Name: John Kenneth Beadles Date of Degree: May 26, 1963

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: THE EMBRYONIC DEVELOPMENT OF THE CIRCULATORY AND RESPIRATORY SYSTEMS OF TELEOST FISHES

Pages in Study: 21 Candidate for Degree of Master of Science

Major Field: Natural Science

Scope and Method of Study: A survey of the literature was conducted to determine the embryonic development of the circulatory and respiratory system of teleost fishes; including a description of pelagic and demersal eggs, and fertilization of the eggs; origin of the circulatory system from the embryonic mesoderm, and the development of the heart; changes that occur in the circulatory system as organs and appendages develop; origin of the visceral arches and changes produced in the circulatory system as gills develop; development of jaws and tongue, with a description of the oral valves; origin of the gas bladder, and its development in physostomous and physoclistic fishes.

Findings and Conclusions: Embryonic development is considered to be the same in all teleost fishes. The differences occur in the time intervals of different stages in development.

ADVISER'S APPROVAL James H. Zant

THE EMBRYONIC DEVELOPMENT OF THE CIRCULATORY AND RESPIRATORY SYSTEMS OF TELEOST FISHES

By

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Bachelor of Science

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1957

Submitted to the faculty of the Graduate School
of the Oklahoma State University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE
May, 1963

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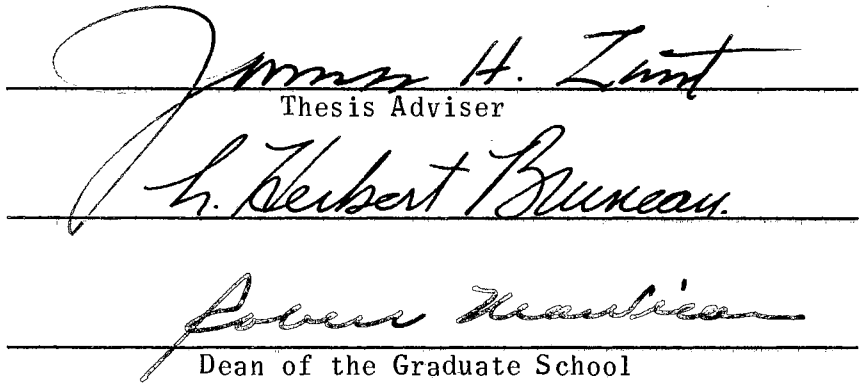
OF THE CIRCULATORY AND RESPIRATORY

SYSTEMS OF TELEOST FISHES

Thesis Approved:



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PREFACE

The purpose of this paper was to survey the literature on the embryonic development of the circulatory and respiratory systems of teleost fishes. This study covers the period from egg laying to hatching.

The writer wishes to express thanks to Dr. R. J. Miller for suggestions and for reading this paper, and to Dr. H. L. Bruneau and Dr. James H. Zant for their encouragement and suggestions.

I am grateful to the National Science Foundation for financial assistance, and making this study possible.

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CHAPTER I

INTRODUCTION

The Problem. An attempt was made to obtain a description of the embryonic development of circulatory and respiratory systems of teleosts. Most work on the embryology of fishes has been on external morphology. Eggs are fertilized and different stages of development photographed and described. The internal development of fishes has not been worked out completely.

Importance of the Problem. The embryonic development of fishes has been utilized in the classroom study of embryology. The reason for this is that some fishes develop in twenty-four hours and different stages of development can be studied in a short period of time.

It is hoped that this survey of the literature will provide information useful to persons attempting to investigate the morphogenesis and differentiation of fish embryos.

CHAPTER II

THE EGGS AND EMBRYONIC DEVELOPMENT OF THE CIRCULATORY SYSTEM

Eggs of Fish. Most fresh water fishes lay demersal eggs either over unprepared bottom, in nests, or among vegetation. Many marine fishes release floating or suspended eggs, some of which are held together by a gelatinous matrix which spreads out in the water covering several feet. Egg size varies with the species. The number of eggs released depends upon whether or not parental care is present.

