into two branches, a right and left, which end shortly. The dorsal duct has the same position as in the preceding stage.

In the following stages there is an increase in the size of the whole pancreas. The dorsal portion comes to lie more and more dorsal to the duodenum and along the right wall of the stomach, while the ventral portion increases in size anteriorly, in front of the anterior duodenal loop.

A description of the parts in a 35 mm. embryo is given as typical of the further development of the pancreas. In this stage the anterior part of the pancreas lies ventral to the gall bladder and is embedded in the peripheral part of the liver (fig.7,B). This part later probably forms the intra-hepatic portion of the pancreas described by Gianelli ('99). Somewhat caudally it is considerably larger in section and separates the liver into dorsal and ventral portions (figs. 11 and 12). In this region just caudal to the gall bladder the hepatic and ventral pancreatic ducts lie embedded in the pancreas. The pancreas is rather prismatic in cross section, its medial side lying along the right side of the stomach, its lateral dorsal side bounded by the duodenum.

Slightly anterior to the ostium of the common duct the pancreas is divided into two masses, one lying ventral and somewhat to the left of the duodenum, the other to the left of the duodenum between it and the stomach (fig.7,C). This latter mass joins the anteriorly directed portion of the dorsal pancreas. The remainder of the ventral pancreas now lies to the lower right side of the stomach, with a part projecting caudalward along the ventral wall of the duodenum (fig.34). The dorsal pancreas is caudal to the ventral and takes a more dorsal position,until it comes to lie above the duodenum which has migrated downward. In cross section the dorsal pancreas near its caudal end extends from the lower right side of the stomach almost to its dorsal margin. About half a centimeter from its caudal end the pancreas forms a very small mass, triangular in section, dorsal to the duodenum.

The ducts of the ventral pancreas of a 35 mm. embryo are shown in a graphic reconstruction in figure 34. The ventral duct arises with the common bile duct from a fold in the lower left wall of the duodenum (fig.7,C). It shortly separates from the common bile duct and extends anteriorly along its right side. It is somewhat ventral to the hepatic duct and divides into dorsal and ventral ducts. The ventral duct shortly sends off branches caudalward to the left ventral portion and extends forward in the ventral anterior part (fig.34). The dorsal of the two ducts divides several times into dorsal and ventral rami. Branches from the dorsal duct extend caudalward and to the right into the anteriorly directed portion of the dorsal pancreas. The dorsal pancreatic duct is given off from the upper left side of the duodenum near the caudal end of the pancreas and extends almost directly upward sending off several short branches anteriorly and posteriorly.

3. Description of the adult pancreas.

In a 15 cm. Amblystoma the anterior end of the pancreas, which is somewhat triangular in section, is embedded in the liver to the right of the stomach. It lies along the upper concave border of the liver with the portal vein and has a small free surface lined with peritoneum. Caudal to this the pancreas lies to the left of the duodenum, between it and the stomach and enlarges in a dorso-ventral direction (fig.35). Now it passes along the left wall of the duodenum but extends both dorsal and ventral to it, the ventral portion being between the duodenum and stomach. About 5 mm. by sections from its anterior end, the pancreas divides into two masses, one along the left ventral surface of the duodenum and the other dorsal to it. The ventral mass remains about in the same position, and extends caudalward almost half the length of the body of the gland. At the caudal end of the ventral portion of the pancreas the dorsal mass which has shifted somewhat to the right and lies above other loops of the intestine as well as the duodenum, is divided into two or three irregularly shaped lobes, one of which is dorsal to the duodenum and directly to the right of the stomach. This part of the pancreas extends a considerable distance caudalwards. As the duodenum shifts downward and to the left with relation to the stomach, this portion of the pancreas lies more and more to the right of the duodenum and for a considerable distance it lies ventral to the stomach. The pancreas extends caudalward almost to the gastro-duodenal loop.

A short distance from the caudal end of the pancreas the dorsal pancreatic duct is connected to the right side of the duodenum (fig.35). This duct extends forward almost to the point where the dorsal pancreas divides into several parts and gives off small branches as it comes to lie more and more in the dorsal part of the gland. The duct of the ventral pancreas joins the common bile duct (fig.35) where it opens into the left side of the duodenum or beside it. The pancreatic duct is ventral to the common bile duct and almost immediately divides into right and left ducts. The left duct is the more ventral and soon divides into branches which turn ventral and caudal (fig.35). The right duct extends anteriorly and upward and sends some branches into that part of the dorsal pancreas which joins the ventral.

