VI. *A System of "Fine" Vessels Associated with the Lymphatics in the Cod* (Gadus morrhua).

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(Plates 84-88.)

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Introduction.

In a paper published in 1926 (4) I described, in the head and forepart of the body of the Angler Fish (*Lophius piscatorius*), "a system of 'fine' vessels probably of a lymphatic nature." These vessels formed delicate and intricate networks in the connective tissues around the arteries and lymph channels and were ultimately distributed to the mucous membranes of the mouth, pharynx and gills, to the walls of the arteries, and to the skin. The individual vessels presented a structure similar to that of a small artery and frequently contained blood; but so far as I could observe the system was not connected in any way with the blood vessels, but was continuous through a terminal capillary network with the lymphatic vessels of normal type described by Trois, Sappey, and other older anatomists.

In young Teleosteans the lymph circulation has been shown (10, 12) to resemble that of the blood, with an outward flow to the periphery and an inward flow in the reverse direction, necessitating afferent and efferent component vessels. From the facts observed in *Lophius*, I put forward the suggestion that the "fine" vessels were probably the afferent component of this double-lymph circulation.

A preliminary examination made upon the Cod showed that there were in that fish

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also vessels of a similar nature, associated (so far as that particular observation went) with the ventral branch of the hypobranchial arteries, and it seemed likely that the system was of general occurrence in Teleosteans. In the present paper, I have pursued the subject further, and have made a detailed study of the distribution of these vessels in the Cod. My object in doing so was, in the first place, to confirm the facts recorded in *Lophius* in some less specialised Teleostean; to determine more surely the relations of the system to the blood vessels and lymphatics; to ascertain its morphological status; and to find evidence of the mode of entry of blood into the vessels, the direction of flow within them, and any structural indications there might be of their physiological meaning.

2. *Material and Methods.*

The Cod (*Gadus morrhua*) was chosen partly because of its convenient size and shape, and partly because it differs widely in habits and relationship from the species previously investigated. The fish used have for the most part been obtained from the market, but I am also indebted for suitable material to Mr. BORLEY, of the Ministry of Fisheries, and to my friend Dr. MUIR EVANS. I have also had an opportunity of injecting the system in a large species of *Pagrus*.

I wish also to take the opportunity of thanking those who have helped me in other ways, and above all Sir ARTHUR KEITH for his unfailing support and encouragement. My assistant (Mr. STEWARD) has given me valuable help in the preparation of photographs, and Miss GLASSCOCK in the preparation of microscopic sections.

The investigation has been carried out by injection, using either TANDLER'S cold gelatine, a mixture of BEALE'S 50 per cent. glycerine medium with a slight admixture of cold gelatine, or BEALE'S glycerine alone, with Indian ink, Chrome yellow, and occasionally Prussian blue, Barium sulphate and Carmine, as colouring matters.

The "fine" vessel system can be injected, so far as my experience goes, only from one of its own components. Of these the most convenient for the purpose is the trunk that accompanies the ventral branch of the hypobranchial artery. This can be readily found by dividing the symphysis of the pectoral arch, and thus exposing a large lymph sinus (sub-pericardial sinus) the walls of which enwrap the artery and its companion "fine" vessel. The "fine" vessel can then be opened, a glass cannula inserted into it and secured with silk, and the injection made in the usual way under water pressure. The pressure used varied from 2–4 inches of mercury. The larger vessels were traced by dissection, the finer ramifications by clarification of pieces of tissue in benzyl-benzoate and to some extent by serial sections.

3. *Distribution of Main Components of "Fine" Vessel System.*

The main stems and larger branches of the "fine" vessel system accompany the various arteries, and, taken as a whole, form what may be described, perhaps more

aptly than in any other way, as an attenuated duplicate of the non-visceral parts of the arterial system. So far as observed their distribution is confined to the head and body and tail, and does not extend to the viscera, with the exception of a few branches to the kidneys and to the anterior end of the alimentary canal.

The following short description in conjunction with figs. 1–3 (Plate 84) will give a sufficiently exact idea of the arrangement and general character of the chief components of the system.

Figs. 1 and 2 are drawn from the same injection. In fig. 1 the floor of the mouth is shown from the dorsal aspect, with the branchial skeleton removed. It will be seen that in each gill arch the efferent branchial vessels and roots of the hypobranchial arterial system are accompanied by one or more branches of the "fine" vessel system. These, in each gill arch, branch and anastomose to some extent (fig. 1, *br.f.*, fig. 12) and, as will be described in more detail later, receive branches from an elaborate plexus in each gill filament. At the ventral extremities of the gills the branchial components of the "fine" vessel system are connected together by a pair of longitudinal trunks (fig. 1, *l.h.br.f.*) that run one on either side of the thyroid body and ventral aorta. Anteriorly these longitudinal hypobranchial trunks are united by a transverse commissure (fig. 1, *tr.c.a*), and are continued beyond it in a cephalad direction to form the roots of a large vessel (fig. 1, *hy,f.*), which accompanies the hyoid artery through a foramen in the hyoid bone and gives off branches to the tongue, the floor of the mouth, the tissues around the hyoid bone, and the branchiostegal membrane.

The main trunk of this hyoid vessel runs backwards along the dorsal edge of the hyoid in close association with the hyoid artery, and can be followed, though usually in an attenuated condition, through the suspensorium of the lower jaw into continuity with the "fine" vessel that accompanies the afferent and efferent arteries of the pseudobranch (fig. 2, *hy.f.*). The vessel is thus separated into hyoid and pseudobranchial sections.

Posteriorly the longitudinal hypobranchial trunks anastomose dorsal to the ventral aorta between the origins of the second and third afferent branchial vessels to form a median vessel (fig. 1, *v.f.*) that accompanies the ventral branch of the hypobranchial artery to the lower surface of the forepart of the body and is distributed to the pelvic fins and the skin in their neighbourhood.

Behind this point of anastomosis, the longitudinal trunks continue caudally, receiving branches from the third and fourth gills, from the inferior pharyngeals and from the floor of the pharynx (fig. 1, *ph.f.*).

Upon the right side of the figure the mandible and part of its suspensorium is outlined to show the distribution of the "fine" vessel that accompanies the mandibular branch of the hyoid artery. This mandibular branch arises from the pseudobranchial section of the hyoid "fine" trunk, as it lies on the outer surface of the mandibular suspensorium, and follows the mandibular artery fairly closely, to the articulation of the jaw. Here it divides into two main branches that run respectively along the outer

and inner surfaces of the jaw, and are distributed to the skin and mucous membrane, more particularly to the papillate mucous membrane of the lip.

Fig. 2 represents the base of the skull of the same individual showing the circulus cephalicus with its chief factors and branches, and the larger components of the " fine " vessel system associated with them. The branchial trunks of the " fine " system (fig. 2, *br.f.*) which are continuous with those shown in fig. 1, emerge, each as a single vessel, from the dorsal extremities of the gills alongside the corresponding epibranchial artery and unite to form an irregular circulus, which in this particular specimen is incomplete upon the right side.

The " fine " vessel circulus is closed anteriorly by an anastomosis (fig. 2, *tr.c.a.*) that runs through the myodome, accompanied by the two corresponding anastomoses between the internal carotid and the efferent pseudobranchial arteries. Posteriorly it is completed by one or more (figs. 2, 3, *tr.c.p.*) anastomoses from which a vessel or irregular plexus of vessels is continued along the aorta to the tail.

Numerous small branches given off from the " fine " circulus (fig. 2, *nut.f.*) accompany corresponding nutritive arteries to the mucous membrane upon and around the epibranchial toothed pads. Other larger branches arising from it at definite points are associated with the chief arteries of the head and trunk : from its hinder part a branch along the subclavian artery to the pectoral fin and shoulder girdle (fig. 2, *scl.f.*) sending twigs (fig. 2 *re.f.*) to the kidney and along the branches of the vagus to the œsophagus ; from its mesial parts between gills 1 and 11 a branch along the external carotid artery (fig. 2, *ext.c.f.*) to the dorsal parts of the head ; and from its anterior part, which runs parallel to the internal carotid artery, one branch forwards along the orbito-nasal artery to the olfactory organ and snout (fig. 2, *an.f.*) and another outward parallel to the anterior border of the pseudobranch along the afferent pseudobranch artery. This branch (fig. 2, *hy.f.*) is continuous (usually by an attenuated anastomosis) with the hyoid " fine " vessel (fig. 1, *hy.f.*) forming its pseudobranchial section ; on the outer side of the mandibular suspensorium it gives origin to the mandibular vessel (fig. 1, *md.f.*) and before perforating the suspensorium supplies several minor branches to the mucous membrane of the palate.

The hinder part of the circulus, which may be a simple transverse loop, as in fig. 2, is more often drawn out longitudinally, as in fig. 3, *tr.c.p.*, the two arms uniting beneath the vertebral column some little way behind the head and sometimes connected by one or two accessory commissures. The loop is continued posteriorly in the angles between the aorta and vertebral column to the caudal fin, forming an irregular and often plexiform vessel or aortic trunk, closely associated with one or both of the sympathetic cords (fig. 3, A, B, C, *aor.f.*). Branches given off from this trunk accompany the segmental arteries (*sg.f.*), passing behind the ribs or transverse processes and curving round the bodies of the vertebræ to follow the neural spines to the dorsal fins, and giving off branches that run in the intermuscular septa to the surface of the body, where they form a fine plexus in the silvery subdermal tissue that covers the surface of the

muscles. Minute branches from this plexus enter the skin at fairly regular intervals of 3 mm. and then break up in a superficial network.

In the tail region branches of special size run ventrally from the aortic trunk along some of the hæmal spines and at the base of the anal fins are connected together by a conspicuous longitudinal anastomosis from which branches are distributed to the fin. Near the root of the tail several large branches radiate both dorsally and ventrally into both lobes of the caudal fin.

In working out the general distribution of the " fine " vessels there were two points that particularly attracted my attention. In the first place it was noticed that although the branches of the system accompanied practically all the arteries distributed to the head, trunk, and tail, very few went to the viscera. These few were given off from the subclavian " fine " vessels and accompanied little arteries ramifying through the head kidney and ran for a short way along the œsophagus mixed with the visceral branches of the vagus. Another very striking peculiarity was apparent when good injections of the " fine " vessels and arteries were compared. In an arterial injection the skeletal muscles were strongly tinged by the colouring matter in the finer branches and capillaries, but not at all by injection introduced into the " fine " vessels. Conversely the mucous membranes of the mouth and pharynx and the skin were but little coloured by an arterial injection, though deeply tinted by the injection mass within the " fine vessels."

Cleared specimens show even more definitely that whereas the blood vessels form rich capillary plexuses within the skeletal muscles, the " fine " vessels do not, but only pass through them here and there, as relatively large trunks, to form capillary plexuses elsewhere, particularly in the connective tissues underlying exposed surfaces such as the skin and the mucous membranes of the mouth and pharynx.

The interest of this difference in distribution lies in the fact that a want of penetration into the skeletal muscles is one of the characteristics of the lymphatic system of vertebrates in general.* This suggests a relationship between the " fine " vessels and the lymphatics, which is borne out (as detailed below) by other and more cogent considerations.

A similar peculiarity in distribution was observed in *Lophius*, but in this Fish, although the system did not extend to the skeletal muscles or viscera, its distribution in the connective tissues other than those underlying the skin and mucous membranes was far more elaborate than in the Cod. In *Lophius* wherever the system extended the connective tissues around its trunks and larger branches were filled with an intricate network of minor branches ; many of these were no doubt direct feeders of the surface capillary plexus, but a considerable number broke up in the walls of the arteries.

In the Cod, this was noticeably not the case. The deeper components of the system, although they gave off numerous branches to form the capillary networks in the skin and mucous membranes, and to a certain extent formed plexuses upon the periosteum

* Schäfer, ' Quain's Anatomy,' XIth ed., vol. 2, Pt. 1, Microscopical Anatomy, 1912, p. 192. Sabin, Keibel and Mall, ' Manual of Human Embryology,' vol. 2, 1912, p. 710.

of the vertebral column and skull, were not themselves surrounded by networks of minor branches and were not distributed, except in the gills, to the walls of their associated arteries.

This difference in the richness of the system in the deeper connective tissues may be due to the different character of these tissues in the two species. In *Lophius* they are extremely abundant and of very loose texture; in the Cod less in quantity, closer and tougher. That this difference in texture may exert some controlling influence is suggested also by the fact that in the Cod, in areas occupied by masses of soft gelatinous connective tissue (such as those met with in the snout and upon the top of the head), the branching of the "fine" vessels is far more rich and elaborate than where the connective tissues are more dense and fibrous.

By comparing the above account of the distribution of the main trunks of the "fine" system in the Cod with that already published for *Lophius* (4, p. 29), it will be apparent that the two agree in their broader outlines, though differing in minor details. There is, however, one very considerable difference: in *Lophius* the system is limited to the head and forepart of the body, but in the Cod it extends along the aorta to the caudal fin.

