REPORT

of

COMMITTEE ON THESIS

THE undersigned, acting as a committee of the Graduate School, have read the accompanying thesis submitted by Walter E. Camp for the degree of Master of Arts. They approve it as a thesis meeting the requirements of the Graduate School of the University of Minnesota, and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Arts.

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THE DEVELOPMENT OF THE SUPRAPERICARDIAL BODY IN SQUALUS ACANTHIAS.

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Contents.

I. Introduction.

A number of investigations dealing with the suprapericardial body or its homologs have been published since the appearance in 1885 of the original communication of its discoverer, Van Bemmelen. Most of these contributions have been of a comparative nature, being purely attempts to correlate the structure throughout the vertebrate series. None of these accounts are devoted to a detailed study of the gland in any one form of the lower vertebrates. Because of the confusion which exists in regard to the significance of the suprapericardial (postbranchial, ultimobranchial) body and because of the singular position it occupies among glands when classified according to form, it was thought that the present study of its development and structure in the form in which it was first discovered --namely Squalus acanthias would be desirable.

The present paper is based upon a study of sectional embryos of Squalus acanthias from 19 to 95 mm. in length, of several specimens of the 'pup' stage varying in length from 20 to 22 cm., of one specimen of newborn and one of

an adult. Most of the sectioned material is from the Harvard Embryological Collection (H.E.C.) while some are from the embryological collection of Dr. R. E. Scammon (S.C.). The older specimens were obtained from the Harpswell Biological Station through the courtesy of Dr. Scammon.

I wish to thank Dr. Scammon for his continued interest and many helpful suggestions, and for the loan of material.

II. Literature

The literature dealing with derivitives of the pharynx wall and gill pouches of fishes and amphibians is very extensive. Identical structures in the same species and homologous structures in other closely related species have been given different names and interpretations by various authors. The name retained in this paper 'the suprapericardial body' is the one originally given to it by Van Bemmelen ('85) because of the dorsal position of the gland with the reference to the pericardium.

Van Bemmelen ('85) in a study of the rudimentary branchial slit of elasmobranchs, describes the suprapericardial bodies as a pair of small epithelial masses lying in the mesenchyma of the ventral pharynx wall, just caudal to the last pair of branchial slits. They advance into about half the thickness of the ventral pharynx wall which here also forms the dorsal wall of the pericardium. Between these epithelial bodies the ventral portion of the copula develops. On either side and slightly anterior is found the last branchial arch. The bodies themselves begin to

form in a stage when the last pair of clefts have just opened, the first trace of embryonic cartilage appears, and when the pericardial cavity is clearly separated from the remaining body cavity.

Originally the body is a simple evagination of the ventral pharyngeal epithelium. Soon, however, its blind end begins to expand and forms a large ventral cyst. From the cyst small epithelial sprouts arise which later acquire lumina and become very much lengthened and coiled. Usually the small neck or connecting piece becomes stunted and remains as an excretory channel, but in some cases it entirely disappears leaving the bodies entirely isolated in the connective tissue.

Histologically the bodies consist of small round follicles held together by scanty connective tissue. The walls of these follicles are composed of columnar or cubical epithelial cells which have large round nuclei. The cavity of the follicles is filled with a structureless mass containing an occasional nucleus. The connective tissue stroma in which the follicles lie is of different

density in the various forms. It is vevy scanty in rays, very dense and rich in nuclei in Torpedo and Aetobatis. In Chimaera it is intermediate in structure. Van Bemmelen was not able to find the nerve and blood supply of the bodies. He thought from their location that possibly their vascular branches were derived from the truncus arteriosus or the axillary artery.

Van Bemmelen described the bodies in all forms of selachian embryos but was unable to find them in mature Heptanchus. In Chimaera the body develops behind the sixth pouch, which completely degenerates without leaving behind any remnants. Often in Acanthias, Scyllium, Pristuris and Galeus the body develops only on one side. In the Raia, Aetobatis, Acanthias and Chimaera the glands remain until maturity and attain a considerable size. In Acanthias he describes and figures the duct opening of the bodies in the free surface of the pharyngeal mucous membrane on either side of the copula. One of the Acanthias embryos showed the suprapericardial body opening into the pharynx by three small ducts. Although these bodies agree

closely with the structure and mode of development of the thyreoid of selachians, Van Bemmelen did not find any union or close relation of the two structures. On the other hand, he considers them as representing a rudimentary pair of seventh branchial pouches which fail to reach the ectoderm and have lost their original function. In support of this hypothesis he argues that the suprapericardial bodies are degenerate structures and are homologous with epithelial derivitives of the spiracle and mouth in selachians, which he also considers as rudimentary clefts.

This same author ('89) continued in a more general way the study of the suprapericardial body or its homologes in the higher vertebrates. In ganoids, amphibians and in Lacerta he found the body clearly defined and well developed. In Acipenser the body consists of follicles as in elasmobranchs, but they have longer lumina and are more dilated. In one of the two examples of Acipenser studied the body was found only on the left side. In amphibians the body is bilateral. It very early loses its connection with the pharynx and develops into a relatively large, thin-walled

cyst lying free in the connective tissue. It remains in this simple cystic form for quite a long period but ultimately sends out diverticula which develop into small independent cysts. He did not find the body in teleosts. In Lacerta the body is present only on the left side and lies much further forward than it does in selachians and amphibians. Histologically it is very similar to that found in amphibia. In mature Anguis fragilis Van Bemmelen ('86) found the suprapericardial only on the left side. It consists of small acinose epithelial bodies held together by connective tissue. In reptiles the bodies arise from the ventral pharynx wall but in their later development they come to lie in between the lobes of the thymus. In birds and mammals Van Bemmelen found great variation in the pharyngeal derivitives of the cervical region in the different forms. He gives a complete review of the literature of the pharyngeal derivitives in vertebrates and homologizes with the suprapericardial body of selachians, the "accessory thyreoids" of De Meuron in birds and mammals; the "post branchial bodies" of Maurer in Amphibians; the "Body Y" of

Mall in birds; and the "lateral thyreoids" of Born and His in mammals.

In a study of their pharyngeal derivitives in the higher forms, Van Bemmelen urges great care in differentiating between those that arise from the pouches themselves and those which spring directly from the pharynx wall. This is particularly true in mammals where these derivitives, although very similar in structure, are to be distinguished by their mode and place of origin. He believes that the suprapericardial bodies in reptiles and their homologues in birds and mammals, as in the selachians and amphibians represent a rudimentary pair of branchial pouches.