4. Discussion.

As has been found in other Amphibia, the pancreas in Amblystoma is developed from three anlagen, two ventral and one median dorsal. As in other forms the dorsal develops earlier and, as Stöhr and others have stated, from only one evagination. This is found just caudal to the anlage of the stomach. In none of the embryos studied is there evidence of an outpouching toward the left as Goeppert ('91) described in another form. Older embryos show that there has been considerable growth of the dorsal pancreas in a cranio-caudal direction with the lengthening of the duodenum, and a division of the anterior end into several processes, one of which joins the ventral pancreas.

In the very earliest stages the ventral anlagen are caudal to the gall bladder. Goeppert ('91) and Choronshitzky ('00) have described these anlagen as lateral to the cystic evagination in the forms studied by them. The two ventral pancreas unite very early along their median sides. Braun ('06) has described the union of the dorsal and the right ventral pancreas as occurring before the union of the right and the left ventral anlagen. The appearance of considerable pancreatic tissue from the left side of the ventral anlage would indicate that there is growth from this evagination. Goette apparently thought this outpouching was rudimentary. The presence of a left duct in some 12-13 mm. embryos indicates that there is growth from the left side. Later stages show that there is more growth on the right side.

Although the lumen of the dorsal pancreatic anlage at first extends anteriorly, the duct later extends upward and in the adult again forward. Short lateral branches extend into the surrounding pancreas. The ventral ducts fuse to form a single one which divides into a right and left pancreatic duct. These again divide into smaller rami, of which some from the right side extend into the portion uniting with the dorsal pancreas. The dorsal and ventral ducts, however, always remain separate.

It is clear that in Amblystoma there is no complex pancreatic duct system as Oppel ('90) has observed in Proteus. In possessing a single dorsal duct Amblystoma resembles the Necturus as described by Kingsbury ('94). The posterior set of ducts emptying into the ductus choledochus as described by Oppel is quite different from the single ventral duct in Amblystoma. Nor does this conform to Kingsbury's description of two posterior pancreatic ducts each of which open into hepatic ducts. Nor can I confirm Bates' ('04) observations concerning the several pancreatic ducts which he stated opened into the hepatic ducts within the pancreas. A table of the ducts as they have been described in various urodeles may be of interest.

Table V

Table of the pancreatic ducts in the various urodeles

Form	Author	Dorsal pancreas	Ventral pancreas
Cryptobranchus japonicus	Hyrtl ('65)	1 (?)	1, joining with ductus choledochus
Salamandra perspicillata Geotriton fuscus	Wiedersheim ('75)	1 (?)	1, joining the two hepatic ducts
Proteus anguineus	Oppel ('89)	10, 33	9, 11 forming network with duct.chol.
Menobranchus lateralis	Goeppert ('91)		2, joining duct.chol.
Salamandra maculata }	"	1	1, joining duct.chol.
Salamandra altra }	"		3, " " "
Triton alpestris }	"		2 { 1, " " "
Triton taeniatus }	"		2 { 1, opening near duct. chol.
Cryptobranchus japonicus	2	6	1, opening near duct. chol.
Necturus maculatus	Kingsbury ('94)	1	2, joining separate hepatic ducts
Triton	Gianelli ('02)	1	1, joining hepatico cystic duct
Amblystoma	Bates ('04)	--	Several joining various hepatic ducts
Amblystoma	Baumgartner ('15)	1	1, may or may not join duct. chol.

As is well known the duct of the dorsal pancreas does not persist in Anura. However, Goeppert ('91) and Vogt and Yung ('94) have described several pancreatic ducts in the ventral pancreas some of which joined the ductus choledochus or hepatic duct. It is seen from the table that there is considerable variation in the pancreatic duct system of the urodeles. The complex system of some forms may be due, as Goeppert suggested, to a later union of the lesser pancreatic ducts with the duodenum or common duct.