It is possible that this difference in distribution is apparent only and is due to discontinuity of the cephalic and trunk portions, so that injection of the one part does not fill the other. That this may be so is suggested (1) by the fact that FAVARO (7) figures in a cross-section of the tail of *Lophius* a vessel similar in position and appearance to the main aortic trunk of the "fine" vessel system in the Cod, and (2) because in different individuals of the Cod there is great variety in the size of the aortic "fine" vessel in the abdominal region. In some it is easy to find when empty, in others (though fish of larger size) it could not be seen at all, and in one specimen, in which the system was injected from the gills, it was small, and vanished about the middle of the abdomen.

The "fine" vessel system in Pagrus.—An injection of the "fine" vessels was made in a large species of *Pagrus*, the mass being introduced into the branch of this system that accompanies the ventral branch of the hypobranchial artery. The injection mass penetrated well enough to discolour, in patches, the mucous membrane of the tongue, gill-arches and palate. So far as I could ascertain it was confined to the "fine" vessel system and had not gained entry to the larger lymphatics. Certainly none whatever had found its way into either the arteries or the veins.

Dissection, which was difficult owing to clotting in the connective tissues, showed that the larger trunks of the system were well filled and, as in the Cod and *Lophius*, accompanied the various arteries of the head and throat, though everywhere sharply differentiated from them, without the least indication of open connection.

It was not possible to trace the distribution of every branch in detail, but so far as they were traced they conformed in their distribution in all essential particulars to those of the Cod; with, however, the important exception that the hinder epibranchial branches did not extend backwards along the aorta through the trunk to the tail.

Apart from this the findings are, so far as they go, on all fours with the facts observed in greater detail in the Cod and increase the probability that a system of "fine" vessels complementary to the arteries is not an isolated occurrence but is common to Teleostean Fishes in general.

4. *Morphological Status of the "Fine" Vessel System.*

With only the facts furnished by my investigation of *Lophius* at my disposal, I was unable to offer any suggestion as to the morphology of the "fine" vessels beyond pointing out the similarity of their structure to that of small arteries (4, p. 41).

The extension of the system into the caudal region, now observed in the Cod, led me to investigate more fully than I had done the literature dealing with the vascularisation of the tail in Fishes, and has opened up a contact with the work of previous observers hitherto wanting, and thrown considerable light on the morphological status of the system as a whole.

At first the possibility suggested itself that this aortic extension of the "fine" system might represent the subvertebral (hæmal) lymphatic trunks described by many anatomists in the hæmal canal and beneath the vertebræ in the abdomen and tail.

The resemblance between these lymph channels and the aortic "fine" vessel may be very striking (particularly so in the Conger), but this resemblance is purely superficial, for the "hæmal" lymph channels (which are usually capacious) open in front directly into the jugular veins, and posteriorly into the caudal lymph heart and within the hæmal canal lie ventral to the caudal vein. These are essential features in which they differ from the aortic trunks of the "fine" system. All question of their identity is, however, set at rest by the presence of both in the Cod, the "fine" vessels close to the aorta, the "hæmal" lymphatics below the caudal vein and along the margins of the swim-bladder.

There have, however, been described in the hæmal canal of Teleostean Fishes, in addition to the aorta, caudal vein and "hæmal" lymphatics, other vessels which I think are undoubtedly the aortic segment of the "fine" vessel system.

These vessels, when the hæmal canal is cut across, may be seen lying in close apposition to one or both of the sympathetic cords in the angles between the aorta and the caudal vein. They are usually very minute and have thick walls similar to those of small arteries, thus corresponding precisely in position and structure to the aortic trunks of the "fine" vessel system. There is, I think, no doubt whatever of their identity, or that the "fine" vessel system is, in its entirety, the completed extension of this system of little vessels hitherto described in the tail and hinder end of the abdomen.

The history of these caudal "fine" vessels is not extensive. They were discovered by RAFFAELE in 1889 (14) in *Atherina*. He considered them to be identical with MAYER'S vasa vasorum (11) in the tail of Elasmobranchs, and described them as "two longitudinal vessels running parallel to the aorta one on each side and a little dorsal to it. They are

relatively slightly developed at the beginning of post-embryonal life and seem to run the whole extent of the abdomen and tail, becoming more capacious in the region of the abdomen." (Tranlation.) He further states that he observed a connection between these vessels and the intervertebral veins and has no hesitation in terming them " veins."

Subsequently in 1906, FAVARO (7) in an extensive monograph on the vascularisation of the tail of Fishes, describes these vessels and figures them in cross-sections of the tail of a number of species of Teleosteans. He terms them the arteriæ longitudinales vasorum intermediorum and regards them as homologous with the arterial connectives of MAYER'S vasa vasorum.

In a figure of *Atherina* he depicts a connection between one of these vessels and a segmental artery, and in his letterpress gives the impression that such a connection is the general rule. It is not clear to me whether he was able to inject the vessels from the aorta and thus follow them by dissection or whether his statements regarding their connections with the arteries are based on the study of sections alone. He describes them as longitudinal vessels accompanying the aorta in the region of the tail, but, I think, does not pursue their distribution to its capillary termination.

In 1910, ALLEN (1), in a description of the lymphatics in the tail of *Scorpaenichthys marmoratus*, describes in this genus and in *Clinocottus* a small longitudinal vessel accompanying the aorta in the tail region and hinder part of the abdomen. This he calls the minor caudal artery, but it is obviously the same vessel as FAVARO'S arteria longitudinalis vasorum intermediorum.

His description, which is accompanied by a figure that leaves no doubt of the identity of these vessels with the caudal part of the " fine " vessel system, runs as follows :— (1, p. 5) " In the caudal peduncle region of *Scorpaenichthys* and in all sections of *Clinocottus* this vessel was found running parallel with the caudal artery, sometimes lying to one side, and again below it. At frequent intervals this artery gives off branches which cross the lower side of the caudal artery. Often these branches have as great a caliber as the main stem, and so far as could be ascertained they were destined to supply the blood vessels of the hæmal canal. For their branches were observed going to and breaking up on the surfaces of the caudal and intersegmental arteries . . . In the single specimen in which the origin of the minor caudal artery was traced, it was found to branch off from the left side of the dorsal aorta a few millimetres cephalad of the posterior end of the kidney . . . Shortly after leaving the body cavity the minor caudal artery . . . separates into two forks . . . there are frequent cross branches between these two stems . . . producing a ladder-like appearance . . . The minor caudal artery divides into a dorsal and a ventral minor caudal fin artery. As a rule these branches traverse the basal canal of the fin with . . . the corresponding caudal fin arteries and like them send off a branch, the minor caudal ray artery. These minor branches . . . follow the dorsal and ventral surfaces of each ray, but so far as could be determined they did not extend caudal of the intrinsic muscles of the caudal fin. They appear, however, to furnish the principal supply for these muscles ; while the caudal fin ray arteries

supply the fin rays and the membrane connecting them. . . . As stated above in *Scorpaenichthys* no connections with the intersegmental arteries were observed."

A further reference in earlier work to what may be part of the " fine " vessel system is to be found in the description by ALLIS of an artery in the epibranchial region, called by him " the artery X." The description of this vessel is to be found on p. 57 of his great paper on the Cranial Anatomy of the Mail-cheeked Fishes (3). It may be summarised as follows :—

> The vessel is formed by the union of what seem to be small arteries that arise in some sort of relation to the efferent arteries of the first three branchial arches. It runs forward close to the common carotid and separates into two branches—internal and external. The internal branch accompanies the internal carotid and was traced as far as the internal carotid foramen. The external branch closely accompanies the external carotid, passes through the trigemino-facialis chamber and divides into three branches, one of these accompanies the sclerotic-iris branch of the external carotid; the second accompanies the branch of the external carotid that goes to the levator arcus palatini; the third turns back, gives off a branch along the portion of the carotid that communicates with the arteria hyoidea, and itself continues along the side of the skull to the region of the adductors and levators of the hyomandibula and opercle.

This vessel was described by ALLIS from sections of young *Scorpœna*, *Trigla*, *Lepidotrigla* and *Dactylopterus*, but he adds " the results were so unsatisfactory that I am preparing material for a further study of it.* It is so small a vessel that it was not looked for in any of the adults."

In a later paper (2) ALLIS mentions that in a specimen of *Scorpœna* (on one side) " the main vessel X is connected with the external carotid . . . by a short commissural vessel." And later (p. 141) states that in a 43 mm. larva of *Amia* a similar vessel X " arises in a glomus that lies mesial to the dorsal end of the first branchial arch, and this glomus is supplied by a small branch of the hyo-opercularis artery." From this origin the vessel runs forward and separates into two branches, both of which pass through the trigemino-facialis chamber and accompany respectively the hyo-opercularis and external carotid arteries.

These descriptions of artery X, particularly in their reference to the small size of the vessel, to its obscure origin from a plexus on or near the efferent branchial arteries, and to its close association with various arterial branches, leave little doubt in my mind that ALLIS was observing part of the supra-branchial portion of the " fine " vessel system.

If I am right in thus regarding the various somewhat enigmatic vessels described by RAFFAELE, FAVARO, ALLEN and ALLIS as parts of the " fine " vessel system, one cannot but conclude that the system as a whole is morphologically an off-shoot of the blood

* Mr. ALLIS informs me that he has not had an opportunity of carrying out this further study.

vascular system, probably of the arteries. For, although none of the above authors agree in the exact position of the point of continuity of the "fine" vessels with the blood vessels, all agree that there is such a continuity, and (with the exception of RAFFAELE) that the connection is with some part of the arterial system. The arterial origin of the "fine" vessels is also suggested (as I stated in my paper on *Lophius*) by their structure.

Contrary to expectation, I failed, in the Cod, to find by injection a direct connection between the "fine" vessels and any of the trunk arteries, either in the places indicated by FAVARO and ALLEN or elsewhere. It then occurred to me that possibly this system which in its distribution so closely duplicates that of the arteries, might like them arise in the gills either independently from the respiratory laminæ or from the efferent branchial vessels as an extension of their nutritive branches.

To test this idea, I made a more detailed study of the vessels within the gill, and was able to demonstrate (at least in this species of Fish) a minute connection between the efferent filamentary vessels and the plexus of "fine" vessels that surrounds them. As my injections seem also to throw light on certain obscurities in current accounts of the nutritive branchial circulation, I propose at this point to interpolate, with the description of the "fine" vessels, a short digression upon the rest of the non-respiratory circulation of the gill.

5. *The Non-respiratory Circulation of the Gill.*

To simplify the following descriptions, a diagram (Plate 84, fig. 4) is introduced showing in a transverse section through a gill arch, the position of the chief structures in the hollow of the arch and in the gill filaments and the terms adopted.

From a survey of the literature it seems that, although our knowledge of the respiratory circulation is fairly exact and up to date, there has been, and still is, considerable uncertainty about the nature and anatomical relations of the various vessels that supply and drain the general tissues of the gill. The latest account of the nutritive circulation is given, so far as I can ascertain, in a paper published more than forty years ago by RIESS (15). This author, working on the Pike (*Esox*) distinguishes in the gill filament and gill arch three kinds of nutritive vessels: arteries, veins, and lymphatics.

(*a*) *The nutritive arteries* (p. 543).—The arteries, he says, arise both from the afferent and efferent branchial vessels ("sowohl aus der Arteria, als auch der Vena branchialis"), but describes only those springing from the afferent. These arise at intervals from the proximal surface of the afferent branchial vessel; each sends arborisations to the tissues of the common base of the filaments, and gives off a larger branch that curves round the afferent branchial vessel to its distal surface, forming there a longitudinal trunk for the supply of several filaments. Each individual filamentary artery, after

supplying the intrinsic muscles divides into two branches which accompany the efferent filamentary vessel to the distal extremity of the filament.

These double filamentary arteries correspond apparently with the vessels described by MÜLLER (13, p. 207) as nutritive veins opening into the supra-ligamentous vessels. In other respects also RIESS's description of these arteries does not entirely tally with that given by other anatomists, particularly in his statement that they arise from the afferent branchial vessels. Thus both HYRTL (9, p. 247) and MÜLLER (13, p. 206) state that the nutritive arteries are branches of the efferent branchial vessels, arising either from their main trunks or (MÜLLER) both from the main trunk and its filamentary branches.

In the Cod, injection of the efferent vessels of the gills fills a system of small nutrient arteries, distributed to the gill arches and their muscles and to the intrinsic muscles and general tissues of the gill filaments.

The larger of these, which, ventrally, form the hypo-branchial system of arteries and dorsally (arising from the epibranchial arteries and circulus cephalicus) supply the levator muscles of the gills and the surrounding mucous membranes, need no special mention. Within the gill arch nutritive arteries of some little size arise here and there from the roots of the filamentary efferent vessels (Plate 85, fig. 5,*n.a.*), but not so far as I have seen from the main efferent branchial. These little arteries break up and form within the tissues around the main branchial vessels a rich plexus, from which fine branches pass between the articular bases of the gill rays to supply the mucous membrane of the arch and the intrinsic muscles of the filaments. Other small arteries, given off more distally from the roots of the filamentary efferent vessels as they traverse the outer surface of each articular base of the gill rays, pass mesad between the individual filaments to the distal surface of the afferent branchial vessel and there form by anastomosis an irregular longitudinal trunk, winding in-and-out between the roots of the afferent filamentary vessels, in the position occupied by the longitudinal nutrient artery figured by RIESS (15, p. 543, Plate XVI, fig. 5, *a.n.*), but described by him as taking origin from the afferent branchial vessel.

