A CONTRIBUTION TO THE EMBRYOLOGICAL STUDY
OF SQUALUS SUICILII, GIRARD

WITH NOTES ON THE LIFE-HISTORY

by

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INTRODUCTION

The study of the embryology and life-history of Squalus sucklii, Girard, was commenced at the University of British Columbia in the winter of 1928, continued at the Pacific Biological Station at Departure Bay the summer of 1929 where some material was obtained from the Reduction Plant in Nanaimo, and again continued at the University during the last session.

A particular study is made of the embryology of a 21 mm. series, although, for sake of comparison, series were made of embryos of 10 to 40 mm. in length. The data concerning the life-history, particularly that on the period of gestation, were found to be in part similar to that of Squalus acanthias and in part dissimilar. The differences and similarities are discussed in conjunction with the considerations of the paper of E. Ford, 1921, from the Plymouth Biological Station.

I should like to express my appreciation of the assistance and suggestions given by Dr. C. McLean Fraser and Dr. W.A. Clemens. My thanks are also due to G.J. Spencer for procuring literature and for many suggestions on technique.
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I PERIOD OF GESTATION

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EXTERNAL APPEARANCE.

On opening the egg-capsule the opaque, yellowish white embryo and the yolk sac are readily separated from the watery albumen. The embryo is attached to the yolk sac by a long yolk stalk which, even at an early stage of development, allows a good deal of movement. The embryo is quite active moving with the typical wave-like motion of the adult. The total length of the embryo is 2.10 cm., the head being two-sevenths of the total length.

The body is quite straight; the head large, the rest tapering evenly to the tail. The mid-brain is the most anterior portion with the fore-brain at an angle of ninety degrees with the main axis of the body. The eyes are prominent; the choroid fissure showing distinctly on the posterior margin. The olfactory vesicles are simple pits. The first gill slit is distinctly differentiated into the spiracle having closed ventrally and moved to lie at an angle of forty-five degrees with the second gill slit. The second gill slit extends two-thirds of the distance across the side of the body; the remaining slits growing progressively smaller, the sixth being half as long as the second. Gill filaments show from all the gill slits; the greatest development is in the second where the filaments are 1.5 mm. in length, the least in the spiracle where there are six short knobs. The mouth remains as a triangular opening into the buccal
cavity showing an indication of the development of the slit-like adult mouth. The middle lateral portion of each gill arch has grown posteriorly over the next to form the gill pouch or pocket.

The rudiments of the fins are well developed giving indication of the unpaired dorsal, second dorsal and caudal, the paired pectorals and pelvics. The dorsal and second dorsal, however, show no indication of the anterior fin spines.
The most noticeable fact about the brain is the extreme flexion that it has undergone. The fore and mid-brain are literally curved over the end of the notochord. The flexure starts in the mid-brain which results in bringing this region into a position approximately anterior to the end of the notochord. The movement at the same time brings the fore-brain directly under the notochord with its original anterior end facing postero-ventrally.

Constrictions have divided the brain into fore-brain, mid-brain and hind-brain. The fore-brain has divided into the telencephalon and diencephalon, the hind-brain into the metencephalon and the myelencephalon. The mid-brain remains single as the mesencephalon.

The telencephalon is large, far larger than the posterior portion of the prosencephalon, the diencephalon. The lateral portions which are adjacent to the thin wall of the dorsal cleft dividing the tel- and diencephalon are slightly folded around the smaller diencephalon. The optic stalks are given off laterally from the wide canal connecting the tel- and diencephalon. Separating the anterior part of the telencephalon from this portion are slight ventro-
lateral constrictions.

The diencephalon is separated dorsally from the telencephalon by a deep, wide, thin-walled cleft, and ventrally by a slight constriction. The anterior wall of the diencephalon is very thin and flattened, the laterals walls thickened. It is connected posteriorly with the telencephalon by a wide canal and separated from the mesencephalon by lateral constrictions. Posterior to the above mentioned cleft and in the roof of the diencephalon the epiphysis arises as a long, simple tube tapering to the tip. On the floor dorsal to the optic stalks the infundibulum is developed as a round evagination having thin walls and a slightly constricted base.

The mesencephalon is more distinctly marked off from the fore-brain than from the hind. The lateral walls are thicker than the roof and floor, the cavity elliptical in shape.

The mes- and metencephalon are joined by a wide channel. The middorsal line of the metencephalon is thin walled; the lateral walls thickened in four places to form distinct horns which project out into the ventricle, the dorso-lateral projections, the alar plate, being greater than the ventro-lateral basal plate.
The myelencephalon has a very thin roof extending laterally to the median line in its greatest development. It looks just as if the walls had been stretched apart at the dorsal line to form a wide open V leaving a very thin strip of nervous tissue across the top. The lateral walls are quite thick and close in on one another dorsally as the myelencephalon tapers towards the spinal cord. The basal plate projects farther into the neurocoele, the alar plate less than in the metencephalon, thus forming midventrally a deep sulcus around which the ependymal layer is more evident than in the lateral walls.