Generally fish eggs ripen or mature in the ovary. The eggs of fish, except for livebearers, are released into the water. Some eggs immediately take up water through the micropyle, while others do not take up water until after fertilization. The spermatozoan enters the egg through the micropyle, and the egg becomes impermeable to water and its contents. According to Hisaoka and Battle (1958) in Brachydanio rerio, the chorion separates from the egg after fertilization and becomes transparent. Within a few minutes the cytoplasm begins to emerge at the animal pole and a large oil droplet appears at the vegetal pole.

The formation of the blastodisc from the cytoplasm, in Brachydanio rerio, causes a streaming effect. The blastodisc is visible as a clear homogeneous cone-shaped mass of finely granular cytoplasm. This mass flattens out approximately twenty-five minutes after fertilization (Hisaoka and Battle, 1958). Thirty-five minutes after fertilization the fertilized egg undergoes the first cleavage, which is a median vertical division, forming two globular blastomeres. Cleavage continues at different intervals, usually vertical and at right angles to the previous plane. Several hours after fertilization, the many celled blastoderm appears as an elevated cap of loosely organized cells at the animal pole.

According to Wilson (1889), in the spreading of the blastoderm in the sea-bass, the posterior margin or dorsal lip of the blastopore

remains a fixed point, while the anterior margin and lateral margin travel around the yolk mass.

During the encirclement of the yolk by the blastoderm, an area becomes marked off in the region of the posterior margin. This area is more or less triangular and thicker than the surrounding blastoderm. It is formed by movement of cells into the area, and by a rapid proliferation of cells in the region of the dorsal lip of the blastopore. Known as the embryonic shield, it develops into the embryo proper (Ingersol, 1953).

Developmental stages. Oppenheimer (1937) gives the developmental stages of Fundulus heteroclitus as follows:

Stage 1. The unfertilized egg.
Stage 2. One celled embryo (1 hour).
Stage 3. Two celled embryo (1 1/2 hours).
Stage 4. Four celled embryo (2 hours).
Stage 5. Eight celled embryo (2 1/2 hours).
Stage 6. Sixteen celled embryo (3 hours).
Stage 7. Thirty-two celled embryo.
Stage 8. Early high blastula. The blastoderm is elevated into a domed, cap-like structure and periblast is being established (5 1/2 hours).
Stage 9. Late high blastula Cells of blastoderm are smaller than in Stage 8.
Stage 10. Flat blastula. Blastoderm has become a flattened disc, rather than elevated bulge as formerly (8 hours).
Stage 11. Expanding blastula. Blastoderm has begun to grow over yolk.
Stage 12. Early gastrula. Germ ring and embryonic shield formed and blastopore just opening (16 hours).
Stage 13. Middle gastrula. About half of yolk covered by blastoderm, neural keel just visible in midline of embryonic shield (19 hours).
Stage 14. Late gastrula. More than half of yolk covered by blastoderm, embryonic shield narrowing, neural keel more clearly visible (22 hours).
Stage 15. Closure of blastopore. Little embryonic differentiation except formation of rudiments of central nervous system and perhaps of optic vesicles and first somites (26 hours).
Stage 16. Expansion of forebrain begins (for formation of the optic vesicle). Three primary vesicles visible in brain.
Stage 17. Formation of cavity in optic vesicles, mesodermal segmentation provides one to four somites.
Stage 18. Formation of the auditory placode. Somites range from four to fourteen and extra embryonic coelom appears as a cavity developed by yolk sac epithelium (36 hours).

Stage 19. Cavity appears in neural cord behind brain. Ectoderm thickens to form lens of eye and olfactory pit. Somites range from fourteen to twenty (42 hours).
Stage 20. Expansion of midbrain to form optic lobes. Somites range from twenty to twenty-five. Melanophores appear about neural cord and present over yolk. Pericardium established. Heart visible, tubular, and pulsing. Location of pectoral fin becoming visible by concentration of cells.
Stage 21. Motility. Muscular contractions come at about twenty-eight somite.
Stage 22. Circulation. Circulation starts with about thirty-five somites. Forebrain walls forming cerebral hemispheres.
Stage 23. Otoliths appear in ear. Melanophores appear in pericardium and blood flows in yolk vessels.
Stage 24. Pectoral fin bud pointed.
Stage 25. Formation of urinary vesicles (as an outgrowth of hindgut).
Stage 26. Formation of liver and peritoneal cavity.
Stage 27. Pectoral fin becomes rounded.
Stage 28. Pigmentation of peritoneal walls.
Stage 29. Circulation established in pectoral fin. Fin becomes motile.
Stage 30. Rays appear in caudal fin. Lower jaw is formed.
Stage 31. Formation of gas bladder (diverticulum of gut). Eyes and jaws become motile.
Stage 32. Hatching. Some yolk is still present (11 days).
Stage 33. Pigmentation and growth of gas bladder.
Stage 34. Yolk absorption completed (12 days or more).