De Meuron ('86) in his studies on the development of the thymus and thyreoid glands, gives a brief account of the suprapericardial body in selachians and amphibians. He homologizes the body in these forms with the accessory thyreoid of reptiles, birds and mammals, of which he gives a more detailed account.

In Acanthias vulgaris (Squalus acanthias) De Meuron describes the suprapericardial body as a small, rather

elongated, diverticulum, arising from the ventral pharynx wall, caudal to the last branchial cleft and on a level with the anterior part of the heart. Although the body may, primarily, arise symmetrically on the two sides, only the one on the left continues to develop. The right body rapidly atrophies and completely disappears. The left body later in its development separates from the pharynx, divides into many small follicles and remains buried in connective tissue between the walls of the pharynx and pericardium.

In amphibians (Rana and Bufo) the bodies arise symmetrically on the two sides of the pharynx caudal to the branchial clefts and about on the level with the anlage of the trachea. Here the bodies always separate completely from the pharynx and form small isolated cysts composed of rather elongated yolk laden cells with a relatively small central cavity. Later the central cavity disappears, the surrounding connective tissue invades the organ dividing it into two or three small lobules. In the adult these bodies ascend along the neck and come to lie so

near the thyreoid that they are considered, by De Meuron, as accessory thyreoids.

In Lacerta embryos of about 6-8 mm. in length there arises behind the fourth gill pouch on either side a ventral diverticulum of the pharynx wall. The diverticulum on the right side atrophies very early, while that on the left side persists and develops rapidly. De Meuron calls this singular body the accessory thyreoid. In consideration of its place and mode of origin he believes it is homologous with the suprapericardial body of selachians and amphibians. In embryos of about 9 mm. the diverticulum separates from the pharynx and forms a large thin-walled cyst. In its later development it forms a mass of closely packed follicles about 1 mm. in diameter. It descends to the left side of the base of the heart and becomes attached to the trachea and large vessels by dense connective tissue.

In birds and mammals De Meuron describes symmetrical diverticula arising from the ventral extremity of the 4th pair of gill pouches. He considers these as homologous to

the accessory thyreoids of reptiles and the suprapericardial body of selachians and amphibians. These accessory thyreoids are evidently the same structures which Born described as the lateral (paired) thyreoids; and which Stieda considered as the sole anlage of the thyreoid.

In the higher vertebrates, according to De Meuron, the fourth pouch gives origin to three derivitives - a dorsal, which is the anlage of the carotid body (Stieda); a ventral, the anlage of the accessory thyreoid; and a middle, the anlage of the fourth thymus component.

The accessory thyreoids in the chick approach the primitive (median) thyreoid and become surrounded by follicles of thyreoid tissue. They remain as distinct bodies lying in the posterior portion of the thyreoid. In human embryos and embryos of the sheep the accessory thyreoids become completely fused with the thyreoid proper and cannot be differentiated from it histologically. De Meuron believes that these two structures - the thyreoid proper and the accessory thyreoids - separate in the beginning because of the long respiratory intestine, approach one another slowly, as the pharynx becomes shortened owing to the

atrophy and disappearance of branchial pouches, as we ascend the scale in the vertebrate series. The pouch which gives origin to the suprapericardial body or the accessory thyreoids, is to be considered always as the seventh in its position, regardless of its numerical order in a given species. The intermediate pouches, he believes, degenerate in the course of vertebrate development without leaving behind any vestiges. This conception is not supported by Van Bemmelen in his later paper ('89).

Maurer ('87) working on the Amphibia describes the suprapericardial bodies and calls them postbranchial bodies because of their position behind the last branchial pouch. In Anuria they arise symmetrically from the ventral pharynx wall behind the fifth branchial pouches, about on the level with the opening of the larynx. In embryos of Rana esculenta of about 7 mm. in length they form as rounded hollow evaginations of the pharyngeal epithelium. The cells forming the anlagen contain brown pigment granules and are more cylindrical than those of the pharynx wall with which they are continuous. In 8 mm. embryos the bodies have become

separated from the pharynx and form either a single large follicle or a complex of from four to six small ones. They have a small lumen surrounded by two or three layers of rather large cells. The pigment granules (yolk?) have disappeared and occasionally the cells may bear cilia. The follicles never develop colloid but almost always in some phase of their development contain a serous secretion. Throughout the larval period the bodies lie medial and dorsal from the cartilage of the fourth arch, under cover of the pharyngeal mucous membrane. In the adult the bodies lie dorsal from the hyoid bone on either side of the opening of the larynx.

In Urodels the postbranchial body develops only on the left side. It arises as a solid epithelial bud which early acquires a small central lumen. This strand separates from the pharynx and becomes placed obliquely to the long axis of the pharynx. In some cases it buds off a few smaller epithelial masses. The lumen become larger but colloid does not appear in it. There is no indication of the formation of a postbranchial body on the right side. In the

adult Triton and Salamander the left postbranchial body has about the same position as in the Anuria. Maurer did not find the postbranchial bodies in teleosts.

According to Maurer's description, the postbranchial bodies in amphibians in no way resemble the thyreoid and cannot be called accessory thyreoids. They do not unite with the median thyreoid as is described by De Meuron, but always remain near the place of their origin in the region of the fourth arch. They occasionally show a serous secretion but never develop colloid. Maurer believes that De Meuron described correctly the origin of the postbranchial bodies, but that he has confused their later development with the epithelial derivitives of the pouches which come to lie near the thyreoid. He agrees with De Meuron, however, that the postbranchial bodies in Anuria are homologous with the suprapericardial bodies of selachians. He leaves entirely undecided the question of the homology of the postbranchial bodies and the derivitives of the fourth pouches in Birds and Mammals. The unilateral development of the body in Urodels, and its rather

marked variation in structure from that found in Anuria suggests to Maurer that possibly in Urodels the post-branchial body represents a remnant of the Ductus oesophago-cutaneous of Bdellostoma.

Platt ('96) working on Necturus, described the supra-pericardial bodies as arising from the ventral pharynx wall between the fourth and fifth branchial clefts on either side. They appear in embryos of about 15 mm. in length as small vesicles connected to the pharyngeal epithelium by small stems. In a 46 mm. embryo they are composed of several small vesicles embedded in the connective tissue of the pharyngo-pericardial wall. They retain their primitive position and show no fusion with the thyreoid. The view of Van Bemmelen--that the bodies are to be regarded as rudiments of a posterior pair of gill clefts--is not supported in Necturus. The position of the bodies here opposes also the conception of Maurer that these structures are postbranchial. As to the probable significance of these structures Miss Platt says: "It therefore seems not impossible that we have in the thyreoid and suprapericardial

bodies modifications of organs belonging primarily to the pronephritic system".