Nearer the respiratory portion of the filament yet other little nutrient arteries (Plate 85, fig. 6, *n.a.*) arise from the efferent filamentary vessel and branch out distally into the free part of the filament. The chief of these vessels accompanies the efferent filamentary vessel, lying just deep to it and to the main filamentary branch of the "fine" system.

No nutrient arteries were seen arising from the efferent vessel in the respiratory portion of the filament as described by MÜLLER (13, p. 206), and as I observed myself in *Lophius* (4, p. 39).

(*b*) *The Nutrient Veins.*—RIESS states that the chief nutrient veins of each gill filament run between the two nutrient arteries deep to the efferent filamentary vessel from the apex of the filament to its base, and here open into two or three vessels (supra-ligamentous vessels) that run along the arch between the afferent branchial

vessel and the transverse elastic ligament that unites the articular bases of the filamentary rays.

In the Cod, an injection of the jugular and inferior jugular veins fills a system of venous factors within the gill arches and filaments. MÜLLER and others have already observed this fact correctly, but are, I venture to think, in error, in regarding the supra-ligamentous vessels (Plate 84, fig. 4, *s.l.v.*) as the path by which the blood is conveyed to the jugular veins from the gills. As I hope to show below the supra-ligamentous vessels are the chief lymph channels of the gills, as FOHMANN thought, and have nothing to do directly with the venous circulation.

From injections made into both the jugular and inferior jugular veins it is clear that trunks in connection with these veins emerge from both the ventral and dorsal extremities of the gills. Those that emerge ventrally join one or other of the larger branches of a system of veins that drain the thyroid body and floor of the pharynx and open into the inferior jugular. Within the gill arch the venous factors form an irregular plexus (Plate 85, fig. 7), the larger components of which lie for the most part near the branchial nerve proximal to the other vascular contents of the arch concavity (Plate 85, fig. 8 B). Minor components run longitudinally in the tissues that surround the main branchial vessels and receive from the filaments contributory vessels (Plate 85, fig. 7) which reach them by following the mesial aspect of the articulations between the bases of the gill rays, thus alternating in position with the efferent filamentary vessels and following the same course as the main filamentary lymphatics.

Distal to the articular bases of the gill rays these main filamentary factors divide (fig. 8A*), one branch passing diagonally outwards to the filamentary efferent vessel, along which it runs deep to the nutritive artery, the other passing mesially between the roots of the afferent filamentary vessels and running in a similar way towards the apex of the filament deep to the afferent vessel.

(*c*) *The lymphatics.*—In the connective tissues of the filaments RIESS describes reticular spaces, that contain red corpuscles as well as lymphocytes. These he regards as lymphatics and states that their contents are carried proximally to two or three large vessels that run longitudinally in the arch between the afferent branchial vessel and the transverse elastic ligament. These longitudinal vessels (" supra-ligamentous " vessels) have, he says, the structure of lymphatics but carry blood and receive not only the lymphatics of the filaments but also (as stated above) the veins.

The various accounts of the lymphatics and nutrient veins of the gills given by older observers agree neither amongst themselves nor with that of RIESS. Thus FOHMANN (8) describes in the Eel afferent lymph vessels (venæ lymphaticæ advehentes) issuing from the subvertebral lymph trunk and entering the dorsal end of each gill. Branches from these run to the distal extremity of each filament and are there reflected to open at the base of the filament into a longitudinal arch vessel (vena lymphatica revehens) that runs ventrally, parallel and distal to the afferent branchial vessel, to open eventually into the inferior jugular vein. TREVIRANUS (16, p. 14) describes in the

Carp a vessel within each filamentary ray. This and its fellows from the other rays connect at the base of the filaments with one of a pair of longitudinal arch vessels, that at the dorsal end (treten . . . aus dem hintern Ende) of the gill arch open into the jugular veins. He apparently regards these vessels as (anyhow in part) lymphatics.

HYRTL (9, p. 236) and MÜLLER (13, pp. 205, 207) consider that these great longitudinal vessels ("supra-ligamentous" vessels) previously described as lymphatics or veno-lymphatics are veins. MÜLLER states that their filamentary factors are a pair of vessels lying in each filament on either side of the efferent vessel, and that their main (arch) trunks open dorsally into the jugular veins and ventrally into the inferior jugulars.

From this short résumé it is evident that there is some confusion with regard to the venous and lymphatic circulation in the gills, and in particular as to the exact nature of the supra-ligamentous vessels, some holding that they are lymphatics, some that they convey both lymph and venous blood, and some that they are veins.

From my own observations on the Cod it seems clear that the lymphatic circulation in the gills is distinct from the venous, and that the main drainage channels of the lymph are the supra-ligamentous vessels. For in practically all the injections that I have made of the veins these supra-ligamentous vessels remain empty (Plate 85, fig. 8B, *s.l.v.*), though in some a mere trace of colouring matter could be detected in their walls. In one exceptional case a moderate amount of venous injection mass lay in one of these vessels, though in less quantity than in the neighbouring veins. How it entered I am unable to say, but in face of the evidence afforded by the other venous injections it is not improbable that its presence was accidental.

In this connection it should be noted that around these vessels there is a very close network of minute veins, from which slight extravasation might easily invade them, and that in parts of their course they are closely associated with a large component of the venous plexus, separated from it by a delicate membrane only. This latter circumstance may account for MÜLLER'S statement that these vessels are filled with blood (13, p. 207), a condition in which I have never found them. In my preparations they were always empty.

A simple test serves to demonstrate the nature of the supra-ligamentous vessels. When a gill is cut across these vessels can readily be seen, between the afferent branchial vessel and the transverse elastic ligament, as shown in Plate 84, fig. 4. If an injection is now introduced into them from the cut surfaces in ventral and dorsal directions, the ventral injection appears in the inferior jugular vein, the dorsal injection flows out freely from the supra-neural and abdominal lymph channels, but does not appear in the heart or ducts of Cuvier. From this it is evident that the vessels are not veins, but form part of the lymphatic system connected dorsally with the great supra-branchial lymph sinuses and ventrally with the inferior jugular vein. This latter connection is probably, as in *Lophius* (4, p. 16) guarded by valves, otherwise injection into the inferior jugular would fill the supra-ligamentous vessels, and this, except in the one partial case cited above, does not take place.

Within the gill arch the supra-ligamentous vessels run longitudinally distal to the ligament for the greater part of their course, but pass to its proximal surface (Plate 85, fig. 9, *s.l.v.*) as they approach the ventral extremities of the gills. Opposite each articulation between the bases of the gill rays, each receives a large filamentary factor (Plate 86, figs. 10, 11, *lph*) composed, as are the corresponding factors of the veins, of branches coming from either border of the filament. The main factors near their entry to the supra-ligamentous vessel appear to be valved against flow to the filament (Plate 86, fig. 11, *vv*).

(*d*) *The "fine" vessels of the Gills.*—As previously stated (pp. 337 and 338), one or more main trunks of the "fine" vessel system run from end to end of each gill arch, joining the hypobranchial network of this system below, and its epibranchial network above (Plate 84, figs. 1, 2, *br.f.*). Within the concavity of the arch the trunks anastomose here and there to form a network of a few meshes situated between the chief branchial nerve and the efferent branchial vessel (Plates 86, 85, figs. 12, 8, *f.v.*). Opposite the origin of each filamentary branch of the efferent branchial vessel the main arch trunk gives off two or more delicate anastomosing branches. These accompany the filamentary efferent vessel, closely enmeshing it with an intricate network of dendrites, many of which dip into its walls (Plate 87, fig. 16A, B).

Within the free part of the filament the "fine" vessels assume a more regular disposition, and can be separated into a main trunk (Plate 86, fig. 13, *m.f.*) lying just deep to the efferent vessel and (connected with the main trunk by numerous short anastomoses) a close plexus surrounding each of the radicles of the efferent vessel. Deep and superficial to the radicles this plexus is connected up longitudinally to form a pair of irregular, broken subsidiary trunks (Plate 86, fig. 13, *s.f.*) lying one on either side of the main efferent filamentary vessel.

From the main trunk and from these subsidiary plexiform trunks numerous branches spread out over the general surface of the filament and connect with a network of larger and more irregular vessels, which from their appearance should be lymphatics. Many of the components of the plexus that envelopes the radicles of the efferent filamentary vessel closely embrace these little arteries as they enter the main filamentary vessel; so closely, in fact, that in some cases little but the endothelium of the artery separates the cavities of the two, though I did not observe any actual opening from one to the other. In all the injections made of these "fine" vessels in the gills it was very noticeable that they were distributed to the connective tissues underlying the mucous membrane of the gill arches and filaments, with special concentration around the efferent filamentary vessels and their radicles, but that they did not supply the intrinsic muscles.

The disposition of the non-respiratory vessels in the gills of the Cod, though in certain particulars in harmony with one or other of the older descriptions, differs from them all in various ways, and indicates that there are in the gill four systems of vessels other than those purely concerned with respiration. These (each of which can be injected to the exclusion of the others) are nutrient arteries, veins, lymphatics and "fine" vessels.

With regard to the first three little need be said, as their nature and uses are fairly obvious, but with regard to the fourth—the " fine " vessels—it is otherwise, and it is not easy to explain either what they are, or what part they take in the vascularisation of the gill. An important point to be noticed in their distribution is their very intimate association with the whole length of the filamentary efferent branchial vessels and with the little radicles that connect these vessels with the respiratory laminæ. That this association has some special value is, I think, suggested by the fact that in *Lophius* in which the fourth gill has no respiratory filaments, the arch is not accompanied, as are the others, by a leash of " fine " vessel trunks, but is supplied indirectly from the pharyngeal " fine " vessel.

In the respiratory region the contact between the " fine " vessels and the arteries is very close, as pointed out above, but there was no proof of actual continuity. In the non-respiratory region, that is the segment of the filamentary vessel between the laminar area of the gill filament (Plate 84, fig. 4, *rsp.l.*) and the main efferent vessel within the arch, evidence is, however, forthcoming of an actual open connection, though of the very slenderest description. This will be described more fully in dealing with the general relation of the " fine " vessels with the arteries, but it is convenient to refer here to certain observations made by HYRTL (9) on the gill of the Salmon (*Salmo hucho*) which may have some bearing on the question.

In this fish HYRTL observed a close plexus of small vessels associated with the radicles of the efferent filamentary vessels, which, in its position and general features, is highly suggestive of the network of " fine " vessels enmeshing the efferent radicles in the Cod.

HYRTL says (9, p. 240) that each of the vessels that emerge from the capillary network of the gill laminæ before entering the efferent filamentary vessel is dilated to form an elliptic swelling.* All these little bulbi or aneurysmata are united one to another by anastomoses and produce many extremely fine lateral twigs, which together form throughout the whole length of the filament a peculiarly delicate and minute network which covers the radicles of the efferent filamentary vessels from the bulbi to the filamentary vessel.

The network thus described, and of which HYRTL gives a figure (9, Plate II, fig. 1), has certainly a very close resemblance to the plexus of " fine " vessels in a similar position in the Cod, but I have been unable to trace any open connection with the efferent radicles or their bulbi, such as HYRTL mentions; the connection which I have observed between the two systems occurs proximal to the respiratory segment of the gill filament.

6. *The Relations of the " Fine " Vessels to the rest of the Vascular System.*

The evident identity of certain parts of the " fine " vessel system with the minor caudal artery or arteria longitudinalis of ALLEN and FAVARO, the possible identity of

* These little swellings were seen by HYRTL in a number of species; RIESS failed to observe them in *Salmo salar*. They are very conspicuous in the Cod.

other parts with the artery X of ALLIS and with the plexus on the radicles of the efferent branchial vessels of HYRTL, combined with the fact of the artery-like structure of the vessels and their frequent blood contents, leaves very little doubt that morphologically this system is, or at any rate originally was, part of the arterial system.

Injections in the Cod, *Lophius* and *Pagrus* show that in these fishes it is not now an integral part of it. The connection with it, where such has been described, is evidently extremely slight and probably inconstant, otherwise it is difficult to account for the fact that in the numerous careful injections of the blood vascular system of Teleosts that have been made by HYRTL, MÜLLER, VOGT, ALLEN, ALLIS, COLE, and other anatomists the system as a whole has been overlooked.

In attempting to determine the place now occupied by the "fine" vessels in the general scheme of vascularisation of the tissues, the first essential is to establish with as much accuracy as possible their connections with every other member of the vascular system.

Relations between the "fine" vessels and the blood vascular system: veins.—Connection between the "fine" vessels and the veins might occur in one of three ways: directly, as venous factors, by anastomosis between branches, through a common capillary network. There is no evidence to show that the "fine" vessels are venous factors. Apart from the fact that both veins and "fine" vessels are distributed to the same areas, injection of the veins never fills any part of the "fine" system. For the same reason it would appear that there is no anastomotic connection.

