PHILOSOPHICAL TRANSACTIONS.

I. *A Contribution to the Anatomy of the Ductless Glands and Lymphatic System of the Angler Fish* (Lophius Piscatorius).

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(*Communicated by Sir* Arthur Keith, *F.R.S.*)

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[Plates 1–3.]

The Angler (*Lophius piscatorius*) is a fish much modified for a bottom habit, and apart from many peculiarities of form and structure associated with this particular mode of life, is remarkable for the looseness of its skin and the abundance of soft connective tissue that separates it from the underlying fascia and muscles.

Within this layer of loose connective tissue lie many of the larger trunks of the lymphatic system, mostly of very considerable size and easy to inject. The fish thus furnishes material better than most for the study of this system.

In a specimen of the Angler presented some eighteen months ago by the Zoological Society to the College of Surgeons for use in the Museum, I was much struck by the prominence of these great subcutaneous lymph channels, and was led by degrees from a preliminary study of their general distribution to the investigation of their relation to the thyroid body and mode of connection with the veins, and incidentally to the observation of certain structural peculiarities of the thymus body and to the presence of a system of minute vessels, which were new to me, intimately associated with certain of the blood-vessels and apparently connected in some way with the general system of lymphatics.

In carrying out this work I have been very much indebted to Dr. Allen, Director of the Marine Biological Association's Laboratory at Plymouth, for providing me with the necessary material in a condition suitable for injection. I wish also to thank especially my chief and friend, Sir Arthur Keith, for giving me, as always, much inspiration and kindly encouragement. My thanks are also due to Dr. H. A. Harris, of University College, and Mr. Redding, of Guy's Hospital, for kindly preparing for me radiographs of barium sulphate injections; to my assistant, Mr. Steward, for much technical help and for the microphotographs that accompany the paper; and to Miss Glasscock for the preparation of numerous microscopic sections.

The subject matter of this paper is to some extent disjointed, and for that reason is best presented in separate sections as follows:—

1. The thymus body and its connection with the pharynx.

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2. The thyroid body and its relation to the ventral superficial system of lymphatics.
3. A system of " fine " vessels (apparently lymphatic in nature) intimately associated with certain of the arteries.

1. The Thymus Body.

The thymus body of Teleostean Fishes was discovered in the year 1850 by Stannius (20). Since that date several papers have been published on it, culminating in an important memoir by Hammar in 1909 (6). This seems to be the last work of importance that has appeared upon the subject.

From Hammar's researches, and from the older work, of which he gives a full summary, it is evident that one of the most striking and characteristic features of the Teleostean thymus is that it retains normally throughout life its original continuity with the epithelium from which it arises. In the majority of the considerable number of species described by him, the organ forms a flat ovate placode of epithelial and lymphoid tissue, situated upon the mesial wall of the gill chamber above the gills, in front of the fold that connects the gill arches with the operculum; and is continuous by its whole outer surface with the epithelium of the wall of the gill chamber, forming an integral part of it.

In some few species (Cyprinus, Gobius, etc., Hammar (6), pp. 13, 14) the deeper parts of the organ project as a plug of thymic tissue into the underlying structures, and the organ is separated more or less late in life from the epithelium overlying it by a thin layer of connective tissue. It will thus be seen that the gland in Bony Fishes is throughout life in a very primitive condition, presenting anatomical features similar to those shown by the same organ in higher Vertebrates at a very early stage of development.

From some of the older anatomical descriptions, and particularly from that of the cod given by Stannius, it would seem that, at any rate in some species, the freedom of the adult thymus from its epithelial matrix is greater than one would gather from Hammar's researches. This most certainly is the case in *Lophius*, where the gland lies free beneath the mucous membrane of the pharynx, separated from it by a considerable layer of loose connective tissue.

The thymus in this genus was originally noticed in a few words by Stannius (20, p. 506). He remarks upon its relatively enormous size and compares the nodulation of its surface with that to be observed in the thymus of the cod. A fuller account is given by Trois (24), in which the position, form, and anatomical relations of the organ are accurately described, as well as some few and imperfect details of its minute structure.

In 1893 Schaffer (17) entered somewhat more fully into the naked-eye appearance and the position of the gland, and gave a more detailed account of its histology. As to the latter, he states that the organ consists of a close intermingling of epithelial and lymphoid

cells, in which the lymphoid cells are distributed in a system of irregular strands, or tracts, amongst islands of epithelial cells. The whole organ is surrounded by a fibrous capsule, from which strong trabecular strands of connective tissue pass into the interior. Within these strands are numerous wall-less spaces. SCHAFFER was unable to detect any structures resembling HASSALL's corpuscles, but noted the presence throughout the organ of great mucous-secreting goblet cells, the secretion of which is discharged into peculiar cavernous spaces. The exact position of these particular spaces is not defined; presumably, they were in some part of the general connective-tissue framework.

So far as the general anatomy of the thymus is concerned, I have little new to add to the descriptions of TROIS and SCHAFFER. Owing to the bottom habit of the fish, and the consequent flattening and expansion of the head region, the branchial cavity is very much extended, and forms, behind the gills, an elongated non-respiratory passage opening to the exterior beneath the root of the pectoral fin. This passage lies mainly upon the ventral surface of the horizontal arm of the clavicle and the pterygiophores of the fin, but its outer part is carried upwards outside the shoulder girdle, so that the mucous membrane that forms its mesial wall invests the outer surface of the clavicle, extending for some distance upon its ascending arm. Between the mucous membrane and the shoulder girdle and its muscles is a layer of loose connective tissue.

The thymus body lies, as stated by TROIS and SCHAFFER, behind the dorsal extremities of the gills, partly deep to and partly above the dorsal reflexion of the mucous membrane of the branchial chamber, just described, in a hollow upon the outer surface of the ascending arm of the clavicle just in front of the lower end of the supra-clavicle. In front it is bounded by the levator clavicularis muscle.

Its position relative to the gills is thus (due allowance being made for the modified form of the pharynx) practically the same as in fishes of more normal build—*i.e.* at the upper extremity of the gill chamber behind the gills and in close proximity to the upper end of the shoulder girdle.

Surrounding the gland is a capacious lymph sinus which passes dorsally into the great cephalic sinus situated beneath the hinder part of the cranium and amongst the levator muscles of the gill arches, and at its ventral end communicates with irregular lymph spaces and channels connected, on the one hand, with the lymphatics of the pectoral fin, and, on the other, with the great pectoral sinus that follows the mesial border of the horizontal arm of the clavicle.

Between the walls of this thymic lymph sinus and the surface of the gland are scattered trabeculæ, which become so numerous towards its outer surface that the cavity of the sinus upon this aspect of the gland is nearly obliterated and is represented only by a system of narrow anastomosing channels. From the lymph sinus offshoots pass into the substance of the thymus in the interlobular connective tissue.

The thymus is supplied with blood by a branch of the subclavian artery, and is drained by a factor of the jugular vein, the main trunks of these thymic vessels being situated respectively upon the deep and outer surfaces of the gland.

The thymus (fig. 1, *thm.**) is most readily exposed by removing the skin from the dorsal surface of the head, together with the thin sheet of the levator opercularis muscle that runs diagonally forward from the side of the cranium across the levator clavicularis to the opercular spine. The upper part of the gland is thus laid bare, lying in its lymph

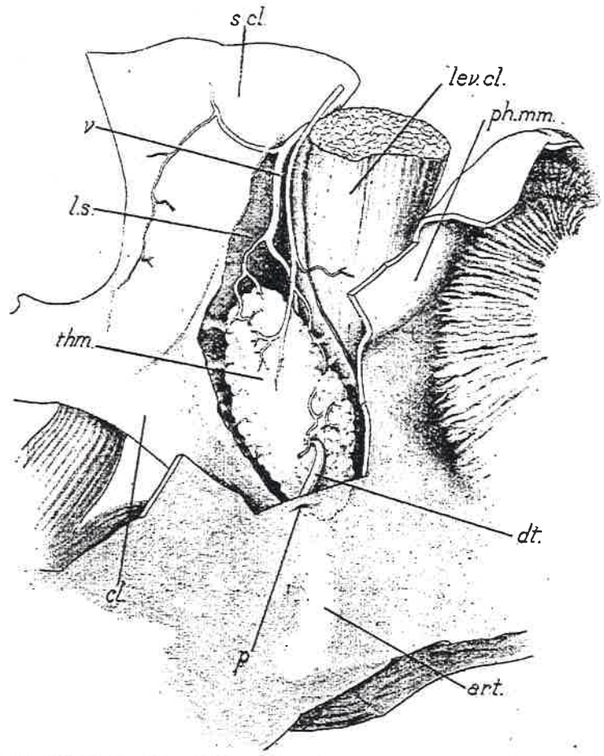


FIG. 1.—Dissection of the right shoulder girdle of *Lophius*, from the upper (morph. outer) aspect. Part of the inner wall of the post-branchial extension of the gill chamber has been cut away to expose the ventral end of the thymus and the "duct" by which it opens into the cavity of the pharynx.

sinus (fig. 1, *l.s.*) between the clavicle and the levator clavicularis, with its lower part covered by the dorsal reflexion of the wall of branchial chamber. This part of the wall of branchial chamber (fig. 1, *ph. mm.*) can easily be turned back from the surface of the gland, but there comes a point at which further reflexion is impeded by a strand of tissue (fig. 1, *dt.*) that emerges from a slight hollow in the face of the gland, and is attached at the other end to the deep surface of the pharyngeal mucous membrane.

A careful examination of the free surface of the mucous membrane opposite this spot, in the region of the claviculo-pterygial joint shows, though often with considerable

* For list of reference-letter abbreviations see p. 54.

difficulty, a small slit-like pore (fig. 1, *p.*). Through this a bristle can be passed up the connecting strand of tissue into the thymus. The strand of tissue is, in fact, a duct-like tube, opening at one end into the branchial cavity and at the other entering the substance of the thymus, and to the naked eye presenting all the characters of the duct of an ordinary ducted gland.

Sections through this "duct" and the parts of the thymus adjacent to it show, however, that the relation of the two is not, strictly speaking, that of a duct to its gland, but that the tube is rather an out-pushing of the wall of the branchial chamber intimately associated at its distal end with the reticulum and reticular spaces of the thymus, but not connected, as the duct of a gland would be, with definite secreting alveoli or tubules.

The tube (Plate 1, fig. 1) is lined by a mucous membrane exactly similar to that of the branchial chamber, consisting of several layers of smallish polygonal cells (Plate 1, fig. 1, *p.c.*) with central lightly staining nuclei. Amongst these cells are a number of large mucous cells (Plate 1, fig. 1, *m.c.*) irregularly arranged. In the deeper parts of the mucous membrane, apparently both in and between the small polygonal cells, are masses of small highly refringent granules (Plate 1, fig. 1, *gr.*). These granules, which form a striking and very characteristic feature of the mucous membrane, stain dark red with Eosin and brilliantly yellow with van Giessen, and seem, so far as one can tell to be similar, except for their smaller size, to the granules described by HAMMAR (6, p. 20) in the thymus and its overlying epithelium in *Esox*. He says: "Bei Esox, aber bei keiner der übrigen untersuchten Arten, habe ich in der Thymus und zwar von allem, wenn auch nicht ausschliesslich, in der Randschicht, homogene Kügelchen angetroffen, die in Homogeneität, Grösse und Färbbarkeit eine gewisse Ähnlichkeit mit den kernlosen roten Blutkörperchen der Säuger darbieten. Sie färben sich mit Hämatoxylin-Eosin rot, mit Malloryfärbung gelb, mit Bendafärbung violett. Sie kommen sowohl intercellulär wie intracellulär vor. . . . Für die Thymus sind sie jedenfalls auch nicht eigenthümlich, denn sie kommen auch im umgebenden Epithel, wenngleich spärlicher, vor."

The granules in *Lophius*, though similar in character and position to those thus described by HAMMAR in the pike, are far smaller than mammalian blood corpuscles.

The tubular extension of the branchial cavity, which is lined, as just described, by a mucous membrane similar in all respects to that of the rest of the pharynx, and is surrounded by a fairly thick layer of connective tissue, passes to the outer surface of the thymus accompanied by blood-vessels and offshoots of the circum-thymic lymph sinus. Near the surface of the thymus the tube enlarges* and becomes enveloped by an increased

* The relations of the extremity of the pharyngeal tube to the thymus seem to be liable to some individual variation. At least, in a second series of sections examined, the tube was constricted rather than dilated at its distal end, and appeared to pass directly into a projecting lobule of the thymus. Unfortunately, in this specimen, the epithelia were not well enough preserved to allow a satisfactory examination to be made of the transition zone between the epithelium of the tube and the reticular tissues of the thymic lobule.

amount of connective tissue continuous with the capsule of the gland. The enlargement (Plate 1, fig. 2, *t.e.*) is very irregular in shape and penetrates the substance of the thymus for some little distance, forming a branching sac from whose deep surface strands of connective tissue riddled with cleft-like spaces pass up into the mass of the gland and become continuous with the trabecular framework connected with the capsule that separates the thymic tissue into lobules and supports it. The sac and its associated connective tissue form, in fact, a sort of hylum, or focus, upon which the interlobular trabeculæ in the neighbourhood converge.

The spaces within this mass of connective tissue appear to be of different kinds: some are continuous with the thymic lobules and with the cavity of the sac-like termination of the pharyngeal tube; others are lined by an endothelium and apparently are lymphatic spaces connected with the circum-thymic lymph sinus; others are blood-vessels.

As the terminal sac of the pharyngeal tube breaks up within this mass of connective tissue, its epithelium opens out, the polygonal cells, growing smaller and stellate, merge into the small stellate cells of the thymic reticulum (Plate 1, fig. 3, *tr.c.*, *r.c.*) and their interspaces become to some extent infiltrated by leucocytes. In the meshes of the network formed by this transformation of the polygonal epithelial cells are masses of the refringent granules mentioned above. Similar, though smaller, masses of these granules can also be observed scattered here and there amongst the reticulum of the thymic lobules throughout a considerable surrounding area. The mucous cells of the epithelium become fewer as the polygonal cells grow less coherent, but can be seen scattered, though sparsely, throughout the reticulum of the thymic lobules. as was observed by HAMMAR (6, p. 27) in the genera that he examined. In other respects also the structure of the thymic tissue agrees with the description given by HAMMAR. The curious large striated cells which he describes (6, p. 24) occur in considerable numbers (Plate 1, fig. 4), and are for the most part grouped around the interlobular trabeculæ. With them are associated large oval or polygonal cells, staining feebly with eosin, aggregated into groups or islands by short connecting dendrites. These cells, though not unlike the large spirally striated cells in shape, size and general appearance, show no striation. They are evidently the same as those described by SCHAFFER (17, p. 341) as forming islands between the strands of leucocytes, and by HAMMAR (6, p. 23), and would seem to be of an epithelioid nature, though distinguishable by their large size from the small stellate cells of the general reticulum. No structures comparable to HASSALL'S corpuscles were seen.

From the description given above it is evident that in *Lophius*—at any rate, in examples of moderate size*—the thymus, unlike that of most Teleosts, has migrated for some distance from its seat of origin, but has maintained its connection with it by means of a tubular diverticulum of the pharyngeal mucous membrane. In this it presents an

* The specimens examined were of the length most usually caught, *i.e.* 2 to 3 feet. According to DAY ('The Fishes of Great Britain,' 1880–84, vol. 1, p. 77) the length may be as much as 7 feet.

interesting condition reminiscent of the adult tonsil or of a developmental stage of the thymus of higher Vertebrates—such a stage, for instance, as that described by Sir ARTHUR KEITH* for the thymus of the human embryo of the sixth week, when he says: "In the sixth week the third pharyngeal pocket has assumed the form . . . where its lower and hinder wall is . . . extended in the form of a flask-like process lined by a thickened epithelium, the embryological basis of the thymus. The neck of the glandular thymic pocket becomes separated from the pharynx in the seventh week and usually disappears, but a strand of tissue frequently persists and represents the stalk of the outgrowth."†

The constitution of the thymus of Teleosteans is of unusual interest, for, as is evident from the descriptions of its intimate structure given by HAMMAR and others, signs of its epithelial origin are more clearly retained in the adult than they are in the thymus of higher Vertebrates. Thus, it is not only possible to trace in the adherent thymus of Teleosts a direct connection between the cells of the pharyngeal mucous membrane and the reticular cells of the underlying thymic tissue, but mucous and other glandular epithelial cells characteristic of the pharyngeal epithelium are scattered irregularly throughout its substance (HAMMAR, 6, pp. 18–31).

These epithelial characteristics are fully apparent in the thymus of *Lophius*, and the original glandular foundation of the organ is even more clearly indicated than in the placodal adherent type of thymus common to other species. For it is possible to trace the epithelioid stellate cells of the reticulum, and the scattered mucous and granular gland cells of the thymic lobules, through irregular connective-tissue spaces lined by an epithelium of a transitional character to a duct-like diverticulum of the pharynx, in which the mucous membrane differs in no respect from that lining the general surface of the branchial cavity.

The condition present in this fish is such, in fact, as would result from the breaking up of the deeper parts of a follicular mucous gland (such as those characteristic of the base of the tongue of a mammal) by an excessive invasion of leucocytes amongst the cells of its lining epithelium, spreading apart the stratified cells to form a supporting reticulum and scattering the gland cells throughout the resulting adenoid and reticular mass.

* KEITH, 'Human Embryology and Morphology,' 4th ed., 1921, p. 261.

† Since the above was written Prof. J. P. HILL has referred me to a paper by VAN WIJHE ('Proc. Koninkl. Akad. v. Wetensch. t. Amsterdam,' vol. 26, 1923, p. 727), in which he describes in a 63-mm. embryo of *Heptanchus* a transitory condition of the thymus remarkably similar to that presented by *Lophius*. In this embryo there is, he says (p. 729), "an excretory duct *in optima forma* for each of the thymus divisions (thymomeres) which are formed on both sides of the body, one for each side from the second to the seventh branchial cleft." Each duct is lined by two layers of flattish epithelial cells and extends from the top of the branchial cleft to the body of the thymus without entering it. In an embryo of 225 mm. these ducts had disappeared. VAN WIJHE infers that "the original function of the thymus could not have been internal secretion only, but it must have removed products through its excretory ducts," and compares the thymus at this excretory stage with the branchionephros of *Amphioxus*.—[February 5, 1926.]

The anatomical structure here shown by a fully formed thymus is of interest, however, not only because it affords peculiarly clear evidence of the epithelial and glandular origin of the organ, but perhaps even more because it links up the thymus with the tonsil, and demonstrates the close structural relationship there is between these two bodies. This relationship is suggested by their similar mode and place of origin (the tonsil from the upper end of the second gill cleft, the thymus (at least in non-mammalian Vertebrates) from a similar part of any cleft from the first to the fifth), but in mammals the thymus has departed in structure so far from its original epithelial conditions that its relationship to the tonsil is not apparent.