In the tunicates Giard (898) considers the epicardial tube homologous with the postbranchial body, an homology of the same nature as that of the endostyle to the median thyreoid.

Greil ('05) working chiefly on Anuria describes the suprapericardial (postbranchial) bodies and calls them ultimobranchial bodies. By reconstructions of the branchial region of the foregut he found that the anlage of the sixth pouch appears on either side as a shallow outpouching of the lateral pharynx wall caudal and slightly medial to the fifth pouch. The thickened epithelium of the ventral portion of this rudimentary sixth pouch develops into the ultimobranchial body. The bodies develop symmetrically on the two sides. The dorsal and medial segments of the sixth pouch forms a cord of cells which runs caudalwards and unites with the gut. In embryos of 8.4 mm. of Hyla the ultimobranchial body lies between the sixth aortic arch and the musculus dilator laryngis. It is completely

separated from the pharynx and contains a central lumen.

Greil opposes the view of Maurer and De Meuron that the suprapericardial body in Anuria develops as an out-pouching of the pharynx wall. On the contrary he describes it as a solid thickening of the epithelium which develops a central lumen after its separation from the pharynx. He says that Maurer, overlooking the remaining segments of the sixth pouch, described the fifth pouch as the last, and considered the derivitives of the rudimentary sixth pouch as postbranchial structures. He thinks that De Meuron has described the body in a fairly advanced stage of development --after the formation of a central lumen--and has mistaken this for its earliest anlage. Greil was unable to find the suprapericardial bodies in five specimens of Bombinator studied by him. The absence of the body in this form is of interest by the fact that in this species the sixth pouches appear in the same situation as the suprapericardial bodies do in the other species.

In selachians, Greil found the ultimobranchial body only on the left side. In Acanthias he describes the an-

lagen of the seventh pouches arising caudal and medial to the sixth pouches. These rudimentary pouches are short and shallow and are more widely separated than the preceding pouches because of the wide expansion of the underlying heart. The appearance of the seventh pouches is delayed by an elevation of the pharynx wall in the region of the sixth pouches. On the medial side of this elevation the ventral extremity of the seventh pouch on the left side develops into the ultimobranchial body.

Greil agrees with Van Bemmelen that the ultimobranchial (suprapericardial) bodies represent rudimentary seventh pouches, especially their ventral extremities. He thinks that in Chimaera--in which the suprapericardial bodies are formed behind the sixth pouches (which degenerate without leaving behind any derivitives)--it is very probable that the loss of the sixth pouch is to be considered as a unique case, and a phenomenon to which the suprapericardial body has not yet adapted itself, as it has, for example, in the Amphibians. In this latter form the formation of the suprapericardial body is assumed by the sixth pouch. In the higher forms in which the reduc-

tion of the gill apparatus is more advanced and in which there are only four pouches, the suprapericardial body is formed from the last pouch.

Vialleton ('08) in his work on the visceral arches in vertebrates describes briefly the suprapericardial bodies in Torpedo. In large embryos of this form (70 mm. in length) they consist of a short excretory canal closely surrounded by a few glandular acini. The entire gland is small and lies very close to the pharynx wall to which it is attached by its excretory duct. There is no evidence of secretion in the gland at this stage.

III. Topography and Morphology.

The suprapericardial body or gland in Acanthias first appears in embryos of about 20 mm. in length. Although it is usually present later on both sides of the pharynx, its early development is always limited to the left side. The gland on the right side does not make its appearance until about the 33 mm. stage. The anlage of the gland appears as a simple evagination or outpouching of the epithelium of the ventral pharynx wall medial and slightly caudal to the ventral extremity of the sixth gill pouch (Fig.2).

Figure 1 is from a wax reconstruction of the pharynx of an embryo 20.6 mm. in length (H.E.C.1494), showing the position of the gland at the time of its appearance. This embryo is No.28a of Scammon's Normentafeln and corresponds approximately with Balfour's stage N. The pharynx is rather flat and arches dorso-ventrally. Its cranial extremity is broad and relatively thick but rapidly tapers caudally into the thin and narrow oesophagus. The mouth is diamond shaped, slightly elongated from side to side and opens widely at right angles to the long axis of the pharynx. The gill pouches are all developed. They take a

rather wide origin from the lateral margins of the pharynx, and project outward at almost right angles. Their dorsal extremities are bent slightly caudalward and are much more pronounced than the ventral ones which are small, narrow and crowded close to the wall of the pharynx. All of the pouches with the exception of the first are open along their ventral and lateral margins. The first pair of pouches are open along their dorsal and lateral margins, their ventral extremities being short, thin, and closed. Rathke's pouch is a roughly triangular sac projecting upward and slightly forward and is widely open to dorso-cranial region of the pharynx. The thyreoid is represented by a median single elongated mass at about the level of the second pair of gill pouches. It is in close proximity to the ventral wall of the pharynx from which it has but recently lost its connection. The anlagen of the thymus have not yet made their appearance.

The suprapericardial body at this stage is found only on the left side. It arises from the pharynx wall slightly caudal to the origin of the ventral extremity of the

sixth left gill pouch. It is located slightly medial to a continuation of the line joining the origin of the ventral extremities of the pouches. The epithelium forming the gland is slightly thickened and evaginated into the mesenchyma to about half the distance to the pericardium which surrounds the atrium. (Fig.2).

In slightly older embryos (24.7 mm. H.E.C.1492) the suprapericardial body has about the same relative position as in the specimen just described. At this stage also the body is found only on the left side. The small plate of epithelium has become converted into a digitiform tubule which reaches almost to the pericardium. The tubule is slightly constricted at the point of its connection with the pharyngeal epithelium. It contains a very small lumen which communicates directly with the cavity of the pharynx.

Figure 3 is from a wax reconstruction of the left suprapericardial body of an embryo 28 mm. in length (H.E.C. 1357, stage 30 of Scammon's Normentafeln). It will be seen that the digitiform tubule of the preceding stages has become converted into a single cyst with a connecting stalk.

The connecting stalk has a rather broad attachment to the cyst but is constricted at its connection with the pharynx wall. It contains a narrow lumen which communicates above with the pharynx and below with the saccular cavity of the cyst. The stalk is attached to the caudal portion of the cyst giving the gland a cranialward directed development which later becomes more marked.