The development of the heart in Alosa sapidissima. The part of the mesoderm giving rise to the heart is a bilateral symmetrical cord of cells on either side near the median borders of the lateral plates. This area has been called the "moyenne". The moyenne is not very different from the other cells of the mesoderm except for location. The moyenne appears between the somital and lateral mesoderm, which tends to remain in contact with the lateral plate. The moyenne is small posteriad and large anteriad. The anteriad portion of the moyenne forms the endocardium. The moyenne descends on either side between the lateral plate and the now closing pharnyx to gain a ventral position. The posteriad moyenne is blocked from descending, therefore the moyenne is divided. The anteriad moyenne will form the endorcardium, and is connected to the posteriad moyenne by a small portion of the moyenne cells called the isthmus.

The endocardium spreads more to the left side than the right and posteriad. The entire left side of the head seems to be more developed than the right. The endocardium moves slowly posteriad to the mandibular pouch. The backward closure of the pharynx is overtaken by the growth of the endocardium, which now covers a considerable area. The moyenne does not grow anteriad, but posteriad and laterad. The lateral plate grows down and blends in with the ventral aorta. The somatic portion of the head mesoderm spreads ventrally around the lateral margins of the endodermal pharynx in the region between the mandibular and hyobranchial pouches. The cells from the somital mesoderm will form the muscles and supporting framework of the hyoid arch.

The medial margins of the lateral plates have met and blended throughout the anterior three-fourths of the pericardial region except in one region, which encircles a group of cells about to form the root of the aorta. The splanchnic mesoderm of the two sides becomes continuous across the midline. In the process of blending, the coelom continues across the mid-line by the apparent loss of the medial margin of the lateral plate. The medial margins constitute the dorsal mesocardium which is lost early.

The endocardium grows posteriad until it reaches the first body somite. The endodermal pharynx is now closed throughout, forming a flat tube. The ventral surface is hidden by the pericardium and endocardium. The primordal heart is now formed, although it is quite flat. The splanchnic mesoderm forms the anterior wall of the sinus venosus, and the pericardio-peritoneal septum. Part of the somatic mesoderm will become the parietal pericardium. The splanchnic mesodermal cells remaining around the heart will develop into the myo-epicardium.

Before the formation of the heart tube, the splanchnic mesothelial cells migrate to the left and carry with them the underlying endocardium. They move about two-thirds of the way to the left body wall. Now the heart develops rapidly, and soon begins to beat (about fifty-two beats per minute). The heart tube is cone shaped, and the base of the heart is directed anteriad, and to the left.

The head of the embryo tears loose from the yolk, and begins to grow anteriad as the yolk moves posteriad. This tearing of the tissue seems to prepare a place for the heart, because the heart pulls loose and moves into the midsagittal plane. The arterial end of the heart is fixed, and the venous end follows the retreating yolk (Senior, 1909).

Primitive circulatory tubes or blood vessels. The first appearance of the circulatory system (Shumway, 1935) is an aggregate of cells called blood islands in the splanchnic mesoderm on the ventral surface of the yolk mass. Shortly after the blood islands form they are converted into hollow vesicles. These represent the development of the early vitelline vessels.

The vessels develop as capillaries, according to Nelson (1953), and spread over both sides of the yolk mass. A part of the developing capillaries grow forward and dorsally around the gut, where they come together below the notochord and join to form the beginning of the dorsal aortae.

The anterior end of the capillaries develop anteriorly and join the developing subintestional capillaries on the ventral side of the gut and continue anteriad to the region of the foregut. The vessels fuse and join the pulsating heart.