The spinal cord extends from the myelencephalon to the tail tapering to end just anterior to the neurenteric canal. In cross-section it is slightly ovoid, being larger ventrally, with the three primary layers around a very narrow, laterally compressed neurocoele. The innermost layer, the ependymal, which encircles the whole neurocoele is widest laterally where it is half the width of the cord. The middle or mantle layer is composed of two crescent-shaped parts lying on either side of the cord which are only connected by a commissure ventrally. The outer layer is the marginal layer. It is free of nuclei and composed entirely of nerve fibres. This layer is divided into two portions:
an inner densely fibrous one and an outer vesicular part crossed by fibres from the inner nucleated layers.

A very interesting fact concerning the lumen of the spinal cord was noticed and investigated, namely that the walls of the neural tube during a certain period of embryonic development approximated and fused to give two or three lumina. This condition was traced thru a series of embryos which were obtained in different years and at different periods of the year, preserved in different types of fixers and imbedded under different conditions. Because of this variation it was concluded that the condition was not one due to physiological or histological factors but was purely an embryonic structure. Embryos 1.02 cm. in length showed no evidence of the closures while those of 1.15 cm., 1.29 cm., 1.62 cm., 2.15 cm., and 2.97 cm. showed a gradual development thru the series. Embryos of 3.20 cm. and 3.49 cm. had no trace of them. From these facts it was concluded to be of a transitory nature.

The following is a description of the condition in the embryo being studied.

Opposite the second gill slit the first indication of this closure is seen. It seems to be due to the growth of the cells in the basal plate described above. Those plates grow towards one another, fuse and thus close
over the ventral sulcus of the neural tube. This sulcus re-
 mains thin walled as does the dorsal one which is seen in the
 spinal cord where it joins the medulla. Posteriorly the gen-
eral shape of the lumen becomes more rectangular, the sides
more parallel as they approach one another. Opposite the
anterior part of the third gill slit there is an indication
of the enlargement of the two alar plates closing in slight-
ly ventral to the middle of the remaining lumen. At the
posterior part of the third gill slit these plates come to-
gether and fuse. Thus are formed the three lumina of the
spinal cord seen in cross section. The dorsal lumen is
triangular in shape, larger than the other two. The ventral
one is long and narrow; the middle one slightly shorter but
more rounded than the ventral. The two points of fusion
differ in that the dorsal one is about three times as long as
the ventral. Three sections (36 micra) anterior to the
fourth gill slit the ventral fusion disappears and the re-
sulting ventral tube becomes long and narrow with a dilated
dorsal portion which was the middle lumen. Meanwhile the
ventral lumen has become smaller and round assuming the
shape of a long inverted drop. The spinal cord grows smaller
and more round. At the sixth gill slit the cord is oval,
the dorsal lumen quite small; the large ventral lumen ellipt-
ical, its dorso-ventral length slightly less than half the
dorso-ventral length of the cord.

Opposite the yolk stalk where the body cavity becomes continuous with that of the stalk the dorsal fusion disappears and the neural tube assumes a longer elliptical outline than the ventral portion had. Just opposite the posterior border of the yolk stalk the ventral fusion again appears. Four sections (48 micra) posterior to this the ventral one reappears. Two sections (24 micra) posterior to this the middle lumen closes leaving a dorsal and a ventral lumen, the ventral lumen being twice as large as the dorsal. This fusion extends over half the total length of the cord. From here the tube remains in this condition until the neurenteric canal is reached where the fusion disappears and the neural canal assumes a spherical outline.

The spinal nerves consist of a dorsal ganglionated and a ventral non-ganglionated root. These roots unite a short distance from the cord, then divide sending off a lateral and slightly dorsal nerve to the muscle plate, the dorsal ramus, a median ventral nerve to the segmental sympathetic ganglion, the ramus communicans, and a ventral nerve to the body wall, the ventral ramus. At the point where the ramus communicans enters the sympathetic ganglion a ventral nerve is given off the ganglion which runs parallel to the ventral ramus out thru the lateral muscle plate and vent-
rally along its outer border. Branches of both the sympathetic and ventral rami are given off to the pectoral and pelvic fin buds. Opposite the yolk-stalk the sympathetic nerve branches just before passing thru the muscle plate, and sends a nerve ventrally between the muscle plate and the wall of the coelom.