The earliest appearance of the suprapericardial body on the right side is found in embryos of about 33 mm. in length (S.C.8 and H.E.C.186). It has about the same corresponding position as the body on the left side. The relation of the glands to the pharynx and its derivitives at this stage is well shown in figure 4 which is a reproduction of a wax reconstruction of the pharynx of an embryo 33.1 mm. in length (S.C.8). The arching of the pharynx present in the younger embryos (fig.1) has almost entirely disappeared. The mouth is more oval in outline and opens into the pharynx at right angles to its posterior wall. The cavity of the pharynx has become somewhat narrowed in its dorso-ventral diameter because of the

rather rapid growth of the underlying heart. The gill pouches have a rather broad attachment to the lateral regions of the pharynx. The first pair of pouches turns sharply upward and forward at almost right angles to dorsal pharynx wall. They are open narrowly along their lateral margins. Each of the succeeding pair of pouches, the second to sixth inclusive, take origin from the pharynx a little more lateral than the pair preceding. This condition is more apparent than real, due to the fact that the ventral extremities of the more caudal pouches are pushed forward and outward by the growth of the heart. The expanded distal portions of the pouches are arched caudally so as to imbricate the succeeding pouches.

The hypophysis forms a flattened triangular mass placed just in front of the roof of the mouth near its connection with the pharynx. It is still connected with the mouth by a small hollow stalk. Its dorsal portion is expanded and divided into a median and two lateral saculations. The thyreoid is a shield-shaped mass of tissue located in the median line about on a level with the origin of the second

pouches. Remnants of its early connection with the pharynx wall is found in a thin broad pouch just below the mouth. The thymus is represented by knob shaped epithelial thickenings on the dorsal extremities of the last five pair of pouches.

The suprapericardial bodies are medial and slightly caudal to the ventral extremities of the sixth gill pouches. They have assumed a position somewhat more medial than in the younger embryos lying about half way between the sixth pouch and the median line. This slight change in position of the gland is probably due to the rapid growth of the caudal portion of the pharynx in its long axis. The right suprapericardial body is much smaller and more rudimentary than the left. It consists of two slender villous like cords of epithelium connected to the pharyngeal epithelium. They are both of about equal length but the more lateral one is broader and turns slightly forward at its ventral extremity. There is no lumen present in either of the cords. Van Bemmelen describes a similar condition in Acanthias where he found the gland consisting of three

small ducts opening into the pharynx.

The left suprapericardial body in the 33.1 mm. embryo (S.C.8) is roughly triangular in shape. The connecting stalk is attached to the caudal and lateral portion of the ventral mass giving the gland a direction of growth which is distinctly medial and forward. The lumen of the stalk communicates with that of the cyst and with the pharynx. The attachment of the gland to the pharyngeal epithelium is very much constricted. It is indicated by a small depression in the wall of the pharynx.

From the 33 to the 37 mm. stage the suprapericardial body shows great advance in development. In the series of five embryos (S.C.25; S.C.10; S.C.9; H.E.C.186 and H.E.C. 363) studied in this stage the body was found only on the left side. It has about the same position as in the preceding embryo. The form of the gland in embryos of this stage is shown in figure 5. This figure is from a wax reconstruction of the left gland of a 37 mm. embryo (H.E.C. 363). The ventral portion of the gland consists of an elongated thin walled cyst running parallel to the long

axis of the pharynx. It is constricted at about its middle and terminates posteriorly in two rounded knobs. A small bud is found arising on its medial surface. The connecting stalk is long and angular and is attached to the lateral and caudal portion of the ventral cyst. A small bud arising from the stalk is directed cranialward. The lumen of the connecting stalk is small and irregular and does not communicate with pharyngeal cavity nor with the cavity of the cyst. As is shown from the above description two important features appear in the development of the gland at this stage (36-37mm.). They are first, the beginning formation of new tubules by budding and secondly, a disappearance of the earlier communication found between the distal portion of the gland and the pharynx.

At 47.3 mm. (S.C.11 and others) the suprapericardial body is again found bilaterally. The right gland is very small and situated at about the level of the cranial extremity of the left gland (fig.6). The caudal portion of the pharynx at this stage has become arched from side to side because of the dorsal bulging of the heart. This

change in the contour of the pharynx wall has caused the suprapericardial body to assume an oblique position, being directed medially and ventrally from its attachment to the pharynx. Immediately below the sixth pouches the pharynx becomes abruptly constricted transversely to form the oesophagus. The ventral epithelial wall of the oesophagus is thrown into large longitudinally directed folds some of which apparently anastomose. The dorsal wall of the oesophagus is rather flat and smooth except for a large longitudinal fold on either side.

The right suprapericardial body in the 47.3 mm. embryo (S.C.11) is shown in figure 7. It consists of a single distal cyst attached to the pharyngeal wall by a solid connecting stalk. Its external form is very similar to that found in the left gland in the 28 mm. embryo (fig.3). The form of the left suprapericardial body is well shown by figure 8. At this stage of development, the gland has become divided into three distinct parts. The proximal part (A) consists of a single tubule broadly attached to the pharyngeal epithelium. It contains a small lumen which

communicates with the pharyngeal cavity. The medial portion of the gland (B) consists of a longitudinally directed tubule which bifurcates at its cranial extremity. Its upper surface is in contact with the proximal tubule but does not fuse with it. Its lower surface is in contact with one of the tubules of the distal portion of the gland. Their epithelium is shown fused in only one section of 12 u. The distal portion of the gland is formed of a large tubule (C) and a broad ventral cyst (D). These two masses are united at their caudal extremities and have a common cavity. Both C and D give rise to small tubules and epithelial buds. By comparing figures 5 and 7 it will be seen that the early connecting stalk has in the older embryo become broken up into segments which correspond to A, B and C. The ventral cyst has steadily increased in size and now gives rise to a few small tubules. It still retains its connection with the stalk element (C). In a slightly older embryo 50 mm. long (H.E.C.444) these changes have become somewhat more marked. The growth of the gland has been chiefly in its cranio-caudal axis. The ventral

cyst has become very much elongated. The stalk element is represented by many small tubule and buds, one of the most proximal of which unites with the pharyngeal epithelium.

At 60 mm. (H.E.C.427) the position of the gland is shown in figure 9. It is attached to the wall of the pharynx by a rather long tubule and also by a small cord of epithelial cells situated just above the tubule. It has about the same general form as in the 50 mm. embryo but has many more new formed tubules. Some of these tubules are completely isolated and lie free in the mesenchyma of the pharyngeo-pericardial wall.