The glandular portion of the ventral and dorsal pancreas fuse as is clearly shown in figure 33. This fusion of the glandular parts takes place immediately after the two parts come in contact. The union of the two parts is at first only a narrow neck of tissue, which remains small even in adults.

In a 35 mm. embryo and in smaller ones attention was called to a small part of the ventral pancreas lying below the gall bladder and separating the liver into upper and lower parts.

The peripheral portion of the liver grows more rapidly and surrounds this part on the outer side. It then has a peritoneal surface only on the medial upper side. This corresponds to Gianelli's intrahepatic portion of the pancreas. However, as stated by Goeppert, the pancreatic and hepatic tissues are always clearly separate. Goeppert ('91) has given a description of the relations and lobes of the pancreas. The pancreas in Amblystoma resembles that in those forms which he described in having a ventral part or lobe caudal to the liver and in intimate relation with it, and a dorsal or caudal part. Kingsbury described five more or less distinct parts. The following table shows a correlation of the lobes of the pancreas which various investigators have described with those of Amblystoma.

Table VI.

Table of the parts of the adult pancreas in Amphibia.

Proteus Oppel ('89)	Vordere Theil	Mittlere Theil	Hintere Theil		
Salamandra, Rana, etc. Goeppert('91)	Dorsal oder vordere Theil	Ventral oder hintere Theil	Hinterste Theil		
Necturus Kingsbury('94)	Lobe along intestine	Central part near gall bladder	Lobe along dorsal wall of liver	Lobe along splenic vein	Lobe along mesenteri[c] vein
Triton Gianelli('02)	Corpo, estremità posteriore	Estremità craniale	Pancreas intra-epatico		
Alytes obstetricanus Reuter ('06)	Kopf	Wurzel			
Amblystoma	Dorsal portion	Ventral portion	Portion along dorsal concave border of liver		

Goeppert mentioned that there were usually several other prolongations of pancreatic tissue. This is also true for Amblystoma, particularly from the anterior end of the dorsal portion were there several prolongations. It is to be remembered that "vordere" is used by Oppel and Goeppert with reference to the cranial end of the intestinal canal and not to the anterior end of the animal.

III. General Summary.

1. The liver begins as a median ventral projection of the lumen of the gut, then as an anterior outpouching from this lumen.

2. There is a later shifting of the posterior part of the liver to the right and dorsally, due to crowding of the stomach and development of the duodenum on the left.

3. A later growth on the left side results in an adult organ with right and left lobe, the right side always remaining more dorsal on the lateral side of the stomach.

4. The ductus choledochus develops as the early anteriorly directed lumen from the gut.

5. The right and left hepatic ducts develop as divisions of the ductus choledochus and by growth and division form the hepatic rami and branches.

6. The gall bladder begins as a median ventral outpouching of the posterior part of the liver anlage. It is first widest laterally, then becomes larger in its craniocaudal diameter, then its dorso-ventral and finally its longer axis is nearly transverse.

7. There is an early right lateral shifting of the gall bladder as of the liver, due probably to the same causes. Along with this there is a constant shifting of direction of the cystic duct in keeping with the dorsalward migration of the gall bladder.

8. The cystic duct is early closed off with the right hepatic and due to the caudalward growth and division of the hepatic duct is finally attached to the lateral branch of this duct.

9. The ventral pancreatic anlagen are ventro-lateral evaginations of the gut caudal to the cystic anlage. The dorsal pancreas - a single median dorsal evagination - forms the larger portion of the early pancreas, later it is a narrow lobe dorsal to the duodenum.

10. The ventral pancreatic ducts are constrictions of the two ventral pancreatic anlagen. Later these unite and form a single ventral pancreatic duct which opens into the common bile duct or in the intestine at the side of the common bile duct. The dorsal duct remains a single stem with short lateral branches.

11. There are two main parts or lobes in the adult Amblystoma pancreas, a dorsal and a ventral, with one or more lesser projections from these. An anterior extension of the ventral lobe is constant.

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FIGURES

Fig. 1. Sagittal section of an Amblystoma embryo 4.5 mm. long taken at about the median plane. X 25. F.g., foregut; g, caudal extension of gut; He, heart; Li, liver; Y, yolk mass.