The primary sympathetic ganglia lie ventro-laterally from the notochord in the centre of a triangle bounded by the dorsal aorta, the pronephric duct and the dorsal muscle plate. In a few sections small masses of cells have formed dorso-median to the primary sympathetic ganglia. These are the secondary sympathetic ganglia which are connected to the primary ganglia by a commissure.

Only five of the ten cranial nerves are developed, namely the fifth or trigeminal, the seventh or facial, the eighth or auditory, the ninth or glossopharyngeal and the tenth or vagus.

In a section thru the ventral portion of the optic stalk and the mid portion of the infundibulum the origin of the fifth cranial nerve is seen. It arises from the medulla by two distinct roots and enters a large ganglion, the Gasserian ganglion. On emerging from this ganglion it divides into two parts, an anterior one going to lie beside the
optic cup --the ophthalmicus profundus nerve--, and a posterior one-- the mandibular nerve. The mandibular nerve then branches into a small dorsal nerve and a large ventral nerve. Both parts run ventro-posteriorly into the mandibular arch. The anterior branch runs to the ventral wall of the arch, the posterior one lies close beside the muscle plate in the arch and curves ventro-medially when the arch closes under the mouth. The anterior branch is the maxillary division of the trigeminal, the posterior one the mandibular division, supplying the upper and lower jaws respectively.

In a section thru the tip of the diencephalon and the optic vesicle the root of the seventh and eighth cranial nerves is seen. These two nerves are very closely associated arising as they do from a single large ganglion. This root passes into a large ganglion from which is sent anterior a large nerve, the palatine branch of the seventh nerve. This nerve runs ventro-anteriorly near the skin in the angle made by the optic vesicle and the hind brain to supply the region of the palate. After the palatine is given off the main stem runs posteriorly giving off a small dorso-lateral branch to the skin which will eventually supply the superficial constrictor muscles. The main part then passes out to the junction of the upper and lower jaws where it divides into an anterior branch which runs immediately below the
skin towards the angle of the jaw, and a posterior branch which passes along the posterior margin of the hyoid arch.

From the combined three posterior branches of the facial the eighth or auditory nerve is given off opposite the anterior end of the auditory vesicle. This nerve enters a large ganglion which lies close beside the auditory vesicle. From the ganglion nerve fibres are sent out to the semicircular canal rudiments.

Opposite the posterior part of the ear the ninth or glossopharyngeal nerve rises from the medulla oblongata. Passing posterolatero-ventrally it dips ventral to the auditory vesicle where it enters a large ganglion. From this ganglion a small branch is given off dorso-laterally to the lateral line. The main branch then goes to the outer and anterior border of the hyoid arch, enters a ganglion and sends off a small branch to the anterior dorsal wall of the arch—a branchial nervous supply for the external gills. After sending off this branch the main stem passes ventrally to lie beside the muscle plate in the arch.

In an earlier stage the vagus arose as a series of four roots from the posterior portion of the medulla. Gradually the posterior roots were lost and now only the two anterior ones remain. The two posterior ones arise as branches of the first and second root ganglion.
At the extreme posterior border of the auditory vesicle the first root of the vagus is given off the myelencephalon. A short distance posterior the second root is given off. Shortly after leaving the cord each enters a ganglion. From these ganglia each sends off two branches, a small anterior one to the lateral line, the other to enter a large commissure. This commissure rises from the first root, passes directly posterior receiving the branch of the second root and continues posteriorly over the remaining arches to end when the intestinal nerve of the vagus is given off. From this commissure into the third, fourth, fifth and sixth arches and the posterior wall of the sixth gill slit nerves are sent ventro-laterally to the outer, anterior border of the third arch where a small branch goes to the gill filaments. Just anterior to the places where the last three above mentioned nerves are given off small nerves arise and pass dorso-laterally to lie in the groove of the lateral line. The main commissure then continues ventrally and posteriorly to become the intestinal branch of the vagus ending in an enlarged ganglion mass lateral to the oesophagus.

The roots of the glossopharyngeal and the vagus are connected close to the medulla by a commissure which is continuous with the dorsal roots of the spinal nerves. It
is of the same cellular structure as the more ventral commissure although of much smaller size.

ORGANS OF SPECIAL SENSE

Under the organs of special sense are described the olfactory organ, the eye, the ear and the lateral line.

The olfactory organs are simple somewhat triangular pits opening to the outside by a wide circular mouth. There are no indications of Schneiderian folds.

Some parts of the eye are well developed, others indicated so that a general conception is reached as to the nature of the adult structure. In the optic cup the inner retinal layer is thickened and closely applied to the outer narrow pigmented layer. A concentration of mesenchyme about the cup indicates the future development of the choroid and sclerotic coats.