The oblique position of the gland and its shifting to a more medial position which were first noticed in the 47.3 mm. embryo have become more pronounced at 95 mm. (H.E.C. 1882). These features are shown in figure 10 which is a reproduction of a wax model of the caudal portion of the pharynx at this stage. A rather sharp ventral outpouching of the wall of the pharynx is found just lateral to the suprapericardial body on either side. It begins just above the attachment of the gland and runs obliquely outward and backward parallel to the ventral diverticulum of the sixth

pouch. On the dorsal wall of the pharynx and forming its caudal extremity on either side of the oesophagus are found two outpouchings very similar to those described above. These outpouchings, both dorsal and ventral, were first found in an embryo 80 mm. in length (S.C.60), They are parallel to the corresponding extremity of the sixth pouch and are located exactly in the place where one would expect the anlage of the seventh pouch to appear. Immediately below the suprapericardial bodies the epithelial wall of the pharynx and oesophagus is thrown into longitudinal folds similar to those in the 47.3 mm. embryo but much more pronounced.

The suprapericardial bodies are attached to the medial wall of the ventral outpouchings of the pharynx. The right gland is very small and placed about on a level with the base of the left one. It has the form of a single cyst which is partly embedded in the pharyngeal epithelium. Its lumen does not communicate with the cavity of the pharynx (fig.11). The left gland is shown in figures 11 and 12. It is connected to the pharyngeal epithelium by three

small tubules. The connecting stalk has developed into a branching mass of tubules a few of which apparently anastomose. The distal portion of the gland forms an elongated obliquely placed cyst which is directed cranialwards. It gives rise to a few secondary tubules along its margins and dorsal surface. It is fused with some of the tubules above but has an independent lumen.

In embryos of the 'pup' stage 20 to 22 cm. in length and in the newborn and adult the gland is easily found by dissection under the binocular microscope. Although many specimens were examined, particularly of the 'pups', the right gland was never found in these older stages. Upon removing the dorsal pharynx wall the position of the left gland is indicated by a small pit in the floor of the pharynx just lateral to the cardiobranchial (basibranchial) cartilage. Figure 13 is a cleared dissection of the head of a 'pup' 21 cm. long showing the gland in situ. The ventral muscles, heart and a portion of the pectoral girdle have been removed as well as the dorsal musculature of the head and dorsal wall of the pharynx. The body or main

portion of the gland lies between the cardiobranchial cartilage and the fifth arch of the left side. It is partly covered over at its base by the ceretobranchial cartilage and the caudal portion of the coracobranchial muscle.

The caudal half of this gland was reconstructed and is shown in figure 14. The proximal part of the connecting stalk is broadly attached to the pharyngeal epithelium and has in its center a rather deep blind pit. Its distal portion is solid and fuses with some of the adjacent tubules. When compared to the gland in the 95 mm. embryo it is found that the entire gland has advanced quite rapidly in growth. The large ventral mass of tubules and cysts has become relatively farther removed from the pharyngeal epithelium. The connecting stalk is single and much longer, and appears to be a direct outpouching or diverticulum from the epithelial wall of the pharynx. The distal portion of the gland, especially in its cranial half, is formed of a very large dilated cyst, which becomes broken up in its caudal portion into several smaller cysts and tubules. The large mass of tubules between the connecting stalk and the ventral cyst

is very irregular and complicated. Some of the tubules are completely isolated. Many of them are fused over a small area of their walls, but contain independent lumina. Apparently true anastomoses are found in a few places.

The whole gland at this stage appears to be the result of repeated budding and branching of the tubules in the earlier stages. The greatest proliferation has occurred in the caudal half of the gland between the connecting stalk and the large tubules which represent the termination of the distal cyst.

In a newborn 27 cm. in length the gland was found only on the left side. It is very similar in structure to that described in the 'pup' stage. Many of the tubules have become dilated into large follicles which communicate with each other and with the smaller tubules. The cranial portion of the gland at this stage has also developed into numerous small branching tubules and isolated follicles. Two large diverticula of the pharyngeal epithelium are present. They are quite some distance apart, one being in the caudal and the other in the cranial portion of the

gland. The most caudal one fuses with the wall of one of the follicles in the proximal portion of the gland. It contains in its central portion a small cavity filled with mucus but which does not communicate with any of the underlying follicles nor with the cavity of the pharynx. The diverticulum in the cranial portion of the gland is short and solid and does not fuse with the epithelium of the gland follicles.

The study of the gland in the adult could not be completed because of lack of material. One specimen at my disposal, in a poor state of preservation, showed the gland present only on the left side. It consists of large distended follicles with their wall. Most of the follicles are directly continuous with other follicles by small constricted necks. The follicles are closely packed together, their walls being separated only by small amounts of connective tissue and vascular channels. An elongated diverticulum from the pharyngeal epithelium is present containing a rather long narrow lumen which is directly continuous with the cavity of the pharynx. This diverticulum is fused

with the epithelium of some of the proximal follicles but their lumina are apparently not continuous.

The structure of the gland in the adult and its function will be considered more in detail in a future study when material becomes available.

IV. Histology and Histogenesis.

At the time of its appearance the suprapericardial body is formed of a simple saccular evagination of the pharyngeal epithelium. The pharynx at this time is lined by a simple layer of cells, cubical in shape near the median line which gradually become columnar at the attachment of the sixth gill pouches. The suprapericardial body arises just at the point where this transition becomes most pronounced. (Fig.2). The cells forming the anlage of the gland are decidedly columnar in shape. Their nuclei are located in their basal portions; are elongated oval in outline, and show a definite chromatin reticulum. The bulk of the chromatin is found near the nuclear membrane but a few masses are found scattered throughout the nucleus. The nuclei of the cells forming the medial wall of the outpouching at its union with the pharynx are very much elongated and closely crowded together, due to a slight twisting of the mass toward the median line. A definite basement membrane is present and separates the epithelial cells from the underlying mesenchyma. (Fig.16).

Almost immediately after its formation the saccular outpouching becomes converted into an elongated tubule with an expanded blind extremity. Very shortly this blind distal portion expands forward and medial from its attachment. The nuclei of the cells at the connection of this expanded cyst with the stalk are very much elongated and deeply stained. This condition is probably due, in the preceding stage, to the crowding together of the cells at these points of flexure. The nuclei of the cells forming the ventral wall of the cyst are broadly oval and evenly separated.

The gland remains in this condition becoming somewhat larger and more expanded up to about the 36-37 mm. stage. At this time the gland is somewhat variable in its histology. It usually shows a solid connection with the pharynx and its distal portion becomes more or less separated from the connecting stalk. Both the distal cyst and the tortuous connecting stalk show the beginning formation of new tubules. Often the expanded cyst has already become divided up into two or three smaller independent cysts

which also show the formation of new tubules.

