6-1939

# A Comparative Study of the Spiracle in *Cyclostomata, Elasmobranchii* and *Pisces*

Miser Russell Richmond
*University of Tennessee, Knoxville*

To the Graduate Council:

I am submitting herewith a thesis written by Miser Russell Richmond entitled "A Comparative Study of the Spiracle in *Cyclostomata, Elasmobranchii* and *Pisces*." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Animal Science.

Barton C. V. Ressler, Major Professor

We have read this thesis and recommend its acceptance:

Henry Meyer, A. C. Cole

Accepted for the Council:
Dixie L. Thompson

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

May 22, 1939

To the Committee on Graduate Study:

I am submitting to you a thesis written by Miser Russell Richmond entitled "A Comparative Study of the Spiracle in Cyclostomata, Elasmobranchii and Pisces." I recommend that it be accepted for nine quarter hours credit in partial fulfillment of the requirements for the degree of Master of Science with a major in Zoology.

Barton W. Kessler
Major Professor

We have read this thesis
and recommend its acceptance:

Henry Meyer
A. C. Cole Jr.

Accepted for the Committee

Dean of the Graduate School

# A COMPARATIVE STUDY OF THE SPIRACLE IN THE CYCLOSTOMATA, ELASMOBRANCHII AND PISCES

---

A THESIS

Submitted to
the Committee on Graduate Study
of
The University of Tennessee
in
Partial Fulfillment of the Requirements
for the degree of
Master of Arts

---

by

Miser Russell Richmond

June 1939

ACKNOWLEDGMENTS

I wish to express my appreciation to the Department of Zoology of the University of Tennessee for the opportunity afforded me to carry on this study. I am especially indebted to Professor Barton C.V.Ressler for the suggestion of the problem, and for guidance during the study.

I wish,also, to thank the Library Staff of the University of Tennessee for their cooperation in search for literature on the subject.

# TABLE OF CONTENTS

## LIST OF ILLUSTRATIONS

FIGURES PAGE

# CHAPTER I

## INTRODUCTION

Although scientists have been interested in the spiracle for a number of years, very little investigation has been done. In this study the writer shall endeavor to describe the structures and functions of the spiracle in the Cyclostomes, Elasmobranchs and Pisces as well as show the continuous development of any structure as to its function in the animals studied.

As a plan of study the specimens were divided into three general groups according to their classification. The methods used in making the observations will be discussed later.

The work has been done either in the library or laboratories of the University of Tennessee. Specimens for study were supplied from the stock of the University of Tennessee, from the markets in Knoxville, or from fishermen along the Tennessee River.

Classification of forms studied in this thesis:

Phylum-Chordata

Sub-Phylum - Vertebrata

Class A. Cyclostomata

Sub-Class I. Myxinoidea--Hagfishes

Family - Myxinidae

Genus - 1. Bdellostoma--Pacific Forms

2. Paramyxine--Ocean Forms

3. Myxine--Pacific, Atlantic Oceans

Sub-Class II. Petromyzontia--Lampreys

Family - Petromyzontidae

Genus - 1. Petromyzon--Found in rivers and seas of America, Europe and Asia

Class B. Elasmobranchii

Sub-Class I. Selachii

Order 1. Squali--Sharks and Dogfish Sharks

Order 2. Raji--Rays and Skates

Sub-Class II. Holocephali

Order 1. Chimaeridae

Class C. Pisces

Sub-Class I. Teleostomi--True Fishes

Order 1. Crossopterygii--Polypteridae

Order 2. Chondrostei--Paddle-fish and Sturgeons

Family a. Polyodontidae--Paddlefishes

Family b. Acipenseridae--Sturgeons

Order 3. Holostei--Garpikes and Bowfins

Family a. Amiidae--Bowfins

Family b. Lepisosteidae--Garpike

Order 4. Teleostei--Bony Fishes

Suborder (1) Cypriniformes

Family a. Cyprinidae--Carp, Minnows

Family b. Catostomidae--Suckers

Family c. Siluridae--Catfishes

Suborder (2) Clupeiformes

Family a. Salmonidae--Trouts, Salmons

Suborder (3) Acanthopterygii--Spiny-rayed Fishes

Family a. Percidae--Perches

Sub-Class II. Dipnoi - Lung Fishes

Family a. Ceratodontidae - Australian Lung Fishes

Family b. Lepidosirenidae - South American and African Lung Fishes

## CHAPTER II

## LITERATURE

The amount of literature on the spiracle is limited to a few textbooks on Comparative Anatomy and a very limited number of articles and reports in various scientific publications. No recent reports were found.

The spiracle, known as the pituitary canal in the Cyclostomata, does not come to the surface but is associated with the nasal organ and runs from the nasal capsule downward and backward tothe respiratory tube at the velum.

Gill-Slits:

In Petromyzon marinus there are seven pairs of gill-slits and a like number of pouches. The first gill-slit opens just opposite the entrance of the pituitary canal. Water can enter the gill pouches either by the mouth or through the gill-slits.

"The Lampreys differ from the other Vertebrata in the fact that the gills do not open directly into the enteric canal in the adult but into a respiratory tube lying below the gullet."[1] In the adult this tube extends from buccal cavity to above the heart while in the larva it extends from the intestine forward to the pharynx and during metamorphosis loses its connection with the intestine and the gullet is formed.

The gill-pouches have the shape of biconvex lenses, with numerous lamella on the inner surfaces. They are separated by inter-branchial septa. An additional cleft has been found in the larva anterior to the first in the adult series.[2]

The development of the olfactory sac, the pituitary pouch and the pituitary body are closely related. In the embryo, before the stomodeum

---

[1] T. J. Parker and William A. Haswell, A Text-Book of Zoology (London: MacMillan Company, 1928), pp. 126.

[2] Ibid., pp. 127-128.

connects with the mesenteron, two unpaired ectodermal invaginations appear in front of the mouth. The first is the rudiment of the olfactory sac, the second the pituitary sac which opens just outside the stomadeum. Its blind end extends to the ventral surface of the forebrain and ends below the infundibulum. As the embryo develops the olfactory and pituitary invaginations become depressed into a common pit which shifts toward the top of the head with the development of the thick upper lip, the process causing an elongation of the pituitary sac into which the olfactory sac opens posteriorly. Thus the entire passage of the Lamprey is a persistent pituitary sac into which the single olfactory organ opens.[3]

The Cyclostomata of the order Myxinoidei differ somewhat to Petromyzontes. The genera Myxine has no true buccal funnel. A velum separates the buccal cavity from the pharynx. The nostril is a very large, unpaired opening located in the dorsal margin of the buccal space and continuous into the pituitary sac, which opens into the pharynx by an aperture which appears late in the life of the embryo. Myxines live in mud and the respiratory current passes through this nasal aperture to the gills.

In different species of Bdellostoma there are from six to fourteen small gill openings on either side. Each of these connects by a tube with one of the gill-pouches which in turn connect with the pharynx. Just back of the last gill-slit, on the left side, is the opening of the oesophageo-cutaneous duct which leads to the pharynx.

Charles R. Stockard,[4] Columbia University, in his observations of Bdellostoma stouti found that two post hyomandibular gills occur in the

---

[3] T. J. Parker and William A. Haswell, A Text-Book of Zoology (London: MacMillan Company, 1928), p. 129.

[4] Charles R. Stockard, "The development of the Mouth and Gills of Bdellostoma Stouti," American Journal of Anatomy, Vol. V, pp. 481-517.

early embryos and are for some time in advance of the true branchial gills in their state of development. They then begin to degenerate and rapidly disappear.

In Myxine the gill-slits unite to form a single opening posteriorly. Also, in addition to these gill sacs, in the Myxinoids a pharyngo-cutaneous duct passes from the pharynx along the left side to the exterior behind the last sac. Its opening is adjacent to the last gill pore.

Breathing is accomplished by the expansion and contraction of the muscular walls of the sacs; water being drawn in through the median nostril, which leads to the hypophysial canal opening into the pharynx behind and expelled to the exterior along the expiratory tubes.

The Gills:

The gills of Cyclostomes are highly specialized structures, the lamellae being enclosed in rounded sacs with narrow ducts leading into them from the pharynx and out of them to the exterior. Due to their pouch-like shape this group of gills is called marsipobranchii.[5]

The gills are inclosed by the branchial basket which is formed on each side of nine curved vertical bars of cartilage the first just posterior to the styloid cartilage, the second in front of the first gill-cleft and the remaining seven just behind their seven respective gill-clefts. These bars are tied together longitudinally by four longitudinal rods.[6]

The respiratory system of the Elasmobranchii shows greater development, especially in the spiracle which now connects the pharynx with the outside through the spiracular canal. The oral cavity is wide and flattened dorsoventrally. The anterior part is bounded by the jaws formed from the mandibular

---

[5] Edwin S. Goodrich, Studies on the Structure and Development of Vertebrates (London: MacMillan Company, 1930), pp. 492-493.

[6] Parker and Haswell, Op. Cit., pp. 124.

gill arch. The tongue forms a small projection in the floor of the mouth, supported by the hyoid gill arch.

The posterior part of the cavity, the pharynx, is pierced by six internal gill-slits. The first, the spiracle, is a rounded opening in the roof of the mouth just posterior to the mandibular arch. The five remaining gill-slits connect with the visceral pouches which open to the outside by way of the external gill-slits. The visceral pouches are separated by the visceral arches. The arches are made up of a central portion, the interbrachial septum, each side of which is covered with gill filaments, except for the first and last, constituting a demibranch.

In Elasmobranchs and some Ganoids the anterior visceral cleft, the spiracle, is smaller than the others, and opens on the top of the head. This spiracle bears well developed gills in sharks such as the Notidanidae but in those showing higher development it may contain only a vascular network in its walls. In Ganoids and Teleosts it is a pseudobranch receiving blood from the opercular gill which is an ectodermal structure developed in the face of the operculum.