The capillaries proceed anteriad from the heart giving rise to the conus arteriosus and bulbus arteriosus. The conus arteriosus (Kyle, 1926) is believed to have one pair of valves in most teleost fish. The bulbus arteriosus is actually the base of the ventral aorta.

The ventral aorta (Weichert, 1959) develops anteriad, then divides into two aortic arches, one to the right and the other to the left, and continues into the mandibular region. These arches join a primitive capillary which develops posteriad along the upper regions of the developing gut, and gives rise to the dorsal aortae.

Five buds start developing from both sides of the ventral aortae and the dorsal aortae until they meet and fuse to form the six aortic arches, which will pass through the tissues of the pharyngeal gills when the gills develop.

The two developing dorsal aortae continue to develop posteriorly and soon join the capillary networks on each side of the yolk mass.

The primordial circulatory cycle is complete and (Torrey, 1962) the blood is pumped anteriad through the ventral aortae to the aortic arches, the dorsal aortae, and the capillaries on the yolk mass. The blood picks up yolk material and carries it via the vitelline and subintestional veins to the heart. This primordial circulatory cycle transports the food material to the cells of the organism.

The cells that were trapped and pulled into the blood vessels, along with the liquid from the pericardial space are now the transporting medium. More blood cells are formed (Romer, 1955) in the belly floor. In many fishes the kidneys function as a source of blood cells. In sturgeons and paddlefish blood forming tissues are around the heart. The spleen is always an important center in the development of blood cells. The blood cells present now are erythrocytes and leucocytes. In some fishes hemoglobin is absent until hatching, while in others the hemoglobin forms earlier. Most of the maturation of the erythrocytes takes place in the blood vessels.

Upon further development the two dorsal aortae fuse together just posterior to the heart and become known as the dorsal aorta. As this change is taking place the vitelline arteries are forming and join the dorsal aorta, so the source of food to the developing embryo is not interrupted. The dorsal aorta continues posteriad and gives rise to single and paired arterial branches. The dorsal aorta upon reaching the tail region becomes the caudal artery. The branches developing from the dorsal aorta go to all the new developing organs. At the same time the two dorsal aortae in the anterior end continue developing anteriad and give rise to the internal carotid arteries, which supply the brain.

The first and second aortic arches are reduced to become branches of the third aortic arch and are now called the external carotid arteries, which will supply the external parts of the developing head.

Later development of the venous system. The blood capillaries (Weichert, 1959) form the beginning of the cardinal system. The capillaries begin developing over the top of the developing brain. These become the anterior cardinal vein on each side and begin developing posteriad. The postcardinal veins begin developing from the posterior

end of the embryo, and where the anterior and posterior cardinal veins meet on each side, form the common cardinal veins. The common cardinals then develop anteriad and form a collecting chamber on the posterior end of the heart called the sinus venosus.

It would be well to note here that fish have a two chambered heart, with a single atrium and ventricle. The sinus venosus is a collecting chamber for the blood returning to the heart. The conus arteriosus is a slightly enlarged vessel on the anterior end of the ventricle and contains a single pair of valves to prevent the blood from reentering the ventricle. The bulbus arteriosus is the base of the ventral aortae, which may function as a pressure control device to help force the blood through the aortic arches. The circulatory cycle is concerned now with getting yolk material to all the developing areas of the fish embryo.

CHAPTER III

EMBRYONIC DEVELOPMENT OF THE RESPIRATORY SYSTEM

Embryonic development of the gill slits. A survey of literature on the origin of the visceral arches, indicates that the origin is similar in all fishes.

In the cod (Ryder, 1882) the digestive tube starts developing about thirty-six hours after fertilization of the egg. The development starts in the posterior region and progresses anteriad, but soon the digestive tube also begins to form in the pharyngeal region, and develops both anteriad and posteriad.

Early in the formation of the pharyngeal region (Romer, 1955) pouches develop laterally from each side of the endodermal lining of the gut. Extending toward the surface, they interrupt the continuity of the mesodermal plates of this region and come in contact with infoldings of the surface furrows. The furrows and pouches continue developing toward each other until the intervening membrane between them breaks down and the endoderm and ectoderm form a continuious lining for the gill slits.