It is therefore of somewhat peculiar interest to find a fish with a thymus body in a state transitional between that presented by a mammalian tonsil, in which most of the features of a follicular gland are retained, and the organ consists of a branching cavity lined by a glandular epithelium continuous with that of the pharnyx, but surrounded by a mass of adenoid tissue infiltrating the epithelial lining of the glandular recesses, and that presented by the thymus of a higher Vertebrate, in which the original glandular out-pushing of the pharyngeal mucous membrane and the epithelial foundation of the organ has been completely modified and obscured by the assumption of an entirely lymphatic function.

Summary.

1. The thymus is not of the adherent placodal type normal to Teleosteans, but lies free beneath the mucous membrane of the pharnyx, separated from it by a lymph space and loose connective tissue.

2. A duct-like tube extends from the pharynx to the thymus, penetrating its substance for some distance and terminating in an irregular cavity, the extensions of which pass insensibily into the lobules of the thymus.

3. The epithelium that lines the " duct " and its termination is similar to that of the pharynx. Within the thymus its polygonal stratified cells become gradually transformed into the stellate cells of the thymic reticulum, and its mucous and other gland cells distributed throughout the thymic lobules.

2. The Thyroid Body.

Our knowledge of the thyroid body of Teleosteans is founded mainly on the work of Baber (4) on the conger, and more particularly of Maurer (10) on the trout and several species of Cyprinoid and other fresh-water fishes.

In all the species investigated the gland is very similar in structure and anatomical relations, consisting of a mass, usually more or less diffuse, of colloid-containing vesicles lodged in the loose connective tissue that envelops the ventral aorta and its branches.

The vesicles in the species described by MAURER are situated mainly upon the ventral surface of the ventral aorta, extending from a point slightly in front of the origin of the anterior pair of afferent branchial vessels to beyond that of the last pair, and spreading to some extent over its dorsal surface and along the roots of the afferent vessels. The vesicles lie freely scattered in the surrounding connective tissue, and have no direct connection with the ventral aorta or its branches.

In the young the gland is more compact than as age advances; in older fish, owing apparently to the disproportionate growth of the ventral aorta, the vesicles become spread apart and scattered in small, more or less isolated groups or lobules.

Thyroid of Lophius: (*a*) *Macroscopic Anatomy.*—In *Lophius* the thyroid occupies a position similar to that described by BABER and MAURER. When the anterior part of the pectoral arch and the hyoid muscles attached to it are removed, the thyroid (fig. 2, *th.*) is exposed lying beneath a mass of loose vacuolated connective tissue. It is a soft, slightly irregular, oval or pear-shaped body, covering and concealing the short ventral aorta and the roots of the great afferent branchial trunks given off from it, and extending forward beyond the bifurcation of the ventral aorta between the anterior ends of the hyo-clavicularis muscles nearly to the symphysis of the hyoid.

The surface of the body, when freed from the surrounding connective tissue, presents a slightly nodular appearance, due to the presence and projection of the colloid-containing vesicles that form its essential part; but the connective tissue within which these vesicles are embedded is not, as is the case in the species previously described, a continuous reticulum closely investing the vessels of the afferent branchial system, but is hollowed out to form a large sinus or lymphatic cistern (fig. 3, *th.s.*) folded around these vessels and beset practically all over by the vesicles of the thyroid.

This cistern, which may be called the thyroid sinus, is lined by an endothelium, and is continuous with the superficial ventral system of lymphatics, lying on the course of the main channels of this system as they pass from the ventral surface of the body to the heart. Its connections and exact relations to this system of lymph vessels and to the venous system are more fully described below. At present the point upon which I wish to lay stress is that the thyroid body is occupied by, or rather lies around, a large lymph sinus.

The ventral surface of the thyroid, although, as stated, showing in most parts indications of a vesicular structure, is in two small areas smooth and devoid of vesicles. These areas lie one on either side of the mid-line close behind the hypobranchial arteries as these vessels curve backwards across the thyroid to unite to form a common median hypobranchial trunk. In the centre of each is a slit-like opening bordered by thin valvular flaps of membrane (figs. 2, 4, 7, *v.th.v.*).

Removal of the ventral surface of the thyroid (fig. 3) exposes the interior of the thyroid sinus. Within this, projecting from the roof and covered by nodulated thyroid

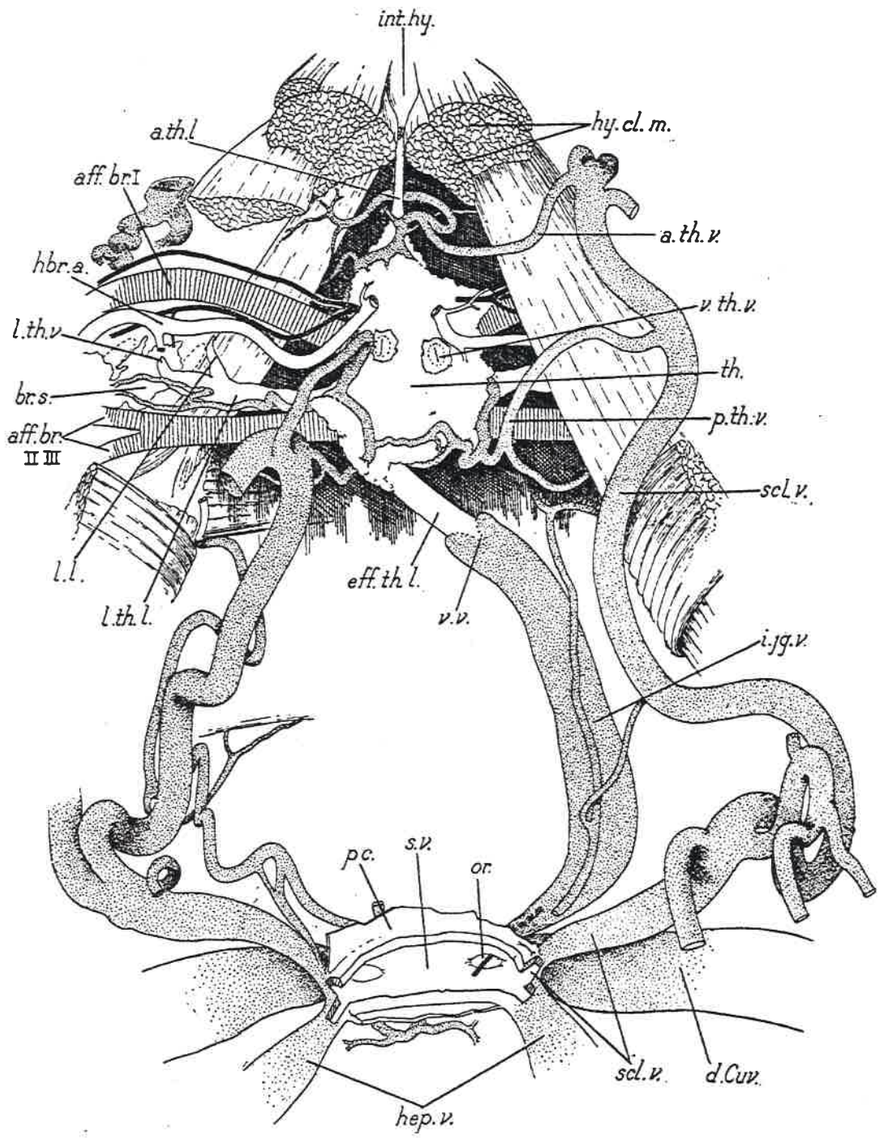


FIG. 2.—A dissection of the floor of the pharynx of *Lophius*, seen from the ventral aspect. The heart and pericardium have been removed, except part of the sinus venosus. Veins: dotted; afferent branchial vessels: cross-lined; "fine" vessels: black.

tissue, are the ventral aorta (fig. 3, *v.ao.*), and the two roots of the afferent branchial vessels given off from it (fig. 3, *aff.br.*). In front of the anterior bifurcation of the ventral aorta the sac is considerably dilated, and is honeycombed by numerous inter-

lacing trabeculæ. Its anterior extremity tapers and passes into a thin-walled tube (figs. 2, 3, *a.th.l.*) devoid of any thyroid tissue, and constituting the termination of one of the trunks of the ventral lymphatic system.

On either side the sinus is produced in a similar way to form a wide thin-walled channel (figs. 2, 3, *l.th.l.*) devoid of thyroid tissue, that passes outwards between the two roots of the afferent branchial vessels towards the ventral extremities of the gills.

Posteriorly, the sac is reflected dorsal to the afferent branchial vessels and ventral aorta, and is continued backwards to the right of the mid-line dorsal to the pericardium

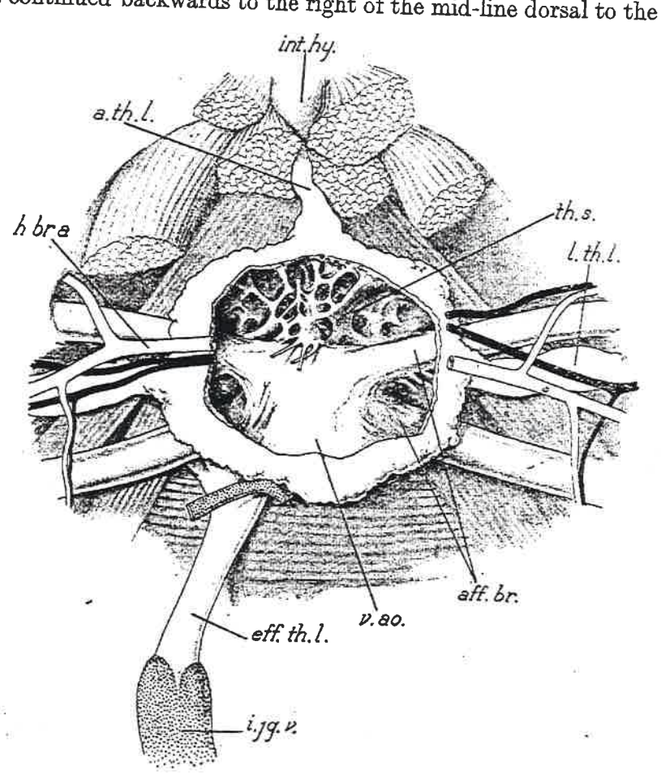


FIG. 3.—The thyroid body of *Lophius*, exposed from the ventral aspect and with its ventral wall removed to show the lymph sinus within it. Veins: dotted; "fine" vessels: black.

as a capacious thin-walled vessel (figs. 2, 3, *eff.th.l.*) devoid of thyroid tissue, which is ultimately connected through a large vein with the sinus venosus of the heart.

(*b*) *Relations between the Thyroid Body and the Lymphatic System.*—The lymphatic system of Teleostean fishes has been described in more or less detail for a large number of species. A full review of the older literature is given by ALLEN (1 and 2) in two papers on the lymphatic system of *Scorpænichthys* and the Ganoids, so that there is no occasion to enter at large into the history of the growth of our knowledge of this subject.

In the older papers (FOHMANN, SHARPEY, etc.) the general arrangement of the main lymphatic trunks and their regional division into several intercommunicating systems was mapped out with some degree of accuracy, and somewhat sketchy descriptions were given of certain large sinuses in the head and fore-part of the body, through which the main vessels of the various regional systems are connected with the veins; but ALLEN was the first, and, I think, so far the last, to describe with accuracy and clearness the topography of these reservoirs and their anatomical relations with the lymphatic trunks on the one hand and the venous system on the other.

For this reason, and because some of these sinuses and their connections are the points with which I am mainly concerned, I propose to use ALLEN's paper on *Scorpænichthys* as a criterion with which to compare the condition observed in *Lophius*.

It is true that so far as *Lophius* itself is concerned, a comprehensive account of the general distribution of the lymphatic system has been given by TROIS (22), and his description is both good and accurate so far as it goes. But his researches are mainly limited to the distribution of the vessels of the various regional systems, and give no very clear information upon the point that concerns me most, namely, their mode of termination.

From TROIS' paper it appears that, as in other Teleosteans, the lymphatic system as a whole can be separated into several regional sections, or systems, freely communicating with one another. There can thus be distinguished primarily a visceral and a muscular system. The latter can again be subdivided into a superficial or cutaneous system, and a deep or submuscular.

The superficial system is composed of four main canals: dorsal, two lateral, and ventral, situated respectively in the dorsal mid-line, beneath each lateral line, and upon the ventral surface of the body, extending in this latter case from either side of the anal fin to the clavicular symphysis.

It is this ventral superficial system with which I am chiefly concerned, and more particularly with its relation to the thyroid body and the venous system.

In *Lophius*, owing probably to the generally lax condition of the tissues (POIRIER and CUNEO, 14), the lymphatics in general are peculiarly large and capacious. Those of the ventral system are further remarkable in various ways. As noted by TROIS (22, p. 769), the main ventral trunk, which normally is single and median, is represented by two, disposed symmetrically on either side of the ventral mid-line from the cloaca to the pectoral symphysis. The vessels composing these trunks, as well as their tributary vessels of smaller size, are somewhat varicose and irregular in outline, and tend to be fasciated—made up of bundles of smaller vessels irregularly anastomosed together and forming in most cases a linear network along the course of the various branches of the hypobranchial artery. The walls of the components of this system are extremely thin and delicate, so that even a vessel measuring some millimetres in diameter is very difficult to detect until it is injected, or unless it contains, as it frequently does, a certain amount of blood.

The account of these superficial ventral lymphatics given by TROIS (22, p. 769), which I have verified, is brief, but as it is supplemented by a detailed figure, between the two an adequate idea can be obtained of their general disposition.

The main trunks of the system, each of which is composed of two or more anastomosing vessels of irregular calibre, arise in the tail, and, passing on either side of the cloaca, proceed forward upon the fascia of the abdominal wall on either side of the mid-line separated from one another by a distance of 2 to 4 cm. On a level with the posterior (mesial) border of the pelvic fins, each trunk receives a large tributary from the mesial extremity of a capacious sinus lying within the embrace of the forked bases of the pelvic fin rays. Anterior to this tributary, the main trunks approach one another, and at their point of closest apposition are united by a variable number of transverse anastomoses.

In front of this connection the trunks again diverge and receive a second great tributary from the pelvic fin continuous with the anterior (outer) extremity of the sinus within the bases of the fin rays just mentioned. The main trunks now pass dorsal to the transverse muscles that unite the ventral branchiostegal rays of either side, and converge towards the symphysis of the pectoral arch, uniting between the origins of the clavicular-pelvic muscles to form a plexiform reservoir from which numerous offshoots spread over the ventral surface of the symphysis intermingled with small arterial branches.

In addition to these two main abdominal trunks and their tributaries, there must also be included in the ventral superficial system of lymphatics a median unpaired vessel situated upon the ventral surface of the intermandibularis and genio-hyoid muscles in front of the pectoral symphysis.

This vessel is formed by the union of a plexus of small vessels situated beneath the skin of the lower jaw, and as it passes backwards, receives numerous lateral tributaries, the posterior of which (situated along the hinder border of the genio-hyoid muscle) is of considerable importance and extends its area of drainage over a large part of the branchiostegal membrane, anastomosing freely with minor tributaries of the main abdominal trunks.

The tissues chiefly drained by this ventral system of lymphatics are the skin and the subdermal and intermuscular connective tissues of the ventral body wall. In the skin itself, and particularly upon and around the pelvic fins, the capillary network from which the vessels originate is, as mentioned by TROIS (22, p. 772), astonishingly close and rich (Plate 3, fig. 13). In the subdermal tissues the plexus is much more open and is largely composed of branches connecting the integumentary network with the main abdominal trunks.

This, in brief, and subject to individual variation in minor particulars, is the arrangement of the chief vessels of the ventral superficial system of lymphatics up to the point where they converge from behind and in front upon the pectoral symphysis. The farther course of the main trunks of the system has not, so far as I know, been hitherto described, and is of interest.

The median anterior trunk at the posterior border of the genio-hyoid muscle bends dorsally around the sublingual reflexion of the buccal membrane between the origins of the hyo-clavicularis muscles, and, after passing through a canal in the basal element of the hyoid, opens freely, apparently without the intervention of valves, into the anterior prolongation of the thyroid sinus mentioned above (p. 11) in the description of the thyroid. At the point at which the vessel dips round the posterior margin of the genio-hyoid, it receives a large tributary from the ventral surface of the tongue.

The main abdominal trunks of the system run together, as we have seen, to form a plexiform sinus behind and above the symphysis of the pectoral arch. This sinus lies upon the anterior end of the pericardium and extends forward, forming between the dorsal surface of the pectoral symphysis and the thyroid body a large lymph cistern subdivided in its posterior region into plexiform intercommunicating channels continuous with the main abdominal trunks of the system and opening out in front, below the thyroid body, to form a single chamber broken up to some extent by folds and trabeculæ.

The general form of this chamber, or sub-thyroid sinus (figs. 4, 7, *s.th.s.*), is that of a blunt arrow-head with its apex directed forward, and its hinder plexiform part connected, as just stated, with the main abdominal trunks of the system, and also communicating by irregular anastomosing channels (fig. 4, *l.ch.*) across the lateral walls of the pericardium, with an extensive sinus associated with the pectoral girdle (fig. 4, *pct.s.*), and through it eventually forming a connection with the great cephalic sinus situated beneath the basis cranii.

This pectoral sinus envelops the pectoro-pelvic articulation in front, extends to some extent over the posterior parts of the pericardium, and at the root of the pectoral fin turns mesially along the ventral (deep) surface of the ascending arm of the clavicle to open widely in the neighbourhood of the kidney into the abdominal and cephalic sinuses.

The irregular anastomoses between the postero-lateral parts of the sub-thyroid sinus and the pectoral sinus were not apparent in every injection. In some in which the injection was light, the subthyroid sinus was circumscribed as outlined in fig. 7, *s.th.s.* I am therefore not absolutely sure that they are natural channels, though their definite outlines, which present an appearance very unlike the diffuseness of an undoubted extravasation, incline me to believe that they are, and that the condition shown in fig. 7 is either a variant or is due to the injection not being sufficiently prolonged. When present, they follow roughly the coracoid branch of the hypobranchial artery, and consist of very irregular spaces of limited capacity flattened between the clavicular pelvic muscles and the pericardium, and so far as I have been able to ascertain, form the only open and direct connection between the sub-thyroid sinus and the great lymph reservoirs situated at the base of the skull through which the chief constituents of the lymphatic system as a whole communicate with the jugular vein. But from the backward trend of these communicating channels it seems unlikely that the lymph in the ventral system passes along them to any extent towards the pectoral sinus; it seems,

in fact, more probable that the flow would be in the opposite direction (as in other tributaries of the ventral system) from the spaces around the pectoro-pelvic articulation towards the sub-thyroid sinus.