The lens is large and ovoid, slightly flattened on the median side. The growth of cells from this flattened side is extensive. They have grown out radially towards the outer wall nearly closing the lens vesicle. The nuclei of this portion are large and faintly staining with few gran-
ules. The outer wall, the lens epithelium, is two cells deep, the nuclei being at different levels and darkly staining.

The short, broad optic stalk is attached to the ventral proximal portion of the cup at the base of the choroid fissure and shows at this point a slight indication of the infolding to form a tube down which the optic nerve fibres from the retina will ultimately grow.

Projecting into the optic cup thru the choroid fissure is a mesodermal structure the processus falciformis which spreads out over the retina to form a flattened disc. From the upper surface of the disc long slightly intertwining fibres radiate out into the posterior chamber. A small blood vessel enters the processus falciformis at the choroid fissure and branches into the pileate structure.

In the ear the three semicircular canal rudiments are quite evident extending as pockets from the otocyst proper. The anterior oblique canal projects antero-dorsally, the posterior oblique postero-laterally and the horizontal laterally towards the skin. The saccus is enlarged ventrally and tapers dorsally into the endolymphatic duct which opens to the exterior postero-dorsally to the posterior extremity of the posterior oblique canal. In the thickened
ventral walls of the canal rudiments the ampullae appear as groups of large clear cells. To the base of each cell is attached a long nervous fibre which is connected to the auditory nerve.

The lateral line has developed anteriorly to the third gill arch and posteriorly to a position opposite the rectal gland. It is formed by a thickening of the ectoderm at the level of the notochord which gives rise to an inner layer, the subsequent mucous layer of the epidermis. The nervous supply of this organ is furnished by branches from the vagus and glossopharyngeal nerves which come to lie in a hollow in the mucous layer.

**ALIMENTARY TRACT AND ITS APPENDAGES**

The mouth or entrance to the buccal cavity is still widely open although assuming the slit-like appearance of the adult. There is no constriction between the buccal cavity and the pharynx. The pharynx extends laterally into the spiracle and gill slits.

The thyroid has lost all connection with the pharynx and lies in the floor of the pharynx opposite the
third gill slit. In shape it is rod-like, triangular in the centre and pointed at both ends.

The pharynx before joining the oesophagus is flattened dorso-ventrally in a wide curve. The oesophagus is small and entirely closed having no lumen whatsoever. Opposite the posterior portion of the ventricle the oesophagus enters the stomach. This is a crescent-shaped laterally flattened structure, curving first to the left side then ventro-medially to enter the intestine. The larger left limb is the cardiac, the median smaller the pyloric division.

The first part of the intestine, the duodenum is short though well defined. Into this segment the ducts of the liver and pancreas and the yolk stalk enter. The walls are thin and where the yolk-stalk enters are thrown into irregular folds.

The main portion of the intestine is taken up by the spiral valve. It is seen to be formed by an ingrowth of the intestinal wall to form a series of annular folds eleven in number, the posterior ones being closer together than the anterior.

The portions of the intestine succeeding the valvular intestine, the colon and rectum, are differentiated by general structure and also by the fact that the rect-
al gland empties into the junction of these two parts. The walls of the colon are thicker, the cells more columnar than those of the rectum. On the other hand the lumen of the former is small and round while that of the latter is crescent-shaped. The rectal gland is a simple antero-dorsolateral outpocketing of the wall of the intestine at the junction of the colon and rectum.

The rectum leads into an enlarged space, the cloaca, which forms a common receptacle for the digestive and urinary, and later the genital systems. It is somewhat flattened laterally and ends blindly after the walls of the segmental ducts have fused with its walls. The proctodaeum is not yet broken thru, there being a close application but no fusion between the ectoderm and endodermal layers.

The posterior portion of the gut which in the earlier stages is called the postanal gut has completely atrophied anteriorly and is only seen in the very tail region where it curves about the posterior portion of the notochord to join the neural tube and becomes the neurenteric canal.
GLANDS.

Under this heading are discussed those parts which are either derivatives of the alimentary tract or are associated with it in the adult.

The main portion of the liver arises as a mass of embryonic liver tissue in that region bounded anteriorly by the sinus venosus and posteriorly by the yolk stalk. From this portion three lobes push posteriorly, a long right and left, and a small median caudate. The gall bladder is situated in the caudate lobe, is drained by a duct which, joined by the other ducts from the lobes of the liver, forms the ductus choledochus and empties into the proximal portion of the duodenum on the dorsal side. Posteriorly the right and left lobes of the liver (the left being the larger) extend opposite the opening of the pancreatic duct into the intestine.

The pancreas is composed of two lobes, a central portion connecting these and a duct. The dorsal lobe is large and expanded into a number of diverticula. From these the central portion leads latero-ventrally to meet the more compact ventral lobe which has a larger number of less branched diverticula. From the ventral lobe the short pancreatic duct leads into the duodenum just anterior to the
first fold of the valvular intestine.