The gill slits develop (Goodrich, 1958) from anterior to posterior, and the number is increased or decreased depending on the organisms. The first gill slit is usually closed but may remain as a spiracle in some fishes. In the majority of Pisces there are five pairs of branchial slits. The earliest known fossil fishes, the Ostracoderm, appear to have usually possessed not more than ten pairs of slits. Traces of the posterior vestigial slits or visceral arches have been described in Selachii. Moreover, the suprapericardial body (ultimobranchial body) is considered to have been formed from a vestigial pouch behind the last branchial slit. In Pisces both the internal

and external gill openings are dorso-ventrally elongated and narrow, the pouches being compressed.

The history of the mesoderm. Most of the mesoderm (Nelson, 1953) of the early embryo exists in the form of epithelium. As development proceeds, much of the mesoderm loses the close arrangement characteristic of epithelium. In doing so the cells become loosely arranged. They also may change shapes and may wonder to distant parts of the body. This loose arrangement of the mesodermal cells forms the primitive mesenchyme.

The mesoderm which forms the head structures contains two basic regions, the heart proper and the branchial region.

The mesoderm of the branchial region represents a direct anterior extension of the mesoderm of the trunk. This portion of the branchial mesoderm is part of the head proper mesoderm, and is associated with the mesoderm of the visceral arches.

The term pre-chordal plate mesoderm signifies that portion of the head mesoderm which is derived from the prechordal plate area located in the anterior end of the foregut. The prechordal plate mesoderm is associated with the foregut endoderm and anterior end of the notochord in the late blastula and gastrula.

The development of the visceral arches. The visceral arches (Weichert, 1959) of the visceral skeleton are modified to form various parts of the skeleton in the head region. Soon after the appearance of the central nervous system during embryonic development, the mesenchymal cells which surround it begin to differentiate forming a membranous layer.

This membranous layer furnishes the material in which the cartilaginous chondrocranium develops. The chondrocranium is made up of several components, first there appears around the notochord, a pair of flat, curved cartilages, the parachordal plates. These extend laterally to the optic capsule, and posteriorly to the point where the tenth cranial nerve emerges. In back of this are two to four occipital vertebrae with which the parachordal plates grow and unite in the midline to

form the basicular plate. This encloses the tip of the notochord and becomes the floor of the mid- and hind-brain. The anterior end of the parachordal plates are united by the acrochordal bar.

Then the prechordal cartilages develop in front of the parachordal plates. The prechordal cartilages fuse and form the ethmoid plate. The ethmoid plate grows anteriad to become the rostrum which later contributes to the formation of the internal septum between the nasal capsule. The prechordal cartilages and the parachordal plates unite, but leave an opening in the center for the pituitary gland and internal carotids to pass through.

At the same time that the prechordal cartilages and parachordal plates are developing, three pairs of capsules make their appearance, the nasal, optic and otic. The nasal and otic capsules unite with the prechordal cartilage and parachordal plates to form the chondrocranium, while the optic remains separated around the eyes.

Next a series of cartilages or pharyngeal arches develop and encircle the pharyngeal portion of the digestive tract. They serve to support the gills and are arranged between the gill slits, one behind the other. They arise from the mesoderm of the gut. The first to develop is the mandibular arch, which becomes divided into a dorsal portion, the palotopterygoquadrate bar (upper jaws), and a ventral portion called Meckels cartilage (lower jaw).

The second arch (hyoid) give rise to the tongue, and the pseudobranch of some fish (Lagler, Bardach and Miller, 1962). The upper division of the hyoid arch forms the connection of the jaws to the cranium.

The four remaining visceral arches are often reduced and are composed of five separate cartilages which are, from dorsal to ventral, the pharyngobranchial, epibranchial, ceratobranchial, hypobranchial and basibranchial. The seventh visceral arch has only the pharyngobranchial which bears teeth but does not support a gill. The cartilages are now replaced by bone.

The gills. On the posterior surface of the early gill arch the epithelial covering produces elongated structures, the external gill filament. These filaments are numerous and give the branchial area

a bushy appearance when viewed externally. The epithelial covering on the anterior face of the gill arch, in the meantime, develops elongated lamella-like folds. The gill arches thus have a series of gill lamellae or plates developed on the posterior and anterior surfaces of the gill arch facing the passageway of the gill slits. The gill lamellae on each surface of the gill arch form a demibranch, and two demibranches form a holobranch or complete gill (Kendall, 1947).