In any case there is, I think, no question that the flow of lymph in the ventral system

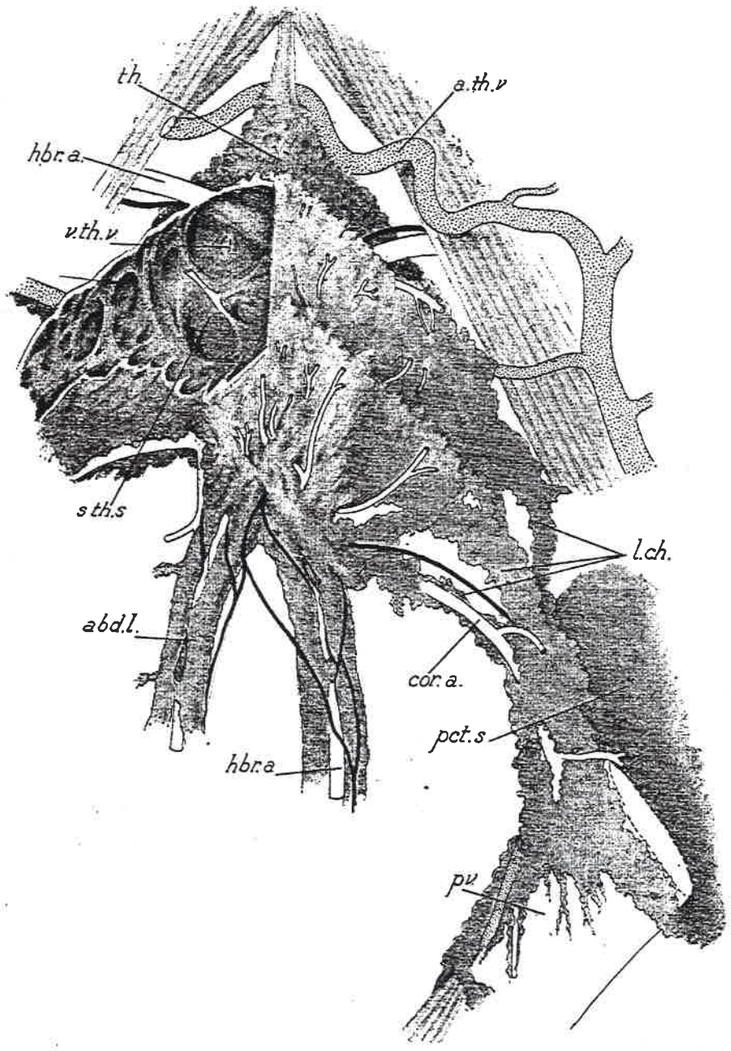


FIG. 4.—The sub-thyroid lymph sinus of *Lophius*, seen from the ventral aspect, after the removal of the shoulder girdle. The right half of the sinus has been opened. Veins : dotted ; arteries : white ; " fine " vessels : black.

as a whole is mainly, even if not entirely, towards the sub-thyroid sinus, and so into the cavity within the thyroid body itself.

This direction of flow is also strongly suggested by the mode of connection between the sub-thyroid and thyroid sinuses; for it will be remembered that in the description of the thyroid body mention was made of a pair of valved orifices in its ventral wall. These openings (figs. 2, 4, 7, *v.th.v.*) are the passages which connect the sub-thyroid lymph sinus with the cavity within the thyroid body. They lie on either side of the mid-line in the spacious anterior part of the sub-thyroid sinus, and when viewed from the cavity of this sinus appear as oval apertures, closed, except for a slit-like median passage, by a pair of very delicate membranous folds. The edges of these folds are inclined towards the cavity of the thyroid, and undoubtedly are valvular in the sense that they prevent the flow of fluid from the thyroid to the sub-thyroid sinus. This can readily be demonstrated by gently compressing the thyroid body; the folds then bulge upwards towards the sub-thyroid sinus; the slit between them is closed, and no fluid can without undue force be passed through it into the sub-thyroid sinus. There can, therefore, I think, be no doubt that the bulk, if not the whole, of the lymph carried by the superficial ventral system of lymphatics flows through the thyroid sinus.

To complete the description of the lymphatic channels afferent to the thyroid body, reference must be made to the two lateral offshoots of the thyroid sinus mentioned previously (p. 11). These channels (figs. 2, 3, *l.th.l.*) are connected with the general cavity of the thyroid between the emergence from its walls of the two afferent branchial arterial trunks. Each passes outwards across the floor of the pharynx towards the anterior extremities of the gills, and about half-way across receives a tributary (fig. 2, *l.l.*) from the tongue curving round the outer border of the hyo-branchialis muscle of the fourth arch. The main channel itself is spindle-shaped, tapering at either end, and extends in front of the gill slits to the interval between the cartilaginous free extremities of the second and third branchial arches; at this point it is blocked by a pair of membranous valves (fig. 2, *l.th.v.*), which prevent injection thrown into the channel from the thyroid sinus passing further even under very considerable pressure. Beyond the valves the channel opens abruptly into a large irregular cavity (fig. 2, *br.s.*) situated above and between the cartilaginous extremities of the branchial arches beneath the mucous membrane of the mouth close behind the tongue. This cavity is the main ventral branchial lymph sinus. It is in connection with a large sinus upon the inner border of the hyoid, and also extends into the tongue and up the concave surface of each gill arch in a system of irregular anastomosing channels that surround the main branchial vessels and open out above the gills into a corresponding dorsal branchial lymph space connected with the great cephalic sinus below the cranium. Within the gills this system of lymph spaces is continuous with a fine but varicose capillary plexus upon the surface of each filament.

(*c*) *Relation of the Thyroid Lymph Sinus to the Veins.*—It was shown above that in *Lophius* the bulk, if not the whole, of the lymph circulating in the branchial lymphatics

and the lymphatics of the superficial ventral system passes into a large reservoir in the centre of the thyroid body. From this reservoir it is conveyed directly to the heart.

In *Scorpænichthys* ALLEN (1) was unable to demonstrate any direct connection between the pharyngeal portion of the ventral lymphatic system and the veins, though the fact that injection thrown into these lymphatics passed into the inferior jugular vein led him to assume that there must be some natural communication between the two.

In *Lophius* this question is not open to doubt, for there is an important open and direct connection between the thyroid sinus and a vein that I take to be the representative of the inferior jugular.

It will be remembered that in describing the cavity within the thyroid, reference was made (p. 11) to the reflexion of the dorsal wall of this lymph sinus above the bifurcation of the ventral aorta, to form a posteriorly directed recess that led into a membranous vessel situated upon the dorsal surface of the pericardium.

This vessel (figs. 2, 3, *eff.th.l.*) always leaves the thyroid sinus to the right of the mid-line, and is of considerable size (averaging 4 mm. in diameter in the examples examined). After a course of some 1·5 cm., the vessel enters the head of a large vein through a pair of strong semilunar valves, so set that back-flow cannot take place from the vein to the lymph channel and thyroid sinus. The vein passes backwards for about 4 cm. dorsal to the pericardium, either longitudinally or diagonally to the left, and enters the dorsal surface of the right or left duct of Cuvier close to its opening into the sinus venosus (fig. 2, *or.*). This vein in all cases (with one exception) had no tributaries other than the lymph channel coming from the thyroid sinus. In the exceptional case an insignificant factor from the transverse pharyngeal muscles entered it close below the valves.

I was at first in considerable doubt whether this unpaired vein was a vessel specially developed to connect the thyroid sinus with the heart, and was without a counterpart in the venous system of the more normal Teleostean, or whether it was one of the usual veins that had lost its ordinary factors and had become transformed to act simply as a channel for the conveyance of lymph.

After further investigation, and particularly by comparison with the excellent descriptions of the Teleostean venous system given by ALLEN for the Loricati (3), and by SILVESTER for the tile-fish (19), I think there can be no doubt that it represents the inferior jugular vein in a specialised condition.

From ALLEN's description of *Ophidion* it appears that the veins that drain the ventral surface of the head and body can be separated into two distinct systems, comprising respectively the inferior jugular vein and the subclavian and ventral veins.

The inferior jugular, which in its anterior parts is mesial in position and unpaired, is composed of factors derived from the tongue, the muscles attached to the anterior parts of the hyoid arch, the ventral parts of the gills, the thyroid body, and the oblique muscles of the floor of the pharynx. It passes backwards as a single vessel dorsal to the ventral aorta, and behind the level of the last pair of afferent branchial vessels

divides into two stems of very unequal size, the right far larger than the left. Each of these stems receives factors from the pharyngeal muscles and passes back close to the pericardium to the duct of Cuvier of its own side, and opens into it at its entry into the sinus venosus.

The ventral veins take their origin from the pelvic fins and ventral trunk muscles, and open into the hepatic sinus, or into the sinus venosus, in close proximity to it.

The subclavian veins, which return the blood from the pectoral fins, can be divided into two systems—one derived from the adductor muscles of the fin, which terminate by breaking up in the kidney, and another derived from the abductor muscles which enters the sinus venosus upon its ventral aspect through the subclavian sinus.

The detailed arrangement of these veins is evidently open to considerable variation (*cf. Lopholatilus*), but the distinction of the two systems, particularly with reference to their mode of entry to the heart, seems to be of a fixed and fundamental character. The inferior jugular is always connected with the duct of Cuvier, entering the antero-dorsal aspect of the sinus venosus; whereas the ventro-subclavian system opens upon the postero-ventral aspect of the sinus venosus in close association with the hepatic sinuses.

When the veins of the central parts of the head, pharynx and body-wall of *Lophius* are compared with the veins of the same regions in the Loricati, or *Lopholatilus*, it is at once apparent that the mode of entry of the vein connected with the thyroid lymph sinus into the heart is similar to that characteristic of the inferior jugular in those fishes. The vein is unpaired, but so is the inferior jugular of *Lopholatilus*. The fact that it may open into either the right or left duct of Cuvier suggests that it is the survivor of an original pair of stems similar to those that in the Loricati connect an unpaired anterior segment of the vessel with the duct of Cuvier of either side. This assumption is strengthened by the marked asymmetry shown by these two stems of the inferior jugular in the Loricati.

It is true that the factors that normally compose the inferior jugulars are absent from this vessel in *Lophius*, and form tributaries of two other large veins (fig. 2, *s.cl.v.*) that lie on either side of the pericardium upon the floor of the pharynx. But these two veins, apart from their reception of these factors, possess all the characters commonly associated with the ventro-subclavian system, particularly as regards their mode of connection with the heart.

They commence in the tongue and genio-hyoid muscles and as they pass backwards beneath the muscles of the floor of the pharynx, receive factors from the gills, the branchiostegal membrane, the pharyngeal muscles, and the thyroid body. Upon a level with the pectoro-pelvic articulation, within the great pectoral lymph sinus that surrounds that joint, they are joined by large factors coming from the pelvic and trunk muscles that arise from the horizontal arm of the clavicle, and turn towards the mid-line to enter the ventral surface of the sinus venosus in conjunction with the hepatic veins (fig. 2,

hep.v.). There can, I think, be no question that these veins, in spite of the fact that some of their tributaries are derived from parts normally served by the inferior jugulars, are, in fact, ventro-clavicular veins, with an extended area of drainage, and that the great branchless vessel that connects the efferent lymphatic channel of the thyroid with the duct of Cuvier is the inferior jugular stripped of its normal factors and specialised to act solely as an efferent vessel of the thyroid lymph sinus.

(*d*) *Discussion.*—From the above description it is evident that the relation of the superficial ventral and branchial lymphatics to the thyroid body in *Lophius* is very peculiar, and though I have been unable to find any parallel to it in any published description of these parts in other fishes, it will be of interest to examine how far it can be compared with the conditions more normally met with.

My own observations in fishes, other than *Lophius*, are at present very imperfect. I have examined sections through the thyroid region of a gold-fish, and have made some preliminary naked-eye investigations of the superficial ventral lymphatics in the cod and hake. From these it appears that the main stem of the ventral lymphatic system opens out anteriorly to form a complex system of lymph spaces between the sterno-hyoideus muscles and around the thyroid body, and that the lobules and vesicles of the thyroid body project into these spaces and are thus freely bathed in lymph. As yet I have been unable to work out in detail the relation of this labyrinth of spaces to the rest of the lymphatic system or to the veins, so that I cannot say how far they represent the sinuses described above.

Little appears to have been published upon the lymphatics in the thyroid region of Teleosteans; in fact, so far as I have been able to find out, the pericardial sinuses, to which the parts described above in *Lophius* are most nearly similar, have been examined hitherto only in the Ganoid *Amia* (7) by HOPKINS, and in *Scorpœnichthys* by ALLEN (1).

In *Scorpœnichthys*, of whose lymphatics ALLEN gives a very full and elaborate account, the pericardial sinuses are highly complex. He describes the main trunk of the ventral superficial system as terminating in front in a large sinus (ventral pericardial sinus) lying longitudinally below the pericardium. Postero-dorsally this chamber is connected on either side behind the pericardium to a large complex cavity (main and posterior pericardial sinuses) which extends upwards to the kidney, and at its dorsal end communicates with the abdominal and cephalic sinuses.

On the level of the bulbus cordis the ventral pericardial sinus is constricted and can thus be separated into two lineally arranged chambers (anterior and posterior ventral pericardial sinuses).

The anterior of these two chambers underlies the ventral aorta, and on a level with the gap between the roots of the second and combined third and fourth afferent branchial vessels, bifurcates, passing upwards and forwards on either side of the thyroid body and second afferent branchial vessel. In front of this vessel each fork (pharyngeal lymphatic) divides into two branches, which run respectively to the first and second afferent branchial vessels, but could not be traced beyond their entry to the gills. From the

point of bifurcation of the ventral pericardial sinus a small medial vessel passes to the thyroid body.

Now, when one compares Allen's description of these ventral pericardial sinuses of *Scorpænichthys* with what has been observed in *Lophius* (fig. 5), there is without question a strong sub-stratum of similarity between the two. It seems fairly obvious that the lymph sac situated in *Lophius*, between the pectoral symphysis and the thyroid body (sub-thyroid sinus), represents the posterior ventral pericardial sinus of *Scorpænichthys*; for not only is it directly continuous with the main trunks of the ventral superficial system of lymphatics, but it is (at least in some cases) in connection postero-dorsally

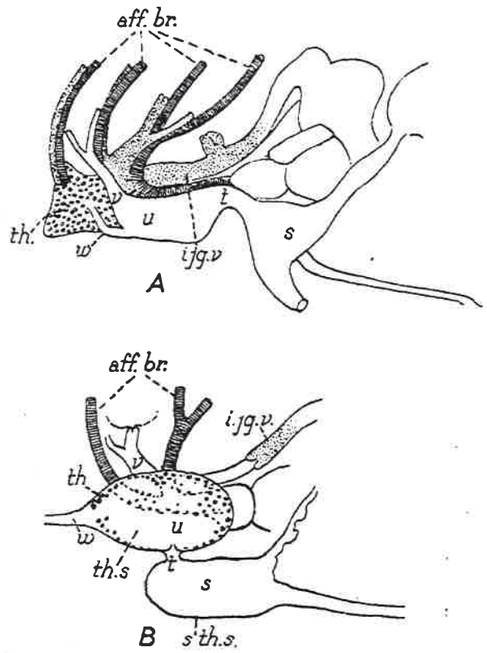


FIG. 5.—Diagrams illustrating suggested comparison between the pericardial lymph sinuses of *Scorpænichthys* and *Lophius*. A. *Scorpænichthys* (after Allen), B, *Lophius*.

with a large sinus that spreads from around the pectoro-pelvic articulation on to the hinder part of the pericardium and communicates with the abdominal and cephalic sinuses, thus corresponding in some degree with the main and posterior pericardial sinuses of *Scorpænichthys*.

The constriction between the anterior and posterior divisions of the ventral pericardial sinus of *Scorpænichthys* may be represented by the valved passages between the subthyroid and thyroid sinuses of *Lophius*. It is true that in the former the passage is single, and in the latter double; but a difference of this kind is not likely to be of

morphological importance, particularly in view of the great tendency to subdivision and anastomosis shown everywhere by the main lymphatic trunks in *Lophius*. In this particular instance the duplication is probably an adjustment made necessary by the confluence of the hypobranchial arteries to form a single stem, occupying the median position originally appropriate to a single unpaired lymph passage.

If this comparison is just, the sinus within the thyroid body should represent the anterior division of the ventral pericardial sinus of *Scorpænichthys*, its lateral channels the pharyngeal lymphatics, and its anterior extension the small unpaired thyroid lymphatic.

This comparison with what may be considered (in want of more extended knowledge) as the condition normal to Teleosteans gives, I think, a clue to the manner in which the curious arrangement of parts and large intra-thyroid lymph sac in *Lophius* may have come about.

The shifting forward of the pectoral symphysis in *Lophius* far in front of the heart, and the shortening of the ventral aorta, may well account for the altered relations of the two divisions of the ventral pericardial sinus, so that instead of being arranged lineally one behind the other, they have come to lie vertically with the anterior sinus above and but slightly in advance of the posterior.

In *Scorpænichthys* the thyroid body lies between the anterior division of the pericardial sinus and the ventral aorta, with its vesicles scattered, no doubt, as in other Teleosteans, in the connective tissue around the ventral aorta and its branches.

From such a relation of parts it is a short and easy step to the invasion of the connective tissue around the anterior division of the ventral pericardial sinus by thyroid vesicles, and such an invasion might without hindrance gradually extend till the whole surface of the sinus became more or less embedded in thryoid tissue and a condition result similar to that actually present in *Lophius*.

From the facts at our disposal it seems, therefore, far more likely that the thyroid body has grown round the thyroid lymph sinus than that the sinus has insinuated itself into the substance of the thyroid.

(*e*) *Microscopic Anatomy of Thyroid Body.*—The vesicles of which the thyroid body is composed show a very great variation in size, ranging from a diameter of some 0·8 mm. to a diameter of 0·05 mm. or less.

Those of small or moderate size are mostly of oval or globular shape, but the larger ones often show an irregularity of form, appearing in surface view to be indented and lobulated and presenting in section a branching stellate outline. The impression given is that of a central chamber with bud-like prominences and recesses.

The individual vesicles, when of any considerable size, are roughly clumped together in oblong masses (Plate 1, fig. 5), which by their appearance suggest that each individual mass is the product of a single rudiment or primary vesicle. A lobular arrangement of the vesicles was also observed by MAURER (10, pp. 140, 147) in the genera that he investigated, but apparently occurred only after a certain age, and is interpreted by

him as the result of the breaking up of an originally continuous layer of vesicles brought about by the disproportionate growth of the blood-vessels around which the thyroid is laid down.

In *Lophius* this lobular arrangement, although fairly definite in some parts, is not everywhere equally distinct, at least so far as the masses of larger vesicles are concerned; but in the case of the smaller ones, which are apparently in process of formation and growth, a definite arrangement in separate linear groups is very clearly marked. The smallest form, in fact, long series of closely apposed but separate vesicles arranged in rows like chaplets of beads, which in many places are replaced by, or are continuous with, long, narrow and sometimes slightly tortuous tubes that gradually taper to a solid point.

Many of these rows of small vesicles and tubes lie in close apposition to masses of larger vesicles, and are evidently buds given off from them, as was described by MAURER (10, p. 146) in the development of the thyroid rudiment in the trout; but in other areas (Plate 1, fig. 6) they are the only type of vesicle present and occur as isolated simple or branching vesiculated strands lying freely in the connective-tissue stroma, and suggest foci of new growth which, starting as a solid column of epithelial cells, develop progressively into hollow tubes and rows of vesicles (Plate 2, fig. 7). There can, however, be no question that these strands of growing vesicles, although now isolated, must have taken their origin by budding from pre-existing vesicles, and have subsequently migrated or been separated from their source of origin by the growth of the surrounding stroma.