It is true that in one or two instances injection thrown into the "fine" system has found its way in small quantity into the jugular and inferior jugular veins; but in these particular instances the "fine" vessel injection was more than usually complete and the injection was found only in those parts of the veins situated near the lymphatic-venous junctions and there is little doubt that the intrusion into the veins took place by way of the lymphatics (see below).

If there were a connection between the "fine" vessels and the veins, the close resemblance of the former to arteries would suggest that it would be of a capillary nature. Double injections show clearly that there is no such connection, although the terminal capillaries of the two systems are in close contact with one another (Plate 86, fig. 14). From this preparation it is clear that the black injection introduced into the "fine" vessels has penetrated into a capillary network of relatively capacious vessels, which is entirely separate from the more minute terminal capillary branches of the veins (white).

It may therefore safely be asserted that the "fine" vessels do not pass into the veins through a common capillary network as they should do were they functionally part of the general arterial system. In fact, from a considerable number of injections both single and double, I am confident that there is no direct connection between the "fine" vessels and the veins, a conclusion to which I also came from the work I did on *Lophius*.

Relations between the "fine" vessels and the blood vascular system: arteries.—As I have already pointed out there is every reason to consider that the "fine" vessels are

morphologically very closely related to the arterial system. This relationship is evident in their structure and contents, as previously noted in *Lophius* (4, p. 41) and the similarity between them and small arteries is equally apparent in the Cod. In the section through the ventral branch of the hypobranchial artery and its accompanying " fine " vessel shown in Plate 86, fig. 15, it is impossible to tell except by their size which is the artery and which the " fine " vessel; both vessels also contain a blood clot of similar appearance. The tissues in this preparation were unfortunately not in a very good state of preservation, but the similarity in structure is unmistakable. In two other specimens blood was seen to issue from the cut end of one of the larger " fine " vessels, in others these vessels appeared to be empty.

Although I was unable to demonstrate any direct connection between the " fine " vessels and the arteries in *Lophius*, it seemed more than likely, from the statements made by RAFFAELE, FAVARO, and ALLEN, that somewhere a connection does occur, and that it should be possible to inject the one system from the other. In this I have failed, except in four cases where there was some slight and rather erratic intrusion of injection mass from the " fine " vessels into some of the arteries in the branchial region. The difficulty of passing injection from one system to the other might of course be due to the presence of valves between the two, but were such present they could hardly act in both directions, and physiological constrictions, were such present, would not probably prevent all passage of fluid, or do so to the same extent in various *post-mortem* conditions of the tissues in different individuals.

Neither can the failure to demonstrate free connection with the arteries be due to coarseness of the injection mass, for in at least two of the arterial injections of the Cod, and in a similar injection of *Lophius*, recently made, the mass had passed in quantity into many of the veins, but none could be seen in any of the components of the " fine " system. Conversely in many of the injections of the " fine " vessels the mass had filled superficial capillary networks and had passed thence into larger vessels which, as shown later, are factors of the lymphatic system, but appeared seldom and then only irregularly and in small quantity in some of the arteries.

These cases in which some injection mass passed from the " fine " vessels into some of the branchial arteries are interesting, and seem to indicate a natural though very restricted connection in this region. They were four in number. In one, colour from the " fine " vessels had penetrated on the left side into the proximal parts of the hyoid artery and some of its branches, and to a very slight extent into the ventral parts of the first efferent branchial; in two others traces of " fine " vessel injection mass were found in the first two efferent branchials, the root of the hyoid artery, and the anterior parts of the circulus cephalicus; in the fourth case very slight traces of intrusion were noticed in the ventral parts of the efferent system of the first two gills. In the other injections of the " fine " vessel system, some twelve in number, no intrusion into the arteries was observed.

Surface examination of cleared pieces of the gill showed no anastomosis between the

"fine" vessels and the efferent arteries, but in sections of the same parts minute connections could be demonstrated. These take place between the dendrites of the "fine" vessels that form a plexus in the outer layer of the walls of the basal (non-respiratory) portions of the filamentary efferent vessels and little conical pits that protrude from the lumen of these arteries in this region. These pits, which in cleared specimens of arterial injections have the appearance of little thorn-like projections of injection mass protruding from all sides of the non-respiratory segment of each efferent filamentary vessel (Plates 85-87, figs. 6, 16, *pr*), giving it a hirsute appearance, lie completely within the wall of the artery lined by an outpushing of its intima and elastica interna. From the apex of each runs an extremely fine passage, usually more or less contorted.

In sections cut transverse to the axis of the filament, black injection mass which had been inserted into the "fine" vessels could be traced through this slender passage into the lumen of the artery. Similar appearances were seen in sections of another specimen: a double injection of the "fine" vessels and arteries. In most of the sections one or more pits could be seen; in the majority of these were fragments of black injection mass, and in a few where the lumen of the pit happened to be exposed along its length from the artery outwards the injection mass could be seen extending along it from a mesh of the "fine" vessel plexus to the lumen of the artery (Plate 87, fig. 17).

In an arterial injection of *Lophius* which I recently made, the basal (non-respiratory) parts of the filamentary arteries present precisely the same curious spiny hirsute appearance as do the same portions of these vessels in the Cod, though the individual processes are smaller (Plate 87, fig. 18). This appearance is strictly confined in both cases to this particular segment of the filamentary arteries, and is not to be observed either in the respiratory portions of these vessels or in other arteries. The little outpushings from the lumen of the vessel to which the appearance is due terminate in *Lophius*, as they do in the Cod, in extremely tenuous contorted passages. I was unable in this preparation to trace any connection with the "fine" vessels, but the close similarity both in form and position between the thorn-like protrusions from the filamentary arteries of the Cod which have been actually shown to form part of such a connection and these protrusions in *Lophius*, suggest that a like connection occurs in this case also.

Whether these pits in the non-respiratory segment of the efferent filamentary vessels can in any way be compared with certain curious bud-like processes described by Cole (5) upon the afferent and efferent branchial vessels of *Myxine* is doubtful, though the connection of both with the lymph or pseudolymph system—in the case of *Myxine* direct, in that of the Cod through the mediation of the "fine" vessels—is a point that merits some little consideration.

Relations between the "fine" vessels and the lymphatics.—In the work that I did upon *Lophius*, I was led to the conclusion that the "fine" vessel system communicated by its terminal branches with the capillary networks of lymphatics in the skin and mucous

membranes, and with them alone. This conclusion was based on (1) my inability to demonstrate any connection between these vessels and the blood vessels. (2) The fact that good injections of the " fine " vessels filled also a network of irregular capillaries and larger vessels similar in character to lymphatics. (3) The fact that in these same injections a certain quantity of the mass made its appearance in the main trunks and sinuses of the lymph system.

It seems that in the Cod, although there is no connection between these vessels and the veins, there is probably a very tenuous communication between them and the arteries.

The chief connection in the Cod is, however, certainly with the lymphatics. This has been shown not only by the simple experiment of filling the " fine " vessels and noting that the injection mass emerges after a time from one or other of the lymphatic trunks, but by means of double injections of " fine " vessels and lymphatics checked by counter-injections of the arteries and veins.

When the " fine " vessel system is injected and the injection has been carried so far as to tint the mucous membrane and skin it is apparent in cleared pieces of these tissues (as was the case with *Lophius*) that the vessels containing the injection are of two kinds. (1) An open network of delicate, hard, clearly defined vessels (Plate 87, fig. 19, 20, *f.v.*) continuous with the larger components of the " fine " system, and (2) a richer plexus composed of larger, less regular, and more transparent vessels, presenting an appearance characteristic of lymphatics rather than of blood vessels (Plate 87, figs. 19, 20, *lph.*). The lymphatic nature of this second plexus can be proved by injecting it in the reverse direction from one or other of the large lymphatic trunks.

In practically all the injections I have made of the " fine " system the injection mass has penetrated to some slight extent into this superficial lymphatic plexus even in light injections, but when such an injection is driven further the injection mass not only fills the superficial lymph plexus, but also appears in considerable quantity in the great lymph sinuses.

These results, which confirmed what I had seen in *Lophius* are, I think, conclusive evidence that the " fine " vessels and the lymphatics are in continuity. The " fine " vessels are not, however, branches of the lymphatics, for injection of the lymphatics does not fill them, and when they themselves are injected, the injection must fill their terminal branches before making its appearance in the larger lymphatics and sinuses.

To test further the place and mode of connection double injections of the two systems were made, black being first introduced into the " fine " vessels and subsequently yellow into the lymphatics, using in different cases the lateral trunk lymphatic, the superficial facial lymphatic where it passes the angle of the mouth, and one of the lymphatics of the branchiostegal membrane. These double injections gave the following results :—

1. When both colours had reached the surface of the skin or mucous membrane, the superficial capillary network showed its meshes filled partly with black, partly with yellow (Plate 88, fig. 21) and some of the deeper lymphatics contained both colours ; the " fine " vessels were black throughout.

2. When the black had reached the surface, but the yellow injection had hardly gone so far, but had filled the network of slightly larger vessels close beneath it, many of these lymphatic vessels contained a certain proportion of black mixed with their yellow injection mass (Plate 88, fig. 22). The " fine " vessels were completely black.

3. When neither the yellow (lymphatic) nor the " fine " vessel injection had reached the superficial networks, or when the yellow had done so, but the black had not (Plate 88, fig. 23), neither system was invaded by the injection of the other.

From this one can conclude that the connection between the two systems takes place at or near the superficial capillary lymphatic network in the skin and mucous membranes, and (from the fact that lymphatic injection did not invade the " fine " vessels) that the flow of fluid takes place more readily from the " fine " vessels into the lymphatics, than in the reverse direction. The actual connection might be expected to take place in one of two ways; either insensibly by the gradual breaking up of the " fine " vessels to form a capillary net common to them and the terminal branches of the lymphatics, or abruptly by anastomosis with the lymphatic vessels or their terminal capillary networks. The latter is what, I think, actually takes place.

In both *Lophius* and the Cod it is noticeable that the finer terminal branches of the " fine " system lying close to the surface of the skin or mucous membrane give off here and there short and very slender branches transverse to their long axis (Plate 88, fig. 24, *c.n.*) These branches end upon neighbouring lymphatics and apparently open into them.

As the " fine " vessels are traced further towards the surface they are seen to retain their characteristic sharp contours throughout and to terminate by branching in various directions (Plate 88, fig. 25, *f.v.*) just beneath the superficial capillary plexus connecting with it abruptly here and there by short anastomoses.

It will be noticed in fig. 25 that the capillaries that form the surface network are of considerably greater calibre than the terminal branches of the " fine " vessels that open into them. It is also to be observed that the lymphatic vessels with which this surface network is directly continuous contain, when an injection of them is made through the " fine " vessels, a denser mass than do the actual capillaries, and that in the main lymphatic trunks and sinuses the mass is again less in quantity.

These facts point to the conclusion that the lymph vessels and the superficial plexus of capillaries are parts of one continuous system and that the terminal branches of the " fine " vessels open abruptly into this system, partly into the lymph vessels just deep to the surface plexus and partly by their branching extremities into the meshes of the capillary plexus itself.

In discussing the mode of connection of the " fine " vessels with the lymphatics in *Lophius* (4, p. 44), I pointed out that the little transverse connectives between the two, similar to those described above in the Cod, appeared (in the mucous membranes) to be blocked by valves arranged to direct the flow from the lymph plexus to the " fine " vessels. In the Cod, although the injection mass is often concentrated in these little

connecting vessels (as it was in *Lophius*) in such a way as to suggest some sort of blockage, I have seen nothing that suggests mechanical valves between the two systems; and the readiness with which injection can be passed from the "fine" vessels into the lymphatics makes the presence of such improbable.

Certainly in the mucous membrane of *Lophius* these little blockages on the connectives (4, p. 46) do, by the appearance of their contained injection mass, suggest in some few favourable cases the presence of valves, but this suggestion is not borne out or confirmed by similar preparations of the Cod, though in other particulars there is perfect agreement. This is a detail of some little importance in its bearing on the probable direction of flow of the fluid within the "fine" system, for if mechanical valves are present, their set would determine the direction of flow in the vessels in which they occur. In this instance, if the interpretation of the appearance in *Lophius* was correct, the flow would be from the lymphatics of the mouth and pharynx into the "fine" system.

But other considerations derived from this study of the Cod, particularly the connection of the "fine" vessels with the arterial system in the gills and possibly also in other parts; their blood contents and artery-like structure; the ready passage of injection mass from them to the finer lymphatics, but not in the reverse direction, suggest that the flow in them should be, as in the true arteries, in the contrary direction—that is, from the gills and possibly from some of the systemic arteries to the surface, with a return viâ the lymphatics to the veins and heart.

This seems likely from the facts observed in the Cod, and it is quite possible that the exception offered by seemingly valved vessels in the mucous membranes of the mouth and pharynx in *Lophius* is due to an error of interpretation.