Since the further growth of the gland from this time up until about the 'pup' stage consists chiefly of the multiplication or branching of the gland elements, namely the tubules, this process will be taken up in detail. The bulk of the small newly formed tubules is always found between the distal cyst and the epithelial wall of the pharynx, showing that in all probability the power of growth is greatest in the elements which represent the connecting stalk. In this region in any of the embryos from 37 to 210 mm. the process of budding or new tubule formation can easily be studied.

The formation of new tubules and the branching of tubules will be discussed together as both processes, so far as can be determined, are analogous up to a certain stage in their development. At the site of a future tubule or branch a localized poliferation of cells occurs. This is followed by a direct extension into this bud, of the lumen of the parent tubule. The process may end here, resulting in simple branching or the new sprout may become

constricted at its base and later become cut off forming an isolated new cyst. The first step in the process--a thickening in the epithelium of the parent tubule--is very transitory being followed almost immediately by an extension of the lumen into the new cell mass. The new formed cells are usually not numerous and form only a very small bud which still remains surrounded by the membrana propria. Their nuclei are broadly oval or round and closely crowded together. The cytoplasm of the cells is small in amount and stains rather deeply. Cell membranes could not be distinguished. These small buds of cells are quite numerous and are found both on the sides and at the extremities of the tubules.

The extension of the lumen into the cell mass is probably due to a more rapid growth of the wall of the tubule at this point. When once a definite putpouching is established the cells become radially arranged around the cavity. The attachment of the outpouching to the wall of the parent follicle shows a slight constriction into which the surrounding mesenchymal cells are pushing in. The epithelial cells forming the attachment are very elongated

and closely crowded together on one side due to a slight twisting of the outpouching toward that side. A very similar condition it will be recalled was found in the anlage of the gland.

The newly formed outpouching may remain connected and grow en masse with the parent follicle forming a branching tubule, or may become pinched off forming a new cyst. The former condition is most common when the buds arise from the extremities of the parent tubule. It is not unusual to find in these cases three or sometimes four small sprouts arising from the extremity of a single tubule. (Fig.8 c and fig.12). Secondary branching or dichotomous division of tubules does not occur. A newly formed branch does not give rise to a new gland element until it has become pinched off as a cyst.

The process of separation of the tubules is by simple constriction of its connection with the parent tubule. This process can be found in all its stages, especially in the older embryos where the tubules are more numerous. The connection of the new branch, which presumably persists

for some time, becomes gradually larger as the tubule grows. At the outset of constriction the wall of the branch at its connection gradually grows in across the lumen of the junction. Usually this ingrowth occurs on all sides but if the branch is flexed with the tubule it may occur only on one side. The constriction or ingrowth of the wall is always accompanied by the surrounding mesenchymal cells.

The nuclei of the cells of the ingrowing wall have at first a radial position to the lumen. As the constriction proceeds and the tubules become separated except for fusion of their epithelial walls the long axis of the nuclei become placed almost tangentially to the circumfer- ence of the lumen. When the tubule walls become completely separated the axes of the nuclei again rotate through 90° and assume a radial position to the new lumen. The tubules at first are separated only by a membrana propria but later the mesenchyma and large blood channels intervene.

The cells in the wall of the fused tubules are too numerous and the cell walls are too indistinct to follow the change in the cell itself, but in all probability the

rotation of the axis of the nucleus represents a rotation of the entire cell. If this is true this process would be comparable to a reversal of the changes which has been described by Scammon ('15) in the anastomoses of hepatic tubules in selachians.

From the 'pup' stage to the adult the increase in the size of the gland is due chiefly to the transformation of the tubules into large thin wall follicles. They are lined by a single layer of columnar cells which stain rather deeply. Their lumina are distended with a mucus or mucoid secretion which contains a few necrotic cells. The connecting stalk in the adult as well as in the pup and newborn is formed of stratified squamous epithelium and appears to be a direct down growth from the pharyngeal epithelium. Scattered throughout the layers of this stratified epithelium both of the pharynx and the connecting stalk are found many large mucus 'goblet' cells.

The suprapericardial gland receives a few small arterial twigs from the pharyngeal artery which throughout a part of its course lies in very close proximity to it. This artery develops relatively late in the embryo but in the 95 mm. embryo (H.E.C.1882) it is a good sized vessel lying in the pharyngeo-pericardial wall just lateral to cardio-branchial cartilage on either side. (Fig.11). Throughout its early development the gland is supplied by a small number of rather large capillaries which tend to encircle the mass of gland tubules. Later in the develop- particularly in embryos of the 'pup' stage and in the new- born where the number of the tubules is very great these capillaries increase in number and become enlarged to form sinus like channels which in many places completely sur- round the individual tubules. (Fig.17). In the caudal portion of the gland the endothelium of the blood channels is not infrequently found to lie in direct contact with the epithelium of the gland tubules. In some cases they are separated only by a small layer of mesenchymal cells. In the cranial portion of the gland the tubules or follicles

are often found surrounded on one side by mesenchyma while on the other side the cells of the tubule come in contact with vascular endothelium. These large capillaries or sinusoids communicate laterally with venous channels located both above and below the fifth branchial arch which empty into the linguo-facial vein (of Lewis '09).

The condition of the circulation in the adult could not be determined but apparently the follicles are surrounded by more connective tissue than would justify the assumption that the gland has a sinusoidal circulation. It is not improbable however, that a portion of the gland at least, in its intermediate stage of development has a true sinusoidal circulation. These sinusoids are formed not as the result of interoresepents of the tubules into a large vein but as a direct extension of venous channels around the tubule.

Small ganglia associated with the pharyngeal artery and the linguo-facial vein send nerve filaments to the tubules.

A plexus of lymphatics is not present. A few vessels are found among the tubules but none of them showed evidence of absorption of the secretion.