In typical Elasmobranchs the interbrachial septa extend to the outside of the body directly, on the neck in Selachii and on the ventral surface in Raiea. The Teleosts and Ganoids are similar except the operculum covers the whole external part of the gills.[7]

In Elasmobranchs the spiracle is not merely asimple tube passing from the pharynx to the surface of the body, but it has various outgrowths. Many of the Selachians have a caecal diverticulum on the dorso-internal wall of the spiracle, which passes inward, and, broadening in an antero-posterior direction, becomes firmly attached to the auditory capsule, below the

---

[7] J. S. Kingsley, Vertebrate Zoology (New York: Henry Holt & Company, 1911), pp. 22-23.

projecting ridge that marks the position of the horizontal semi-circular canal, and immediately above the post-orbital groove. The opening of the caecum into the spiracle is never closed, although in some genera (Galeus) it may be very small. This caecum was first observed by Muller[8] who thought it was an accessory to the auditory organ. Muller described the caecum as being present in Scyllium, Pristurus, Mustelus, Galeus and Batoids. Van Bemmelen[9] added Acanthias, Squatina and Heptanchus to Muller's list. In Acanthias it is not the dorsal caecum, but the mucous membrane of the spiracle itself, that is bound to the auditory cartilage.

Projecting inward and forward from the inner wall of the spiracle, at its pharyngeal opening, is another diverticulum, much shallower in extent and with a wide mouth. It is located below the level of the pre-spiracular cartilage and immediately in front of the proximal end of the hyomandibular. Anteriorly it is bounded by the levator maxillae superioris muscle, and posteriorly by the anterior surface of the hyomandibular cartilage and the inferior post-spiracular ligament. The blind end of this caecum is separated only by mucous membrane from the orbital blood sinus.[10]

Norris and Hughes[11] (1895) found an opening on the anterior mesial wall of the spiracular cleft of Squalus acanthias both in the embryo and adult. The very small pore in the spiracular wall leads into a cup-like organ with three diverticula. They seem to be modified ampullae of Lorenzini.

The spiracle in sharks represents only the upper part of the hyoid cleft,

---

[8] W. C. Ridewood, "The spiracle and associated structures in Elasmobranch Fishes," Anatomischer Anzeiger, Vol. XI, Dec. 1895.

[9] Ibid., p. 431

[10] Ibid., p. 430.

[11] G. Pinkus, "The spiracular sense organ in Elasmobranchs, Ganoid Dipnoan," Anatomy Record, Vol. XVIII, pp. 208-209.

the middle and lower portions being obliterated. The pit thus formed is the structure regarded as the internal part of the hyoid cleft by Dorhn[12] in 1886.

Garman (1874) pointed out that the spiracle is of greater importance to the rays than the sharks, due to the fact that rays live on the bottom and this places their mouth at a disadvantage as an incurrent respiratory opening. The spiracle is used as the incurrent opening and is therefore larger than in the sharks. He, also, pointed out that sting rays had a valve in the spiracle which allowed the current to pass inward only. However, in the common skate there is no valve and water may pass either way. It usually goes only inward, but if sand or other foreign material gets into the spiracle, the skate spouts out through the spiracle to remove it.[13]

"When fully open the external opening of the spiracle in the common skate is almost elliptical in outline, but the curvature of its anterior margin is much greater than that of its posterior margin. The anterior lip of the opening bears a rudimentary gill and the closing of the spiracle is effected mainly by the contraction of this gilled lip, while the posterior lip, being nearly straight when relaxed contracts but little."[14]

In respiration the spiracle opens and closes regularly. During rest the movements are slow and the opening is much narrower, but during active respiration the anterior lip of the spiracle moves back and forth quickly and the spiracle opens its maximum width. When the spiracular valve opens the branchial region expands and a strong current of water is drawn through the spiracle, the

---

[12] G. Pinkus, "The spiracular sense organ in Elasmobranchs, Ganoid, Dipnoan," Anatomy Record, Vol. XVIII, p. 433.

[13] Herbert W. Rand, "Functions of the Spiracle in the Skate," The American Naturalist, Vol. XXXXI, May 1907, pp. 288-289.

[14] Ibid., p. 389.

external branchial apertures being closed. The movement of the mouth is practically the same. Some water entered the mouth, however, the greater volume enters the spiracle. The action of the mouth is always a little slow as compared with the action of the spiracle. The mouth and spiracle close together, but the mouth opens slightly later than the spiracles. When the spiracle and mouth are closed, the water is forced out through the gill clefts. Inspirations occur from twenty to thirty per minute and normal spouting every five to ten minutes. Spouting is caused by insufficient oxygen supply, irritation, exercise or induction of bulk material. Also, any irritation to the eye will cause the animal to spout.[15]

Van Bemmelen[16] (1884) searched for a thymus element in the spiracle of rays and in his study observed the ventral spiracular follicle but could not determine its thymus element. In his conclusion Van Bemmelen said, "I incline certainly to the view, which would consider both the vesicular follicle of the spiracle and that of the angle of the mouth as possibly the rudimentary equivalents of thymus-element of these parts.

Ten years later Beard[17] found, in the ray embryo of seventeen mm, a thymus placode in the spiracle. It consisted of but a single regular epithelium of columnar cells containing very few leucocytes. In larger embryos the leucocyte count increased, though the structure of the epithelium changed very little. However, Beard found in some embryos that the placode grows and spreads into a flattened plate of epithelial cells and in others a cone of epithelial cells were formed.

---

[15] J. Frank Daniel, _The Elasmobranch Fishes_ (Berkley, University of California Press, 1928), p. 151.

[16] J. Beard, "Thymus-Element of the Spiracle in Raja," _Anatomischer Anzeiger_, Vol. XVIII, Nov. 1900. (Jena: Verlag von Gustav Fischer, 1909) pp. 358-359.

[17] _Ibid._, p. 363.

In the Scyllium the thymus-elements arise as those of the Raji and for a time their placodes remain very simple, only increasing in area. Later the epithelium becomes tubular and vascular.

Beard made the following conclusions in regard to the thymus-elements:

"1. It arises as a placode of the gill-pouch, and with the rupture of this latter it comes to be epiblastic in position.

2. In late phases it acquired a covering of ordinary epiblast.

3. Connective-tissue septa grow into it.

4. Blood capillaries penetrate it.

5. Its epithelium gives origin to leucocytes.

6. At a later period it becomes more or less constricted off from the branchial epithelium, but apparently unlike a thymus-element, not completely."[17]

The external opening of the gills, directly to the outside in the Cyclostomes, and Elasmobranchs, is replaced by opercular covering of the gill-clefts in the Teleostomi and Dipnoi.

In Holocephali, spiracles are absent in the adult but present in the young of Chimaera. The interbrachial septum is also much reduced and in Teleostomi the reduction is carried still further, the whole gill structure being covered by a movable operculum.[18]

Open spiracles are wanting in most Teleostomi but are retained in the Crossopterygii (Polypterus) and Chondrostei (Acipenser and Polyodon). In the embryos of salmon the spiracle is present but degenerates in the adult. The spiracle in the sturgeon (Acipenser) is a slit-like structure just above the eye. It is a hemibranch of the hyoid arch and is a true gill serving the

---

[17] Beard, op. cit., p. 363.

[18] T. W. Bridge and G. A. Boulenger, Fishes, Ascidians, etc., (London: MacMillan & Company, 1922, pp. 278-279.

same purpose in the circulatory system as in Elasmobranch. Polyodon (Spoonbill) and Polypterus have a suppressed hemibranch while Lepidosteus (Garpike) has two series of lamellae on the inner surface of the operculum. The ventral section is supplied with venous blood, the dorsal with arterial, so that the latter is a definite pseudobranch.[19]

Goodrich[20] found a pseudobranch to be developed in Acipenser, Polyodon, Lepidostens, Amia and most Teleosts. Von Baer (1827) found two pseudobranchs in Acipenser. In 1831 those of Lepisdosteus were worked out by Valentin. Hyrth (1838) proved they were supplied with arterial blood. J. Muller (1839) classified the teleostean psuedobranchs as, (1) free, with gill-lamella projecting into the sub opercular cavity, and (2) glandular, sunk below the epithelium. Granel distinguished four adult types of pseudobranchs, "(1) a free pseudobranch with lamella set along the axis and bearing secondary lamella all covered with ectodermal epithelium. Ex. Trachimus; (2) lamella free but epithelium covers them without sinking between the secondary lamella, Ex. Chrysophrys; (3) the lamella do not project and have sunk below the covering of ectodermal epithelium, Ex. Phoxinus; (4) the whole organ is separated from the superficial epithelium by an overgrowth of tissue. Ex. Gadus, Cyprinus."[21]

Pinkus[22] in his study of Protopterus found a peculiar vesicular sense-organ imbedded in cartilage near the anterior end of the ear capsule, innervated by a small nerve that arises from the main lateral line of the facial nerve.

---

[19] Bridge and Boulenger, op. cit., pp. 283-284.

[20] E. S. Goodrich, Loc. Cit., p. 519.

[21] Ibid., p. 521.

[22] G. Pinkus, "The spiracular sense organ in Elasmobranchs, Ganoid, Dipnoan," Anatomy Record, Vol. XVIII, pp. 208-209.

# CHAPTER III

## DISSECTION AND DISCUSSION

Cyclostomata:

The specimens used to dissect for a study of the Cyclostomata were Petromyzon marinus, a species which is common in the waters of the rivers, seas and oceans in and around America, Europe and Asia. This animal is long and eel-like, having two dorsal fins but no lateral fins. The body is covered with a slimy skin without scales.

The mouth is at the bottom of a circular suctorial funnel, the inside of which is armed with horny teeth which aid in holding on to the fish on which they feed. The nasal organ is a single median organ placed at the posterior side of the hypophysial duct, the opening to which serves as the nostril opening upon the top of the head. The deeper end of the hypophysis expands into a sac which ends blindly at a point even with the first gill-slit.

The gill-slits are tubular, and the folded gills are borne on the walls of pouch-like regions of these tubes.

It is the nasal apparatus in Cyclostomes that is the forerunner of the spiracle in the Elasmobranchs. To show these structures and the related structures the specimens were dissected by making a sagittal section, from dorsal to ventral beginning with the anterior of the buccal funnel and continuing in a mid-line to a point even with the last gill-slit. This represents about 1/5 of the total body length. (Figures 1 and 2)

The nasal aperture opens externally in the mid-dorsal line slightly anterior to the eyes. The nasal opening runs downward to the nasal capsule.