Although no doubt these buds are of a secondary nature, their linear disposition and progressive transformation from solid cell columns to tubes and discrete vesicles is of interest, for it seems to form a link, absent apparently in most fishes, with the columnar and tubular character of the vesicular rudiment in higher Vertebrates and man at a certain period of its development (SCOTT-WILLIAMSON and PEARSE, 18, p. 961). MACKENZIE (8) records that in *Amiurus* the vesicles show a tendency to be arranged in short rows (quoted by THOMPSON, 21, p. 97), but MAURER (10, p. 141) saw no indication of a tubular or columnar condition of the growing vesicles in the Teleostean genera that he studied, nor was a tubular character observed by FERGUSON (5, p. 191) in the thyroid of Elasmobranchs.

Formerly the columnar and tubular phase was supposed to represent a very early stage in the phylogeny of the thyroid, but it has been shown by NORRIS (12, 13) in the Elasmobranchs and Man that what had been taken for columns of cells are in reality a system of fenestrated plates, derived in a somewhat complex way from the vesiculation of the solid mass of epithelium that constitutes the first rudiment of the organ, and that solid columns and tubes, somewhat similar to those observed in *Lophius*, occur later as buds given off from a system of primary vesicles developed within the fenestrated plates.

In face of NORRIS's observations, the secondary tubular phase of development cannot be regarded as representing the earliest condition of the gland after its transformation from the open endostyle period of its existence; but this widespread tendency to grow

by throwing out columns and tubes of epithelium suggests that at some stage in its history the organ had the character of a tubular gland.

The epithelium that lines the vesicles consists of simple columnar cells of an elevated type, with the nuclei situated with great regularity towards the base. In the elongated form of its cells it closely resembles that of the thyroid vesicles of the wolf-fish (*Anarrhichas*) and the conger, examples of which I have been able to examine. The form of the epithelial cells seems, however, to vary in different genera of Teleosteans, as it does in Elasmobranchs (FERGUSON, 5, p. 195), for MAURER figures the epithelium of the vesicles in the trout as cubical, and from his description (10, p. 141) it is to be inferred that a low epithelium of this type was general among the genera with which he dealt. He also states (10, p. 143) that in old vesicles the epithelium becomes quite flat. In *Amiurus* the epithelium is stated by THOMPSON (21, p. 98) to be "difficult to recognise" and never columnar, and I have observed the same to be the case in the gold-fish. The height of the cells in *Lophius* varied to some extent from vesicle to vesicle, and even in different parts of the same vesicle, but I was unable to distinguish any constant or marked difference in height as between vesicles filled with colloid and those that were not, to which FERGUSON (5, p. 195) draws attention in the Elasmobranchs.

The vesicles, both large and small, contain in many cases colloid, which usually forms a homogeneous mass, but sometimes, particularly in the smaller vesicles and towards the periphery of the mass, is broken up, as described by FERGUSON (5, p. 200) in Elasmobranchs into homogeneous spherules (Plate 2, fig. 9). Here and there in the colloid contents of the larger vesicles were the remains of nucleated cells, some of which had somewhat the appearance of red blood corpuscles (Plate 2, fig. 8, *cd.*), though I cannot upon this point be quite sure. Similar cell débris is described by MAURER (10, p. 142) as occurring in the colloid within the older vesicles in the trout.

In the description of the naked-eye appearance of the thyroid (p. 9) it was stated that indications of the presence of vesicles could be observed all over the surface of the thyroid-lymph sinus, except close around the passages leading into it from the subthyroid sinus.

Microscopic examination shows that this is substantially correct, although the number and average size of the vesicles varies very much in different areas.

In the anterior richly trabeculated segment situated in front of the first afferent branchial vessels, vesicles (many of large size) are distributed in quantities in all parts of the walls of the thyroid sinus and in the substance of the trabeculæ (Plate 2, fig. 10).

Farther back, where the first afferent vessels are leaving the walls of the sinus, vesicles are most abundant in the connective tissue between these vessels and the sinus, and in the ventral wall of the sinus; in the dorsal wall they are fewer and mostly of quite small size. Still farther back, in sections taken through the valved openings between the subthyroid and thyroid sinuses (Plate 2, fig. 11), the larger vesicles are aggregated mainly around the first afferent vessels (which at this level lie free within the thyroid sinus) and within the ventral and lateral walls of the sinus; in its dorsal wall they are

relatively few and small. As the point is approached at which the second afferent branchial vessels leave the thyroid sinus, a complex mass of vehicles appears in the roof of the sinus (Plate 2, fig. 12, *m.*). This mass is of some apparent thickness and density, but is, in fact, like the rest of the gland, composed of a relatively thin layer of vesicles surrounding complex offshoots of the general cavity of the sinus, forming a sponge-like intermixture of lymph spaces, and baulks and trabeculæ of connective tissue, within which lie the vesicles. Towards the hinder end of the gland this mass of vesicles more or less surrounds the ventral aorta and roots of the afferent branchial vessels, forming lateral masses in folds connecting these vessels to the lateral walls of the sinus. In other parts at the hinder end of the gland, vesicles, though present in most parts of the walls of the sinus, are relatively few and small.

It is to be particularly noticed that the vesicles everywhere, even when, as just stated, they are apparently massed together to a considerable depth, form in reality quite a thin layer close to the cavity of the thyroid sinus.

They lie embedded in a stratum of connective tissue slightly more condensed than that of the general surroundings. The individual vesicles, and especially those of small size, may be separated from the endothelium of the thyroid sinus by a variable thickness of connective tissue, but a considerable proportion of the larger vesicles project freely into the cavity of the sinus with, at the most, the merest film of connective tissue interposed between their epithelium and the endothelium of the sinus, and in the majority of cases with the epithelial and endothelial cells in actual and close contact (Plate 2, fig. 9).

This intimate relation between the epithelium of a large number of the vesicles and the endothelium of the sinus obtains throughout the gland, not only where the sinus is a relatively simple sac, but in those parts in which it is elaborately folded to form a labyrinth of lymph spaces in the seemingly more solid parts of the organ. The close contact is always obtained by the protrusion of the vesicle into the lymph sac; never, so far as I can see, by the intrusion of lymph vessels from the sac into the stroma and amongst the vesicles embedded in it.

The condition is almost exactly similar to that figured and described by Norris and Ferguson (12, 5) as occurring between the sinusoid veins and the vesicles in Elasmobranchs, where the vesicles project into a large enveloping blood sinus, and the endothelium of the sinus forms a more or less complete investment of the epithelial portions of the gland.

The thyroid body is highly vascular and receives its blood through small branches given off from the hypobranchial arteries. These arterial branches are relatively small, as was found by Norris (12, p. 205) to be the case in Elasmobranchs. In comparison the veins are both large and numerous. Their main factors lie in the connective tissue surrounding the gland outside the vesicular zone. The majority are situated laterally and upon the dorsal surface, forming in the latter position an open plexus around the root of the ventral aorta.

From these anastomosing vessels emissary veins (fig. 2, *a.th.v.*, *p.th.v.*) emerge at either end of the gland; an anterior thyroid vein in front, which, after receiving tributaries from the muscles attached to the symphysis of the hyoid and from the mucous membrane of the floor of the mouth, enters the head of the main trunk of one or both of the subclavian veins (described above, p. 18). The posterior emissary veins in a similar way pass outwards to join the subclavians at a lower level, after receiving factors from the ventral region of the gills.

As might be expected, the arrangement of these veins is open to considerable individual variation, but in it two features appear to be constant—the anastomotic union of the larger tributary veins upon the dorsal and lateral aspects of the thyroid body, and the connection of these tributaries with the subclavians by anterior and posterior emissary veins. The smaller vascular channels and capillaries form around each vesicle an open net-like plexus—far more open in the mesh than the similar plexuses figured by Schäfer for the thyroid of the dog.*

Most of the components of these plexuses are separated by a considerable amount of connective tissue from the epithelial walls of the vesicles, but here and there they come into close apposition to them, with either a film of connective tissue between, or even with their endothelium in actual contact with the epithelium of the vesicle.

The blood vascular arrangement offers a strong contrast to that shown by Ferguson (5, fig. 11) to be characteristic of the Elasmobranchs. In these fishes, in which a lymphatic system has not yet been separated as a morphological entity from the blood vascular system, the thyroid is surrounded and permeated by a lacunar system of venous blood spaces, which closely surround the vesicles, filling in most of the space between them, and are either in direct contact with their epithelium (Norris, 12, p. 205) or separated from it by only a thin layer of connective tissue.

In *Lophius*, on the other hand, in which a lymphatic system is relatively highly differentiated, the condition of the blood-vessels far more closely resembles that characteristic of the thyroid of higher Vertebrates, though the vascular plexuses around the vesicles are more open and consist of larger, and sometimes almost lacunar, component capillaries.

The blood-vessels appear to be the only vascular elements distributed throughout the perivesicular stroma in *Lophius*. I was unable to detect any lymphatic vessels derived from the thyroid sinus or other parts of the superficial ventral system of lymphatics, and no vessels belonging to the special system of "fine" vessels (to be described in Part 3) penetrated to the zone of connective tissue occupied by the thyroid vesicles, though they injected freely in the surrounding areas, lying mainly in contact with the veins and arterial branches.

The intimate connection between the thyroid vesicles and the thyroid lymph sinus is a matter of some little interest, both with reference to the structure of the thyroid

* Quain's "Elements of Anat.," vol. 2, 'Microscopic Anat.,' 1912, fig. 965.

body in man and to the relation that exists between the thyroid vesicles and the vascular system in the Elasmobranch fishes at the other end of the Vertebrate series.

Recently Drs. SCOTT-WILLIAMSON and PEARSE (18) have brought forward evidence to show that in Man a system of sinusoidal lymph spaces in connection with the intralobular lymphatics of the thyroid plays a very essential part in the structure and physiology of the organ. They maintain (18, p. 461) that "the functional gland unit of the thyroid organ is essentially a lymphatic sinusoid, in which float columns of epithelium enmeshed by a highly specialised plexus of blood capillaries." The cells of these columns of thyroid epithelium (or of the vesicles developed from them) are in direct contact with the endothelium of the sinusoid, and the sinusoid and lymphatic vessels in connection with it constitute the main channel for the evacuation of the thyroid secretion, conveying it in the first instance to the parathyroids and the thymus body.

Although, obviously, no direct morphological comparison can be made between the thyroid lymph sinus in *Lophius* and the sinusoids that surround the thyroid units in Man, the similarity that is apparent in the close relation in each case between the thyroid vesicles and the endothelium of a lymph space into which they project, is probably not without physiological significance. And it is interesting to observe that in Elasmobranch fishes, some of the most generalised and primitive of Vertebrates, a somewhat similar condition obtains, although in this group, owing to the still undifferentiated condition of the lymphatics, the sinus that envelops the thyroid vesicles belongs to the blood vascular system rather than to the lymphatic. For it has been shown by NORRIS (12) and FERGUSON (5) that in the Elasmobranchs the thyroid lies within a sinus connected with the inferior jugular vein, surrounded and permeated by it, so that, as NORRIS says (p. 216), "the gland is literally suspended in a lake of blood, the blood being separated from the epithelial structure only by a single layer of epithelial cells."

In comparing this thyroid blood sinus of Elasmobranchs with the lymphatic thyroid sinus of *Lophius*, it is worth while noting that in both cases a valve (NORRIS, 12, fig. 14) is interposed between the sinus and the trunk of the inferior jugular vein with which it is continuous, and probably performs in each case an essential part in the passage of the blood or lymph from the thyroid to the heart. For, as suggested by FERGUSON (5, p. 172), it is likely that "the alternate expansion and contraction of the mouth and pharynx, forcing the stream of water through the branchial clefts, alternately fills and empties the thyroid sinus, so that by means of these respiratory movements the sinus acts somewhat after the manner of a venous heart." Without suitable valves this action would be very uncertain; with a single pair, as in *Acanthias*, fairly efficient; but far more efficient with valves at both entry to and exit from the sinus, as we have seen is the case in *Lophius*.

It will have been noticed that in the above descriptions it has been assumed that the sinus within the thyroid, as far back as the valves situated within the efferent channel, forms part of the lymphatic system.

There can be no question that physiologically this is so, for the cavity contains lymph and not blood; but it is, of course, possible that morphologically both this sinus and its anterior prolongation (anterior lymph trunk) may represent the anterior parts of the inferior jugular vein. This may be so in a sense, and these parts in *Lophius* may represent a specialised portion of the inferior jugular in process of transformation, or segregation, to form part of the lymphatic system--a transformation that in *Scorpœnichthys* has apparently brought about the almost complete separation of the lymphatic pericardial sinus from the inferior jugular vein.

That some such separation of the pericardial lymph sinuses and lymphatics of the thyroid from the inferior jugular system of veins may be taking place in fishes is not altogether unlikely, for there is much evidence to show that the lymphatic system of Vertebrates arises, in ontogeny, from the veins by means of vesicular outgrowths (SABIN, 16, etc.). It is thus in harmony with the results of embryological research to find in the adults of the lower forms of Vertebrates, in which the lymphatics are first to be recognised as an independent system, some confusion between them and the veins, and in the most primitive forms no sharp morphological distinction between the two. Thus in the Elasmobranchs the venous and lymphatic systems are still morphologically one, though the veins, or rather some of them, may sometimes carry blood and sometimes carry lymph. It is therefore not unreasonable to suppose that as the two systems became morphologically distinct, the great thyroid expansion of the inferior jugular vein of the Elasmobranchs became separated into a system of true veins permeating the stroma of the gland, and possibly mainly nutrient in function, and a lymph sinus specially related to the evacuation of the secretions of the thyroid epithelium.

The first beginnings of differentiation seem, in fact, to be already taking place in this group of fishes, for in connection with the venous sinus that envelops the thyroid body, FERGUSON (5, p. 183) describes a plexus of vessels to which he assigns the character of fully differentiated lymphatics, and into some of which he traced the entry of secretion from the cavity of neighbouring thyroid vesicles.

What is apparently an early stage in a similar process of differentiation has been observed by ALLEN (2) in the cartilaginous Ganoid *Polyodon*. In this genus the ventral aorta and its branches are enveloped by a large, irregular, sinus-like expansion of the inferior jugular; but this sinus is not purely venous in character, for there open into it, not only veins, but vessels derived from the lymphatics of the gill arches, containing a fluid poor in red corpuscles, and evidently to be classed rather as lymphatics than as veins.

In Teleosteans the lymphatic system has attained morphological independence, and the separation between the lymphatics and veins in the neighbourhood of the thyroid is complete, except for a connection with the heart through the proximal parts of the inferior jugular. This connection in *Scorpœnichthys* is apparently through some insignificant channel, but in *Lophius* it is effected by the complete incorporation into the

lymphatic system of a large part of the inferior jugular, accompanied by the transference of the blood-carrying factors of this vessel to other neighbouring veins.

Summary.

1. The thyroid body occupies the usual position around the ventral aorta and its branches, but instead of being continuous is hollowed out and occupied by a large lymph sinus, connected, through valved openings, with the ventral superficial lymphatic system and the ventral branchial sinus.

2. The thyroid vesicles project freely into the cavity of this sinus, and in many cases are separated from the contained lymph by the endothelium of the sinus only.

3. The lymph within the thyroid sinus is conveyed direct to the heart by a vein (inferior jugular) which is specialised for this purpose and is without factors.

3. A System of "Fine" Vessels, probably of a Lymphatic Nature.

Whilst making a dissection of the superficial ventral lymphatics, it was noticed that, in addition to the arteries and veins that accompany the fasciculi of large thin-walled channels that form the main trunks of this system, there was an open network of fine vessels of quite a different appearance.

These vessels were relatively minute, and from the thickness and opacity of their walls had the look of delicate white or semi-translucent threads not unlike nerve fibres, with which, indeed, they were at first confused.

The larger components of the system were first noticed upon the ventral surface of the body accompanying the branches of the hypobranchial arteries and anastomosing here and there in an open plexus around these vessels and amongst the fasciculated channels that make up the main trunks of the superficial ventral system of lymphatics.

Little more than this could be made out by simple dissection, as the vessels were very minute, but with suitable injection it became apparent that the system was of very considerable extent, and not only accompanied the branches of the hypobranchial arteries upon the ventral surface of the body, but penetrated into the branchial cavity and was distributed to the mucous membrane of the gill arches, gills and floor of the buccal cavity, and extended above the gills to the cranium and dorsal surface of the body and along the pectoral arch to the vertebral column.

Connected with the larger components of the system there is in all parts of the area to which they are distributed a complex network of extremely slender anastomosing branches (fig. 10), which, owing to their minute size and sharply defined contours, present a very different appearance from the networks formed by the irregular and somewhat varicose vessels of the general lymphatic system (Plate 3, fig. 13). The density of this network differs from place to place; roughly speaking, it is closest and most elaborate upon the mucous membrane of the mouth, upon certain parts of the gills,

upon the periosteum of the gill arches and shoulder girdle, and upon the walls of the arteries and lymph sinuses, and most sparse and open in the loose subdermal and intermuscular connective tissues, and in the muscles.

Although everywhere the main components of the system are surrounded by a multitude of these fine anastomosing vessels, it is often difficult with the naked eye to trace the connection between the two. For in many cases the fine constituent vessels of the network arise independently, or in small bunches, from a main component and not from the breaking up of branches of any noticeable size or length. For this reason it is difficult to treat in one description both the main trunks of the system and their branching networks, and I propose to give an account in the first place of the general disposition of the main trunks, adding later some details of the fine plexuses by which they are surrounded and to which they give rise.

A. *The Main Components.*

In tracing the larger vessels of the system towards the mid-ventral line of the pharynx, either from the open networks that they form amongst the lymphatics and arteries upon the ventral surface of the body, or in the other direction from the plexus that they form in the gills, one is struck by the fact that as the larger vessels of both plexuses come in either direction towards the anterior end of the pericardium, they become simplified and their constituents ultimately combine to form a single trunk* of relatively large size (1 mm. diameter) that forms a common connecting stem between the two (figs. 7, 8, *m.f.*).

This trunk, which lies upon the lateral wall of the thyroid body and extends thence across the ventral surface of the pharyngeal floor to the point of entry of the first afferent branchial artery to the gill-chamber, forms, in fact, a main common stem or focus for the entire system of vessels. From it, on the one hand, branches out upon the ventral surface of the body a plexus of finer vessels, which is ultimately resolved into intricate capillary networks in the skin and elsewhere; on the other hand, from its opposite extremity are given off networks of vessels that break up into capillary plexuses upon the gills, the buccal membrane, and the walls of the lymph sinuses at the base of the skull, and the skin upon the dorsal surface of the head and fore part of the trunk.

The entire system of fine vessels has thus the arrangement commonly associated with a portal circulation—a circulation, that is, in which the circulating fluid is brought from a capillary network to a main trunk, from which it is in turn distributed into a second system of capillaries.