V. Discussion.

The original conception of Van Bemmelen ('85) that the suprapericardial body in selachians represents a rudimentary branchial pouch is probably correct. This conception is shared also by Greil ('05) who describes in selachians a true anlage of a seventh pouch. Although several specimens were examined by me, I have not been able to find the early anlage of the seventh pouch as described by Greil. In the embryos of much older stages, 80-95 mm. in length (S.C.60 and H.E.C.1882), there is present a distinct outpouching of the pharynx wall both dorsal and ventral on either side, and exactly in the place where one would expect a seventh pair of pouches to arise. (Fig.10). The suprapericardial body arises from the medial wall of the ventral outpouching. In the younger stages, particularly at the time of appearance of the gland or shortly before, no such outpouchings are to be found. In one embryo of 28 mm. (S.C.6) the left suprapericardial body has the form of a single diverticulum which extends ventrally as far as the pericardium. It is widely open to

the cavity of the pharynx and is lined by a single layer of tall columnar cells very similar to those of the gill pouches. This gland resembles very closely in its appearance a developing pouch. There is no corresponding structure on the right side or no indication of a dorsal outpouching above it. From the position of the gland, which is medial and slightly caudal to the sixth pouch, and from its mode of development as an elongated diverticulum from the pharynx resembling (very strikingly in one embryo (S.C.6) a developing pouch, I believe we are justified in assuming that in acanthias the suprapericardial body represents the ventral extremity of a rudimentary seventh gill pouch. In many of the specimens which I examined the gland in its early stages had the appearance of a rudimentary pouch which had become stunted in its progress of growth by abutting against the underlying pericardial wall.

The failure of the gland to appear on the right side in many of the specimens is difficult to explain. From the number of specimens at my disposal it appears to be

the rule rather than the exception that the right body fails to appear. Van Bemmelen ('85) found that often in Acanthias, Pristuris and Galeus the body appears only on the left side. He figures a dissection of the 'pup' stage showing the openings of the gland on either side of the cordis-branchial cartilage. Although numerous specimens of the 'pup' stage were examined by me I found the gland only on the left side. (Fig.13). All of these specimens however were not sectioned and it may have been possible that in some cases the right gland was present but too small to be seen with the binocular microscope. De Meuron ('86) says that in Acanthias the body may, primarily, arise symmetrically on the two sides but that the right gland rapidly atrophies and disappears. Greil ('05) in his work on selachians found the body present only on the left side. From these observations and from the fact that the right gland when present appears relatively late (33mm. or later) and is always represented as a single small cyst it is very probable that it entirely degenerates in the course of development.

If the mode of development of the suprapericardial body be carefully analyzed it will be found that it differs both from the ordinary type of branching gland (tubulo-alveolar) and the typical closed follicular ductless gland. The ordinary type of gland in selachians develops as a direct outpouching of the epithelium. This outpouching may be preceded by a thickening of the epithelium to form a gland bud as has been described in the gastric glands by Peterson ('08), but often this does not occur. (Pancreas[1], Liver, Scammon ('15); Digitiform gland, Hoskins ('15).) The blind extremity of this outpouching gives rise to the tubular or saccular end pieces while its proximal portion forms the excretory channel. The end pieces may become secondary removed from the main excretory duct, but they always remain in communication with it (Fig.16,A). The ductless glands, typical examples of which Laguesse ('10) has described as glands with closed follicles, develop as an outpouching of the epithelium which almost immediately becomes

(1) Scammon, unpublished manuscript.

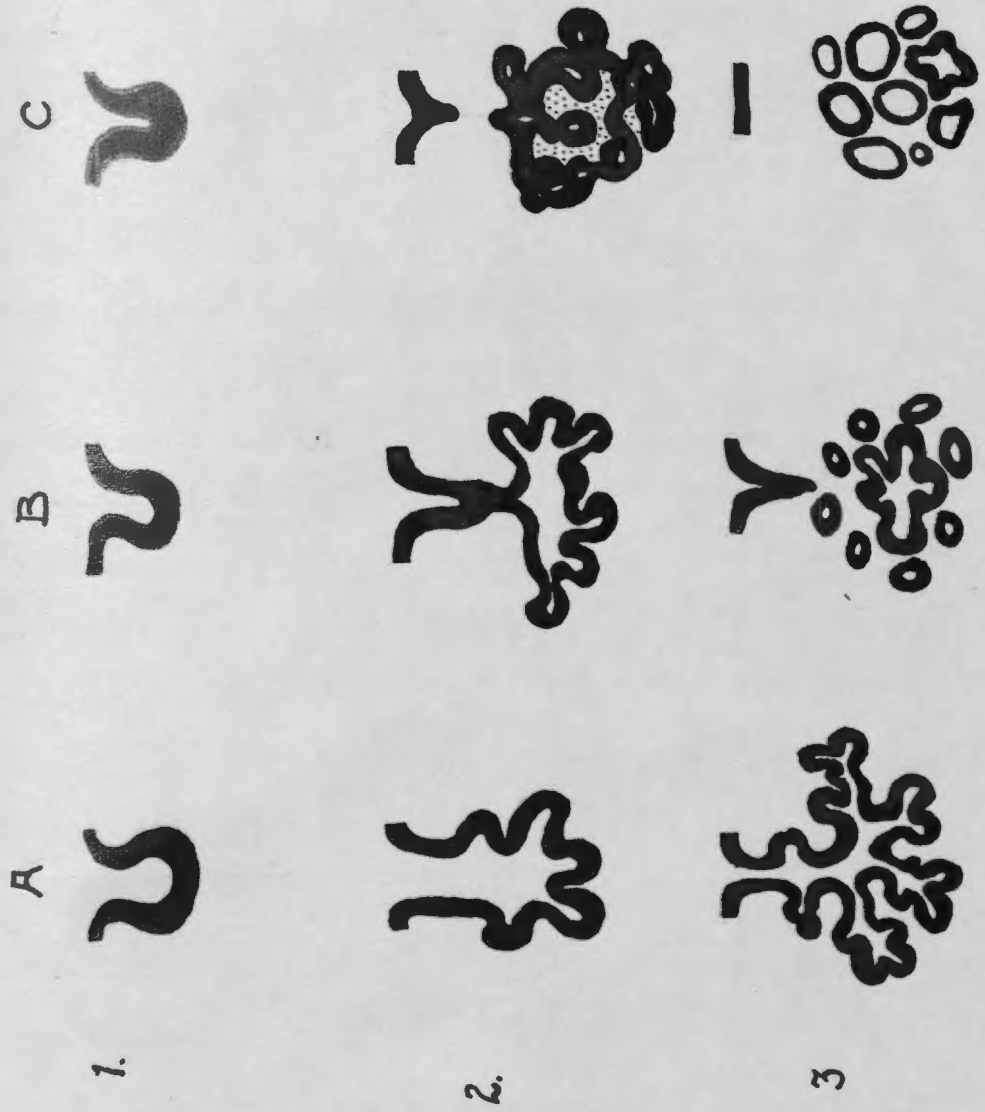

Figure 15.