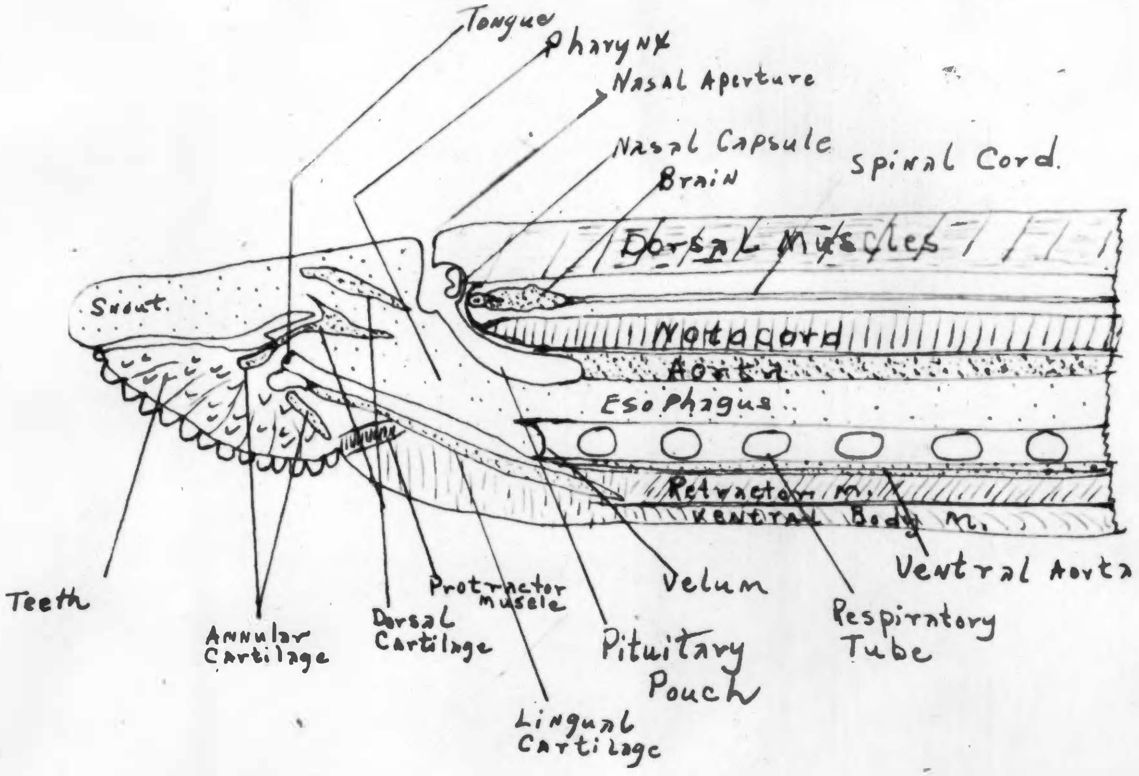


Fig. 1. Petromyzon Marinus - Sagittal section

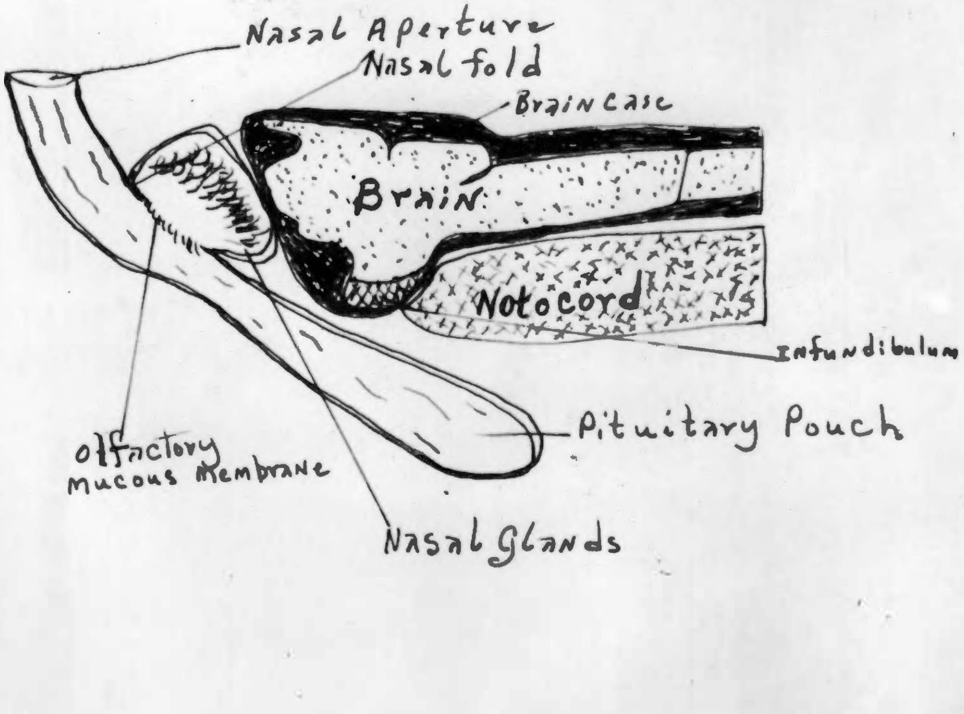


Fig 2. P. Marinus - Sagittal Section through Olfactory Apparatus. X 3

A pouch-like diverticulum separates it from the nasal aperture by mucous membrane and it contains the nasal glands and olfactory nerve endings, then it curves slightly upward and continues on backward ending in a blind pouch just below the notocord at a point even with the first gill-slit. The posterior part of the pouch is known as the pituitary pouch. The whole nasal aperture is tube-like with slight convolutions in the walls running longitudinally. No rudimentary gill structures are present.

The nasal aperture is primarily used in the sense of smell which is located in the olfactory sac which lies in the nasal capsule. When the pituitary sac comes in contact with the infundibulum of the brain, it gives off numerous follicles which form the pituitary body.

The nerve supply to the nasal aperture is the superior opthalmic to the dorsal region and the facial to the pituitary region.

The blood comes from the internal carotid artery through the basilar artery.

Selachii:

The Elasmobranchii include several orders but in this investigation the dogfish shark (Squalus acanthias) and the common skate (Raji erinacea) were used as basic specimens with others referred to for comparison.

In the Elasmobranchii the spiracle is definitely a part of the respiratory system. The spiracle opens to the exterior through the spiracular aperture and to the interior into the pharynx.

Squalus acanthias adults reach a length of about three feet. In this investigation various sizes, from unborn embryos of 5 inches to 25 inches long were studied. The illustrations shown in Figures 3, 4, 5, 6, 7 and 8 were made from a specimen twenty-five inches long to get the various cross sections of the spiracle at different depths. A specimen twenty-one inches long was used in making the cross section of the body through the spiracles.

The spiracle is located posterior to and slightly toward the dorsal line from the eye, in the middle of an imaginary line drawn from the mouth to the nearest point on a mid-dorsal line. (Figure 3)

The opening of the spiracle is somewhat longer than wide with the long axis running horizontal to the eye. Anterior and adjacent to the spiracle is the spiracular pit and just dorsal to the spiracular canal is the rather large spiracular muscle. From an external view the lamella of the pseudobranch may be observed attached to the anterior muscular wall. This muscular wall serves as a valve in controlling the size of the opening of the spiracular canal.

The first plane observed below the surface was from a dorso-lateral view with the skin and superficial muscles removed. (Figure 4)

In this and the illustrations of this series the eye is used as a point of orientation. In this illustration the spiracle appears almost oval with the lamella more distinct on the anterior side. The spiracular pit is still present. The spiracle is protected by the hyoid and mandibular arches on either side and dorsally by the supra-orbital crest.

The second plane of observation (Figure 5) below the surface was made from the same position as the previous one and shows the structures one-fourth of an inch below the surface.

This illustration shows the spiracle to be pressed down by the dorsal spiracular muscle, the spiracular pit is not evident and the lamella of the pseudobranch are somewhat flattened.

In Figure 6 the spiracle has become enlarged slightly and stretched

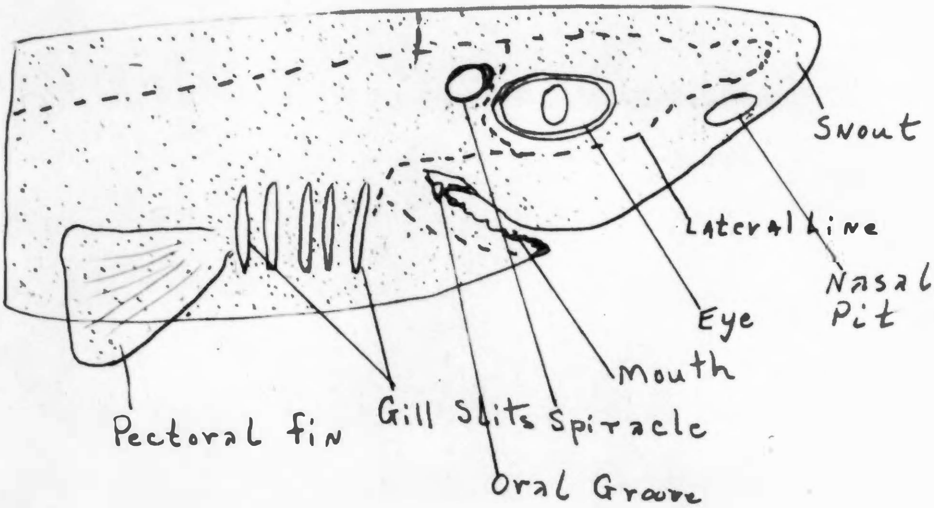


Fig. 3. Squalus acanthias - side view.