This seems to me the only way in which to interpret the convergence of these two vascular networks upon a common central stem. For if the flow of fluid does not take place as in a portal system through this stem from one capillary network to the other, drainage must be from each network towards the central stem, and there must of

* This stem may show subdivision—*see* left side, fig. 6.

necessity be an outlet from the common stem into some other part of the vascular system. But I am convinced, both by dissection and by the study of serial sections, that there is no such outlet from the central main stem. For apart from the fact that injection does not flow freely from this system of vessels into any other, as it almost certainly would do were the common stem of the system, a factor of some other part of the vascular or lymphatic systems, the common stem can easily be traced by dissection from one plexus to the other, and at no part of its course is it in close contact with either a blood vessel or lymphatic channel, but lies practically free in a stratum of loose connective tissue.

B. *Distribution of Main Components on Ventral Surface of Body.*

The main stem (figs. 6, 7, 8, *m.f.*) when followed ventrally is found to pass alongside the root of the hypobranchial artery between the thyroid body and subthyroid lymph sinus towards the mid-ventral line. At the point where the two roots of the hypobranchial arteries unite to form a common longitudinal stem, the vessel subdivides and forms around the arterial union a plexus of a few meshes connecting it with its companion vessel of the opposite side.

Anteriorly this meshwork, or the larger stems from which it arises, gives origin to some minor twigs, and in particular to a couple of branches (figs. 7, *a*) of some size that unite to form a median vessel that runs forward upon the surface of the anterior trunk of the ventral lymphatic system, and after receiving a branch (figs. 7, 8, *b*) derived from the lingual plexus (described below) is distributed to the genio-hyoid muscles, the skin behind the symphysis of the jaw, and a large part of the ventral surface of the branchiostegal membrane.

Posteriorly the united main stems are continued back as a single or double vessel (figs. 7, 8, *c*) on either side of the median trunk of the hypobranchial artery amongst the cavernous spaces of the sub-thyroid lymph sinus to the point where the artery again divides into its right and left main branches. At this level the vessel again subdivides and anastomoses, forming an open longitudinally drawn-out plexus, which is continued backwards on either side along the corresponding branches of the hypobranchial artery and the main channels of the ventral system of lymphatics to the cloaca, either as a single vessel (figs. 6, 7, *d*) or more often as an elongated network of a few simple meshes.

From this vessel, or plexus of vessels, offshoots accompany the integumentary branches of the hypobranchial arteries and lymphatics, spreading beneath the skin upon the ventral surface of the pharynx and anterior part of the body, and forming in particular a rich plexus upon and around the pelvic fins.

Opposite the base of the pelvic fin the main longitudinal trunk, or plexus, gives off two branches of outstanding importance (fig. 6, *e*, *f*) which follow the arteries and lymphatics of the fin, and, like them, form within the embrace of the bifurcated bases of

the fin rays a continuous arcade (fig. 6, *pv.l.*) from which smaller branches pass to the distal extremity of the fin between the rays.

Another constant and important branch is associated in a similar way with the blood-vessels and lymphatics of the pectoral fin. It arises from the main longitudinal trunk close behind the symphysis of the clavicles (figs. 6, 7, *cor.f.*), and passes, in company with

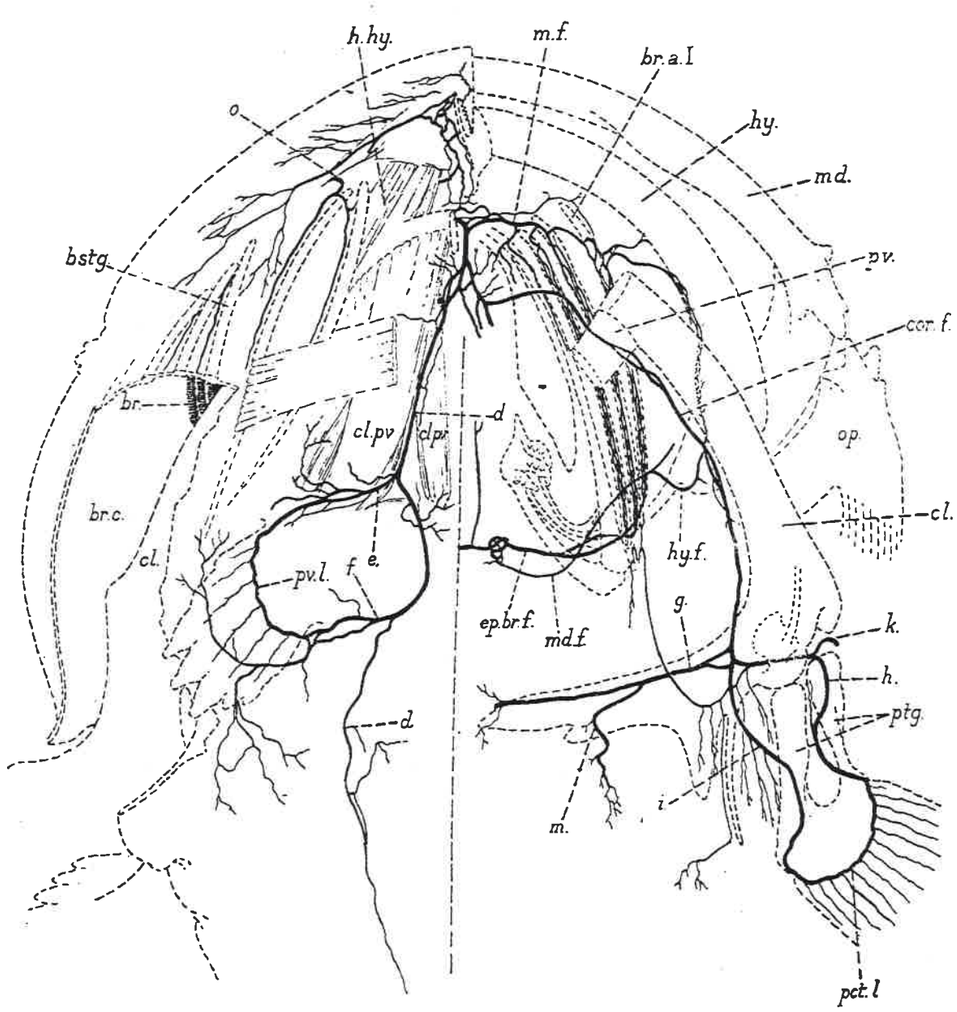


FIG. 6.—Diagram showing the distribution of the larger components of the system of "fine" vessels to the ventral surface of the body, to the paired fins, and to the gills. The diameter of the vessels is not to scale. Surface of body on left, skeleton on right, "fine" vessels: black.

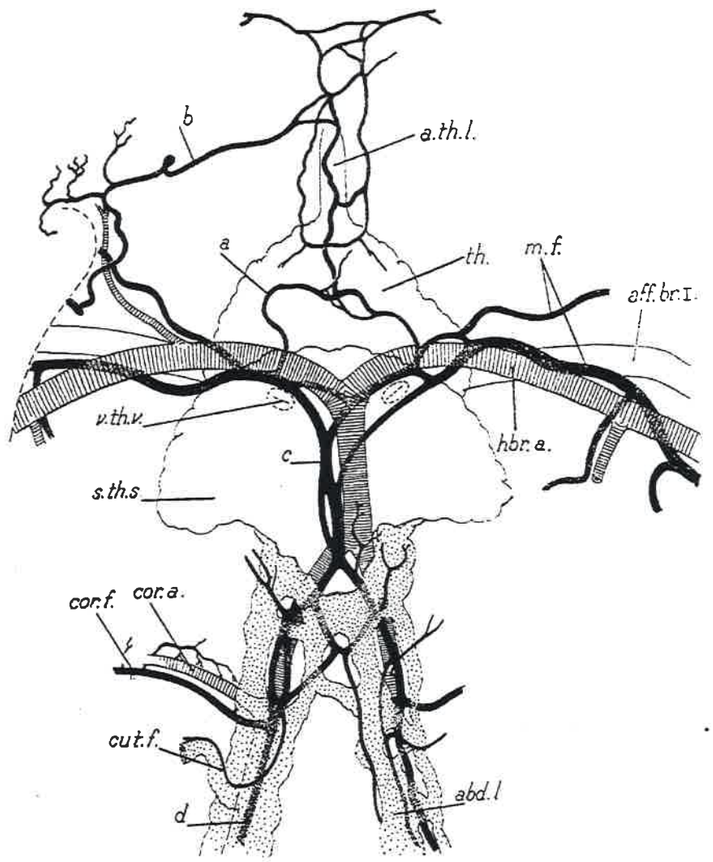


FIG. 7.—The plexus of " fine " vessels issuing from the main trunks of the system between the thyroid and sub-thyroid lymph sinuses, and accompanying the chief components of the superficial ventral lymphatics. Lymphatics: dotted; " fine " vessels: black; hypobranchial artery: cross-hatched.

the coracoid branch of the hypobranchial artery, outwards and dorsal, between the pericardium and the pelvic and trunk muscles that arise from the clavicles, to the joint that unites the pelvis to the pectoral arch. Here it enters the wall of the great pectoral lymph sinus that runs along the mesial border of the clavicle, and, passing dorsal to the pelvis, continues back in the wall of this sinus in close association with the coracoid artery and vein to the junction of this artery with the subclavian upon the inner surface of the ascending arm of the clavicle.

At this point, close to the coracoid cartilage, it breaks up into a small plexus and gives origin to numerous branches. Three of these (fig. 6 *g*, *h*, *i*) are larger than the rest and form, in fact, divergent terminal divisions of the main stem: (1) (fig. 6, *h*), a vessel

that passes outwards, through the coracoid to the outer side of the articulation between the shoulder girdle and the fin, and, passing distally between the pterygiophores, enters the outer margin of the base of the fin, to traverse the canal embraced by the bifurcated ends of the fin rays, and unites with the second division in an arcade (fig. 6, *pct.l*) similar to that described above in connection with the pelvic fin.

At the point where this first division of the coracoid vessel emerges from the joint between shoulder girdle and fin, it gives off a large branch (figs. 6, 9, *k*) that spreads out over the dorsal surface of the hinder end of the gill chamber and in the subdermal tissues of the fin, and, in addition, sends forward a strong branch along the thymic artery (fig. 9, *l*).

(2) The second division (fig. 6, *i*) forms the mesial arm of the arcade just described. It passes from the plexus formed by the breaking up of the main coracoid vessel along the mesial and ventral surfaces of the fin, and enters the canal between the bases of the fin rays at its inner extremity, to become continuous with division 1 (*h*). In its course it gives off numerous small branches that spread richly within the subdermal tissues upon the ventral surface of the fin.

(3) The third division (figs. 6, 9, *g*) follows the subclavian vessels towards the vertebral column, and shortly gives origin to a large branch (figs. 6, 9, *m*) that accompanies the lateral artery into the lateral lymphatic canal and forms upon the walls of the latter an intricate network of finer vessels. The main stem continues its course along the ascending arm of the clavicle to the vertebral column, and passing in front of the first spinal nerve, emerges beneath the skin of the back close to the mid-line. Here it divides (fig. 9, *n*) and, running fore and aft, forms an anastomosing chain of small vessels associated particularly with the muscles and integument of the modified rays of the dorsal fin.

In addition to these three main divisions, the coracoid vessel gives off from its point of subdivision numerous smaller branches, which are distributed mainly to the lateral body muscles and (in rich quantity) to the integument and muscles that border the posterior opening of the branchial chamber.

The above are the chief constituents of the plexus of " fine " vessels distributed mainly to the ventral aspect of the fish. They are closely associated with the hypobranchial arteries and their branches, and, as stated above, unite in front between the thyroid body and the subthyroid lymph sinus, to form on either side a main stem which runs transversely outwards upon the ventral and lateral walls of the thyroid body towards the branchial chamber.

C. *Distribution of the Main Components within the Branchial Chamber.*

The main stem of the system, formed as just stated by the union of the ventral plexus of fine vessels, when traced from its position upon the surface of the thyroid body towards

the gills, may remain single till it enters the branchial chamber (fig. 8, *m.f.*), but more often is divided into two (fig. 7, *m.f.*). It crosses the space between the thyroid body and the anterior end of the gills in company with the hypobranchial and first afferent branchial arteries (fig. 8). Close to its entry with these vessels into the gill chamber it gives off posteriorly a pharyngeal branch (fig. 8, *p*) of some size that accompanies a corresponding branch of the hypobranchial artery, and breaks up with it in the base of

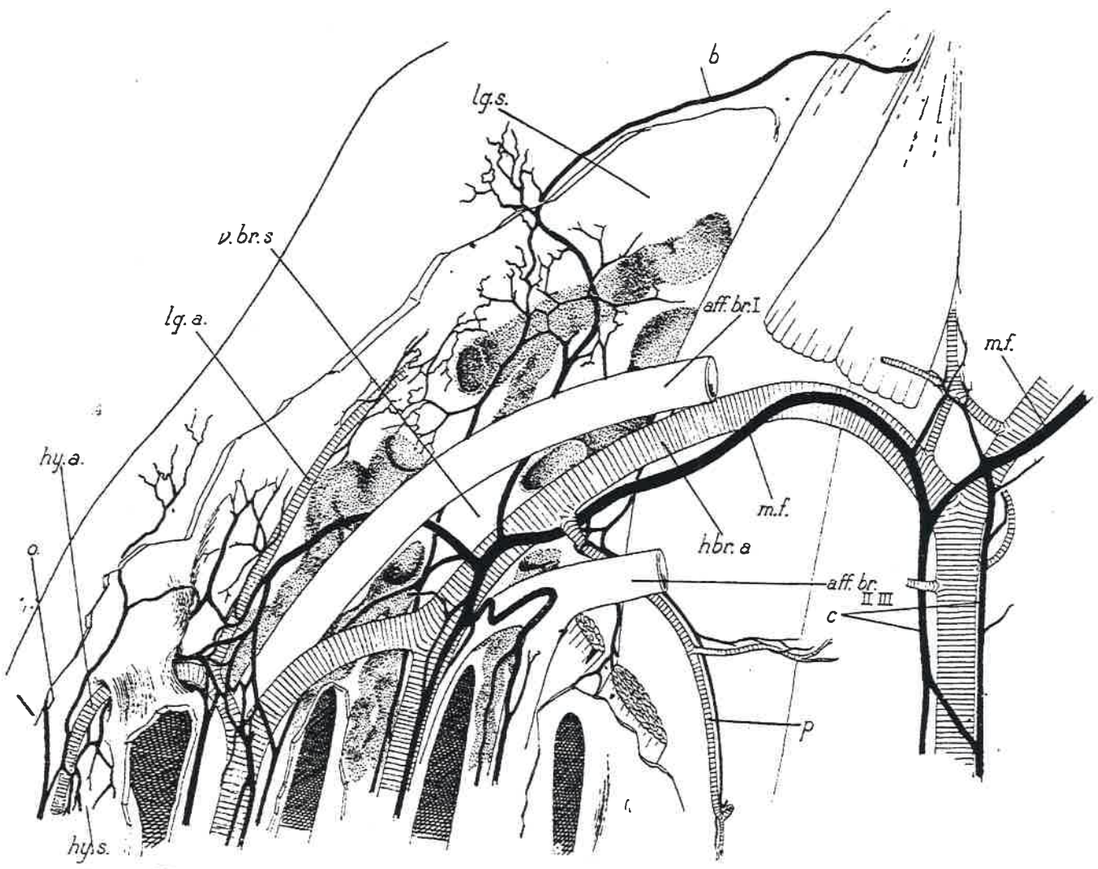


FIG. 8.—The plexus of "fine" vessels (black) issuing from the branchial extremity of the main trunk of the system and distributed to the tongue, hyoid and branchial arches. Veins: dotted, afferent branchial arteries: white, hypobranchial artery: cross-lined.

the tongue dorsal to the transverse pharyngeal muscles, and in the connective tissue that separates these muscles from the pericardium, and also sends branches to the oral surface of the fourth and fifth gill arches.

After its entry into the branchial chamber the main stem (or its two divisions) sub-

divides (fig. 8) to form a network of vessels within the large lymph sinus (ventral branchial sinus) that lies above and around the cartilaginous extremities of the first three branchial arches. This sinus, it will be remembered, communicates mesially through a valved orifice (fig. 2, *l.th.v.*) with the lateral lymph channel of the thyroid sac, and in the opposite direction extends as a meshwork of anastomosing spaces along the branchial vessels lying within the concavity of each gill arch. Anteriorly it is in communication with a large sinus situated along the dorsal margin of the hyoid (fig. 8, *hy.s.*), from which an offshoot runs forward into the tongue (fig. 8, *l.g.s*).

The plexus of " fine " vessels formed within the walls of this sinus by the subdivision of the main trunk sends offshoots of some size into its hyoid and lingual extensions in close association with the hyoid artery and its lingual branch (fig. 8, *hy.a.*, *lg.a.*).

From the major components of the lingual plexus a vessel of considerable size (figs. 7, 8, *b*) runs forward and towards the mid-line to join (as mentioned above, p. 30), the vessels that accompany the anterior trunk of the ventral lymphatic system, and thus to take part in the plexus of " fine " vessels distributed to the ventral surface of the intermandibular space and the branchiostegal membrane.

In a somewhat similar way two or more vessels (figs. 6, 8, *o*) arise from the hyoid plexus, and after curving across the outer face of the hyoid bone, emerge upon the ventral surface between the heads of the branchiostegal rays. From this point they, or their branches, run backwards close alongside the rays, and are distributed to the membrane between them. Other subdivisions of the main plexus in the ventral branchial sinus extend posteriorly within the concavity of the first three gill arches, forming a longitudinally drawn-out network amongst the lymphatic spaces that envelop the branchial arteries and nutrient veins.

At the upper (posterior) extremities of the gills the larger members of the plexus situated within the concavity of the branchial arches emerge, together with the epibranchial arteries (fig. 9, *epbr.f.*) and pass along these vessels towards the basis cranii.

After leaving the gills, the vessels (fig. 9, *epbr.f.*) unite to form a single trunk that passes towards the cranium alongside the first epibranchial artery, between it and the efferent artery of the pseudobranch. On a level with the origin of the internal carotid from the first epibranchial artery, this main vessel divides in a plexiform manner and gives origin to a strong branch associated mainly with the lower jaw and suborbital region of the face.

This branch (fig. 9, *md.f.*) passes outwards upon the hinder wall of the orbit and follows the posterior origin of the adductor mandibulæ, deep to the muscle, upon the outer surface of the suspensorium, to the mandibular joint, its ultimate branches being distributed to the outer and inner surfaces of the lower jaw.

On a level with the attachment of the epihyal to the inner surface of the suspensorium, the mandibular vessel is joined by one of somewhat smaller size (fig. 9, *hy.f.*) which emerges from the deep aspect of the hyoid bone, and is derived from the upper end of the plexus of vessels that accompanies the hyoid artery within the hyoid lymph sinus.

From this vessel minor branches are distributed to the skin overlying the mandibular suspensorium and operculum.