The subnotochordal rod underlies the whole length of the notochord except for the small curved anterior portion. Anteriorly it is very small and shows signs of atrophy. Centrally it shows its highest stage of development as a small mass of darkly staining cells. In the region of the neurenteric canal it is quite rudimentary and shows its origin as a proliferation of the cells of the dorsal wall of the gut.

**MESENTERIES**

The mesenteries and septa which are to form partitions between the different body cavities are being developed. Around the sinus venosus mesenchyme is collecting to form the rudiment of the lateral mesocardium. The single dorsal mesentery which in an earlier stage supported the whole of the digestive tract is beginning to break down to form the adult structure—a large anterior and a small posterior mesentery. This is accomplished by holes appearing in the mesentery; these coalesce and the mesentery disappears. The posterior mesentery extends from the anterior tip of the rectal gland posteriorly. The anterior mesentery extends over the greater part of the remaining portion ending a short distance anterior to the rectal gland. Just before the yolk
stalk enters the body a septum forms and attaches the liver to the ventral body wall. This is, however, the only spot where the two lateral sides of the body cavity are completely separated from one another.

ACCESSORY GLANDS

The interrenal gland is an unpaired rod-like mass of cells lying between the dorsal aorta and caudal vein in the region of the posterior end of the kidney. As yet the cell mass is undifferentiated except that there is a slight indication of a fine membranous covering.

The sympathetic ganglia which form the basis of the suprarenal glands are well developed and have conspicuous branches connecting them with the spinal nerves. Branches which are masses of dark staining cells with a definite lumen are given off to the dorsal aorta. The ganglia themselves show an indication of division into a ventral suprarenal and a dorsal sympathetic portion.

The rudiment of the spleen is seen as a mass of undifferentiated cells derived from a proliferation of mesenchymal cells. This projects out into the body cavity from the left side of the dorsal mesentery opposite the pancreas.
RESPIRATORY SYSTEM

The respiratory tract comprises the mouth, pharynx, gill slits and gill filaments.

The spiracle, the most anterior of the six gill slits, has become definitely differentiated, and lies at an angle of forty-five degrees with the long axis of the body. The second gill slit lies slightly at an angle with the dorsal portion pointing anteriorly. The fifth and sixth slits are at right angles to the body axis.

The branchial arches have lengthened out laterally, the central part becoming a plate, the septum from which the gill filaments arise; the distal part folding over the next posterior arch.

The embryonic gill filaments arise as nodules from the septum of the walls of the gill slits. Each nodule lengthens out and forms a more or less flattened plate about whose outer border a blood vessel circles. Filaments have developed on the anterior walls of the spiracle and the sixth gill slit and on both anterior and posterior walls of the four remaining arches. The filaments from the anterior walls are relatively much longer than those on the posterior walls.
CIRCULATORY SYSTEM

HEART

The heart consists of a large thin-walled auricle lying dorsal to a smaller thick-walled ventricle; anteriorly from the ventricle is a conus arteriosus, posteriorly from the auricle a sinus venosus.

Indications of valves show in the conus arteriosus and between the auricle and ventricle. Those in the conus arteriosus appear as three triangular folds, one dorsal, two latero-ventral, projecting into the lumen of the conus; those between the auricle and ventricle as two folds pointing anteriorly into the auricle.

ARTERIES

The conus arteriosus leads anteriorly into the ventral aorta which gives off the six afferent aortic arches to the branchial arches. The fifth and sixth afferents leave the ventral aorta together dividing shortly after; the rest come off separately. These traverse the outer posterior walls of the branchial arches, send off branches to the gill filaments and run dorsally to join the dorsal aorta. A
secondary arch is developed in the gill filament region. It consists of two branches. The posterior branch arises in the filament region in the posterior wall of the branchial arch, sends three vessels directly anterior to meet the anterior branch in the filament region in the anterior wall of the branchial arch. These are the efferent collectors which, joined by the afferent collectors enter the dorsal aorta.

The dorsal aorta is divided for the greater part of the arch system. It branches immediately to the entrance of the sixth efferent arch and unites again just anterior to the spiracular cleft so that all the arches but the sixth efferent empty into separate right and left dorsal aortae. The single dorsal aorta continues anteriorly to the base of the infundibulum where it again divides sending branches to lie close beside the wall of the mesencephalon. Immediately posterior to this division branches enter from the mandibular regions. These are the pseudobranchial arteries. They arise from the posterior portion of the first afferent collector, run anteriorly under the spiracle, then dorso-anteriorly to join the dorsal aorta. Posterior to the aortic arches the dorsal aorta continues as an undivided vessel to the tail region where it becomes the caudal artery. The one large branch given off opposite to the posterior border of
the ventricle is the omphalomesenteric or vitelline artery. It dips ventrally and to the right side to enter the yolk stalk. Paired branches are given off the aorta to every segment—segmental arteries.