Fig. 2. Sagittal section of an Amblystoma embryo 5 mm. long, taken to the right of the median line. X 25. F.g., fore-gut; G, caudal extension of gut; He, heart; Li, liver; Y, yolk mass.

Fig. 3. Sagittal section of an embryo almost 7 mm. long. X 25. D.chol., ductus choledochus; D.h.d., right hepatic duct; F.g., foregut; G., caudal extension of gut; G.B.,gall bladder; He, heart; Li, liver; Lu., lung; Y, yolk mass.

Fig. 4. Sagittal section of an embryo almost 9 mm. long. X 25. D. chol.,ductus choledochus; D.h.d., right hepatic duct; F.g., foregut; G.B.,gall bladder; He, heart; Li., liver; Lu., lung; Y, yolk mass.

Fig.5. Transverse section of embryo 9 mm. long, X 25. F.g., foregut; L, left portion liver; R, right portion liver.

Fig. 6. Transverse section of an embryo 11.5 mm. long. X 25. F.g., foregut;GB, gall bladder; L, liver.

Fig. 7. A series of transverse sections in the region of the liver. A, embryo of 13.5 mm. X 20; B, embryo of 20 mm. X 15; C, embryo of 35 mm. X 10; G.b., gall bladder; L, liver; P., pancreas; Sp., spleen; St., stomach; x, ostia of ductus choledochus into gut.

~~A 13.5~~	At level of anterior end of liver	About mid-way between first and third drawing	Anterior end of gall bladder	Fig. 9	Level of attachment of cystic duct to gall bladder	Level of ostium of ductus choledochus
A 13.5	"	"	"	Fig. 9	"	"
14 mm.	----	----	----	Fig. 8	"	----
15 mm.	----	----	----	Fig. 10	"	----
B 20	"	"	"	Fig. 11	"	"
C 35	"	----	"	Fig. 12	"	"

Fig. 8. Transverse sections of an Amblystoma embryo 14 mm. long, taken at level of attachment of cystic duct to the gall bladder. X 35. D, duodenum; G.B., gall bladder; Li., liver; P., pancreas; Sp., spleen; St., stomach.

Fig. 9. Transverse section of an Amblystoma embryo 13.5 mm. long, taken at the same level as figure 8. X 35. For abbreviations, see figure 8.

Fig. 10. Transverse section of an embryo 15 mm. long, taken at the same level as figure 8. X 35. For abbreviations see figure 8.

Fig. 11. Transverse section of an embryo 20 mm. long, taken at the same level as figure 8. X 30. For abbreviations see figure 8.

Fig. 12. Transverse section of an embryo 35 mm. long, taken as in figure 8. X 15. For abbreviations, see figure 8.

Fig. 13. A dissection of an Amblystoma 12 cm. long. X 1. The ventral abdominal wall has been cut away and the gall bladder and main hepatic ducts dissected out. D, duodenum; D.chol., ductus choledochus; D.cy., cystic duct; D.h.d., right hepatic duct; D.h.s., left hepatic duct; L.L., left lobe liver; R.L., right lobe liver; St., stomach.

Fig. 14. Diagrammatic drawing of the gall bladder and hepatic ducts of an Amblystoma.

Fig. 15. Graphic reconstruction (lateral view) of an Amblystoma 7 cm. long. X 15. D.chol., ductus choledochus; D.cy., cystic duct; D.h.d., right hepatic duct; D.h.s., left hepatic duct; D.P., pancreatic duct; G.B., gall bladder; L.Br., left branch of common ramus; L.R.l.d., lateral branch right lateral ramus; L.R.l.s., lateral branch left lateral ramus; L.R.m.d., lateral branch right medial ramus; L.R.m.s., lateral branch left medial ramus; M.R.l.d., medial branch right lateral ramus; M.R.l.s., medial branch left lateral ramus; M.R.m.d., medial branch right medial ramus; M.R.m.s., medial branch left medial ramus; R.Br., right branch of common ramus; R.l.d., right lateral ramus; R.l.s., left lateral ramus; R.m.d., right medial ramus; R.m.s., left medial ramus.