The large mandibular vessel in the upper part of its course gives off a large branch forward across the ventral area of the floor of the orbit (fig. 9, *q*), which, after sending a few twigs to the origin of the suborbital muscle sheet, emerges to the surface at the lower anterior border of the orbit and is distributed mainly in a fine meshwork to a gelatinous body described by TROIS (23).

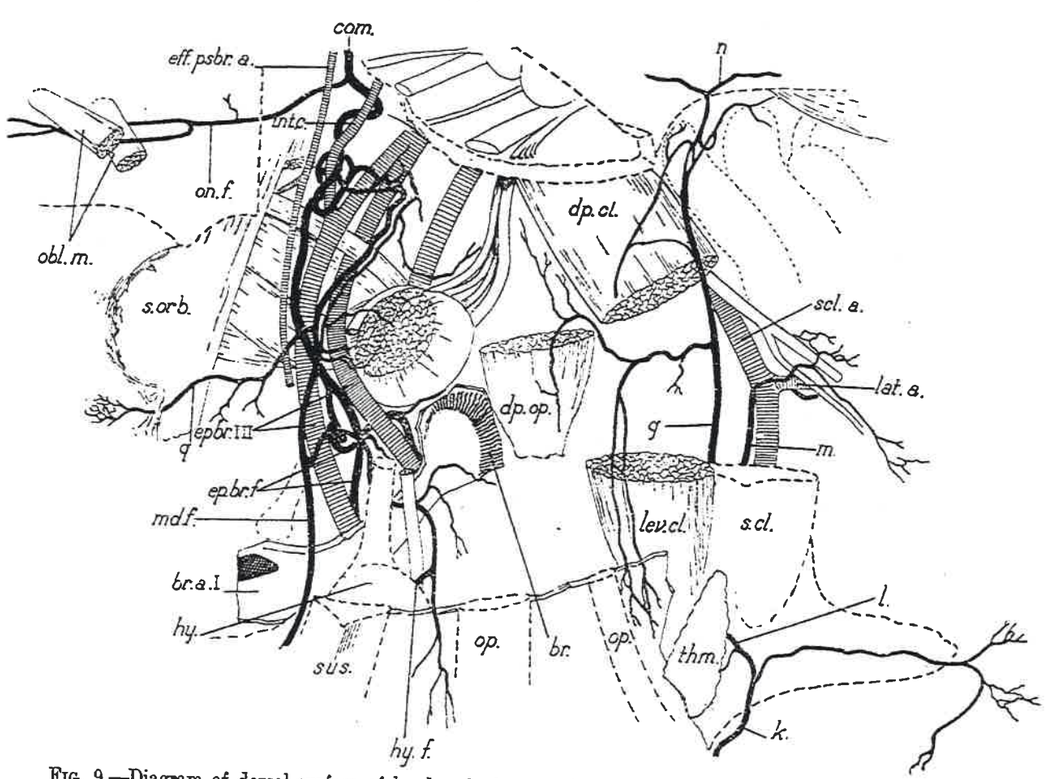


FIG. 9.—Diagram of dorsal surface of head and pharynx showing the termination of the "fine" vessels issuing from the dorsal extremities of the gills, and of the main stem of the coracoid branch.

After the separation from it of the large mandibular vessel, just described, the main trunk coming up from the gills enters the myodome in company with the internal carotid artery, and there forms a commissural connection (fig. 9, *com.*) with its fellow of the opposite side. Whilst within the myodome it gives off a large branch (fig. 9, *on.f.*) that follows the orbito-nasal artery across the dorsal surface of the suborbital muscle sheet, and, passing in two divisions deep to the oblique muscles of the eye close to their origin from the cranium, is distributed to the snout and to the gelatinous body that lies in front of the orbit.

D. *Distribution of the Finer Networks.*

The foregoing description includes only vessels of any noticeable size, but it must be borne in mind that they are but the larger members of a rich plexus of far finer vessels (fig. 10), that ramify in all directions between and around the larger and more conspicuous trunks and form in particular elaborate networks upon the arteries and veins, and in the walls and trabeculæ of the lymph sinuses with which some of these blood-vessels are associated.

The distribution of the minute ultimate constituents of the system was determined by water-pressure injection, using as an injection mass either a weak gum or cold gelatine solution with indian ink, prussian blue, or barium sulphate. In the more successful injections the mass penetrated into the very finest branches, and I am confident that practically the whole system was filled.

As the injection proceeded, a flush of colour spread over the skin of the ventral surface of the body, the mucous membrane of the floor of the mouth and branchial apparatus and other unpigmented parts of the head and anterior end of the body, the colour of the injection being specially marked upon the pelvic fins and the mucous membrane, of the tongue and gill arches and the lining of the branchial chamber.

Examination of pieces of skin and mucous membrane, cleared in oil of winter-green, showed that the coloration was due to the injection of open networks of extremely fine and sharply defined vessels, which differed entirely in character from the closer networks formed by the more or less irregular fasciculated bundles of the ordinary lymphatics (*cf.* Plate 3, figs. 13, 14).

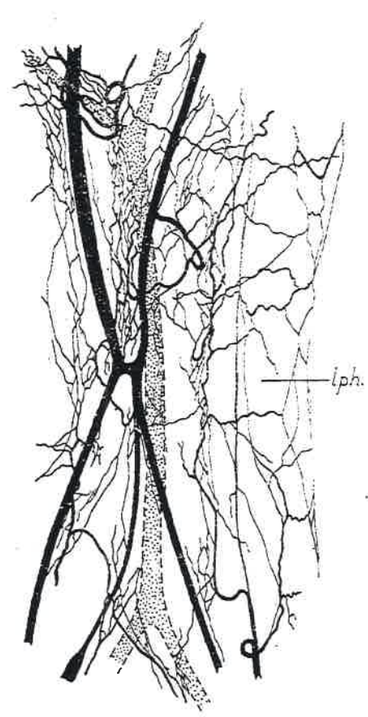


FIG. 10.—Camera lucida drawing of a portion of the hypobranchial artery, showing the chief trunks and networks of the "fine" vessel system associated with it and with the main channels of the ventral system of lymphatics. Artery: dotted; "fine" vessels: black.

In the skin and the mucous membrane of the mouth and pharynx the ultimate network of these "fine" vessels is more open and lies at a slightly deeper level than that formed by the lymphatics, though it is closely applied to it. Its components lie usually alongside a small blood-vessel or capillary. This close association with the blood-vessels is, in fact, characteristic of the system as a whole, and is even more intimate in its deeper and coarser parts; for here the various component vessels of the networks

not only closely accompany the arteries and their branches, but frequently penetrate the outer layers of their walls by small tufts and arborisations (fig. 12, A).

When the skin is removed from the ventral surface of the body, the loose subdermal connective tissues are seen to be riddled by an open plexus of " fine " vessels, resembling nothing so much as a reticulum of the finest hairs. This subdermal plexus serves, no doubt, mainly, if not entirely, to connect the superficial network to the larger vessels of the system that accompany the blood-vessels and lymphatics situated upon the fascia of the muscles of the body and pelvic fins. The subdermal network is richest in the mid-ventral region of the body, more particularly beneath the pericardium, around the clavicular symphysis and upon and around the pelvic fins. From the subdermal tissue it penetrates amongst the inter-muscular connective tissue dorsal to the transverse branchiostegal muscles, and can be traced, though much reduced in quantity, into the substance of the neighbouring muscles, extending posteriorly over the ventral body wall to the anus and passing through the abdominal muscles to the subperitoneal connective tissue.

The plexuses of fine vessels show an increased richness and complexity in the neighbourhood of the main trunks of the ventral lymphatic system (fig. 10), and especially so amongst the anastomosing spaces of the sub-thyroid sinus around and in front of the coalescence of the roots of the hypobranchial arteries, spreading to the surface of the clavicles and covering the ventral surface of the branchiostegal membrane.

Fine but open networks cover the pericardium and extend to the anterior parts of the peritoneum; a delicate reticulum also permeates the loose connective tissue that fills in the space below the floor of the pharynx between the thyroid body and the branchial chamber. Small branches of the system can also be traced into the connective tissue surrounding the thyroid body, but, as mentioned previously (p. 25), seem to be confined to its more superficial parts in association with the larger blood-vessels and to have no relation to the thyroid vesicles.

In connection with the important main branch of the system that follows the coracoid artery is a rich plexus distributed upon the walls and trabeculæ of the large pectoral lymph sinus in which the artery and its companion vein lie. The plexus closely surrounds the blood-vessels and spreads itself upon the periosteum of the clavicle and to some extent penetrates the neighbouring muscles. The posterior part of this plexus follows the subclavian vessels and the great transverse arm of the pectoral lymph sinus in which they lie, being distributed upon and around the blood-vessels and in the walls of the lymph sinus, extending for some distance backwards along the lateral lymph sinus and upon the capsule of the kidney, amongst the roots of the anterior spinal nerves, and upon the periosteum of the vertebral column, spreading thence to the skin upon the dorsal surface of the body.

Beneath the mucous membrane of the mouth and pharynx a looser reticulum connects the surface network with a coarser plexus distributed in the walls and trabeculæ of

the ventral branchial, hyoid, and lingual lymph sinuses, and around the roots of the hypobranchial artery and its hyoid and lingual branches.

Fine plexuses are also richly distributed to the periosteum of the hyoid and branchial arches, and follow the blood-vessels and lymphatic spaces that lie in the concavity of the gill-bearing arches to the dorsal extremities of the gills, spreading thence to the walls of the cephalic lymph sinus situated beneath the cranium and to the epibranchial and internal carotid arteries, and to the roots of the neighbouring cranial nerves.

In connection with the vessels that emerge from the upper ends of the gills and with the terminal branches of the coracoid vessel are rich superficial plexuses distributed over both surfaces of the lower jaw, upon the palate, and upon the skin of the dorsal surface of the face, gill chamber, and trunk. These plexuses are particularly strong at the angle of the mouth, along the lateral borders of the head, and upon the skin of the pectoral fin.

In the hollow of each gill-bearing branchial arch the finer plexuses form a rich network amongst the anastomosing spaces of the branchial lymphatic system, and around their own chief trunks of origin and the main afferent and efferent vessels of the gill. At the base of the filamentous part of the gill they are somewhat condensed, forming on the level of the main afferent vessel a network in which the meshes are mainly drawn out parallel to the long axis of the gill. Offshoots from this longitudinal condensation pass up the edges of each filament, forming a superficial network around the main respiratory vessels of the filament (Plate 3, fig. 16) lying in the connective tissue that surrounds the blood-vessels, and apparently connected here and there across the breadth of the filament by branches running in the septum to which the respiratory laminæ are attached. The individual vessels of the plexus are closely applied to the nutritive blood-vessels of the filament, but are not in open communication with them.

This absence of communication is quite clear from injections of the "fine" vessels and of the blood-vessels, examined both as surface preparations and in section. The several systems injected freely, but in no case did the injection mass show any indication of having passed from one to the other.

As a result of these injections, it can be stated that within the gill filament there are, in addition to the respiratory blood circulation and lymphatics, three systems of vessels: (1) nutrient arteries arising from the efferent filamentary vessels, as described by Müller (11) but denied by Riess (15); (2) nutrient veins; (3) plexuses of "fine" vessels differing markedly in structure and general appearance from the corresponding plexuses of lymphatics (*cf.* Plate 3, fig. 16, text-fig. 11) and without direct connection with the blood-vessels, either nutrient or respiratory.

Injection thrown into any of the blood-vessels was always confined to them and never appeared in the plexus of "fine" vessels and, *vice versa*, injection into the system of "fine" vessels did not find its way into either the nutrient blood-vessels or the respiratory vessels of the gill.

I have entered somewhat fully into the relationships of the blood-vessels and "fine" vessels within the gill filament as it seemed to be a possibility, especially in view of ALLEN's (2) description of the branchial nutritive arteries of *Polyodon*, that the entire

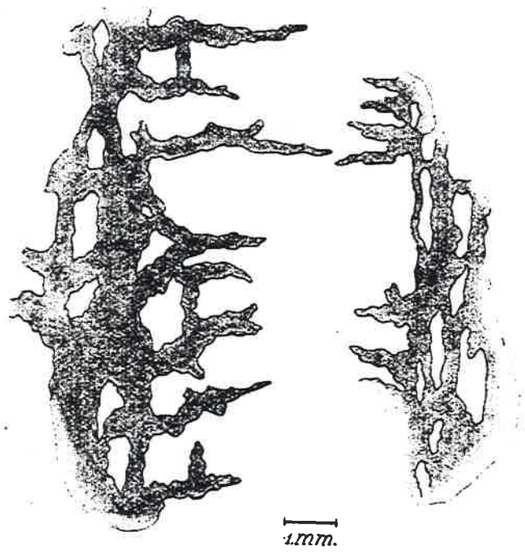


FIG. 11.—Camera lucida drawing of lymphatic network in gill filament.

system of "fine" vessels described above in *Lophius* might belong to the system of nutrient branchial arteries, taking origin from the efferent vessels of the gills and extending thence along the hypobranchial arteries. This possibility, and the further one that the "fine" vessels might find their origin in the gill filaments, if not as nutrient branches of the efferent filamentary vessels, then as offshoots of the afferent respiratory system, must be ruled out.

The above description will, I hope, give some idea of the character and extent of distribution of the fine plexuses in which the main trunks of this system of "fine" vessels terminate. The area of distribution covers practically the whole of the head and fore-part of the body as far back as the cloaca, and agrees in large part with the distribution of the hypobranchial arteries and their main branches.

Everywhere within this area, except upon the abdominal viscera, elaborate networks of "fine" vessels accompany the arteries and the branches of the ordinary lymphatics and permeate the connective tissues, varying in richness in different parts, but forming their finest and most elaborate plexuses upon exposed surfaces, such as the skin, the mucous membrane lining the mouth, the gills, and the walls of the branchial chamber, and upon the walls of the blood-vessels and certain of the lymph sinuses.

Before attempting to discuss the nature of these vessels and their relation to the

rest of the vascular system, there are certain points to be emphasised or considered in further detail. It was noted that the vessels that compose this system were, in comparison with the general run of the lymphatics, remarkably small and thick-walled. The thickness of their walls was noticeable even to the naked eye, and suggested a likeness to a small artery rather than to a vein or lymphatic. A section through the main trunk of the system, when compared with the hypobranchial artery alongside it (Plate 3, fig. 17), shows that in the thickness of their walls there is very little difference between them. In their intimate structure also the "fine" vessels agree very closely with the arteries, though their walls are somewhat more elastic.

The lumen of the vessel is lined by an endothelium of protruding cells, the appearance of protrusion being, I think, mainly due to the strong pleating of the elastica interna. Outside the intima is a muscular "media" varying in depth with the size of the vessel, but taking up, on an average, from one-third of the thickness of the entire wall in the larger vessels to one-fourth in those of lesser diameter.

The media is surrounded by a thick adventitia of felted connective tissue.

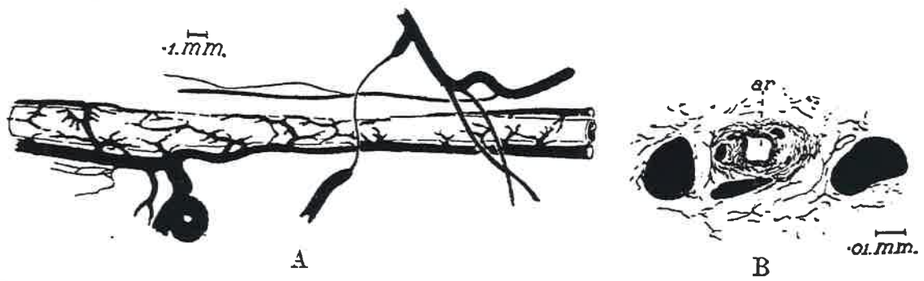
The elastic constituent of the wall is remarkably well developed (*cf.* Plate 3, figs. 18 and 19); it consists of a strong elastica interna, forming a stout, deeply pleated sheet external to the endothelium, and of a close network of elastic fibres in the adventitia; in the media there is little or no elastic tissue.

A similar structure is shown by the larger vessels and those of moderate size, but in vessels of quite small diameter (0·025 mm.) the elastic network is absent from the adventitia, though the elastica interna remains strong and there is still a muscular media one or two cells in thickness.

The structure of these vessels is thus in every way far more like that of an artery of corresponding size than that of a vein. The walls of the latter (in the thyroid body, for example) are practically without muscle and show but little concentration of connective tissue to form an adventitia, and only a very slight development of elastic tissue, with no very clearly defined elastica interna. Still less do the walls of the "fine" vessels resemble those of the spacious channels of the lymphatic system, which consist practically of a layer of flattened endothelium alone, with little or no concentration of fibrous and elastic tissue around it.

In describing the networks of minute vessels derived from the larger trunks of this system of "fine" vessels, it was observed that they were often in close contact with the blood-vessels and lymph sinuses. This close connection is, in fact, one of their most striking peculiarities, for, although the networks permeate in a general way the connective tissues throughout their area of distribution, they are especially rich in and near the walls of the lymphatic sinuses and around the blood-vessels. Their relation to the arteries in particular is of the most intimate character, resembling that of vasa vasorum. From the meshes of the networks that accompany the various arterial branches small offshoots arise here and there and immediately break up against the wall of the blood-

vessel, either in the form of small brushes of minute vessels or short claw-like processes (fig. 12, A) that dip into the wall of the artery and are lost in the adventitia (fig. 12, B).



A B

FIG. 12.—A. Part of a small branch of the hypobranchial artery, showing the distribution upon it of branches of the "fine" vessels. "Fine" vessels, black. B. Transverse section of small artery showing branches of "fine" vessels penetrating its walls. "Fine" vessels, black.

A connection of this kind was not observed to occur between the "fine" vessels and the veins, for, although the networks of "fine" vessels followed the larger veins closely and were in intimate contact with them, they did not appear to send offshoots into their walls. On the contrary, the veins at their capillary ends occupied a relation to the "fine" vessels the reverse of that of the arteries. It was observed, for instance, in the mucous membrane of the tongue, that the smaller veins accompanied the components of the "fine" vessel network, forming around them close plexuses of minute venules (fig. 13).

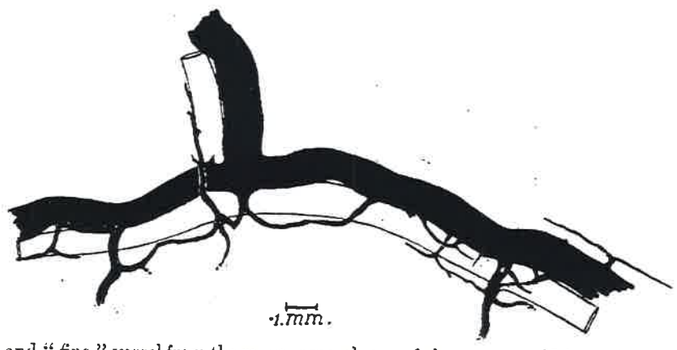


FIG. 13.—Vein and "fine" vessel from the mucous membrane of the tongue. Vein: black; "fine" vessel: white.