7. *Conclusions and Summary.*

In reviewing the foregoing descriptions, it is apparent that a system of "fine" vessels is present and extensively distributed not only in *Lophius* but also in the Cod and *Pagrus*: Teleosteans far removed from each other in habit and taxonomic position. Further, it is legitimate to assume from the published descriptions of parts of the system in numerous other species, that it is of general occurrence in the group; the work of FAVARO and others even suggests that it, or at any rate its caudal part, may find its prototype in the Elasmobranchs.

The general distribution of the system is in essentials similar in the Cod and *Lophius*, but there is evidence to show that in the Cod it is not restricted to the head and fore-part of the trunk as seemed to be the case in *Lophius*, but extends throughout the body to the caudal fin. It does not apparently supply the viscera, except to a limited extent, or the skeletal muscles, but is practically confined to the connective tissues of the head and trunk.

The distribution within the walls of the arteries, which was very conspicuous in *Lophius*, is slight or absent in the Cod, except as regards the efferent filamentary vessels

of the gills. In and around these vessels is an elaborate network of " fine " vessel branches through which the two systems are in attenuated communication. Other connections between the arteries and " fine " vessels have not been traced in the Cod, but reference to previous work on various species of Fishes suggests that such may occur, though in any case the channels of communication between the " fine " vessels and the arteries are evidently of the slenderest description, though sufficient it seems to allow the passage of blood.

The terminal branches of the " fine " vessel system are distributed in part to the periosteum, but chiefly to the connective tissues underlying the epidermis and the mucous membrane of the mouth and pharynx. Here they form an open network which is connected by end branches and short anastomoses with the superficial capillary plexus of the lymphatic system.

The flow of the fluid (blood) in the " fine " vessels is probably from the efferent vessels of the gills (possibly also from other parts of the arterial system) to the lymphatic capillary plexus, but the total capacity of the system is actually so small and, relative to that of the lymphatics, so nearly negligible, that it is hard to imagine what useful purpose it can serve. There is little doubt, however, that morphologically these vessels are closely related to the arterial system, and it is possible, as FAVARO suggests, that they may be (at least as regards their caudal part) homologous with the arterial connectives of the longitudinal vasa vasorum described by MAYER in the tail of Elasmobranchs. But without more knowledge, particularly of their condition in primitive Fishes, it is impossible as yet to make any very definite statements as to their phylogenetic origin and morphological status.

The facts so far ascertained show clearly, however, that these vessels (as they occur in the adult fish) are more intimately associated with the lymphatics than with any other part of the vascular system, and it is therefore to be assumed that their past history is in some way bound up with the evolution of this system of vessels.

What part they actually played in this evolution cannot be stated with any certainty until more is known both of their comparative anatomy and embryology, but the facts regarding them set forth in this paper, and in the previous publication on *Lophius* (4), suggest a picture of what the early history of the rise of the lymphatic system in lower Vertebrates may have been, and of the part in it taken by the " fine " vessels.

This picture, although largely a matter of assumption, and therefore purely tentative, is not, I think, at variance with the facts revealed by comparative anatomy and by embryological studies on the lymphatics in general, and at the same time offers a reasonable explanation of the meaning of the system of " fine " vessels described above in Teleostean Fishes. In brief, it is suggested that the lymphatic system as a whole arose in lower aquatic Vertebrates by specialisation of a part of the pre-existing blood-vascular system, and that this part at the onset of its specialisation consisted, not only, as is usually assumed, of veins, but of both arteries and veins, as do all other parts of the blood-vascular system.

It is further suggested that as the efferent components (veins) of this modified part of the blood-vascular system became increasingly specialised for the carriage of lymph, its afferent components (arteries) became of less and less use, and eventually, when quite superfluous, were lost, leaving the efferent components, or modified veins, as the definitive lymphatic system. Or alternatively, it might be that the arterial components, when no longer necessary as afferent vessels, lost their connection with the rest of the arterial system and became incorporated with the modified veins to form part of the lymphatic system. In either case, the " fine " vessels would, on this general hypothesis, represent the superfluous arterial or afferent components of that portion of the blood-vascular system which in lower aquatic Vertebrates became modified to form the lymphatic system.

A recognisable lymphatic system is first to be found in the more primitive orders of Fishes. In them (*e.g.*, Cyclostomes, Elasmobranchs) its specialisation is, however, still very imperfect, for its constituent vessels carry, from the periphery to the veins, blood in variable quantity, or sometimes lymph and sometimes blood ; it is thus difficult in these lower Fishes to draw any hard and fast line between lymphatics and veins. In Ganoids the distinction is somewhat more pronounced, and in Teleosteans a separate lymph system is definitely established, with vessels corresponding topographically with the main pseudolymphatic trunks of Elasmobranchs, but typically lymphatic in structure and contents.

The facts of comparative anatomy, as may be seen from the work of ALLEN ('Anat. Record,' vol. 2, 1908, p. 65, etc.), FAVARO, COLE and others, suggest strongly that the lymphatic system took its origin in lower Fishes by modification of vessels that at first appearance formed a part of the blood-vascular system, and only later in more highly organised forms became definitely set aside for the carriage of lymph alone. This conclusion is, in fact, that come to by most who have studied the vascular system in the adult.

An assumed close relationship between the lymphatic system in the early stages of its evolution and the blood-vascular system rests, however, not only on the findings of comparative anatomists, but is to some extent suggested by the facts of embryology. It is, of course, notorious that embryologists differ profoundly in their interpretation of the appearances presented by the lymphatic vessels at their first differentiation, and upon the question of the source and mode of development of the endothelium that lines these early rudiments. According to one idea, due originally to RANVIER, but associated now chiefly with the name of SABIN,* the lymphatics are direct outgrowths of the veins ; their endothelium sprouts from the pre-existing endothelium of the veins and their growth takes place centrifugally from the veins to the periphery.

In opposition to this view it is maintained by MCCLURE, HUNTINGTON and numerous others, that the lymphatics arise, as at an earlier stage do the blood vessels, from

* SABIN'S view of the question is given fully in KEIBEL and MALL'S ' Manual of Human Embryology,' vol. 2, 1912.

numerous independent and isolated spaces in the mesenchyme, which become lined by an endothelium derived from the mesenchyme cells that surround them, fuse with one another to form a plexus, and (growing centripetally) form connections with certain of the veins.

Although these two views are opposed to one another in their interpretation of the source from which the endothelium of the lymphatics comes and upon the method of their growth, they do not seem to me to be in conflict upon the broader and more fundamental question of the derivation of the lymphatic and blood-vascular systems from a common vascular basis. On SABIN'S hypothesis the relationship is one of direct sequence, the lymphatic vessels being outgrowths from veins already formed. On the other hypothesis the common origin of the two systems is put back to an earlier stage, symbolised in ontogeny by the development of both in a similar way from discrete spaces in the mesenchyme. Thus the one system does not actually grow from the other, but both arise from a common vascular bed.

This fundamental relationship of the two systems in a common mode of development is well expressed by MCCLURE when he says: "The development of the general vascular system—hæmal and lymphatic vessels—is a uniform process which consists in a local origin (genesis) of endothelium from mesenchymal cells and a growth of endothelium after it has once been formed. It would, therefore, appear that the lymphatic problem in its broadest sense should not be interpreted in terms either of a venous or non-venous origin, but rather in terms of the uniform phases of genesis and growth which may characterise the establishment of vascular channels in general." ('Mem. Wistar Inst.,' No. 4, 1915, p. 71.)

And again by HUNTINGTON in discussing the origin of vascular endothelium. After suggesting that a mesenchyme space originates by the accumulation of fluid between two mesenchyme cells, he continues: "The cells, whose opposing surfaces have become freed by the development of an intercellular space and are subjected to fluid pressure, will react as a whole, become flattened and be transformed into endothelial cells forming the parietal limit of an originally intercellular mesenchyme space, which is the font and origin of all vertebrate vascular development, independent of the question as to the ultimate destiny of the space in the organisation of the vascular system of which it forms a part. The particular space in question may become a constituent of the heart, of the arterial, of the venous, of the hæmal capillary, or of the lymphatic components of the entire vascular complex." ('Amer. Jour. Anat.,' vol. 16, 1914, p. 289.)

In pursuing this idea it should be observed that HUNTINGTON, MILLER and others describe in several of the major groups of Vertebrates (though not in Teleosts) an early condition of unusual interest, a condition in which the first appearing rudiments of the lymphatic system are both morphologically and functionally not lymphatic but venous.

A full review and discussion of this primitive blood-carrying or "hæmophoric" stage in the development of the lymphatics, is given by HUNTINGTON in 'Amer. Jour. Anat.,'

vol. 16, 1914, p. 259. Without, however, going into unnecessary detail, the essential features of the process are indicated in the following quotation from a shorter paper by HUNTINGTON in 'Anat. Record,' vol. 8, 1914, p. 76.

"In certain regions of amniote embryos lymphatic vessels develop, during the early stages, primarily for the purpose of conveying red blood cells formed *in situ* in the adjacent hæmopoietic mesenchyme directly into the venous channels. During this period they offer no morphological criteria differentiating them from the adjacent hæmal canals."

These hæmophoric vessels are apparently the first part of the lymphatic system to appear, and after thus acting as blood carriers, temporarily lose their connection with the veins, to resume it secondarily after taking up lymph vessels developed independently in the surrounding mesenchyme.

This hæmophoric phase passed through by the lymphatic vessels in the earliest stages of their development, when their constituent vessels are indistinguishable from blood-vessel rudiments except by reference to their subsequent history, seems to me to afford a most important indication of the original identity of the two systems; when to this is added the similarity in the mode of development of the lymph and blood vessels in the embryo, and also the facts shown by a comparative study of their anatomy in the adult, there seems reason to suppose that the lymphatic system (whether we adopt the SABIN or MCCLURE interpretation of its ontogeny) at the inception of its phylogenetic evolution formed an integral part of the blood-vascular system.

Whether the further assumption that this modified part of the blood-vascular system before the onset of its specialisation for a lymph-carrying function comprised both arteries and veins is a justifiable one is a problem of greater difficulty. If SABIN'S interpretation of the facts of the early ontogeny are correct and the evolving lymphatics were direct outgrowths from veins already in existence, there seems to be no special reason to suppose that such outgrowths designed from the first for a centripetal circulation only, should carry with them in their growth towards the periphery complementary arterial branches for which there would be no use. Should, however, the lymphatics be a specialised part of a primitive blood-vascular system, it is highly probable that whilst the coming lymphatics were still blood carriers—in a condition, that is, represented in ontogeny by the "hæmophoric" stage—they would include in their circulation both afferent and efferent channels.

The probability that this was so and that such a double circulation persisted to some extent even after the lymphatic system was well established, is borne out by the observation made by JOURDAIN and MAYER (10, 11) of an afferent and efferent circulation of lymph in young Fishes. So, although it cannot be regarded as by any means certain, it is not unreasonable to suppose that in the earlier stages of their evolution the lymphatics, like the rest of the vascular system, included both afferent and efferent components.

This idea is in harmony with FAVARO'S views (7, p. 253) on the relation of the vas intermedium of Elasmobranchs to the hæmal lymph trunk of Teleosts, and seems also to be supported by the researches of COLE on the vascular system of *Myxine* (6). In this low type of Fish, COLE distinguishes vascular channels of four kinds—arteries, veins, red lymphatics, and white lymphatics.

The red lymphatics form capacious sinuses associated mainly with the skin and gills with extensions to various parts of the head and to the mucous membrane of the pharynx and œsophagus. This lacunar system is in direct continuity on the one hand with the arterial system through branches of the carotid arteries and through curious perforated papillæ distributed along the respiratory blood vessels, and on the other hand with the venous system through valved openings. It contains blood in greater or less quantity that enters it directly through its arterial tributaries. The white lymphatics are apparently fully differentiated lymphatics without blood contents or arterial connections. They contain lymph only and derive important factors from the viscera.

If, as I am assuming from the facts observed in Teleosteans, the lymphatic system took its origin in the specialization of a part of the blood-vascular system that included both arteries and veins, the condition that one might expect to find at the commencement of this specialization would be something similar to what COLE describes in the red lymphatics of *Myxine*.

Probably an important factor in calling forth the lymphatic system was the necessity for an improved means for the conveyance of extraneous fluid from the periphery to the centre, either fluid of the surrounding medium transfused through the skin and the mucous membrane of the mouth and pharynx, or food material absorbed by the alimentary canal. The vessels most readily adaptable for this purely centripetal circulation would be the veins. One would thus expect to find in the earlier stages of this evolutionary process signs of modification in some of the veins, such as those of the skin, but not necessarily a corresponding alteration in their associated arteries, except possibly indications of degeneration. And this is very much what is to be observed in the condition of the red lymphatics of *Myxine* ; for these blood-containing spaces which underlie the skin and surround the gills are " not true lymphatics but belong rather to the blood-vascular system " (COLE, p. 335), and yet they cannot be regarded simply as veins, for although they contain blood, the blood varies much in quantity, and the regions in which they are distributed have in addition to them a blood supply of normal type.* On the other hand, that they are not true lymphatics but in a sense belong

* " *Polistotrema* (a Myxinoid) in the adult possesses a distinct system of lymphatics or veno-lymphatics, supplying a region amply furnished with veins " (ALLEN, " Studies on the development of the veno-lymphatics, in the tail region of *Polistotrema*," ' Quart. Jour. Micro. Sci.', vol. 59, 1914, p. 348).