The operculum, which is dermal in origin (Harrington, 1955) is supported by the bony skeleton and forms a hinged anteriorly armor like door, which may be opened by opercular muscles. The bony branchiostegal rays usually extend from the inner surface of the operculum to the ventral body wall, and support the branchiostegal membrane, which will serve as a one way valve permitting water to leave the branchial chamber through the gill slit but does not allow it to enter.

Oral valves. Breathing valves are best known in bony fishes according to Gudger (1935). Dahlgren (1898) was the first to give an account of these structures. He figured and described oral valves in the sunfish and the flounder, and stated he had observed their action in over fifty species of fresh and marine teleosts. It was pointed out by Gudger (1935) that Amia calva has only the maxillary valve present. The best description of the oral valves of teleosts and their importance was given by Mitchell (1904).

The valves are sheets of membrane composed of elastic connective tissue covered with a mucous membrane continuous with the lining of the mouth. They are situated in the oral cavity just posterior to the maxillary and mandibular teeth (teeth are not present in all fish). The valves are placed with their edges pointing downward and backward at an angle of less than forty-five degrees to the axis of the body.

CHAPTER IV

CHANGES IN THE CIRCULATORY SYSTEM

Changes in the circulatory system with the development of gills. The original aortic arches divide into efferent and afferent branchial arteries with capillaries developing between them in the gill lamellae. The afferent branchial carries the blood to the afferent capillaries, which empty into the efferent branchial artery, which connects to the dorsal aortae, and circulation continues as before (Nelson, 1953).

Changes in the circulatory system with the development of fins. In stage twenty-four of the developing embryo the paired appendages begin to grow, therefore the circulatory system must change again. The subclavian artery and vein develop in the pectoral fins. The subclavian artery develops from the median aorta and proceeds into the pectoral fin, breaks up into capillaries and the blood is collected from the capillaries into the subclavian vein which leads into the anterior part of the postcardinal. In adults it empties into the common cardinal vein.

The iliac artery develops from the median aorta, and proceeds into the pelvic fins, breaking up into capillaries. The capillaries lead into the iliac vein which joins the postcardinal vein (Weichert, 1959).

CHAPTER V

THE DEVELOPMENT OF THE GAS BLADDER

Gas bladder. The gas bladder in the majority of clupeoid fish consists of an elongated, tubular chamber extending the length of the body cavity. The pneumatic duct arises from a point near the middle of the gas bladder and extends to the blind end of the stomach sac. The gas bladder of Stolephorus mitchilli, differs from the typical clupeoid gas bladder because it is divided into an anterior and posterior chamber by a constriction (Tracy, 1911). The posterior part is a large expanded thin walled chamber which occupies the greater portion of the posterior visceral cavity. The pneumatic duct opens into this part of the gas bladder directly behind the constriction. The anterior chamber is in the form of a thick-walled, opaque tube which extends anteriad to the skull. On the dorsal surface of the anterior chamber, a small tube arises, divides and continues into the skull where it expands into squamosal and pro-otic bullae in a similar manner to that found in other clupeoid fish. The external appearance of the gas bladder in these species resembles that of the carp.

The gas bladder first appears in larvae three to five millimeters long. It grows from the left side of the dorsal wall of the gut just in front of the liver duct, passing through the mesentery, and then grows posteriad and expands into a chamber of large capacity. This stage seems to correspond to an early stage of the carp gas bladder (Tracy, 1911). In specimens four to five millimeters in length, there arises from the anterior end of the gas bladder, a bud from which a solid cord grows forward in about the mid-line dorsal to the coelom. The anterior end of this cord grows anteriad to the base of the skull, and divides into two brahches. Each grows forward under the ear capsule, then up through the floor and into the anterior chamber of the

ear capsule. The distal end begins to expand into an air vesicle in young five to seven millimeters in length. The squamosal vesicle is developed at a later stage in specimens about thirty millimeters long. It appears as a swelling in the tube leading to the pro-otic vesicle, and rapidly expands to fill a cavity which appears in the squamosal bone.