Although the relation of the "fine" vessels to the blood-vessels is of this intimate character, there is no evidence whatever to show that there is any direct communication between them—in no case has injection passed either from the blood-vessels into the "fine" vessels or from the "fine" vessels into either the arteries or the veins.

The relation of the "fine" vessels to the lymphatics is a question that has caused

me a great deal of perplexity, and upon which the evidence is not complete or fully satisfactory.

It has been mentioned that the "fine" vessels accompany the ordinary lymphatics and form peculiarly rich plexuses in the walls and trabeculæ of many of the lymph sinuses. I have not, however, been able to detect any communication between the larger components of these plexuses and the cavity of the sinus, although such evidence as I have is sufficient to show that the "fine" vessels do form a connection with the lymphatic system.

Repeated injections have produced somewhat contradictory results. Injection thrown into the "fine" vessels has sometimes, though not always, made its way to some extent into the lymphatics, appearing most often in those situated in front of the clavicular symphysis upon the intermandibular floor or in those distributed over the branchiostegal membrane and partially filling several of the large sinuses. The fact that injection passes only with difficulty and sometimes not at all from the system of "fine" vessels to the lymphatics, added to the fact that no connection could be traced by dissection between the two systems, suggests that the connection between the two cannot be of an open nature, but that it takes place probably through the capillary ends of the two systems, or at least between their finer constituents.

When dealing with such delicate structures as the lymphatics of *Lophius*, there was always the danger that constituents of the "fine" vessel system, when injected, might rupture into one of the fasciculated lymph channels or sinuses with which they are often in such close contact; and the capriciousness with which injection found its way into the lymphatics made me for a long time hesitate to assume that there was, in fact, a natural connection between the two systems. As the result of a recent and more perfect injection (cold gelatine and prussian blue) I am, however, certain that there is a connection, and that it takes place, at any rate in part, in the mucous membrane of the mouth and pharynx through the terminal branches of the "fine" vessels and lymphatics.

In the injection in question the mass was inserted into the "fine" vessel system through the main trunk issuing from the ventral end of the gill chamber, and was found to have penetrated into the lymphatics in the skin and the mucous membrane of the mouth and pharynx, and to some extent into most of the main lymph channels and sinuses of the fore-part of the body.

Although the injection mass only partly filled those of the larger lymph trunks and sinuses into which it had penetrated, the smaller and more superficial lymph vessels were well filled in every part that I examined (skin, branchiostegal membrane, mucous membrane of the mouth, gill chamber and branchial arches). These minor vessels presented the irregular plexiform appearance characteristic of the lymphatics, and could everywhere be readily distinguished, both by this appearance and also in most places by a less deep coloration of the injection mass within them, from the networks of sharp outlined and densely injected "fine" vessels by which they were accompanied. In the mucous membranes, for instance, or the skin, the "fine" system could be traced as

an open network of simple, sharply defined vessels lying upon, but independent of, an accompanying plexus of irregular freely anastomosing channels (figs. 14, 15).

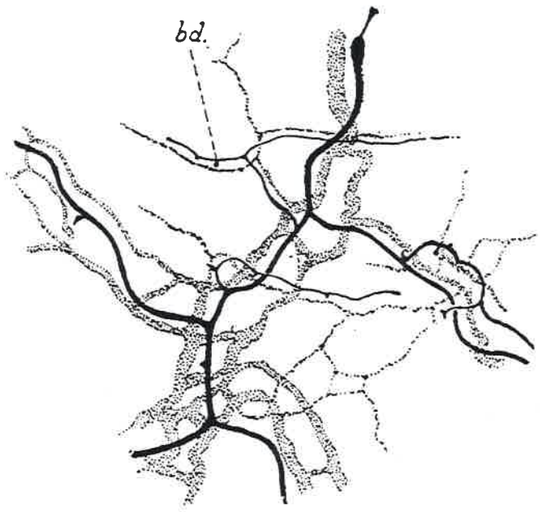


FIG. 14.—Part of the superficial plexus of "fine" vessels and lymphatics in the mucous membrane at the outlet of the branchial chamber. "Fine" vessels, black; lymphatics, dotted.

This irregular plexus may (especially in its deeper parts) (Plate 3, fig. 15) be distributed without any very definite relation to the course assumed by the "fine" vessels, but in most parts the relationship between the two (probably determined by the course of a blood-vessel) is very characteristic, with the "fine" vessel disposed in the centre of an irregular ladder-like plexus of lymphatics (fig. 15).

The two systems of vessels (except for the connections to be described later) remain separate to their finest extremities, and it seems that the ultimate network beneath the epithelium of the skin or mucous membrane consists solely of capillaries in direct continuity with the ordinary lymphatics, but united (as described below) by small transverse connectives to the accompanying independent network of "fine" vessels.

In the mucous membranes the smaller branches of the "fine" vessel system show at intervals, projecting at right angles from their surface, curious little club-shaped processes (figs. 14, 16, *bd.*), like buds. In the apex of each of these the more solid parts of the colouring matter of the injection mass were concentrated, so that each bud showed up black in contrast to the deep blue of the vessel from which it projected. In almost all cases the extremities of the buds lay near or upon one of the components of the accompanying lymph plexus, and in a few favourable instances a feebly injected vessel could be seen connecting the apex of the bud to the lymphatic (figs. 16 *con.*, 17).

Wherever a bud was not thus in close association with the lymphatics, but lying at a distance from them and apparently ending blindly, it was observed that its apex was in close apposition to the wall of a minute blood-vessel, though not in open communication

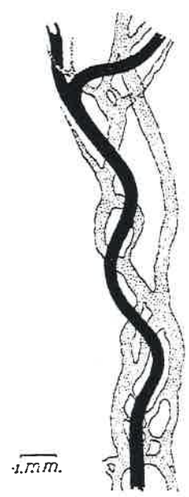


FIG. 15.—" Fine " vessel and accompanying lymphatic plexus from the skin in the neighbourhood of the pelvic fin. " Fine " vessel, black; lymphatics, dotted.

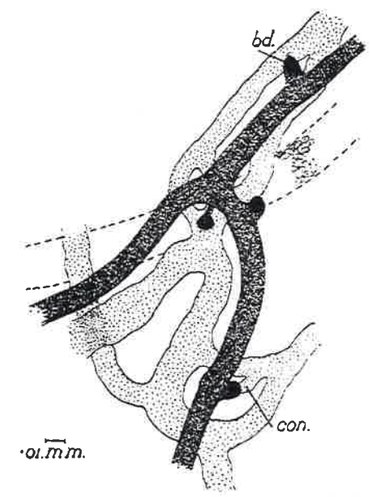


FIG. 16.—" Fine " vessels (dark) and lymphatics in mucous membrane of tongue, showing bud-like valved connectives between the two.

with its lumen. It seems that the buds may be of two kinds, blind protrusions applied to a blood-vessel, or short connectives joining the " fine " vessel network to the neighbouring plexus of lymphatics. In the latter case, which is far the more usual condition, the deeply pigmented swelling represents, no doubt, a point of blockage upon the course of the connective. Swollen connectives of this kind are, so far as I have observed, restricted almost entirely to the networks in the mucous membrane of the mouth, pharynx, gill chamber and gills. In these membranes they are quite numerous; I have also seen one or two in the skin of the branchiostegal membrane in the neighbourhood of the exhalent orifice of the gill chamber, but was unable to find any connections of this particular kind between the " fine " vessels and lymphatics in the rest of the skin. From the general appearance of these small swollen " buds " there is little doubt that they mark a point of hindrance to the passage of fluid from the " fine " vessels to the lymphatics. This is clearly indicated by the local swelling in the connective, by the

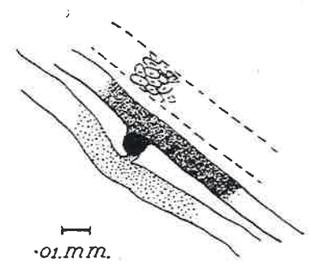


FIG. 17.—Valved connective between " fine " vessel (dark) and lymphatic in mucous membrane of tongue.

accumulation in this swelling of the colouring matter of the injection, and by the loss of colour in the injection in the continuation of the vessel from the swelling to the lymphatic. As to the nature of the impediment, it might either be physiological, due to the action of a local sphincter muscle, such as those described around the smaller veno-lymphatics of Rays by MAYER and others, or it might be mechanical, due to the automatic action of valves. I have been unable to demonstrate the presence of any definite sphincter muscles at the points of blockage, but, on the other hand, the form of the "buds" is in many cases suggestive of the presence at these points of valves directed away from the lymphatics.

In favourable cases (fig. 18) under high magnification the mass of injection within the bud appears to be divided into two parts, lying side by side, as it would do were it held

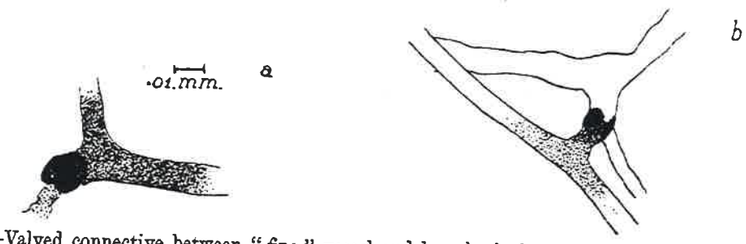


FIG. 18.—Valved connective between "fine" vessel and lymphatic from mucous membrane at outlet of gill chamber, showing lobed appearance suggestive of valves.

up in the cavities of two semilunar valves; and at the apex of the "bud," where the feebly injected continuation of the vessel emerges, there is sometimes to be seen a slight indentation between the two deeply pigmented masses within the swelling—an indentation such as would appear between the apposed bases of a pair of valves. For these reasons I feel pretty sure that in these small connectives between the system of "fine" vessels and the lymphatics of the oral mucous membranes, there are valves so directed as to hinder the flow of fluid from the "fine" vessels into the lymphatics.

It is highly improbable that these valved passages in the mucous membranes are the only means of communication between the "fine" vessel system and the lymphatics. The fact that the connections in the mucous membrane are valved against outflow from the "fine" vessels, and that injection was evidently forced through them only with difficulty into the lymphatics, while at the same time the smaller lymphatics in the mucous membrane, skin, and branchiostegal membrane were well filled with injection introduced through the "fine" vessels, indicates, I think, pretty clearly that the two systems must somewhere have means of communication other than through the valved passages in the mucous membrane. Theoretically also there should be some means by which fluid entering the "fine" vessels from the lymph plexus in the mucous membranes through these valved passages can re-enter the circulation. Where the re-entry takes place, I have been unable to demonstrate with any certainty.

I was unable by dissection or by the examination of cleared specimens or of radiographs of barium sulphate injections, to find an entry of any of the deeper and large branches of the " fine " vessel system into the lymphatic trunks or sinuses. These negative results, taken in conjunction with the fact that injection of the " fine " vessels, when not pushed to extremes, or when a finely granular mass is used, does not penetrate into the larger lymphatics, whereas a more perfect injection with a fluid mass fills the peripheral lymphatics more completely than it does the larger trunks and sinuses, and also the fact that in a very complete indian-ink injection of the abdominal trunks of the lymphatic system (Plate 3, fig. 13) none of the mass penetrated into the " fine " vessels, make it, I think, safe to assume that any connection there may be between the two systems other than through the valved connectives in the mucous membrane must take place peripherally through their finer branches or ultimate capillary networks.

I have, in fact, seen in the skin and branchiostegal membrane a very few delicate open connectives (fig. 19), not valved like those in the mucous membrane, but far too

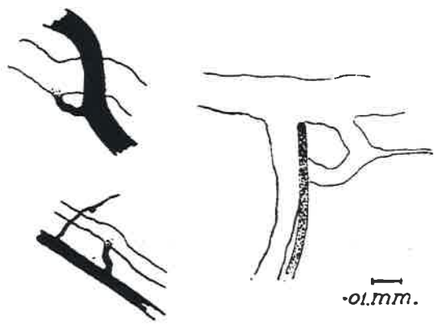


FIG. 19.—Open connections between the " fine " vessel network and the lymphatics, in the skin. " Fine " vessel : black or dotted.

few to account for the comparatively large amount of injection mass that can be introduced from the " fine " vessels into the lymphatics. The comparative freedom with which the lymphatics of the branchiostegal membranes and pelvic fins fill by injection of the " fine " vessels suggests that possibly there may be means of connection here that I have been unable to trace.

The " fine " vessels normally contain blood, sufficient in many cases to show through their walls to the naked eye as a pink central line, and to ooze out, when the vessel is cut, as richly red as the blood within the true blood-vessels. Sections through a segment of such a vessel from the ventral branchial plexus (Plate 3, fig. 20), which had been tied off before removal, showed a mass of some 130 to 150 red corpuscles. White corpuscles could not be seen with certainty, and were evidently, if present in the section, relatively few.

In other cases, though red corpuscles were present, they were relatively few and

were considerably outnumbered by leucocytes. In a transverse section through a vessel of 0·2 mm. diameter, upon the margins of a large granular clot were not more than eight red corpuscles, and around and within the clot some 17 leucocytes.

The presence of red blood within these vessels, though its quantity is remarkable, does not necessarily imply that they are part of the true blood vascular system, for in fishes the lymphatics normally contain a fluctuating number of red corpuscles. This fact has been generally observed, and I can confirm it in the case of the lymphatics of *Lophius*, although in this fish the proportion of red corpuscles in the lymph seems never to be high, though sufficient sometimes to give to the contents of the larger lymphatic trunks a pinkish hue. In a smear made from the contents of the main abdominal lymphatic trunk the proportion of red to white corpuscles was about 3 to 16.

Discussion.

It seemed probable that *Lophius* was not the only fish in which these vessels occur. On *a priori* grounds it would be unlikely that a system of vessels so extensive and well defined should be restricted to one particular species of fish, and it was therefore with some satisfaction that I observed in some preliminary investigations that I have made upon the cod, vessels of an exactly similar character associated with the hypobranchial artery in that species.

Although I have not yet been able to work out fully the distribution of these vessels in the cod, I have no doubt of their presence, nor of their essential similarity to those described above in *Lophius*. A more complete study of them may, I hope, throw some more definite light upon their nature and relation to the rest of the vascular system.

Such search as I have made through the literature dealing with the lymphatic and blood vascular systems of fishes and other Vertebrates, though furnishing no actual account of "fine" vessels such as those described above, offers indirectly some evidence as to their nature.

Of particular import is the work of JOURDAIN (7A) and MAYER (11A) on the circulation of the lymph in the fin membranes of young flat-fishes. It was discovered by JOURDAIN, by the examination during life of very young and therefore transparent specimens of *Pleuronectes*, that the lymph circulation is comparable to the blood circulation, some vessels transporting lymph to the periphery, others returning it to a central reservoir. He states that each fin ray is accompanied by six vessels. Two of these contained blood and were respectively an artery and a vein united at intervals by connectives. The other four contained lymph and were arranged in pairs accompanying the artery and the vein. The members of each pair were in continuity at their distal extremities, and JOURDAIN observed that in each of them the flow of lymph was in an opposite direction: in one from the base of the fin to the periphery, in the other from the periphery to the base, thus constituting an afferent and efferent circulation, similar to that of the blood vascular system. JOURDAIN thus concluded that in *Pleuronectes*, and probably in Tele-

ostean fishes in general, the lymph circulation is comparable to that of the blood. Some vessels, which he calls "lymph arteries," carrying the lymph from the centre to the periphery, and a complementary set, "lymph veins," returning it from the periphery to the centre. A similar afferent and efferent lymph circulation is said by JOURDAIN to have been noted by FOHMANN in the gills.

These observations of JOURDAIN have more recently been confirmed in several species of flat fish by MAYER (11A), so that there seems to be no doubt of their accuracy.

In these researches on young living fish the terminal branches of the lymphatics in the fins only were suitable for study, owing to the relative opacity of the body; thus no information could be given either of the anatomical relations of the larger components of the two systems or of any possible difference in the structure of their individual vessels. The fact, however, that in Teleosteans there is a complete two-way circulation of lymph, and not, as in land Vertebrates, a flow only from the periphery to the centre, is in itself of very great interest, and incidentally suggests strongly that the "fine" vessels described above in *Lophius* are the afferent component (lymph arteries) of the lymphatic system and the ordinary lymphatics the efferent component (lymph veins).

Neither JOURDAIN nor MAYER give any indication of the source from which the afferent vessels derive their contents, nor any very satisfactory explanation of the means by which the lymph circulation is driven, though it is suggested by JOURDAIN that the flow is probably effected by the muscular respiratory movements, and by MAYER that the source of propulsion is the heart. JOURDAIN gives no idea what the object of this type of lymph circulation may be, but MAYER is led to suppose that it is to convey nutrient material (in the form of granules in the leucocytes) from the viscera to the peripheral parts.

When one reviews, in the light of JOURDAIN's and MAYER's researches, the whole of the facts set forth above, I think that the conclusion to which one must come, at least provisionally, is: (1) That the vessels of the "fine" system here described are the afferent part of a lymphatic system with a double circulation (similar to that of the blood vascular system), the terminal parts of which in the fins were seen in action by JOURDAIN and MAYER. (2) That the system commences in an open network in the mucous membrane of the mouth, pharynx, and gills, receiving its contents through small-valved connectives from a fine network of lymph capillaries situated close beneath the mucous epithelium. (3) That from this origin its vessels are distributed alongside the ordinary (efferent) lymphatics throughout the anterior part of the body to the arteries, connective tissues and skin, and that probably (though of this I have little direct evidence) in these areas of distribution its terminal networks connect up with the terminal branches of the ordinary lymphatics, and thus through them complete the path of circulation, returning the lymph from the periphery *viâ* the ventral system of lymphatics to the sub-thyroid and thyroid sinuses and thence to the heart.

The fact that I have not seen any parts of this system of "fine" vessels distributed to the alimentary viscera makes me hesitate to agree with MAYER that it serves to

carry nutrient matter from the digestive organs to the periphery; but, on the other hand, its wide distribution upon the mucous membrane of the mouth, pharynx and gills—where, as JOURDAIN points out, its terminal factors would be in as close association with the water as are the branchial respiratory vessels—suggests that possibly its contents may here take up some constituent of the water and convey it to the walls of the blood-vessels and lymph sinuses, and to the skin. This suggestion is possibly supported by the fact that a complete two-way circulation of lymph is, so far as known, peculiar to fishes, and does not occur in land Vertebrates, the flow in them being in one direction only—from the periphery to the heart.

It will be obvious that the above suggestions are very tentative, and that many anatomical points remain obscure. It is not, for instance, certain how red blood corpuscles, in excess of those found in the ordinary lymphatics, gain access to these vessels; exact information with regard to the connections between this system and the lymphatics is still very imperfect; and it is not clear how the propulsion of the lymph is brought about, though with regard to this latter point the probable sucking action due to the respiratory movements of the pharynx acting upon the valved lymph sinus within the thyroid, should not be overlooked (p. 26).