VEINS.

Blood is collected from the head region by the anterior cardinal veins which receive vessels from about the di- and mesencephalon and the optic vesicles. Continuing posteriorly they swerve laterally and come to lie ventro-laterally from the auditory vesicles near the skin. In the branchial region they lie lateral to the dorsal aorta. In the heart region they dip ventro-laterally to enter the common cardinal veins.

Blood is collected in the tail region by the caudal vein immediately ventral in position to the caudal artery. Opposite the anterior end of the rectal gland this vein divides to form the two postcardinals. These continue anteriorly on the median side of the kidney and enter the common cardinal veins at the same time as the anterior cardinals.

The hepatic veins run along the lateral walls the
entire length of the liver lobes and enter separately into the posterior part of the sinus venosus. The omphalomesenteric or vitelline vein enters the central portion of the liver and gives off two vessels which run along the median walls of the left and right liver lobes.

_NOTOCORD_

A section cut at right angles to the longitudinal axis of the body and passing thru the infundibulum also passes thru the anterior end of the notochord. In cross section the notochord consists of large vacuolate cells the nuclei of which are concentrated at the outer margin, and a definite non-cellular sheath. In the oesophageal region the notochord becomes flattened on the ventral side. Opposite the pancreas it is as large as the neural tube. From this point posteriorly it tapers off keeping the same size as the neural tube and ends at the beginning of the neurenteric canal.
The muscle plates are developed from the somites which form the segmental plates of the body. Each somite has divided into a dorsal segment and a ventral segment. The dorsal segment consists of an outer layer, the dermatome, and an inner, the myotome. The dermatome has again divided into an outer layer of cells with small nuclei and an inner layer of closely packed cells of larger nuclei. From the inner and ventral edges of the myotome loose sclerotomal cells have proliferated and formed a triangular mass opposite the upper part of the notochord. Within the myotome muscle fibrillae have formed which give the myotome a white fibrous appearance. These will ultimately form the muscles of the back. From the outer ventral edge of the myotome and from the ventral edge of the dermatome outgrowths extend ventrally close to the ectodermal wall. These outgrowths fuse and form the ventral plate.

The ventral segment of the somite forms the lateral plate which lies close beside the wall of the coelom.
The urinary system consists of a pronephric or segmental duct and segmental tubules. The pronephric duct lies in the genital ridge and extends from the cloaca anteriorly to the origin of the omphalomesenteric artery from the dorsal aorta. At its anterior end it is open to the body cavity, at its posterior end it has a slight swelling which is the rudiment of the urinary bladder. The walls of this vesicle are closely applied to the dorsal wall of the cloaca.

The segmental tubes and nephrostomes appear more posteriorly, near the entrance of the bile duct into the duodenum. Each segmental tubule consists of a nephrostome opening to the body cavity. The segmental duct grows dorso-laterally from the nephrostome and dilates into the median vesicle which later forms the tissues for Bowman's capsules. The short renal tubule leaves the median ventral portion of the vesicle and empties into the larger primitive collecting tubule. The total number of segmental tubules present at this stage of development is thirty-one with the indication of two more at the anterior end.
GENITAL SYSTEM

On either side of the dorsal mesentery the coelom-
ic epithelial cells have become columnar and formed the
rudiments of the two gonads. In each segment groups of
primordial germ cells appear as large clear cells in the
germinial epithelium. In the highest stage of development
these cells have begun to wander into the gonad rudiment,
there to divide and multiply. The secondary groups so
formed are bounded by cells of mesenchyme.

There is no trace of the horizontally splitting
of the pronephric duct to form the Müllerian duct.
LIFE-HISTORY NOTES

PERIOD OF GESTATION.

General collections of embryos were made in the summer of 1929 from May 15 to August 1, and at the beginning of the year, 1930, from January 1 to March 15. It was found that small germinal discs were obtained over a period of three months namely, January, February and March. There is the possibility that this period may be as long as that of Squalus acanthias recorded by S. Ford, page 503, who says that "newly formed embryos were obtained from November until the middle of May."

At the same time, January to March, embryos of 16 to 17 cm. were also obtained. Similarly embryos of two sizes were obtained in the summer collecting, the smaller ranging from 2.0 to 4.0 cm., the larger from 17.0 to 22.0 cm. In the fall of 1914 Dr. C. McLean Fraser took some measurements of embryos. With these results to bridge over the winter months it was seen that the period of gestation extends over a space of about twenty-three to twenty-four months. This is illustrated in the graph of Plate 1.
In general these observations coincide with those of E. Ford on the life-history of *Squalus acanthias* but there are some points of difference. I shall give below the parts of the summary of his paper which deal with the early stages of development and shall discuss each part as to the differences and similarities of the two species.