" It is largely by the anterior terminal branches of the external carotid artery that blood enters the subcutaneous sinus. . . The external carotids otherwise supply the gut . . . , and also the skin of the snout" COLE, (6) p. 314.

to the blood-vascular system is indicated by the fact that they *do* contain blood, and by their distinct connection with arteries.

The condition of the vascular system in these lowly Vertebrates thus seems to present, as COLE suggests, an early stage in the evolution of lymphatics, in which "the 'lymphatic' spaces are neither true lymphatic nor true blood-vascular spaces, but partake of the nature of both. We have in the Myxinoids the final stage in the separation of the blood-vascular from the lymphatic system. In other words, the two systems are in the act of segregating out." (COLE, 5, p. 229.)

Some such condition may well represent, in a general way, a stage through which the lymphatic system of Teleosteans has passed, a stage in which the pre-Teleostean lymph vessels still partook of the characters of veins and were still in direct connection with branches of the arterial system, the present condition being attained by further segregation from the rest of the blood-vascular system, though still showing indications of the original arterial connections in the system of "fine" vessels described in this paper.

In this attempt to refer back the lymphatic system of Teleosts to a condition represented at the present day in Cyclostomes, it is perhaps of interest to note that the distribution of the red lymphatics of *Myxine* (which show arterial connections) corresponds in a general way with that of those lymphatics in Teleosteans with which "fine" vessels are associated; and that the white lymphatics, which in *Myxine* are apparently fully differentiated and have no arterial connections, are distributed mainly to the viscera, as are those lymphatics of Teleosteans to which I could find no "fine" vessel counterpart.

Should it indeed be the case that the lymphatic system at the commencement of its evolution included both venous and arterial components, it would open the way to a plausible interpretation of the nature of the "fine" vessel system in Teleosteans; for one could then regard these vessels, with some confidence, as the superfluous arterial component of a part of the blood-vascular system in process of lymphatic transformation, the complementary venous component being represented by the lymphatics with which the "fine" vessels are in capillary communication. This, so far as I can see at present, is the most reasonable interpretation of their nature and meaning, which will serve as a provisional hypothesis to be tested by further investigations.

Many questions still remain obscure. One would like to know, for instance, why the "fine" vessels, if they represent the arterial components of transformed veins, constitute a self-contained and continuous system complementary to the arteries. One would further wish to know whether a similar system of "fine" vessels is to be found in any of the more primitive Fishes, and if so, under what guise; is it, as in Teleosts, in the form of a more or less complete and self-contained network of vessels or does it occur as independent arterial branches, as in Cyclostomes; is it, if present, in more open connection than in Teleosts with the rest of the arterial system; and what are its relations to the pseudolymphatic vessels? Again, what is the meaning of the very

slight connection there is between the "fine" system and the arteries in Teleosts; is it a step between open continuity and complete separation preparatory to a final disappearance; or is it leading up to separation and the incorporation of these vessels with the rest of the lymphatic system? It is perhaps suggestive that the lymphatics of Cæcilian Amphibians are of two sharply contrasted types, one slender, thick-walled, elastic and muscular, the other delicate and capacious.

These and many other questions await an answer.

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DESCRIPTION OF THE PLATES.

Reference Letters.

a.b., articular base of gill ray.
a.p., arterial plexus.
aff.br., afferent branchial vessel.
aff.fil.v., afferent filamentary vessel.
aff.psbr.a., afferent artery of pseudobranch.
an., anastomosis.
aor.f., aortic trunk of " fine " vessel system.
br., I-IV., gills.
br.a., branchial arch.
br.f., branchial " fine " vessels.
br.st.f., " fine " vessel branches to branchistegal membrane.
cm.a., cœlio-mesenteric arteries.
eff.br., I-V., efferent branchial vessels.
eff.fil.v., efferent filamentary vessels.
eff.psbr.a., efferent artery of pseudobranch.
epbr.a., epibranchial arteries.
epbr.r., attachment of epibranchial retractor muscle.
ext.c.f., " fine " vessel accompanying external carotid artery.
f., gill filament.
f.v., " fine " vessel.
hy., hyoid arch.
hy.f., hyoid " fine " vessel.
hy.ph., inferior pharyngeal.
int.m., intrinsic muscle of gill filament.
l.hbr.f., longitudinal hypobranchial trunk of " fine " system.
lg., tongue.
lg.f., lingual " fine " vessel.
lph., minor lymphatic vessels or capillaries.
md., mandible.
md.f., mandibular " fine " vessel.
n., branchial nerve.
n.a., nutrient artery.
nut.f., " fine " vessels accompanying nutrient arteries.
o.n.f., orbito-nasal " fine " vessel.
pal.f., " fine " branches to palate.
pct.f., " fine " vessels to pectoral fin.
ph.f., pharyngeal " fine " vessels.

pr., thorn-like pits in wall of non-respiratory segment of efferent filamentary vessel.
ps.br., Pseudobranch.
r., gill ray.
rad., radicles connecting respiratory laminæ to efferent filamentary vessel.
re.f., "fine" vessel branches to head kidney.
rsp.l., respiratory laminæ.
scl.a., *scl.f.*, } subclavian artery and "fine" vessel.
sg.f., segmental branches of "fine" system.
s.l.v., supra-ligamentous vessels.
sus., suspensorium of jaw.
tr.c.a., *tr.c.p.*, } anterior and posterior transverse commissures in hypo- and epibranchial segments of "fine" vessel system.
tr.l., transverse elastic ligament.
v.a., *v.f.*, } ventral branch of hypobranchial artery and of hypobranchial segment of "fine" vessel system.
v.v., valves.

Explanation of Plates.

Plate 84.

Fig. 1.—The floor of the mouth, dissected from the dorsal aspect to show the main "fine" vessels (black) and the efferent branchial and hypobranchial arteries (grey). On the right side the fourth gill and inferior pharyngeal have been removed to show the ventral artery and "fine" vessel (*v.f.*), running ventrally towards the pelvic fins.

Fig. 2.—The circulus cephalicus with its main factors and branches (grey) and the larger components of the "fine" system that accompany them (black).

Fig. 3.—Diagram of the branches of the "fine" vessel system to the pectoral fin and along the aorta; arteries, grey; "fine" vessels, black. A. and B, from the circulus cephalicus to the second hæmal spine; C in the tail. Caudal artery, cross hatched.

Fig. 4.—Diagram of cross-section of gill to illustrate the orientation of its different parts and the terms used.

Plate 85.

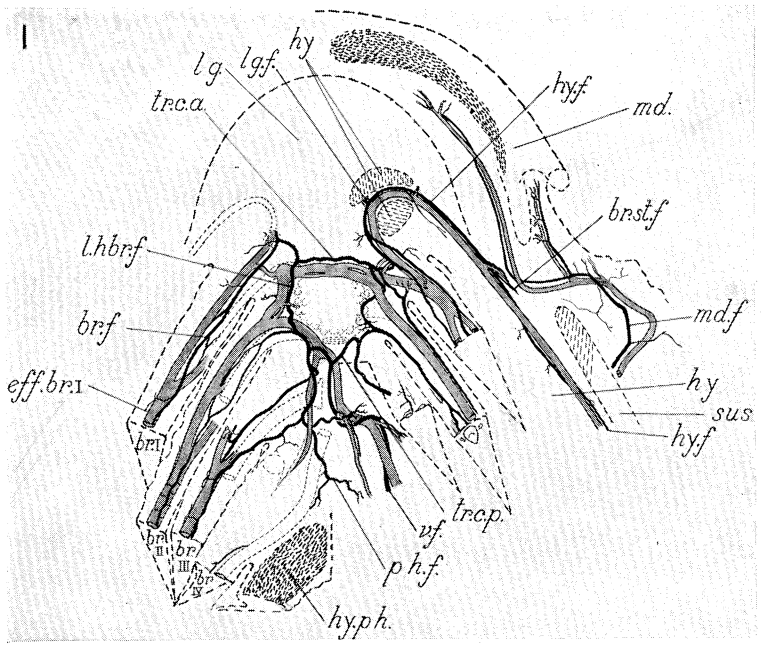
Fig. 5.—Two drawings, from microphotographs, of segments of the efferent branchial artery, showing origin of nutrient arteries from the roots of efferent filamentary vessels.

Fig. 6.—Drawing, from microphotograph, of efferent filamentary vessel, showing nutrient arteries of the filament and spine-like processes in basal parts of the artery.

Fig. 7.—Drawing, from microphotograph, of venous plexus within concavity of branchial arch. A-B: long axis of arch.

Fig. 8.—Drawings, from microphotographs. A. Basal part of filament, showing the venous factors. B. Transverse section of arch, showing venous plexus and main filamentary factors. Veins: grey; "fine" vessels: black. * Corresponding point in figs. A and B.