Fig.16. Graphic reconstruction (ventral view) of an Amblystoma 10 cm. long. X 15. For abbreviations, see figure 15.

Fig. 17. Graphic reconstruction (lateral view) of an Amblystoma 15 cm. long. X 15. For abbreviations, see figure 15.

Fig. 18. Graphic reconstruction (lateral view) of the biliary apparatus of an Amblystoma embryo 13 mm. long, X 100. D., duodenum; D.chol., ductus choledochus; D.h.d., right hepatic duct; D.cy., cystic duct; g.b., gall bladder; R.l.d., right lateral ramus; R.l.s., left lateral ramus; R.m.d., right medial ramus; R.m.s., left medial ramus. X, pancreatic duct.

Fig. 19. Graphic reconstruction (lateral view) of the biliary apparatus of an embryo approximately 13.5 mm. long. X 100. For abbreviations, see figure 18.

Fig. 20. Anterior view of a reconstruction of the lumina of hepatic ducts and gall bladder of a 9 mm. embryo. X 100. D.h.d., right hepatic duct; D.h.s., left hepatic duct; g.b., gall bladder; R.l.d., right lateral ramus; R.l.s., left lateral ramus; R.m.d., right medial ramus; R.m.s., left medial ramus.

Fig. 21. Transverse section of an Amblystoma embryo 9 mm. long, taken in the region of the gall bladder. X 25. D.chol., ductus choledochus; F.g., foregut; D.cy., cystic duct; g.b., gall bladder.

Fig. 22. Sagittal section of an embryo 12.5 mm. long. X 25. F.g., foregut; g.b., gall bladder; Li., liver.

Fig. 23. Drawing of a model of the gall bladder of an Amblystoma 14 mm. long. A, anterior view; B, left lateral view. X 40.

Fig. 24. Lateral view of a reconstruction of the pancreatic anlagen of a 9 mm. embryo. X 40. D.pan., dorsal pancreas; Li., liver; St., stomach; V.pan., ventral pancreas; Y, yolk gut.

Fig. 25. Lateral view of a reconstruction of the lumina of the gut and pancreatic anlagen. X 40. G.b., gall bladder; other abbreviations, ~~same~~ as in figure 24.

Fig. 26. Drawing of a section through the ventral anlagen of an embryo 9 mm. long. X 30. F.g., foregut; v.pan., right and left ventral pancreases.

Fig. 27. Drawing of a section through the ductus choledochus of an 11 mm. embryo. X 30. D.chol., ductus choledochus; St., stomach; V.pan., ventral pancreas.

Fig. 28. Drawing of a section about 80 u anterior to the preceding. X 30. For abbreviations, see figure 27.

Fig. 29. Drawing of a section through the dorsal pancreas of an 11 mm. embryo. X 30. D., duodenum; D.pan., dorsal pancreas; Y, yolk gut.

Fig. 30. Lateral view of a model of the pancreatic anlagen of an 11 mm. embryo. X 40. D.pan., dorsal pancreas; G.B., gall bladder; Li., liver; St., stomach; V.pan., ventral pancreas; Y, yolk gut.

Fig. 31. Lateral view of a model of the pancreas of a 13 mm. embryo. X 30. D.pan., dorsal pancreas; G.B., gall bladder; St., stomach; V.pan., ventral pancreas; Y, yolk gut.

Fig. 32. Drawing of a section showing the united acini of the dorsal and right ventral pancreas. X 180. D.pan., from dorsal pancreas; V.pan., from ventral pancreas; bl., blood vessel.

Fig. 33. Lateral view of a model of the pancreas of a 15 mm. embryo. X 30. D.pan., dorsal pancreas; D., duodenum; Li., liver; St., stomach; V.pan., ventral pancreas.

Fig. 34. Graphic reconstruction of the pancreas and pancreatic ducts of a 35 mm. embryo. X 20. D., duodenum; D.pan.d., dorsal pancreatic duct; D.pan., dorsal pancreas; Lt.pan.d., left ventral pancreatic duct; Rt.pan.d., right ventral pancreatic duct; V.pan., ventral pancreas.

Fig.35. Graphic reconstruction of the pancreas and pancreatic ducts of a 20 cm. Amblystoma. X 5. For abbreviations, see figure 34.