"2. The female, before becoming sexually mature, undergoes an extended adolescent period during which the initial set of ovarian eggs are maturing."

It was noticed that in some females bearing embryos of the second year cycle there were maturing ovarian eggs which measured 1 to 1.5 inches in diameter in January and 1.5 to 1.75 inches in May. This shows that as the embryos are developing in the oviduct there are eggs maturing in the ovaries at such a rate as to be ready for fertilization at the beginning of the third year cycle.

"5. In a pregnant female the embryos are of the same general size, and similarly the ovarian eggs."

"4. Males and females are equally represented in the embryos and may occur together in the same uterus; they do not differ in size at any corresponding stage of embryonic
development."

A typical example of this is shown in the embryos from a female caught on June 22, 1929.

<table>
<thead>
<tr>
<th>Length of embryo</th>
<th>Sex</th>
<th>Oviduct</th>
</tr>
</thead>
<tbody>
<tr>
<td>21.6 cm.</td>
<td>♂</td>
<td></td>
</tr>
<tr>
<td>21.6 &quot;</td>
<td>♀</td>
<td>right</td>
</tr>
<tr>
<td>21.6 &quot;</td>
<td>♂</td>
<td></td>
</tr>
<tr>
<td>20.9 &quot;</td>
<td>♂</td>
<td></td>
</tr>
<tr>
<td>21.6 cm.</td>
<td>♀</td>
<td></td>
</tr>
<tr>
<td>21.6 &quot;</td>
<td>♀</td>
<td></td>
</tr>
<tr>
<td>20.9 &quot;</td>
<td>♂</td>
<td>left</td>
</tr>
<tr>
<td>20.3 &quot;</td>
<td>♂</td>
<td></td>
</tr>
<tr>
<td>20.3 &quot;</td>
<td>♀</td>
<td></td>
</tr>
</tbody>
</table>

This also shows that, as the total volume of the two oviducts are almost the same, that oviduct which has the fewer number of embryos will have larger ones than the other oviduct with more embryos.

5. The number of embryos carried by one fish, if the length of the parent is ignored, is most frequently from three to four in an observed range from one to eleven. It may be possible, however, that the number of embryos is dependent on the length of the parent, for the largest number of embryos was found in the largest fish."
In *Squalus sucklii* the observed average is nine to ten in the largest fish and five to six in the smaller, the range being five to twelve. In fact there were no females caught in which there were less than five embryos or five developing ovarian eggs.

"6. The remains of the egg-capsule in which the earlier developmental stages are undergone may continue in the uterus until the embryos are ready for birth."

There has never been observed any remains of the egg-capsule in the oviducts of *S. sucklii* after it has become ruptured. This may be explained that, because of the thin membraneous structure of the capsule, it may be absorbed or it may pass out of the uterus more easily than can the hard horny one of *S. acanthias*.

Ford does not give the time of the cycle when the egg-capsule is ruptured leaving the developing embryos free in the oviduct. This evidently occurs sometime in the fall of the first year cycle as embryos in August have a capsule while those in November have none.

It has been noted by Balfour that Elasmobranch eggs possess no membrane other than a surface tension one at the interfaces of the yolk and albumen. It may be that the egg-capsule is used to form a protecting surface about these. As the blastoderm grows it spreads over the yolk.
forming a yolk membrane which eventually surrounds the whole yolk. When this stage is reached the egg-capsule is no longer required and it is perhaps then that it is passed off allowing more space and freer movement for the developing embryos.

"8. Newly formed embryos were obtained from November until the middle of May."

This has been discussed above.

"12. The constitution of the shoals of adult fishes is governed by the factors of size and sexual condition.

As all observations were made on fish caught by set lines only the larger fish were observed, but it was noticed that among these catches there was a definite segregation according to size and sex. One scow-load brought into the Reduction Plant at Nanaimo, B. C. consisted of two catches from the mouth of the Fraser River, about seventy percent of which were large mature males, the other thirty percent made up evenly of immature males and females of the same size. The same day, May 20, 1929, a catch from Snake Island near Nanaimo from shallow water consisted of large females carrying embryos. Another catch brought in pregnant females and a small amount of immature males and females. This tends to show that the immature males and females have a wider range of occurrence, the mature males and pregnant
females keeping in definite shoals.
LITERATURE


Beard, J. On the development of the common skate (Raja batis). Fishery Board for Scotland. 1889.


PLATE I.

Figure 1. - Cross-section of medulla oblongata

Figure 2. - Fusion of basal plate - b.