Fundulus and Menidia. The larval stages of these fishes may be partly passed in the egg (Tracy, 1911). Very soon after hatching, the young begin to swim freely and effectively. The gas bladder is well developed, consisting of a posterior extending sac with a small cavity, and is connected with the right side of the esophagus by an open pneumatic duct. The cavity enlarges greatly as a result of gas passing into the gas bladder. In Fundulus heteroclitus, gas is taken into the gas bladder after hatching, but in Menidia it occurs six or seven days after hatching. At this stage of development the pneumatic duct is still present, opening into the anterior end of the gas bladder, and the duct opening is surrounded by the red gland. The red gland allows gas to diffuse into the gas bladder. The pneumatic duct soon loses its lumen and gradually atrophies as the adult organ is developed.

The embryonic pneumatic duct opens into the anterior end of the gas bladder. This association of pneumatic duct with gas bladder appears to be the more primitive.

The gas bladder in Opsanus tau (Toadfish) is a heart shaped organ deeply bilobed in front by a longitudinal, vertical septum which divides only the anterior half of the organ (Tracy, 1911). A longitudinal band of muscles extends from the anterior to the posterior end of the organ.

Soon after hatching, the gas bladder appears as an evagination from the dorsal side of the esophagus just anterior to the liver duct. It then grows upward through the mesentery into the region bounded dorsally by the aorta and laterally by the kidneys. The proximal end remains as a pneumatic duct connected with the esophagus while the distal end swells to form a vesicle which grows forward causing the duct to open into the posterior end of the gas bladder. The pneumatic duct then pulls away from the esophagus, leaving a stump pointing downward from the posterior end of the gas bladder.

The gas bladder is composed of cuboidal epithelium, and is invested with a compact layer of cells which come from the splanchnic mesenchyme. The ventral portion of these cells are invaded by a branch of the coeliac axis which flattens and spreads. Subsequently the flattened vessels develop the bundle of capillaries which are to form the blood supply to the future red gland. Shortly after the establishment of the inner layers, amoeboid mesenchyme cells collect between the kidneys and peritoneum, and apply themselves to the outside of the vascular layer, which is the origin of the tough, shining white outer connective tissue layer of the gas bladder. The muscle band grows on later arising from a mass of embryonic cells from the muscle plate of the first somite.

The secondary chamber develops and the wall thickens on the posterior chamber and thin out in the anterior. The larva hatches and the gas bladder increases in size. The columnar cells lining the chamber just in front of the passage to the posterior chamber remain as a single layer, and form the red gland while the rest of the cells flatten into squamous epithelian cells.

When the young pipefish (Siphostoma fusium) are released from the brood-sac of the male, they are about eight to ten millimeters in length (Tracy, 1911). The gas bladder consists of a single chambered vesicle. The pneumatic duct arises from the posterior end and connects with the esophagus. The distal end atrophies, and the duct grows posteriad forming a curved u-shaped tube. The limb of the u which is attached to the gas bladder then greatly enlarges, thus forming the posterior chamber. The other limb of the u-shaped tube remains for sone-time as a vestige embedded in the wall of the gas bladder, then disappears.

In the porgy, Stenotomus chrysops, the posterior end of the lumen of the gas bladder becomes contracted into a tube which turns somewhat to the left of the median line, then extends posteriad a short distance and ends abruptly (Tracy, 1911). At the posterior end the epithelial lining is continuous with a solid cord of cells which bend around to the left and run anteriad a short distance into the wall of the gas bladder. This cord of cells could be the remains of the pneumatic duct, which has

atrophied. In older specimens the gas bladder appears to be divided into an anterior and posterior chamber connected by a small tube.

CHAPTER VI

SUMMARY AND CONCLUSION

This report is a survey of the literature including a description from eggs to hatching of fishes.

Development of Fundulus heteroclitis, and stages in its development.

Development of the heart and movement of the heart into the mid-line of the body.

Development of primordial blood vessels, both arterial and venous.

Development of the gill slit, and a discussion of the mesoderm and its importance.

Development of the visceral arches and the changes produced in the circulatory system resulting from the development of the visceral arches.

Discussion on the gills of fishes, and the tissues involved.

Changes in the circulatory system as a result of gill and fin development.

Formation of the gas bladder and differences between physostomous and physoclistic fishes.

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