A diagram showing three corresponding stages in the development of (A) a typical branching gland in selachians, (B) the suprapericardial body, and (C) a closed follicular gland (the thyreoid).

solid. This solid anlage becomes broken up into solid cell cords which acquire lumina and develop into follicles the most of which are completely closed cysts. (Thyreoid) (Fig.15,c). The connecting stalk or excretory canal completely disappears early in the development. The closed follicular type of gland usually develops a sinusoidal circulation but does not always retain it (Thyreoid). The suprapericardial body in its development and structure is intermediate in type between the ordinary gland and the ductless gland. It arises as an evagination of the epithelium which remains cystic especially in its distal portion. The proximal portion of the connecting stalk remains connected with the epithelium and becomes solid. The distal portion of the connecting stalk develops rapidly into branching tubules, many of which become cut off as separate cysts or closed follicles. The blind extremity of the original outpouching becomes transformed into a large isolated cyst. Later in the development these cysts and branching tubules become expanded into large distended follicles many of which communicate. (Fig.15,B).

The circulation of the gland also is intermediate in type. Although primarily capillary in form, later in the development of the gland the vascular channels become expanded and their endothelium comes to lie in immediate contact with the epithelium of the tubules.

Since this paper is devoted solely to a study of the gland in one form the question of the homology of the suprapericardial body with similar glands in other forms will be discussed only briefly. De Meuron ('86) describes small epithelial bodies arising behind the last gill pouch in amphibians, reptiles, birds and mammals which he calls accessory thyreoids and which he considers as homologs of the suprapericardial body of selachians. From De Meuron's description, as Maurer ('87) has already pointed out, it is very probable that De Meuron has confused the postbranchial body with the epithelial derivitives (epithelial bodies III and IV) of the gill pouches. Maurer ('87) describes in Amphibia a derivitive of the pharynx posterior to the last gill pouch which he calls the postbranchial body and considers this as the homo-

logue of the suprapericardial body. Greil ('05) working on Amphibia found that the postbranchial body of Maurer developed from the ventral extremity of a rudimentary sixth pouch and believes for this reason as also in selachians that the body is ultimobranchial. In the higher vertebrates an homology with the suprapericardial body is difficult to make because of the rudimentary development of the pharyngeal pouches. In his later communication Van Bemmelen believes that the Body "Y" of Mall ('88) in birds and the "lateral thyreoids" of Born ('83) and His ('80) are homologous to the suprapericardial body. Later writers, Rabl ('07) (Birds), Grosser ('10) (Man), and particularly Verdun ('98) (Mammals) describes a diverticulum arising from the pharynx near the connection of the fourth pouch. This body unites with the thyreoid and forms a small cyst which in some forms contains colloid. (Hermann and Verdun ('99).) Recent investigations in thyreoids which have become atrophic (Getzowa ('11) shows that the ultimobranchial body does not form thyreoid tissue but remains cystic or entirely degenerates.

VI. Summary.

1. The suprapericardial gland in Acanthias appears in embryos of about 20 mm. in length. Its early development is always limited to the left gland. The right gland is inconstant in its development and does not appear until about the 33 mm. stage.

2. The right gland has the form of a single cyst or solid cord of cells and probably degenerates entirely in the course of development.

3. The left gland, arises as an outpouching of the ventral pharynx wall, medial and slightly caudal to the sixth pouch. In its position and mode of development it corresponds to the ventral extremity of a rudimentary seventh pouch.

4. In its later development the gland consists of a solid connecting stalk and a mass of branching tubules and isolated cysts.

5. In its development and structure the suprapericardial body represents a type of gland intermediate in character between the ordinary branching gland and the

typical closed follicular gland.

6. The blood supply of the gland is from twigs derived from the pharyngeal artery. The circulation although primarily of a capillary type, later becomes both capillary and sinusoidal. The venous channels drain into the linguo-facial vein (of Lewis).

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Description of Figures.

List of abbreviations.

Ao., Aorta

At., Atrium

Cb.c., Cardiobranchial Cartilage (Basibranchial)

C.C., Ceretobranchial Cartilage

D.O., Dorsal Outpouching

H.S., Hypophesial Stalk

L.S.B., Left Suprapericardial Body

M., Mouth

M.Cb., Musculus coracobranchialis

Nch., Notocord

Oes., Oesophagus

P.C., Pericardial Cavity

P.G., Pectoral Girdle

Ph., Pharynx

R.P., Rathke's Pouch

R.S.B., Right Suprapericardial Body

S.B., Suprapericardial Body

S.Nch., Subnotocordal Rod

Som., Somite

Sp.C., Spinal Cord

T., Thyreoid

Th., Thymus

V.B.W., Ventral Body Wall

V.O., Ventral Outpouching

Vt., Ventricle

I to VI, First to sixth gill pouches.

Figure 1.

Ventral view of reconstruction of the pharynx of an Acanthias embryo 20.6 mm. long (H.E.C.1490) X 35.

Figure 2.

Cross section through the pharynx of an embryo 20.6 mm. long (H.E.C.1490) at the level of the suprapericardial body.

Figure 3.

Lateral view of a reconstruction of the suprapericardial body of an embryo 28 mm. long (H.E.C.1357). X 250.

Figure 4.

Ventral view of a reconstruction of the pharynx of an embryo 33.1 mm. long (S.C.8). X 35.

Figure 5.

Reconstruction of the left suprapericardial body of an embryo 37.0 mm. long (H.E.C.363). X 250.

Figure 6.

Ventral view of a reconstruction of the posterior part of the pharynx of an embryo 47.3 mm. long (S.C.8) X 35.

Figure 7.

Reconstruction of the right suprapericardial body of an embryo 47.3 mm. long (S.C.11). X 250.

Figure 8.

Reconstruction of the left suprapericardial body of an embryo 47.3 mm. long (S.C.11). X 250.

Figure 9.

Parasagittal section of the pharynx of an embryo 60 mm. long (H.E.C.427). X 80.

Figure 10.

Ventral view of a reconstruction of the posterior portion of the pharynx of an embryo 95 mm. long (H.E.C. 1882) X 18.

Figure 11.

Transverse section of the pharynx and suprapericardial body of an embryo 95 mm. long (H.E.C.1882) X 80.

Figure 12.

Medial view of a reconstruction of the left suprapericardial body of an embryo 95 mm. long (H.E.C.1882)X250.

Figure 13.

Dissection of the ventral pharyngeal region of an embryo of the pup stage (210 mm. long) showing the supra-pericardial body in situ. X 6.

Figure 14.

Medial view of a portion of the left suprapericardial body of an embryo of the pup stage (210 mm. long). X 250.