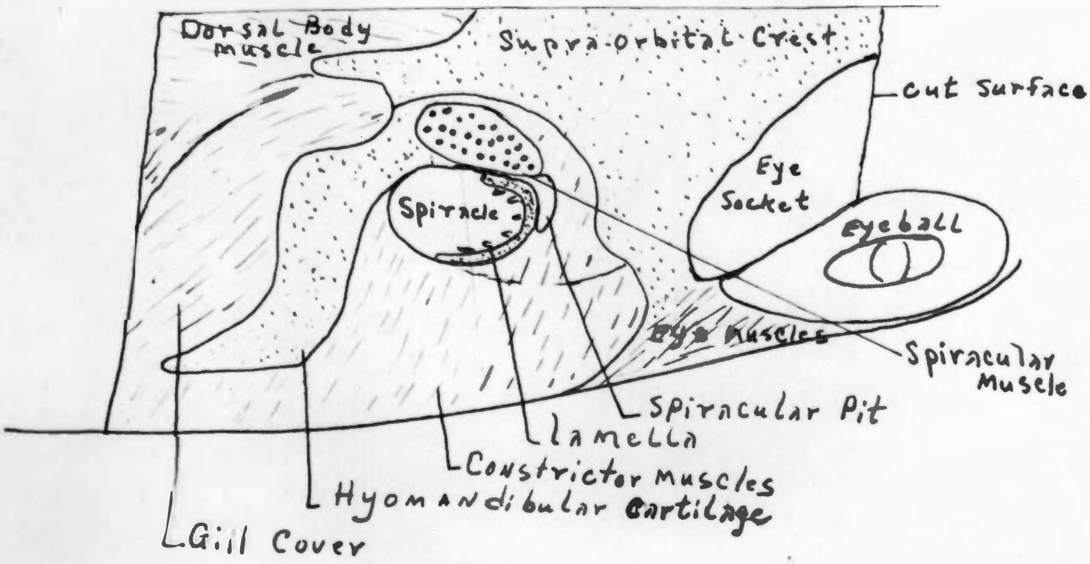


Fig. 4 Squalus acanthias - Dorso-lateral View showing structures under the skin and skin muscles

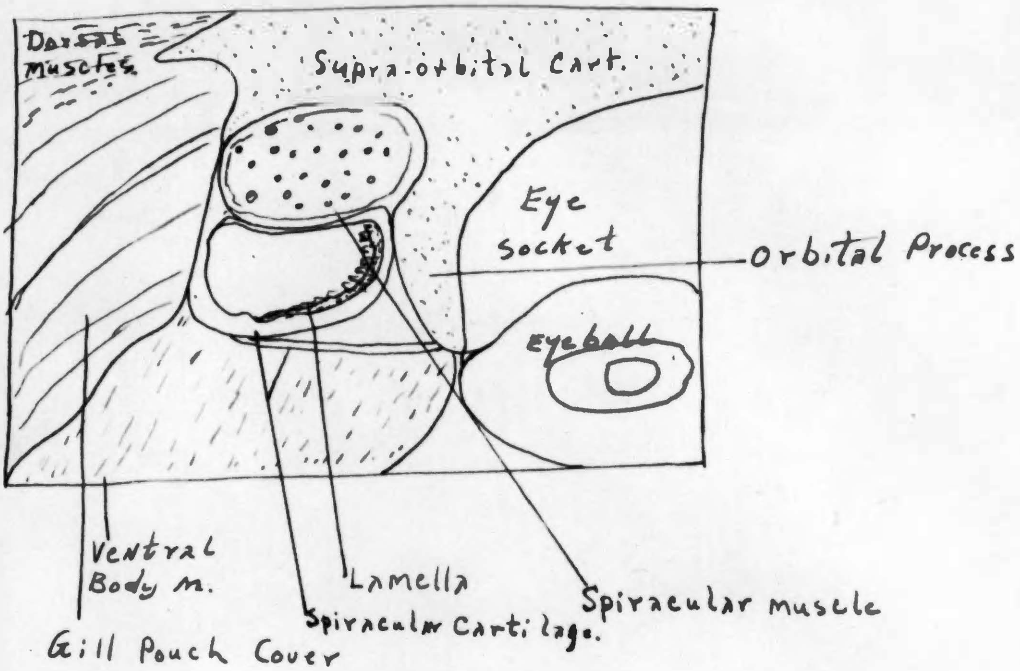


Fig. 5. Squalus acanthias - Dorso-lateral View showing Structures ¼ inch below the surface.

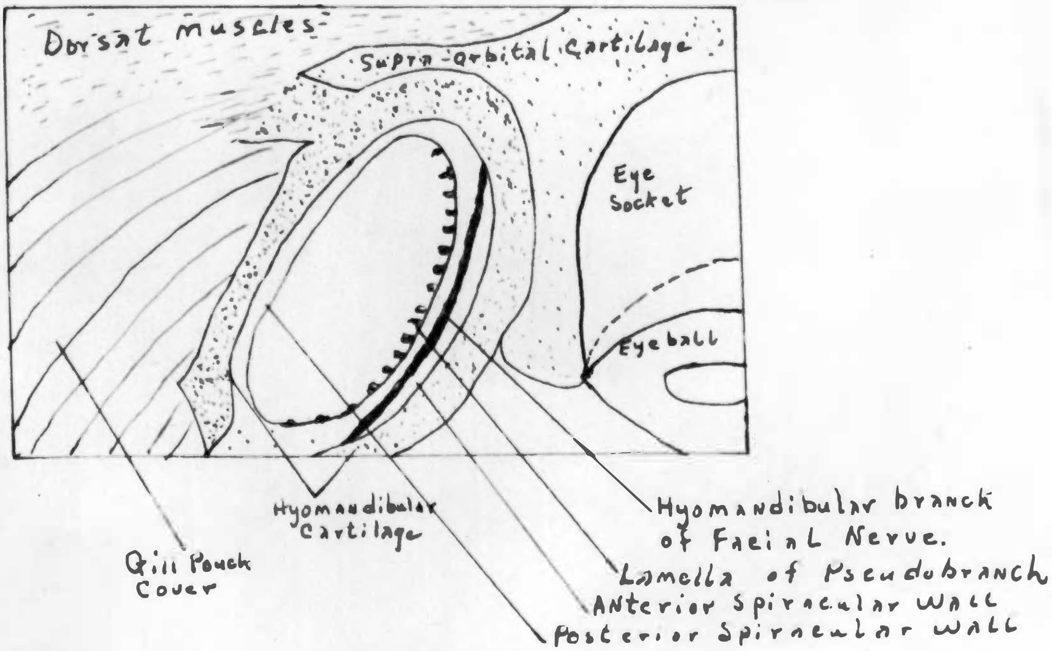


Fig. 6. Squalus acanthias - Dorso-lateral View showing Structures ½ inch below the skin.

toward the base of the supra-orbital crest. The dorsal spiracular muscle has disappeared. The hyomandibular branch of the facial nerve is seen coming from the supra-orbital crest and running across the anterior wall of the spiracle. The lamellae have become greatly reduced in size and now appear more as ridges of vascularized tissue. The spiracular artery supplies the pseudobranch with blood from the first afferent artery.

Figure 7 shows the structures exposed on a plane three-fourths of an inch below the surface. The spiracle has been somewhat flattened by the hyoid and mandibular arches. The hyoid and mandible are exposed. The base of the supra-orbital cartilage has pushed downward and backward causing the spiracle to appear to have two protrusions in a craniad direction.

The final illustration in this series, Figure 8, shows the base of the spiracle as it enters the pharynx. The walls are irregular and contain many irregular folds filled with mucous. There is a posterior-ventral diverticulum between the mandible and the hyoid which appears to be due to pressure rather than being a true diverticulum. The front of the spiracle widens toward the oral groove. Through the opening, the floor of the pharynx may be observed covered with mucous and having the gill rakers and gill bars opening to the gill pouches in a ventro-lateral direction.

Since Squalus acanthias was the only type available for dissection the investigator has used two illustrations, one from Goodrich and one from Ridewood of Scyllium canicula (Figures 10 and 11) as a means of comparison.

In a transverse section through the spiracles it was observed that the spiracular canal of Squalus acanthias is practically straight with only slight bulges in the inside walls and a pseudobranch with poorly developed lamella on the anterior wall. In Scyllium canicula, however, the spiracle

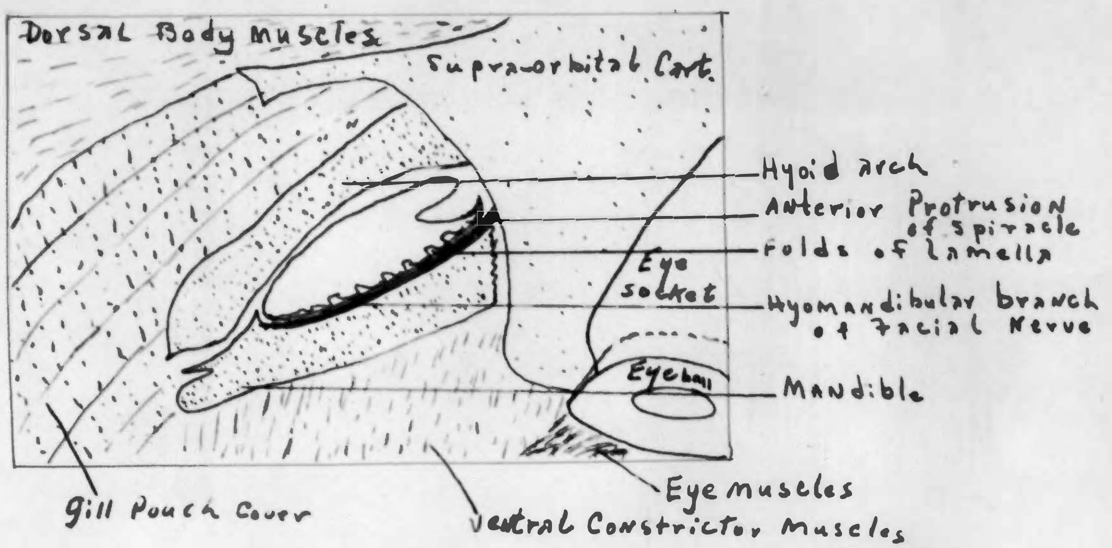


Fig. 7. Squalus acanthias - Dorso-lateral View showing structures 3/4 inch below the surface.