Fig. 9.—Drawing, from microphotograph, of contents of branchial arch, in cross-section, showing supra-ligamentous vessels passing to proximal surface of ligament, and lymphatic factors at base of filament. Lymphatics: grey; "fine" vessels: black.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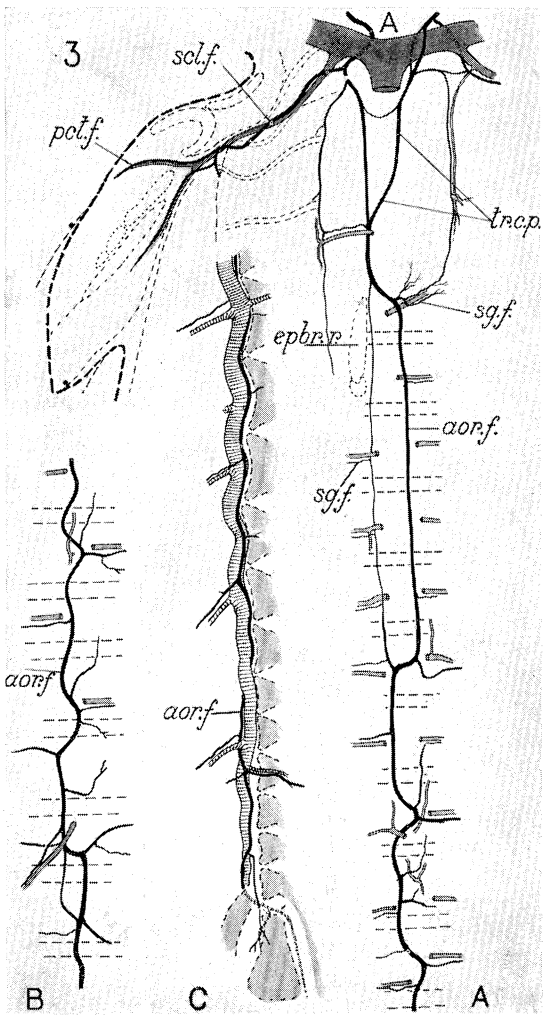
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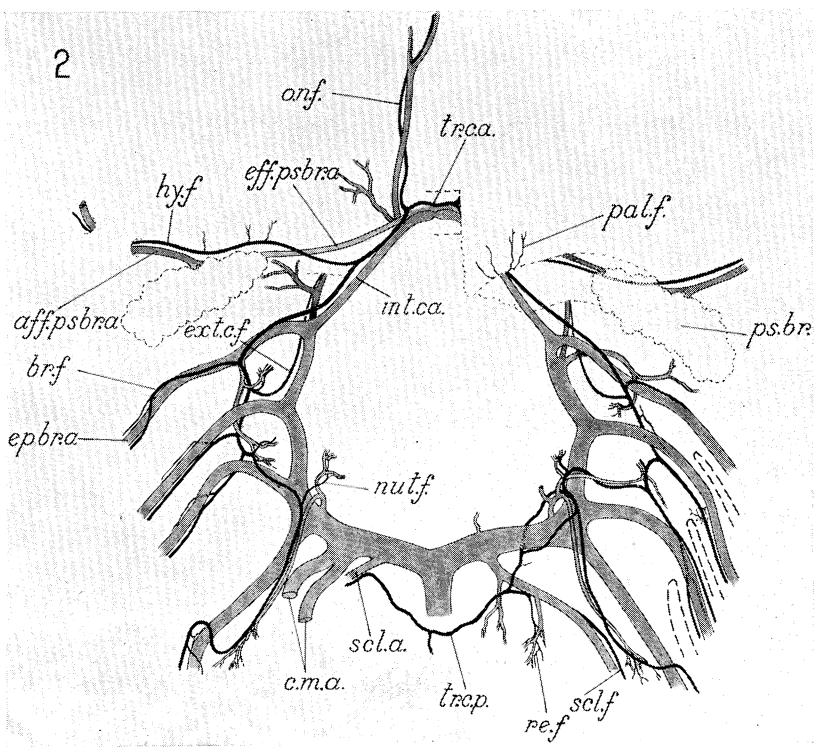
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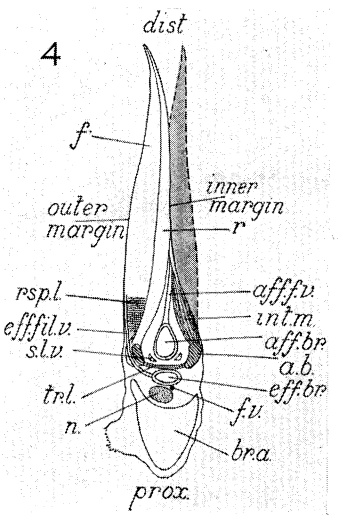
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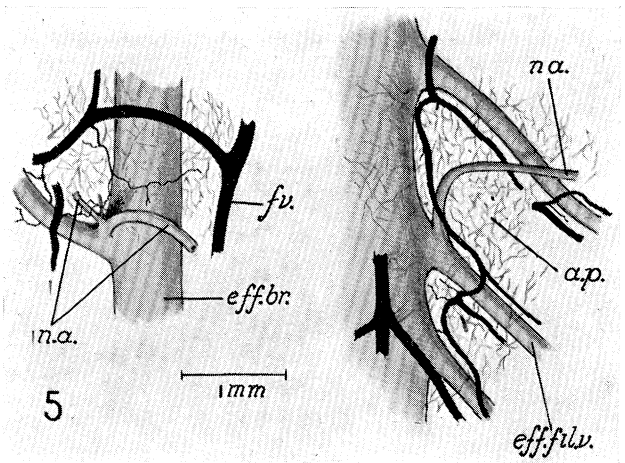
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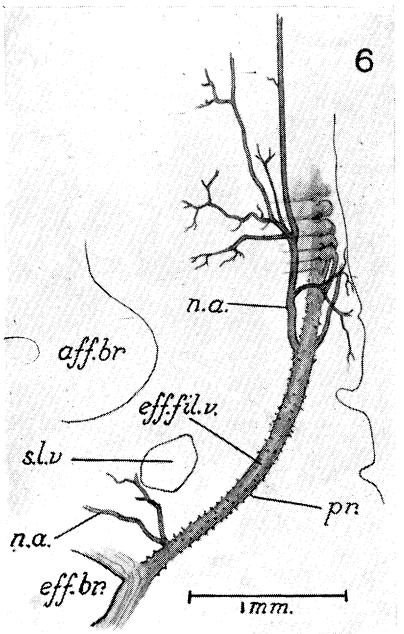
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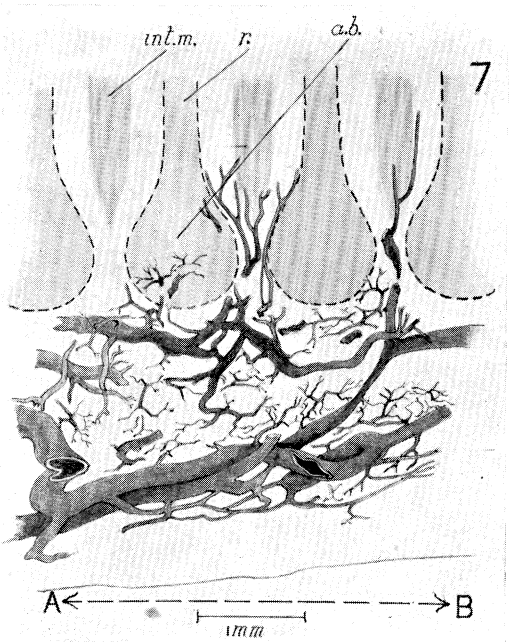
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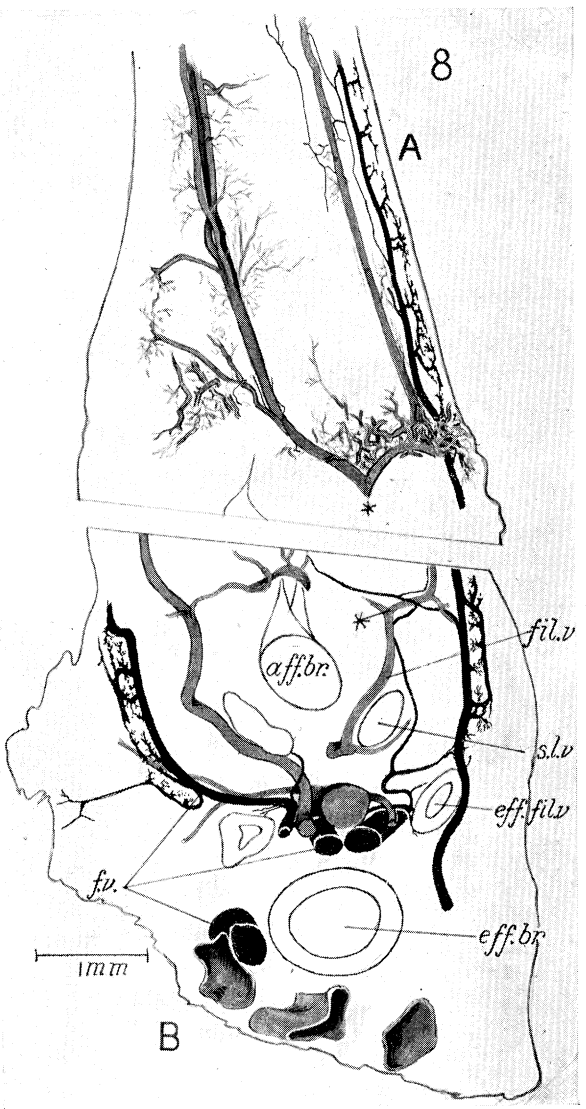
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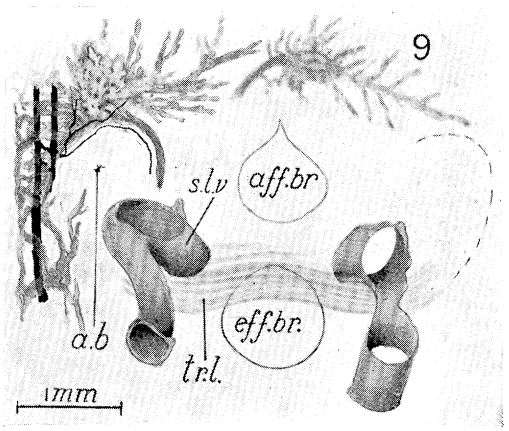
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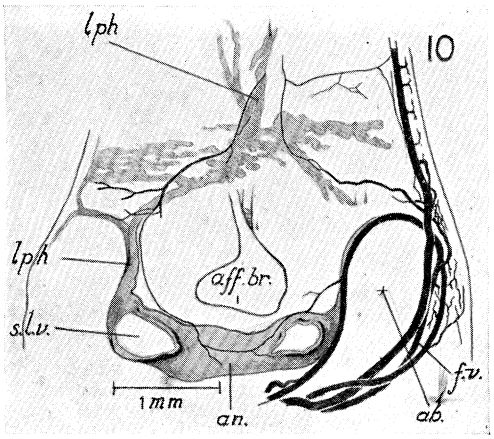
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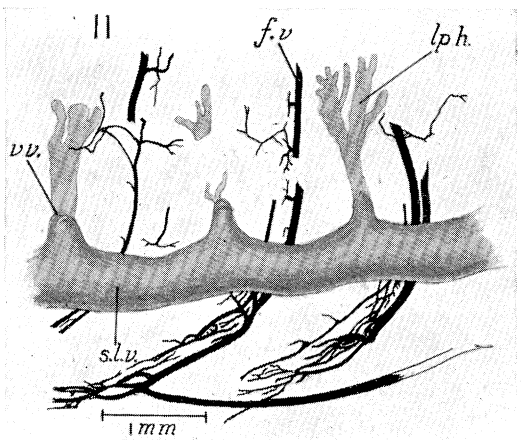
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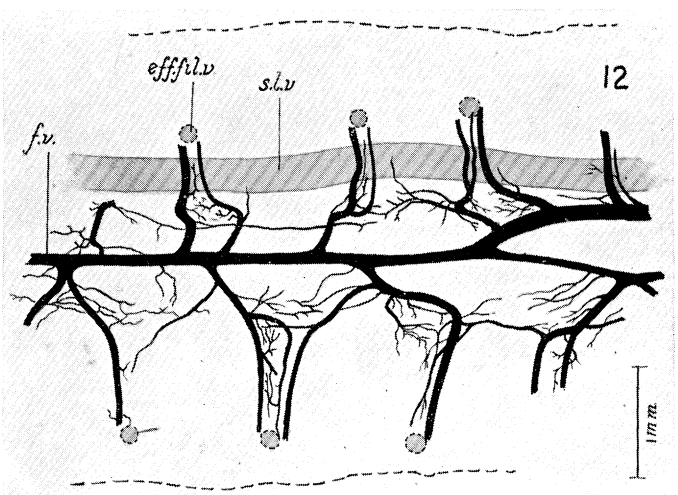
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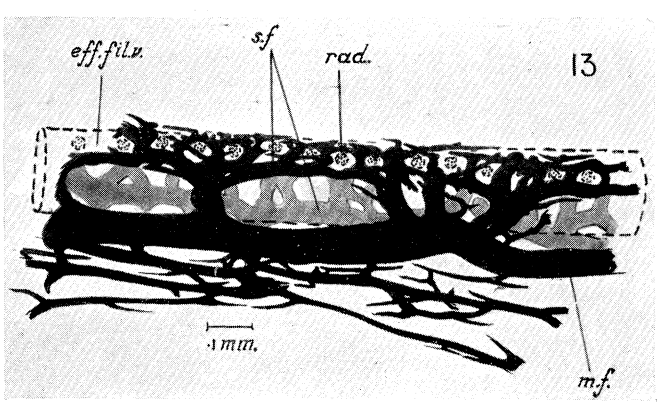
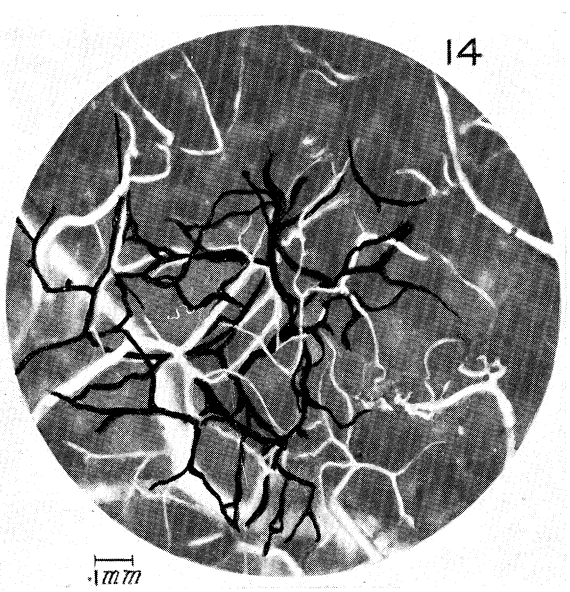