Plate 1.

36. Median view of right and left halves of a reconstruction of the liver of an Amblystoma embryo 7 mm. long. X 70.

37. Median view of right and left parts of a reconstruction of the liver of an Amblystoma embryo 9 mm. long. X 70.

38. Posterior view of a reconstruction of the liver of an Amblystoma embryo 9 mm. long. X 100.

d., early anlage of duct	D.h.s., left hepatic duct
D.chol., ductus choledochus	G.B., gall bladder
D.cy., cystic duct	Li., liver
D.m., dorso-medial duct	Lt.,Rt.,left and right
D.h.d., right hepatic duct	parts of hepatic anlage.
	v.l., ventro-medial duct

Plate 2.

39. Ventral view of a reconstruction of the hepatic ducts and gall bladder of an Amblystoma embryo 14 mm. long. X 100.

40. Dorsal view of the same reconstruction. X 100.

41. Ventral view of a reconstruction of the hepatic ducts and gall bladder of an embryo 13.5 mm. long. X 100.

42. Dorsal view of a reconstruction of the hepatic ducts and gall bladder of an embryo 15 mm. long. X 100.

43. Right ventral view of a reconstruction of the hepatic ducts and gall bladder of an embryo 20 mm. long. X 100.

D., duodenum

D.chol., ductus choledochus

D.cy., cystic duct

D.h.d., right hepatic duct

D.h.s., left hepatic duct

D.P., pancreatic duct

g.b., gall bladder

L.Br., left branch of common ramus

L.R.l.d., lateral branch right lateral ramus

L.R.l.s., lateral branch left lateral ramus

L.R.m.d., lateral branch right medial ramus

L.R.m.s., lateral branch left medial ramus

M.R.l.d., medial branch right lateral ramus

M.R.l.s., medial branch left lateral ramus

M.R.m.d., medial branch right medial ramus

M.R.m.s., medial branch left medial ramus

R.Br., right branch of common ramus

R.l.s., left lateral ramus

R.l.d., right lateral ramus

R.m.s., left medial ramus

R.m.d., right medial ramus

Z., extra duct in 13.5 mm. Amblystoma embryo

Plate 3.

44. Right ventral view of a reconstruction of the hepatic ducts and gall bladder of an Amblystoma embryo 35 mm. long. X 70.

D., duodenum

D.chol., ductus choledochus

D.cy., cystic duct

D.h.d., right hepatic duct

D.h.s., left hepatic duct

D.P., pancreatic duct

g.b., gall bladder

L.Br., left branch of common ramus

L.R.l.d., lateral branch right lateral ramus

L.R.l.s., lateral branch left lateral ramus

L.R.m.d., lateral branch right medial ramus

L.R.m.s., lateral branch left medial ramus

M.R.l.d., medial branch right lateral ramus

M.R.l.s., medial branch left lateral ramus

M.R.m.d., medial branch right medial ramus

M.R.m.s., medial branch left medial ramus

R.Br., right branch of common ramus

R.l.d., right lateral ramus

R.l.s., left lateral ramus

R.m.d., right medial ramus

R.m.s., left medial ramus

Plate 4.

45. Anterior view of the pancreas and ventral pancreatic ducts of a 13 mm. embryo. X 60.

D., duodenum

D.pan., dorsal pancreas

G.B., gall bladder

Lt.pan.d., left ventral pancreatic duct.

Rt.pan.d.,right ventral pancreatic duct.

St., stomach

V.pan., ventral pancreas

Y, yolk gut

46. Anterior view of the pancreas and ducts of a 15 mm. embryo. X 60.

D.chol., ductus choledochus; V.pan.d., ventral pancreatic ducts.

For other abbreviations, see figure 45.

Footnotes

(1) The terms used by Scammon ('13) in describing the ducts of Elasmobranchs have been used in this paper.

(2) In the further study of the pancreas it was found that this duct was attached by means of a small tubule to the left side of the ventral duct of the pancreas. The epithelial lining resembled that of the gall bladder, for which this duct was mistaken at first. It might very well be a pancreatic bladder. The pancreatic duct in this embryo was to the right of the enlarged duct.