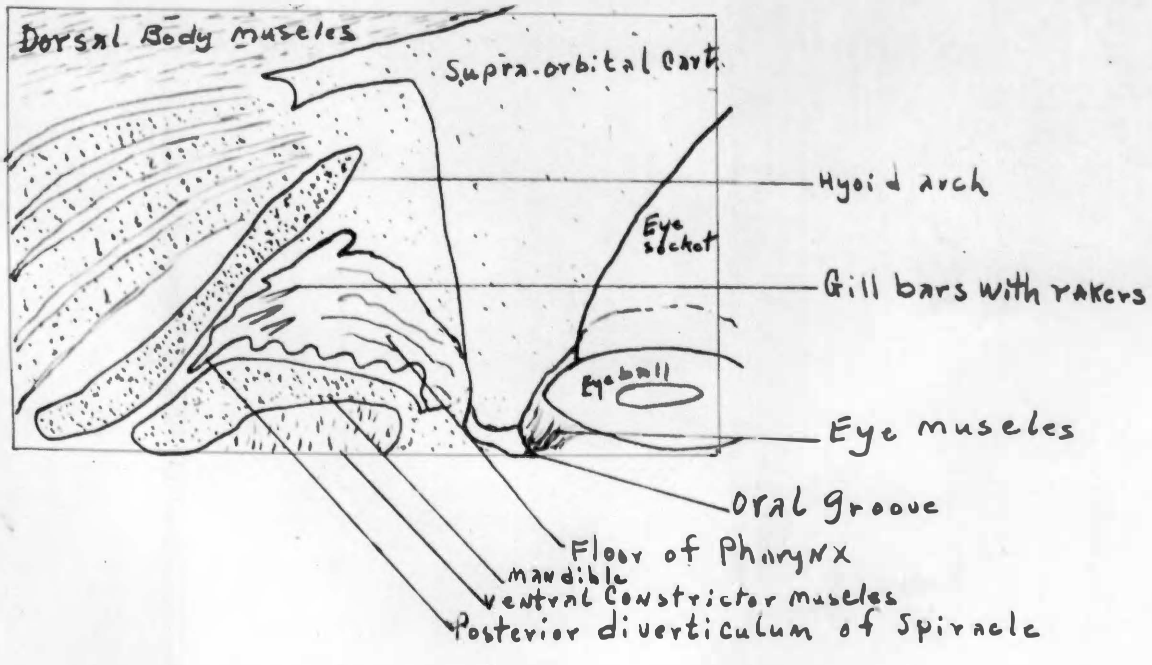


Fig. 8. Squalus acanthias - Dorso-lateral View showing structures where spiracle meets pharynx.

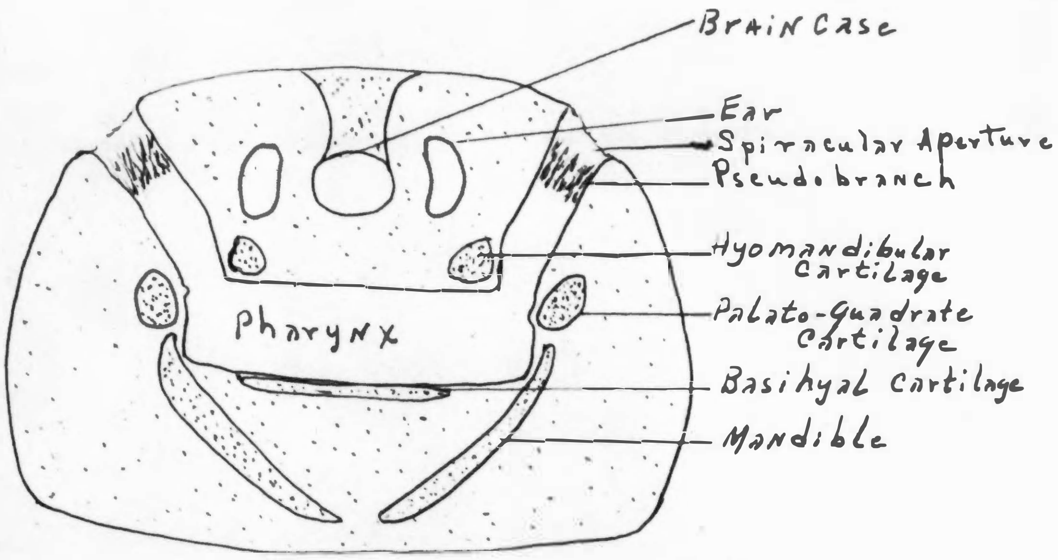


Fig. 9. Squalus acanthias — Transverse section through spiracles.

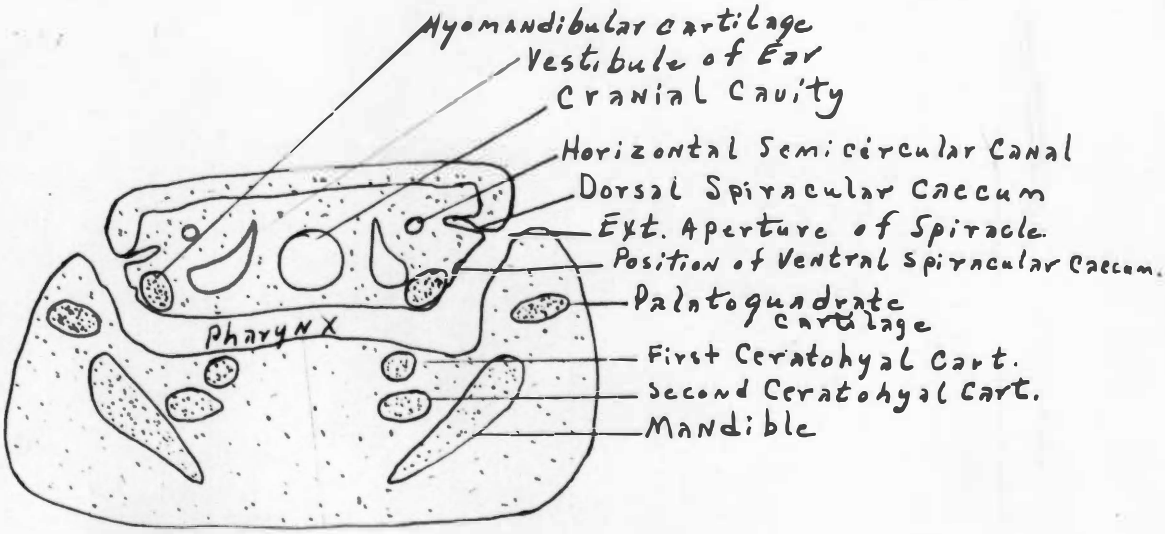


Fig. 10. Scyllium canicula — advanced embryo — Transverse sect. (Ridewood)

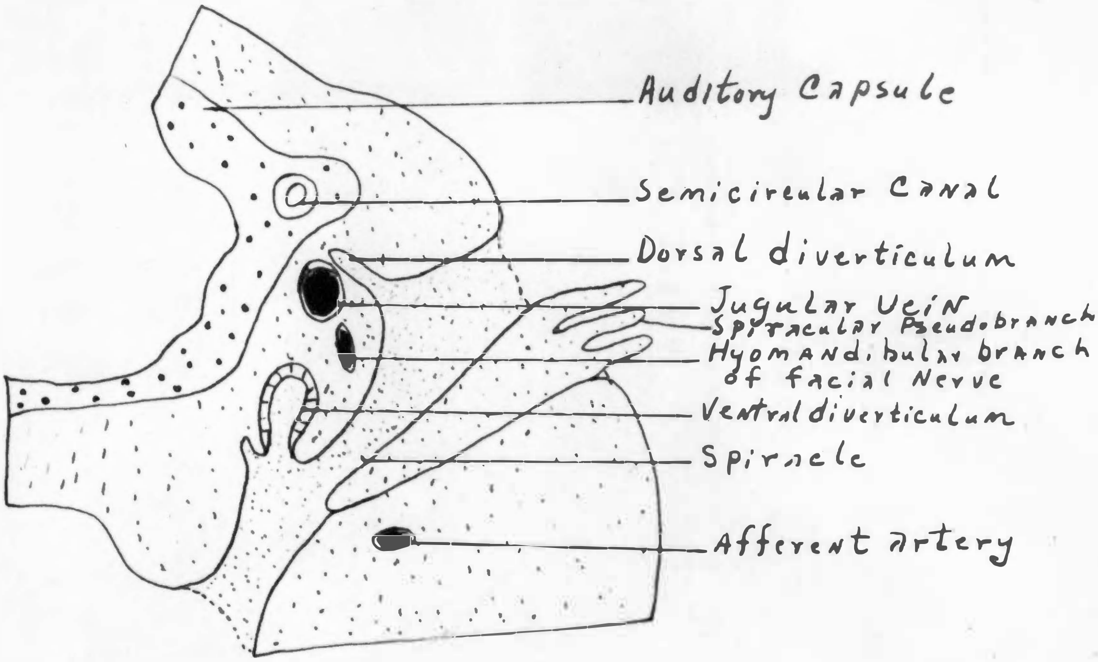


Fig. 11. Scyllium canicula, advanced embryo. Transverse section through the spiracle. (Goodrich)

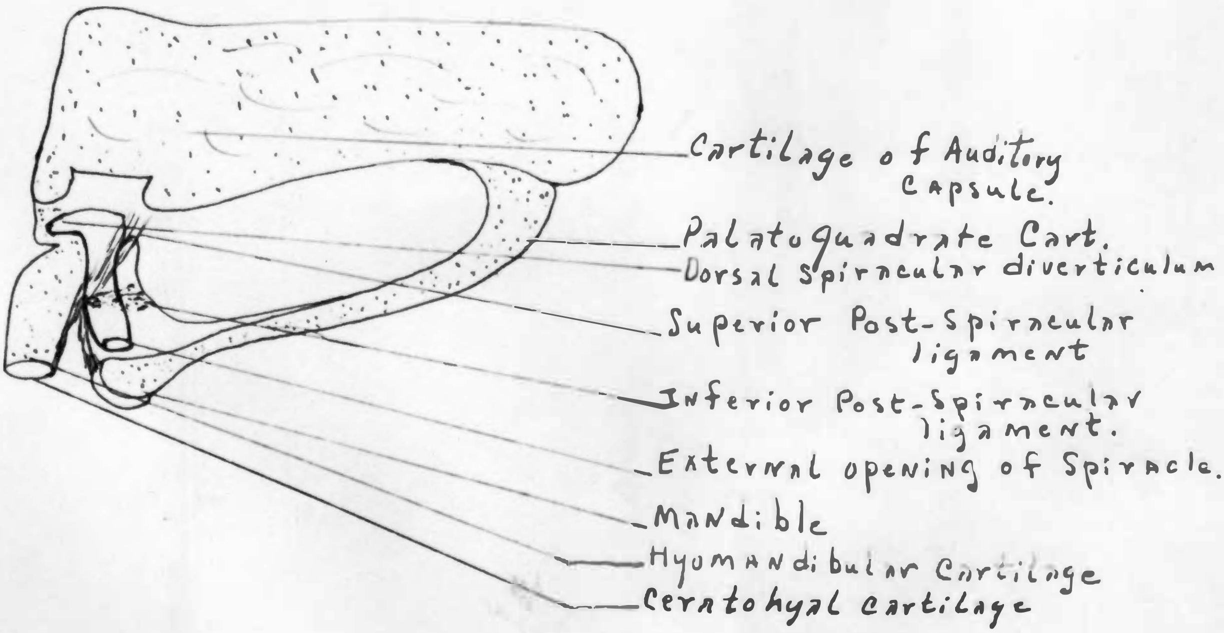


Fig. 12. Scyllium canicula, dorso-lateral view of skull showing relation of the post-spiracular ligaments and the dorsal spiracular caecum.
(Anatomischer Anzeiger Vol. XI)