Figure 3. - Fusion of a and b
PLATE I

Fig. 1

- Thia roof of the medulla
- Ependymal layer
- Mastic layer
- Marginal layer
- Fusion of basal plates
- Ventral sulcus
- Commissure

Fig. 2

- Air plate
- Basal plate

Fig. 3

- a
- b
- c
- 2
- 3
Figure 1. - Opening of b
Figure 2. - Fusion of b for the second time
Figure 3. - Closing of 1 by the lengthening of a
Figure 4. - Same as 3. This condition continues posteriorly for some distance
Figure 5. - Same as 3.
PLATE III

Figure 1. - Reopening of both a and b
Figure 2. - Fusion of a for second time
Figure 3. - Fusion for third time of b
Figure 4. - Complete closure of 2

The condition found in Figs. 1, 2, and 3 is of very short duration being found in three consecutive sections

Figure 5. - In the tail region
Figure 6. - Same as 5.
Figure 7. - Junction of the neural tube and the postanal gut to form the neurenteric canal
PLATE III

Fig. 1

Fig. 2

Fig. 3

Fig. 4

In the tail region

Fig. 5

In the tail region

Fig. 6

Neurenteric canal

Fig. 7
PLATE IV.

Figure 1. - Reconstructions of segmental tubule from cross-sections

Figure 2. - Reconstruction of segmental tubule from longitudinal sections

Figure 3. - Reconstruction of brain
PLATE V.

Figure 1. - Reconstruction of 5th cranial nerve - trigeminal

Figure 2. - Reconstruction of 7th and 8th cranial nerves - facial and auditory

Figure 3. - Reconstruction of 9th and 10th cranial nerves - glossopharyngeal and vagus
PLATE V

Fig. 1

Root of 5th nerve
Gasserian ganglion
Mandibular branch
Ophthalmic branch

Fig. 2

Root of 5th nerve
Branch to constrictor muscle
Auditory nerve
Branch to hyoid arch
Branch to skin
Palatine branch

Fig. 3

Root of 5th nerve
Root of 7th and 8th nerve
Root of 9th and 10th nerve
Branches to lateral line
Intestinal branch of vagus
Branches branches
PLATE VI.

Figure 1. - Reconstruction of aortic arches
Figure 2. - Reconstruction of vascular system
Figure 3. - Valves of conus arteriosus
PLATE VII.

Figure 1. - Section thru optic cup to show falciform process and inrolling of optic stalk

Figure 2. - Falciform process

Figure 3. - Lens
PLATE VII

Fig. 1
- Optic cup
- Lens
- Processus labiiformis
- Choroid eit
- Infolding of optic stalk

Fig. 2
- Vitreous humor
- Processus labiiformis

Fig. 3
- Lens epithelium
- Lens fibres
PLATE VIII

Figure 1. - Section thru anterior portion of auditory vesicle
Figure 2. - Section thru posterior portion of auditory vesicle
Figure 3. - Structure of ampulla of auditory vesicle
Figure 4. - Nasal pit
PLATE IX.

Figure 1. - Reconstruction of spinal nerve
Figure 2. - Lateral line
PLATE IX

Fig. 1

Dorsal root
Spinal ganglion
Ventral root
Notochord
Nerve of lateral line
Ramus communicans
Ventral ramus
Sympathetic ganglion
Posterior cardinal vein
Ventral muscle plate
Fin bud

Fig. 2

Epidermis
Nerve of lateral line
Myotome
Dermatome
Figure 1. - Solid oesophagus
Figure 2. - Structure of valve in spiral intestine
Figure 3. - Structure of pancreas
Figure 4. - Section thru posterior end of liver
Figure 5. - Cross-section of thyroid
PLATE X

Fig 1.
Solid oesophagus

Fig 2.
Dorsal mesentery
Spiral valve
Intestinal wall

Fig 3.
Dorsal pancreas
Pancreatic duct
Ventral pancreas
Junction of yolk-stalk and duodenum

Fig 4.
Embryonic trabeculae
Hepatic anuluscd

Fig 5.
Thyroid
Mesoderm
PLATE XI.

Figure 1. - Primitive ova

Figure 2. - Fusion of segmental duct to wall of cloaca

Figure 3. - Budding of cells from postanal gut to form subnotochordal rod
PLATE XI

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Fig. 1

- Peritoneum
- Connective Tissue
- Primitive ova
- Germinal epithelium

Fig. 2

- Collecting tubule
- Segmental duct
- Notochord

Fig. 3

- Notochord
- Subnociocordal rod
- Posterior gut

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PLATE XII.

Showing that the period of gestation extends over a space of approximately 24 months.
PLATE XII

SQUALUS SUCKLII, GIRARD

Period of Gestation