Though I have little doubt, from the suggestion afforded by JOURDAIN'S discovery, that the " fine " vessels are the afferent component of a two-way circulating lymphatic system, I have found in the literature no direct reference to any vessels at all comparable to them in structure or anatomical relations, except possibly in the paper by TROIS (22) on the lymphatics of *Lophius*, in which part of the description of the branchial lymphatics seems to refer to the network of these vessels around the main respiratory afferent and efferent vessels in the concavity of the gill arches. In describing these parts (p. 774) he mentions that the lymphatic trunks of the gills are of different sizes, the most noticeable being four to six anastomosing vessels in the concavity of each branchial arch, ensheathing the main afferent and efferent branchial vessels and forming an elaborate reticulated plexus around them. He describes superficial coarse and fine networks, remarkable for the gibbosity of their constituent vessels. It is not quite certain from the description and figure given whether the reticulum of vessels around the branchial vessels refers to the ordinary more or less lacunar lymph spaces, or to the " fine " vessels described above; probably, I think, the latter; but TROIS evidently did not realise that they formed a system distinct from that of the general lymphatics.

The resemblance between the branchial plexuses of the " fine " vessels and the plexuses formed by the nutrient arteries in the gills and upon the mucous membrane of the gill arches in *Polyodon*, described and figured by ALLEN (2, p. 107, Plate XI, fig. 20, *d*), suggested at first that the two might be of the same nature. But this comparison is negatived by the fact that these vessels in *Lophius* have no connection with the arterial system, and that there is in addition to them a fully formed system of nutrient arteries.

If, as seems no doubt to be the case, these vessels are part of the lymphatic system, it is possible that certain facts recorded by FERGUSON (5) in his paper on the thyroid

of Elasmobranchs may have a bearing on their morphological status. In Elasmobranchs the thyroid is stated by FERGUSON to be surrounded by a large venous, or veno-lymphatic sinus, connected through a hyoid sinus with the jugular veins. In the walls of this sinus FERGUSON demonstrated a peculiarly rich plexus of fine vessels, which he regarded as of a definitely lymphatic nature. He says: "The vessels form perivascular lymphatics about the venous sinuses. Ink or a coloured fluid injected into the connective tissue about the hyoid and thyroid sinuses readily fills the anastomosing vessels, forming a sheet-like mass of peculiar form. Ink thus injected can also be traced into the perivascular lymphatics of the hypobranchial arterial vessels as far backward as the walls of the coronary arteries; it can likewise be found in small perivascular lymphatics in the walls of the thyroid arteries, and to some extent in the broad venous spaces between the vesicles of the thyroid gland, indicating that the lymphatic vessels to some extent may open into the veins of the thyroid (5, p. 185)"; and, further (p. 171): "The thyroid sinus is surrounded with connective tissue containing a network of lymphatic vessels. Ink injected in the living animal into the space between the lateral margin of the thyroid sinus and the ventral end of the first branchial cleft will, after a few minutes, be found filling many of the lymphatic vessels of the thyroid sinus, as well as many other perivascular lymphatics in relation with most of the cervical veins and the arteries of the hypobranchial system."

Thus it seems that in the Elasmobranchs in which the lymphatic system is still almost entirely undifferentiated from the veins, there is appearing in connection with the veno-lymph sinuses of the thyroid and hypobranchial regions a system of small vessels more definitely lymphatic in character and associated mainly with the walls of the veno-lymph sinuses and the hypobranchial arteries.

In FERGUSON's description of these lymphatic vessels two points in particular are of interest in connection with the question of the origin of the system of "fine" vessels in *Lophius*: in the first place, the intimate connection between these lymphatic networks and the *walls* of the arteries and venous sinuses (see FERGUSON's fig. 8, p. 182); and, in the second, the association of their distribution with that of the hypobranchial system of arteries.

The resemblances between these lymphatics and the system of "fine" vessels in *Lophius*, both in their relation to the walls of the blood-vessels and in the limits of their distribution, are certainly striking and seem to me suggestive of morphological identity. As might be expected from the still undifferentiated condition of the lymphatic system in Elasmobranchs, these vessels are in them in a very simple and rudimentary condition, and show neither the marked independence nor the structural peculiarities of the "fine" vessels of *Lophius*; but their distribution and their relation to the arteries and veno-lymphatic sinuses seem to point to their possible genetic relationship.

On the other hand, the sharply defined outlines, regularity of contour, and the remarkable thickness and elasticity of the walls of the "fine" vessels in *Lophius* and the cod, present a combination of characters very unlike those presented by the lymphatics

described by FERGUSON, and, indeed, unlike those commonly associated with lymphatic vessels in general.

The only lymph vessels of a similar structure that I know were described in the Cæcilian Amphibian, *Hypogeophis*, by MARCUS (9). These vessels, which, thanks to Prof. J. P. HILL, I have myself had the opportunity of studying in *Siphonops*, are found beneath the skin, in connection at one end with a series of small segmentally placed lymph hearts, and opening at the other into large thin-walled lymph channels disposed in various parts of the body. The vessels are narrow tubes with thick, highly elastic walls, which are stated by MARCUS to consist largely of muscle.

The similarity in structure between these Amphibian lymphatics and the "fine" vessels of *Lophius* has probably no morphological significance, but it shows that such a structure, though unusual, is in no way incompatible with the character of a lymphatic.

Summary.

So far as one can judge from the facts ascertained, there are in *Lophius* and in the cod, and probably in other Teleostean fishes, lymphatic vessels of two kinds, differing from one another in structure and contents :—

1. An extensive system of vessels of the ordinary lymphatic type ; delicate in structure, irregular in outline, inclining to lacunar or sinus-like expansion ; separable into regional but freely intercommunicating systems ; draining lymph with a slight admixture of red blood corpuscles from all parts of the body and viscera ; opening directly into the veins through sinus-like reservoirs situated in the head or fore-part of the body.

These are the lymphatics that have been described in greater or less detail by ALLEN, TROIS, FOHMANN, and many others.

2. A system of narrow, sharply defined vessels ; thick-walled, muscular and highly elastic, arranged somewhat after the manner of a portal system, with one end branching out upon the ventral surface of the body and paired fins, and the other distributed to the gills, buccal membrane, and dorsal parts of the head and trunk ; connected in the mucous membrane of the mouth, pharynx and gills by narrow valved branches with the peripheral networks of the ventral system of lymphatics, and intimately associated with the walls of the arteries ; containing sometimes lymph, but more often rich red blood.

3. At present such evidence as there is suggests that these vessels derive their contents from the lymphatic networks in the mucous membrane of the mouth, pharynx and gills, and that the flow of fluid in them is to the skin of the fore-part of the body and to the walls of the arteries and of some of the lymph sinuses.

From the work of JOURDAIN and MAYER it is inferred that these vessels form an afferent system of lymphatics, complementary to an efferent system represented by the lymphatics of ordinary type, and that by it lymph, possibly containing salts or other

substances derived from the sea water, is conveyed from the mucous membranes of the mouth and respiratory organs to the blood-vessels and body surface, whence it is returned to the heart through the ventral system of ordinary lymphatics.

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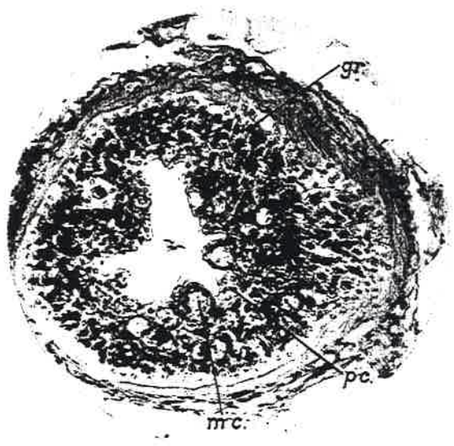
Reference Letters.

a. th. l., anterior thyroid lymphatic.
a. th. v., anterior thyroid vein.
abd. l., main trunks of ventral lymphatic system.
aff. br. I., II., III., afferent branchial vessels.
art., articulation of pectoral fin.
bd., bud-like swelling on valved connectives between "fine" vessels and lymphatics.
br., gills.
br. a. I.-V., branchial arches.
br. c., branchial chamber.
br. s., ventral branchial lymph sinus.
bstg., branchiostegal rays.
cl., clavicle.
cl. pv., claviculo-pelvic muscles.
com., "fine" vessel commissure in myodome.
con., connective between "fine" vessel and lymphatic.
cor. a., coracoid artery.
cor. f., coracoid branch of "fine" vessel system.
cut. f., cutaneous branch of "fine" vessel system.
d. Cuv., duct of Cuvier.
dp. cl., depressor claviculæ.
dp. op., depressor operculi.
dt., thymic duct.
eff. psbr. a., efferent artery of pseudobranch.
eff. th. l., efferent lymphatic channel of thyroid.
ep. br. I., II., III., epibranchial arteries.
ep. br. f., "fine" vessels emerging from dorsal ends of gills.
gel., plexus of "fine" vessels in suborbital "gelatinous" body.
h. hy., hyo-hyoideus muscle.
hbr. a., hypobranchial artery.
hep. v., hepatic vein.
hy., hyoid.
hy. a., hyoid artery.
hy. cl. m., hyo-clavicular muscles.
hy. f., "fine" vessel emerging from hyoid sinus.
hy. s., hyoid sinus.
i. jg. v., inferior jugular vein.
int. c., internal carotid artery.
int. hy., interhyal.
l. ch., lateral lymph channels connecting subthyroid and pectoral sinuses.
l. l., lingual lymphatic.
l. s., lymph sinus.
l. th. l., lateral thyroid lymph channel.
l. th. v., valves in lateral thyroid lymph channel.



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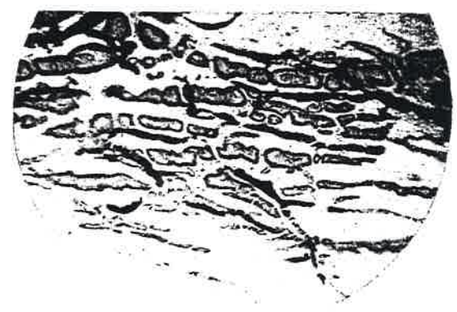

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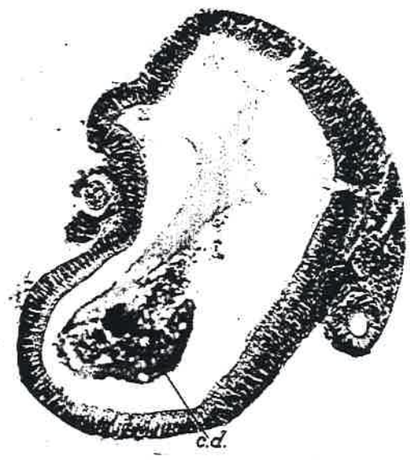

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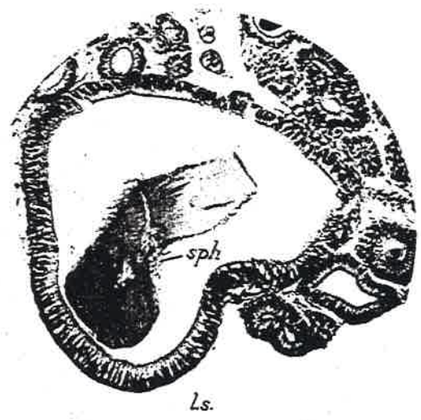

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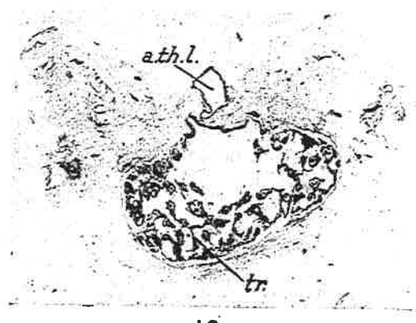

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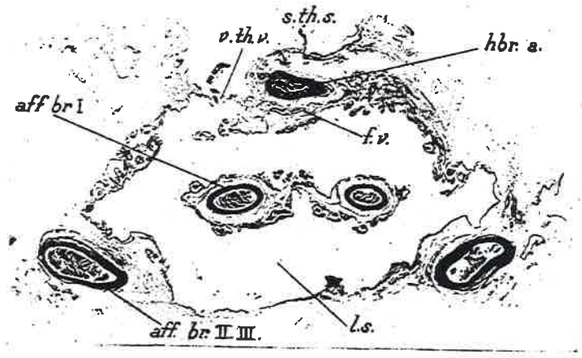

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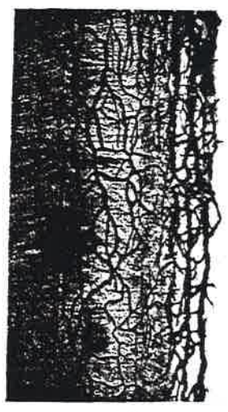

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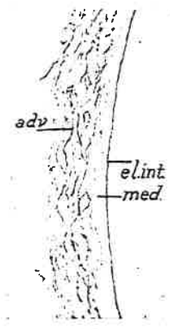

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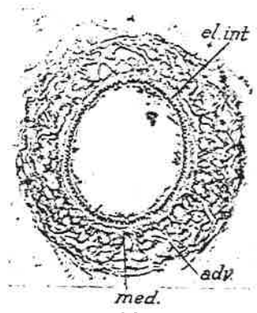

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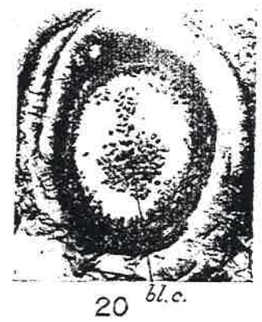

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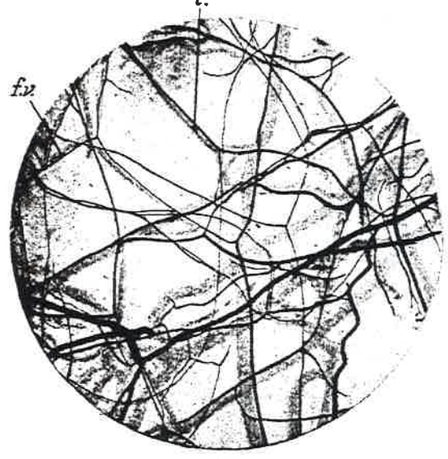

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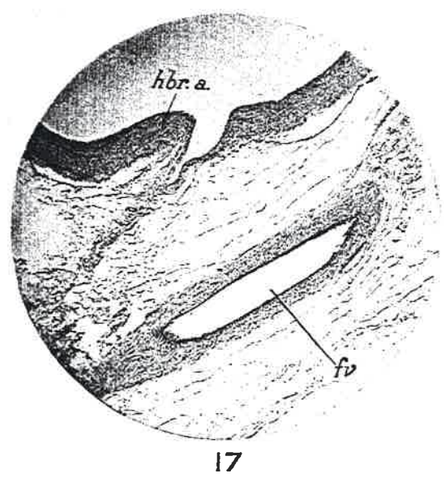

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lat. a., lateral artery.
lev. cl., levator claviculæ.
lg. a., lingual artery.
lg. s., lingual lymph sinus.
lph., lymph channel.
m. f., main trunk of "fine" vessel system.
md., mandible.
md. f., "fine" vessel to mandible.
on. f., orbito-nasal branch of "fine" vessel system.
obl. m., oblique muscles of eye.
op., operculum.
or., entry of duct of Cuvier and inferior jugular vein to sinus venosus.
p., orifice of thymic "duct."
p. th. v., posterior thyroid vein.
pc., pericardium.
pct. l., "fine" vessel arcade in pectoral fin.
pct. s., pectoral lymph sinus.
ph. mm., pharyngeal mucous membrane.
ptg., pterygiophores.
pv., pelvis.
pv. l., "fine" vessel arcade in pelvic fin.
s. cl., supra-clavicle.
scl. a. & v., subclavian artery and vein.
s. orb., suborbital muscle sheet.
s. th. s., subthyroid lymph sinus.
sus., mandibular suspensorium.
s. v., sinus venosus.
th., thyroid.
th. s., thyroid sinus.
thm., thymus.
v., thymic vein.
v. ao., ventral aorta.
v. br. s., ventral branchial sinus.
v. th. v., valved openings from sub-thyroid to thyroid sinus.
v. v., valves between efferent thyroid lymph channel and inferior jugular vein.

EXPLANATION OF PLATES.

Plate 1.

Thymus and thyroid of *Lophius piscatorius*.

Fig. 1.—Thymic "duct"; trans. sect. × 180.

Fig. 2.—Transverse section of thymus through point of entry of "duct." × 48.

Fig. 3.—Epithelium of thymic "duct" in process of transformation into reticulum. × 180.

Fig. 4.—Island of large epithelioid cells upon interlobular trabecula. × 180.

Fig. 5.—Portion of thyroid, showing massed arrangement of vesicles. × 20.

Fig. 6.—Young thyroid vesicles, showing linear arrangement. × 20.

dt., thymic "duct"; *e*, normal epithelium of "duct"; *e.c.*, large epithelioid cells; *gr.*, granules; *m.c.*, mucous cells; *p.c.*, polygonal cells; *r.c.*, reticulum cells; *str.c.*, striated cells; *t.e.*, terminal expansion of "duct"; *tr.c.*, transitional cells.

Plate 2.

Thyroid of *Lophius piscatorius*.

Fig. 7.—Young thyroid vesicles (longit. sect.) showing elongated beaded, tubular and solid stages. × 180.

Fig. 8.—Thyroid vesicle, showing cell débris in colloid contents. × 180.

Fig. 9.—Thyroid vesicle projecting into lymph sinus, and in extensive contact with its endothelium. × 180.

Fig. 10.—Trasn-section through anterior end of thyroid, showing relation of vesicles to thyroid lymph sinus. × 5.

Fig. 11.—A similar section through the passage from the sub-thyroid to the thyroid sinus. × 5.

Fig. 12.—A similar section through the hinder part of thyroid. × 5.

a.th.l., anterior lymphatic trunk; *c.d.*, cell débris; *f.v.*, "fine" vessel, main trunk; *l.s.*, lymph sinus; *m.*, mass of vesicles interspersed with offshoots of lymph sinus; *r.*, solid cylinder of thyroid tissue; *sph.*, homogeneous spherules; *tr.*, trabeculæ; *v.*, tubular vesicles.

Plate 3.

Lymphatics and "fine" vessels of *Lophius piscatorius*.

Fig. 13.—Cutaneous network of lymphatics from ventral body wall. × 20.
Fig. 14.—Network of "fine" vessels from wall of branchial cavity. × 20.
Fig. 15.—Plexus of "fine" vessels and lymphatics in skin behind symphysis of clavicles. × 20.
Fig. 16.—Plexus of "fine" vessels upon branchial filament. × 20.
Fig. 17.—Section through hypobranchial artery and main trunk of "fine" vessel system. × 45.
Fig. 18.—Part of wall of hypobranchial artery, stained for elastic tissue. × 180.
Fig. 19.—"Fine" vessel, from ventral plexus, stained for elastic tissue. × 180.
Fig. 20.—"Fine" vessel, from ventral branchial plexus, showing blood contents. × 180.
adv., adventitia; *f.v.*, "fine" vessel; *l.* lymphatic; *med.*, media; *el.int.*, elastica interna; *bl.c.*, blood corpuscles.