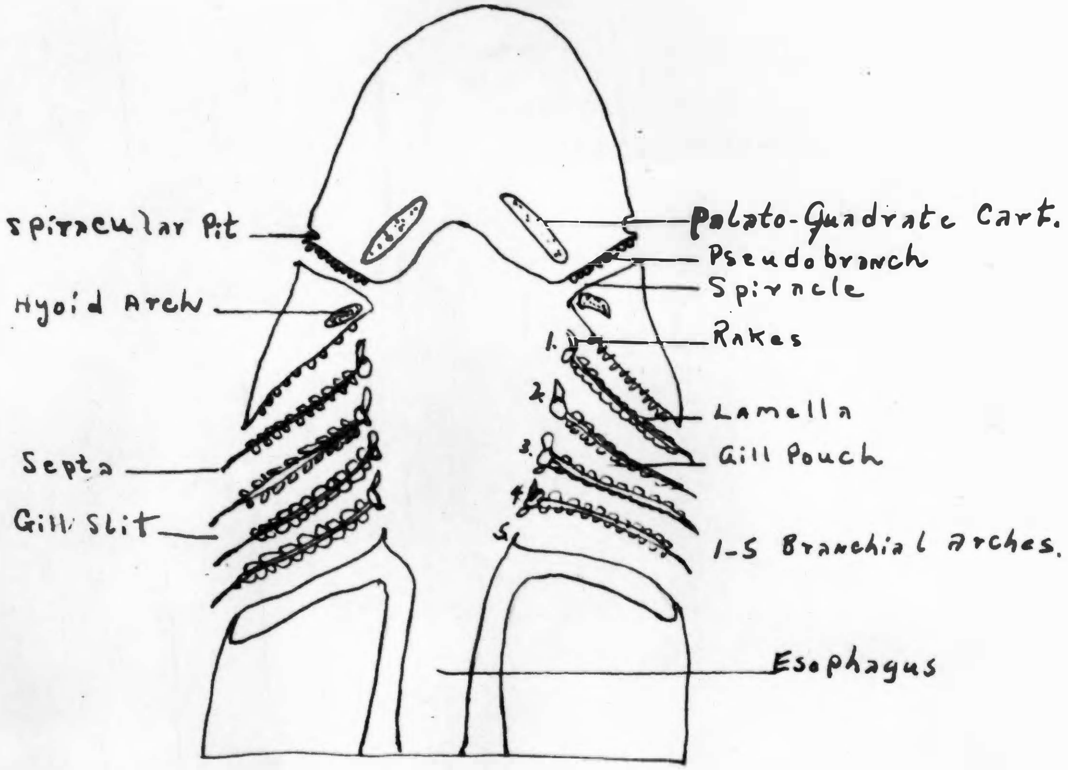


Fig. 13. Horizontal Sect. Elasmobranch (Squalus acanthias)

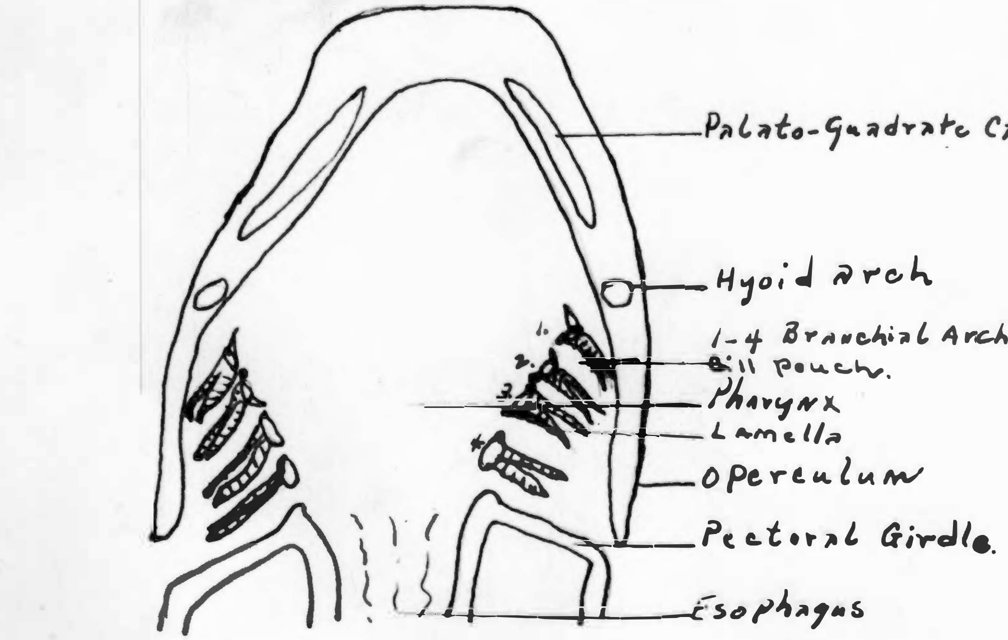


Fig. 14. Horizontal Sect. Teleost (Perca flavescens)

shows two diverticula (Figures 10 and 11). The dorsal diverticulum projects from the antero-medial wall of the spiracular pocket toward the auditory capsule and may be attached to it above the post-orbital groove. At its beginning the diverticulum is almost closed but becomes enlarged as it approaches the auditory capsule.

The embryonic specimens studied were little different from the adult except that the spiracle was larger in proportion to the total body size and assumed more of a wedge shape with the blade pointing toward the mouth. The lamellae appeared as very small ridges almost covered with mucous.

Norris and Hughes (1920)[1] claimed the dorsal diverticulum in Squalus acanthias is divided into two or three small diverticula each of which is supplied by a branch of the ramus oticus VII nerve. He considered it a modified ampulla of Lorenzini.

The second diverticulum on the anterior medial wall of the spiracular canal is located ventrally near the union of the canal with the pharynx. It is more shallow than the dorsal diverticulum and is connected to the canal by a short neck.

The spiracular pocket is supplied by the hyomandibular branch of the facial nerve and by the spiracular artery.

In the Squali the spiracle functions as an accessory respiratory organ, water being taken into the spiracle as well as the mouth. It is thought by some that the spiracular diverticula form a part of the auditory system.[2]

Raji:

The common skate (Raji erinacae) used for study was eleven inches wide and nineteen inches long.

---

[1] J. Frank Daniel, Loc. Cit., p. 149.

[2] Ibid., p. 149.

The spiracles are located immediately posterior and slightly lateral to the eyes. (Figure 15) From an external view the spiracle appears to slant (as a Chinaman's eyes). On the anterior wall at the opening, the muscular spiracular valve is located and immediately below this structure the pseudobranch may be seen when the spiracle is open. The spiracular valve is composed of a stiff crescentic fold of connective tissue which is constantly opening and closing during respiration. This fold is held in place by the crescentic spiracular cartilage which is attached at each end by ligament. The closure of the spiracular valve is by the dorsal constrictor muscles.

The spiracle, in the Raji, is the main opening for the entrance of water into the pharyngeal cavity since the mouth is against the bottom of the stream most of the time. (Figure 16)

At the posterior of the pharyngeal cavity six internal gill-slits break the lateral wall of the cavity into the visceral pouches which open to the outside through the external gill-slits. The visceral arches separating the visceral pouches are made of a central interbranchial septa with branchial filaments on either side. These are supplied with blood from the ventral aorta which gives off branches to each demibranch through the afferent arteries. The blood from the gill filament is collected by the post-trematics on the anterior face of the gill-arch and the pre-trematics on the posterior face of each gill-arch which join to form the efferent branchial arteries which connect with the dorsal aorta.

The hyoidean artery arises near the middle of the front pre-trematic and goes forward to supply the rudimentary gill of the spiracle and the adjacent muscles. The branches to the spiracle reunite forming the ventral carotid which joins the internal carotid.

The spiracle, beside being supplied by the infra-orbital canal of the lateral line system, is supplied by the hyomandibular branch of the facial nerve.

A cross section through the spiracles (Figure 17) shows them with related structures. The body is much flattened, the lateral sides being the muscular lateral fins. The spiracular canals run from the orbital crest at the eye downward and inward into the pharynx. The muscular valve and pseudobranch appear near the exterior opening of the spiracular canal. Below and to the side of the pharynx is the large pectoral muscles.

Teleostomi:

The spiracle in the Teleosts is either greatly modified or entirely absent. The salmon (Salmo) have a spiracle in the embryo but as adults they have a small rudimentary pseudobranch left under the operculum. Sturgeons (Acipenser) have a small spiracle opening from a small slit-like opening above the eye and running downward and inward to connect with the pharynx. No pseudobranch is present on either anterior or posterior wall. The spoonbill (Polyodon) has a small spiracle behind the eye. The operculum contains no opercular bones and is extended into a pointed process. There are no branchiostegal rays in the spoonbill.

The writer examined specimens of the catfish, sucker, trout, perch, carp and branch minnows, chiefly silversides, and found the spiracle to be absent.

Gills in the Teleosts are covered with a partially ossified structure, the operculum, which is a new structure in the bony fishes. (Figure 14)

The spiracle in most Teleosts is closed on the outside by the operculum,

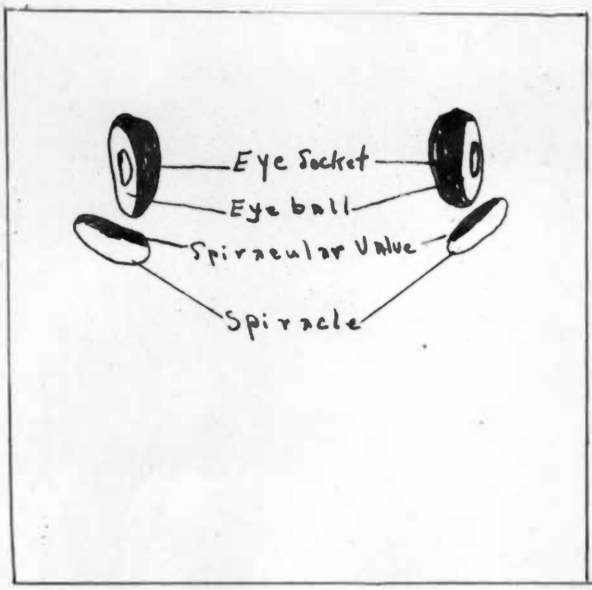


Fig. 15

Dorsal View of a section 3 x 3 inches of Raji erinaceae to show relationship of Spiracle to other structures

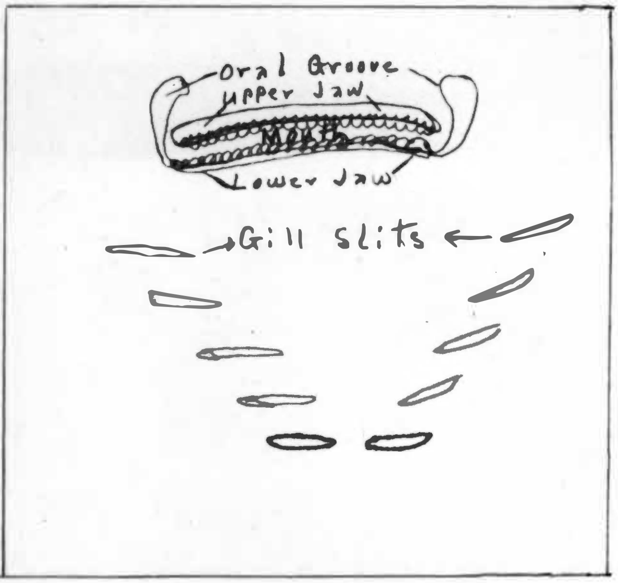


Fig. 16

Ventral View of a section 3 x 3 inches of Raji erinaceae to show relationship of structures.

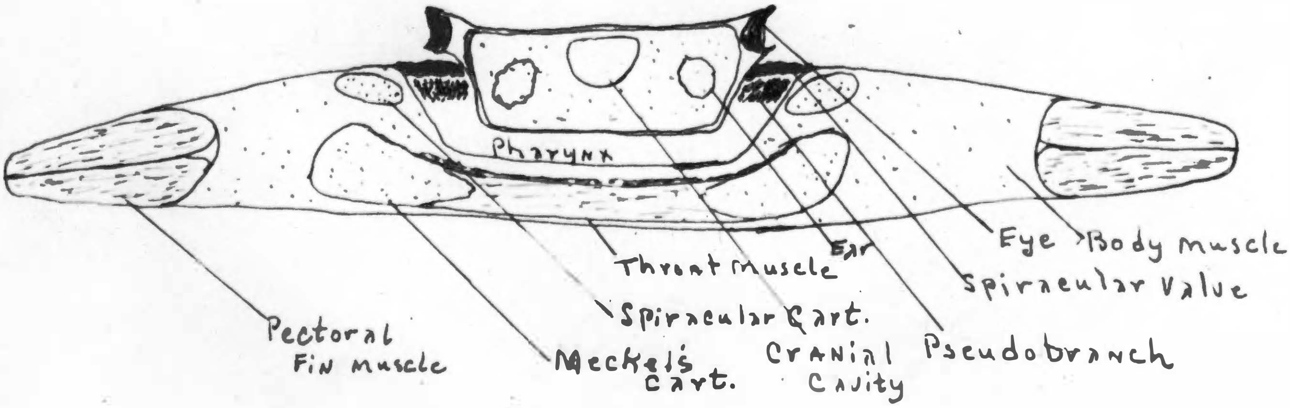


Fig. 17 Raji erinaceae, Cross section through the spiracles

the inside structure from the throat ending in a pouch-like diverticulum just beneath opercular roots. This diverticulum has a protuding arm toward the labyrinth of the ear. This protrusion does not appear to penetrate the auditory capsule but the circulating water within affects the sensitive part of the ear. This blind spiracular canal is the primitive Eustachian tube, but, since there is no middle ear in fish the tube is not a true Eustachian tube. In the Amphibians the middle ear appears in Anura and we find a definite Eustachian tube connecting the vestible of the middle ear with the throat.

Ear:

Since the ear is so closely related to the spiracle the writer observed the ear in the specimens of Petromyzon marinus, Squalus acanthias, Raji erinacea, and Perca flavescens and will describe to some detail their structures.

Petromzon marinus (Figure 18) has an ear which is very simple and could be called a neuromast of the lateral line system. It does not serve the purpose of hearing but of equilibrium. The ear is paired taking the form of sacs located on each side of the brain behind the eyes in the cartilaginous skeleton. The labyrinth bears two semicircular canals, anterior and posterior, each of which bears an ampulla containing statoliths. The statoliths contain calcium particles in a mucous substance which when moved produce a sensation on the auditory nerve. Connection to the outside is maintained through the endolymphatic duct which emerges in a pit just back of the median nostril. The canals and the auditory sac are filled with endolymph.

The Elasmobranchii, also, have a lateral line system in connection with the auditory apparatus.

The ear of Squalus acanthias (Figure 19) shows a marked advance over P. marinus in having three semicircular canals. Each of these canals has an

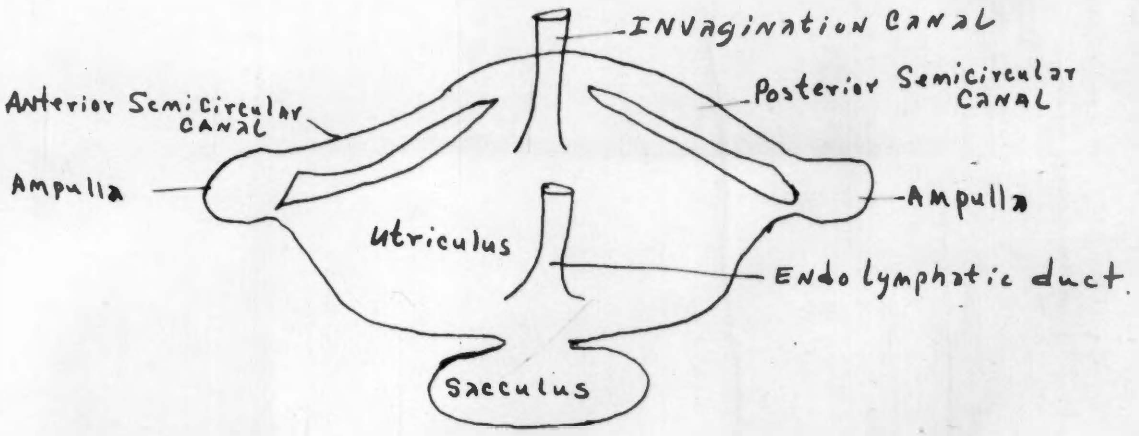


Fig. 18. Ear of Petromyzon marinus

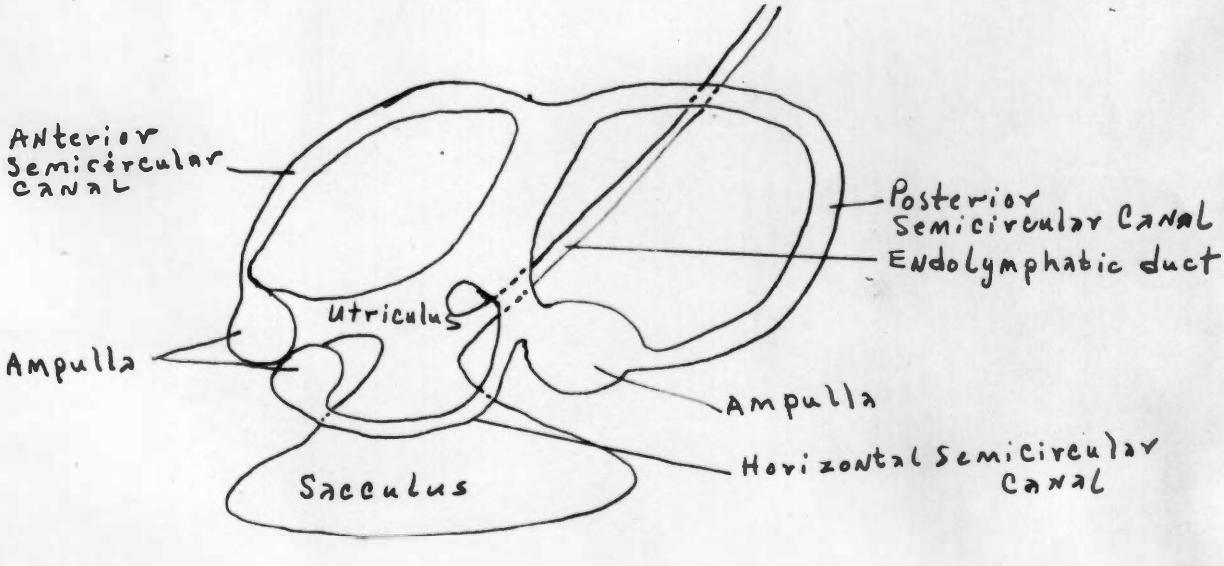


Fig. 19. Ear of Squalus acanthias

ampulla containing a number of hair cells innervated by the auditory nerve. The cavity of the statocyst retains its connection to the outside through the endolymphatic duct which contains water instead of endolymph. The sacculus has become further separated from the utriculus and is connected only by the canalis reuniens. The sacculus has developed an outgrowth, the lagena. The lagena does not function and it is believed that the ear is chiefly an organ of equilibrium. The whole apparatus is located in a cartilaginous capsule fused with the cranium.

The ear of Raji erinacea (Figure 20) is similar to that of Squalus acanthias in the number of semicircular canals, ampulla and hair cells. A crystalline stone is present in the utriculus. The connection to the outside is through the endolymph duct and endolymphatic vestibule. The ear with its canals filled with perilymph and the ducts and vestibule with endolymph function both in hearing and balance. As in Squalus the whole auditory apparatus is enclosed in a cartilaginous cranium which appears as an elevation between the spiracles and mid-line.

Perca flavescens (Figure 21) has the same number of semi-circular canals as the Raji. However, the Perca has a large utriculus and a much larger sacculus than previously found. The endolymphatic duct now grows out of the sacculus to the exterior. The bony auditory capsule is connected with the cranial cavity. In function the auditory apparatus is for hearing and equilibrium.

Hearing in any of the fishes is the perception of mechanical vibrations of low frequency. Fish are capable of hearing with their auditory organs but not to the extent that land vertebrates are which are subject to vibrations of the air.

When forms leave the water for a land habitat, they no longer breath by

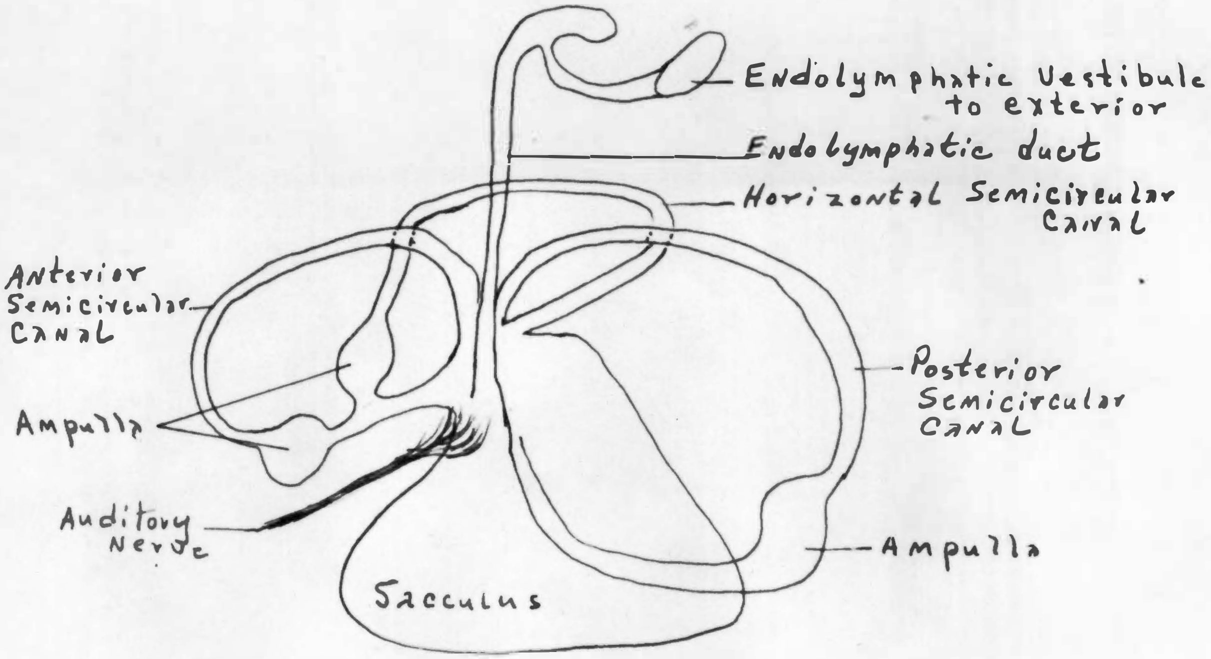


Fig. 20. Ear of Raji erinacea

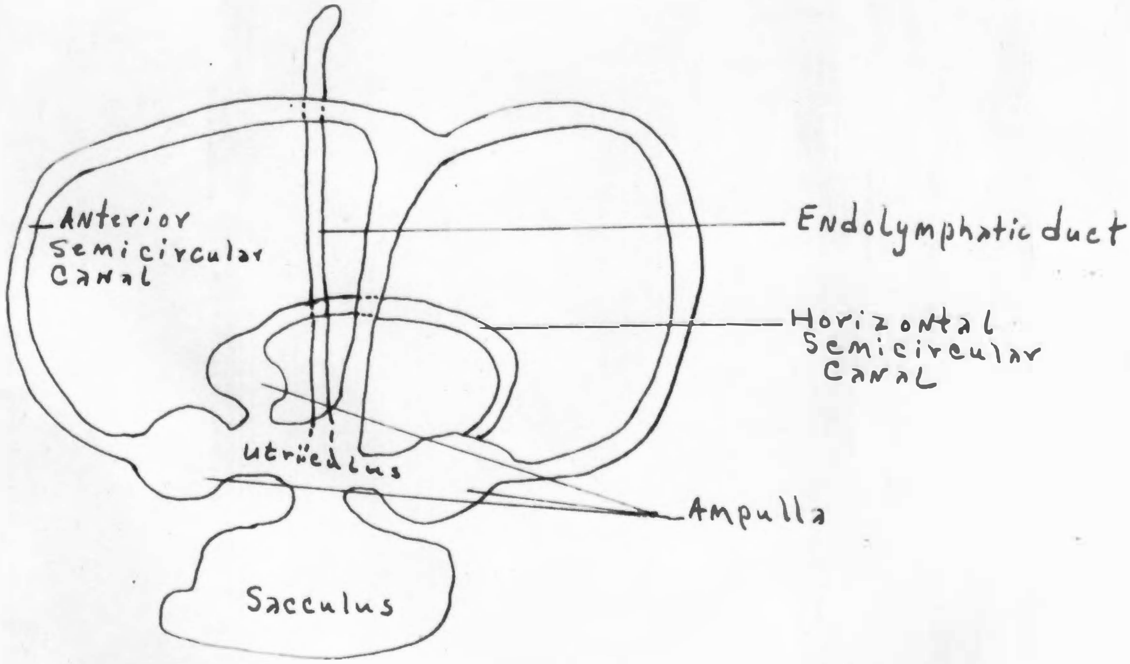


Fig. 21. Ear of Perca flavescens

gills. Therefore, the spiracular cleft and hyomandibular arch are no longer needed in their primitive function and differentiate into the middle ear, Eustachian tube and the columella (stapes) respectively. The incus develops from the quadrate of the lower vertebrates while the malleus came from the proximal end of Meckel's cartilage which was cut off from the total structure.

## CHAPTER IV

## SUMMARY AND CONCLUSIONS

1. The *Cyclostomata*, *Elasmobranchii*, and *Pisces* have respiratory systems using gills to take the oxygen from the water.

2. All forms live in water during their entire life.

3. All forms have a structure related to the respiratory system usually known as spiracle, or a derivative from it.

4. The spiracle in its typical form is a modified gill-cleft derived from the first pharyngeal pouch and containing a rudimentary gill structure as in the *Elasmobranchii*. Through this canal water passes from the exterior to the pharynx.

5. The *Cyclostomata* possess a primitive form of spiracle in the median nasal canal. In *Petromyzon marinus* the nasal capsule ends as a blind sac, the pituitary pouch, which opens only to the exterior, while *Myxines* maintain a connection with the pharynx.

6. In the *Raji* the spiracle is equipped with a valve which regulates the flow of the water into the pharyngeal canal.

7. The *Teleosts*, except *Acipenser* and *Polyodon*, have no spiracular opening to the exterior. The upper end has been closed off by the formation of the operculum (*Salmon* has a rudimentary pseudobranch under the operculum).

8. The spiracle is related to the auditory apparatus. Diverticula were found protruding from the spiracular canal toward and in some cases

connecting with the auditory structures.

9. When the tympanum is formed it originates from structures around the spiracular canal and closes the opening to the exterior, the lower part forming the Eustachian tube.

10. The development of the tympanum and the Eustachian tube parallels the development of the auditory receiving mechanism which appears in the land forms that must adjust themselves to recording air waves. The first true tympanum and Eustachian tube appear in the Anura.

# BIBLIOGRAPHY

# BIBLIOGRAPHY


Adams, Leverett Allen, An Introduction to the Vertebrates, New York: John Wiley & Sons, Inc., 1938.

Beard, J., "A Thymus-Element of the Spiracle in Raji," Anatomischer Anzeiger, November 1900, Vol. XVIII, Jena: Verlag von Gustav Fischer, 1901.

Daniel, J. Frank, The Elasmobranch Fishes, Berkley: University of California Press, 1928.

DeBeer, G. R., Vertebrate Zoology, New York: The MacMillan Company, 1928.

Goodrich, Edwin S., Studies on the Structure and Development of Vertebrates, New York: The MacMillan Company, 1930.

Horner, S. F. and Shipley, A. E., Fishes and Ascidians, Etc., The Cambridge Natural History Series, Vol. VII, New York: The MacMillan Company, 1922.

Hegner, R. W., College Zoology, Fourth Edition, New York: The MacMillan Company, 1936.

Hyman, Libbie, H., A Laboratory Manual for Comparative Vertebrate Anatomy, Chicago: The University of Chicago Press, 1922.

Kingsley, J. S., Textbook of Vertebrate Zoology, New York: Henry Holt and Company, 1911.

Kuhne, Eugene R., A Guide to the Fishes of Tennessee and the Mid-South, Nashville: Tennessee Department of Conservation, 1939.

Neal, Herbert V. and Rand, Herbert W., Comparative Anatomy, Philadelphia: P. Blakiston's Son and Company, Inc., 1936.

Norris, H. W. and Hughes, Sally P., "The Spiracular Sense-Organ in Elasmobranchs, Ganoid, Dipnoan," Anatomy Record, Vol. XVIII, pp. 205-209.

Owen, Richard, Anatomy of Vertebrates, Vol. I, "Fishes and Reptiles," London: Longman's, Green and Company, 1866.

Parker, T. Jeffrey and Haswell, William A., A Text-Book of Zoology, Fourth Edition, London: MacMillan and Company, 1928.

Ridewood, W. G., "On the Spiracle and Associated Structures in Elasmobranch Fishes," Anatomischer Anzeiger, December 1895, Vol. XI, Jena: Verlag von Gustav Fischer, 1896.

Stockard, Charles R., "The Development of the Mouth and Gills of Bdellostoma Stouti," American Journal of Anatomy, Vol. V, pp. 481-517.

Wilder, Harris H., The History of the Human Body, New York: Henry Holt and Company, 1923.

Wieman, H. L., An Introduction to Vertebrate Embryology, New York: McGraw-Hill Book Company, Inc., 1930.

Woodruff, Lorande Loss, Animal Biology, New York: The MacMillan Company, 1938.