eff.fil.v.
s.f
rad.
13
1 mm.
m.f.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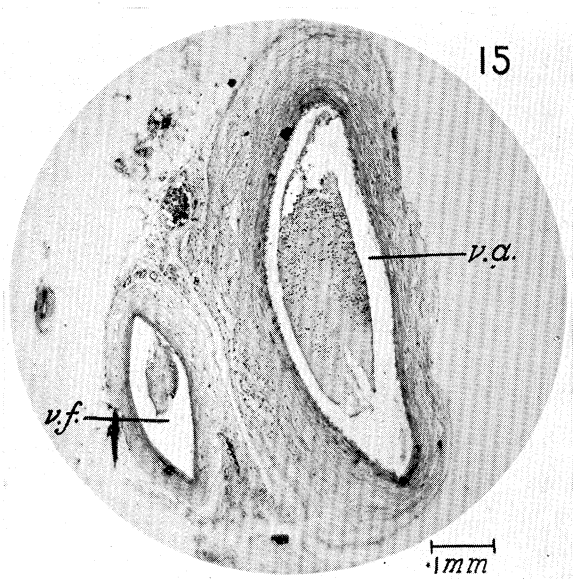
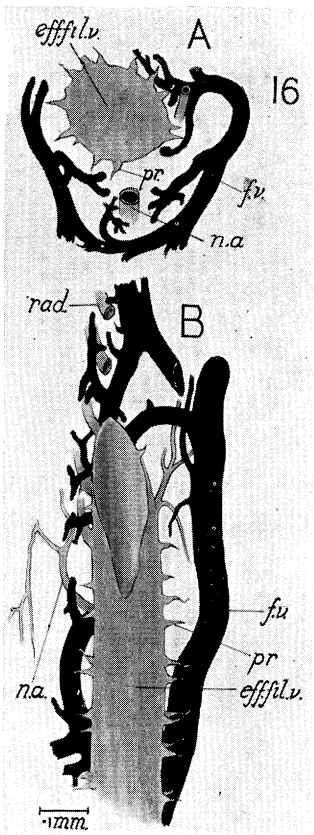
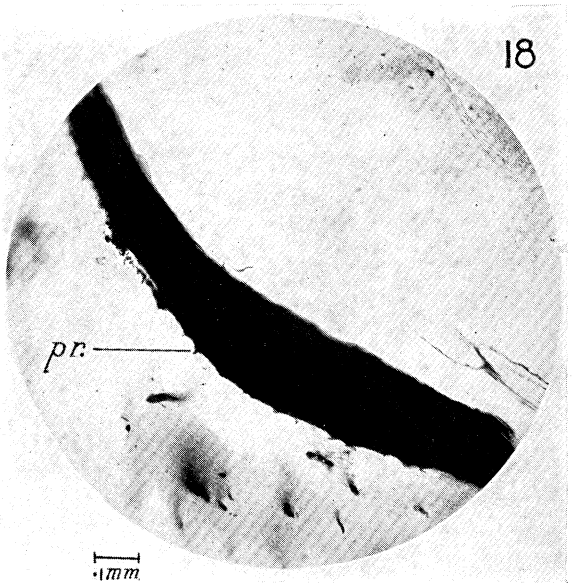
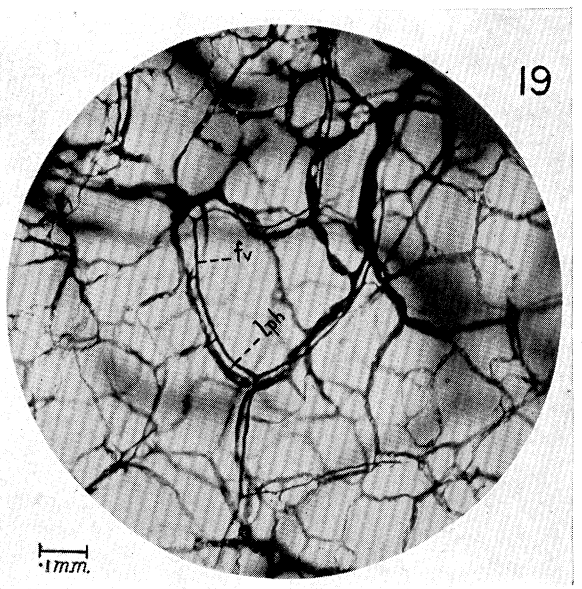

15
v.a.
v.f.
1 mm


A
efffil.v.
pr.
f.v.
n.a
B
rad.
f.u
pr
n.a.
efffil.v.
·1mm.

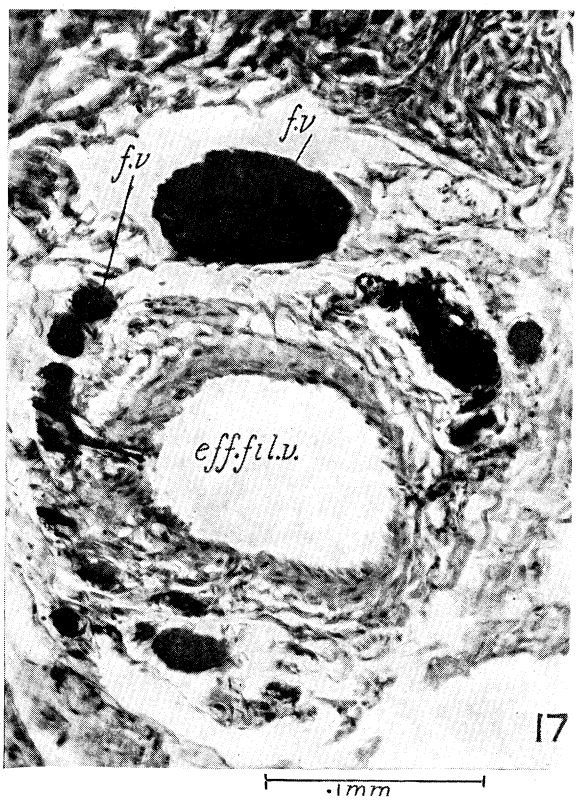
16


pr.
·1mm.

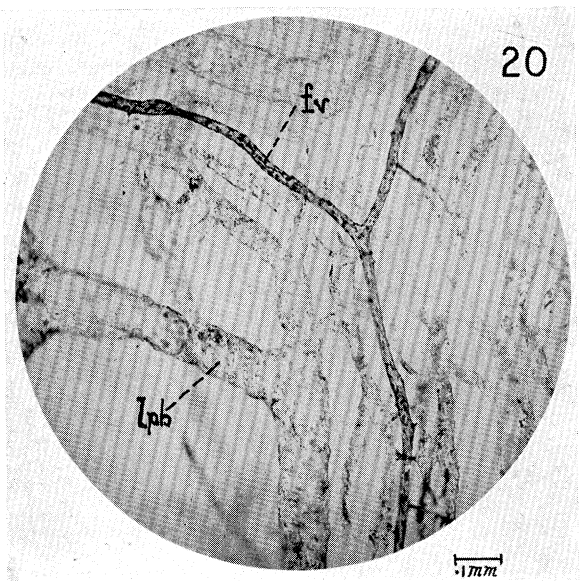
18


f.v
lpb
·1mm.

19


f.v
f.v
eff.fil.v.
·1mm

17


fv
lpb
·1mm

20

PLATE 86.

FIG. 10.—A figure similar to No. 9, showing connection between the supra-ligamentous vessels and the main filamentary factor. Lymphatics: grey; "fine" vessels: black.

FIG. 11.—Supra-ligamentous vessel, viewed parallel to long axis of branchial arch, showing valved entry of filamentary factors. Lymphatics: grey; "fine" vessels: black.

FIG. 12.—Contents of branchial arch viewed from proximal aspect; showing "fine" vessel network and its filamentary branches. One of the supra-ligamentous vessels contains faint injection introduced through the "fine" vessels.

FIG. 13.—Part of outer margin of filament, showing main and subsidiary trunks of "fine" vessels surrounding efferent filamentary vessel and its radicles. *Eff. fil.v.*, position of efferent filamentary vessel; *m.f.*, main filamentary "fine" vessel trunk; *rad.*, position of radicles of efferent filamentary vessel; *s.f.*, secondary plexiform filamentary "fine" vessel trunks.

FIG. 14.—Microphotograph (retouched) of a piece of the mucous membrane of the tongue with the veins injected yellow, and the "fine" vessels and lymphatic (?) capillaries: black.

FIG. 15.—Microphotograph of transverse section through ventral branch of hypobranchial artery and its accompanying "fine" vessel.

PLATE 87.

FIG. 16.—Basal (non-respiratory) segment of efferent filamentary vessel, showing thorn-like projections from lumen. Arteries: grey; "fine" vessels: black. A. transverse section. B. longitudinal view.

FIG. 17.—Transverse section through non-respiratory segment of efferent filamentary vessel, showing passage of injection (black) from "fine" vessel plexus to artery.

FIG. 18.—Microphotograph of non-respiratory segment of efferent filamentary vessel of *Lophius piscatorius*, showing thorn-like projections (*pr.*) from lumen; part of one side only is in focus.

FIG. 19.—Microphotograph of mucous membrane of tongue with "fine" vessels injected, showing vessels of two kinds filled with injection mass.

FIG. 20.—Microphotograph of mucous membrane of tongue with "fine" vessels injected black taken at a deeper level than Fig. 19. In this preparation the larger vessels (*lph*) contain both black and yellow introduced respectively from the "fine" vessels and from the lymphatics (see Fig. 23).

PLATE 88.

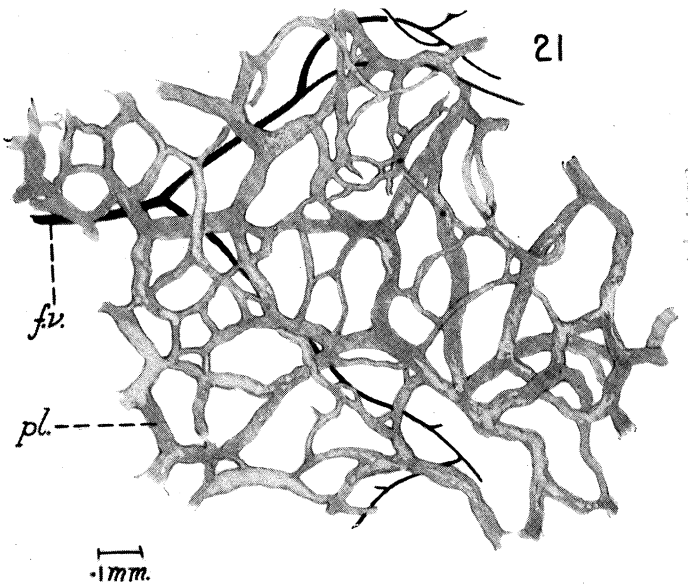
FIG. 21.—Superficial plexus in skin above eye. Black injection was introduced into " fine " vessels and subsequently a yellow injection into the lateral superficial lymphatic trunk. The superficial capillary network (*pl.*) contains black injection mixed with yellow.

FIG. 22.—Mucous membrane of tongue. Black injection introduced into " fine " vessels, yellow into superficial facial lymphatic : intrusion of black injection mass into larger lymphatics.

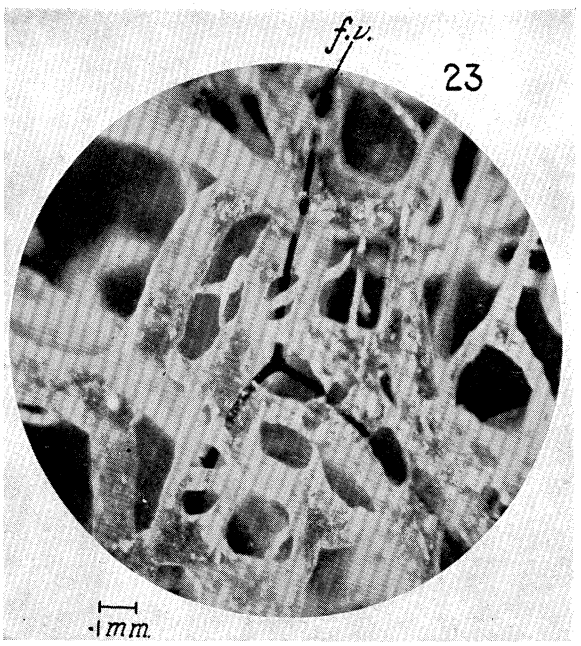
FIG. 23.—Mucous membrane of tongue. " Fine " vessels injected black; lymphatics, yellow from branchial lymphatic. Neither injection reached the surface, no admixture of colours.

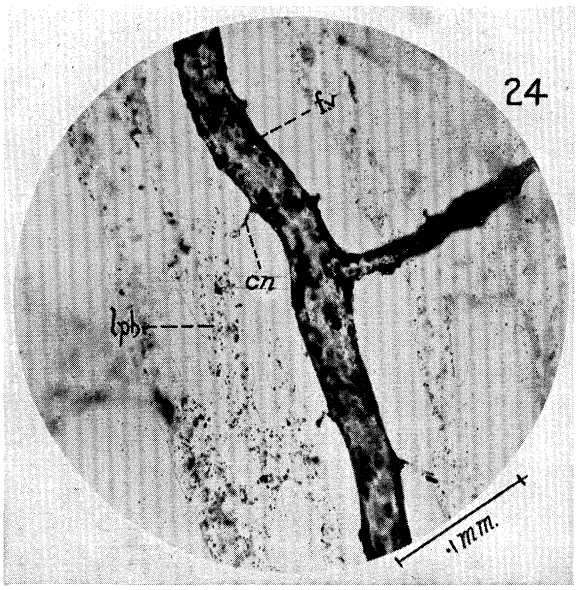
FIG. 24.—Mucous membrane of tongue with " fine " vessels (*f.v.*) injected black, showing slender transverse branches (*cn*) extending from them to the lymphatics (*lph*).

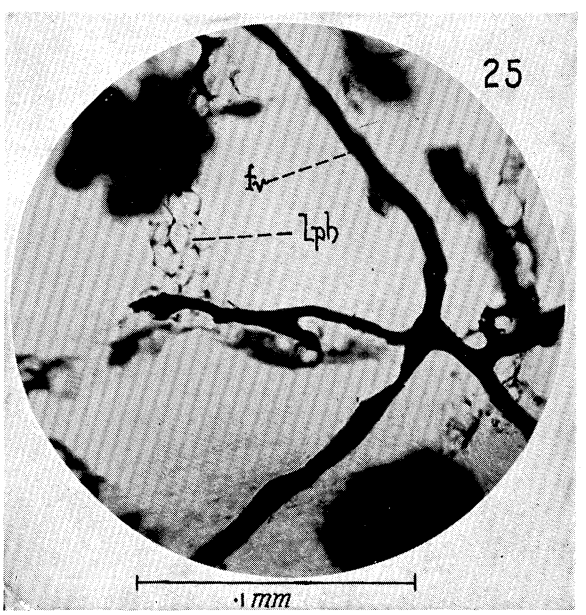
FIG. 25.—Terminal branches of " fine " vessels, forming connections with the meshes of the superficial network of lymphatic capillaries. From the mucous membrane of the tongue.

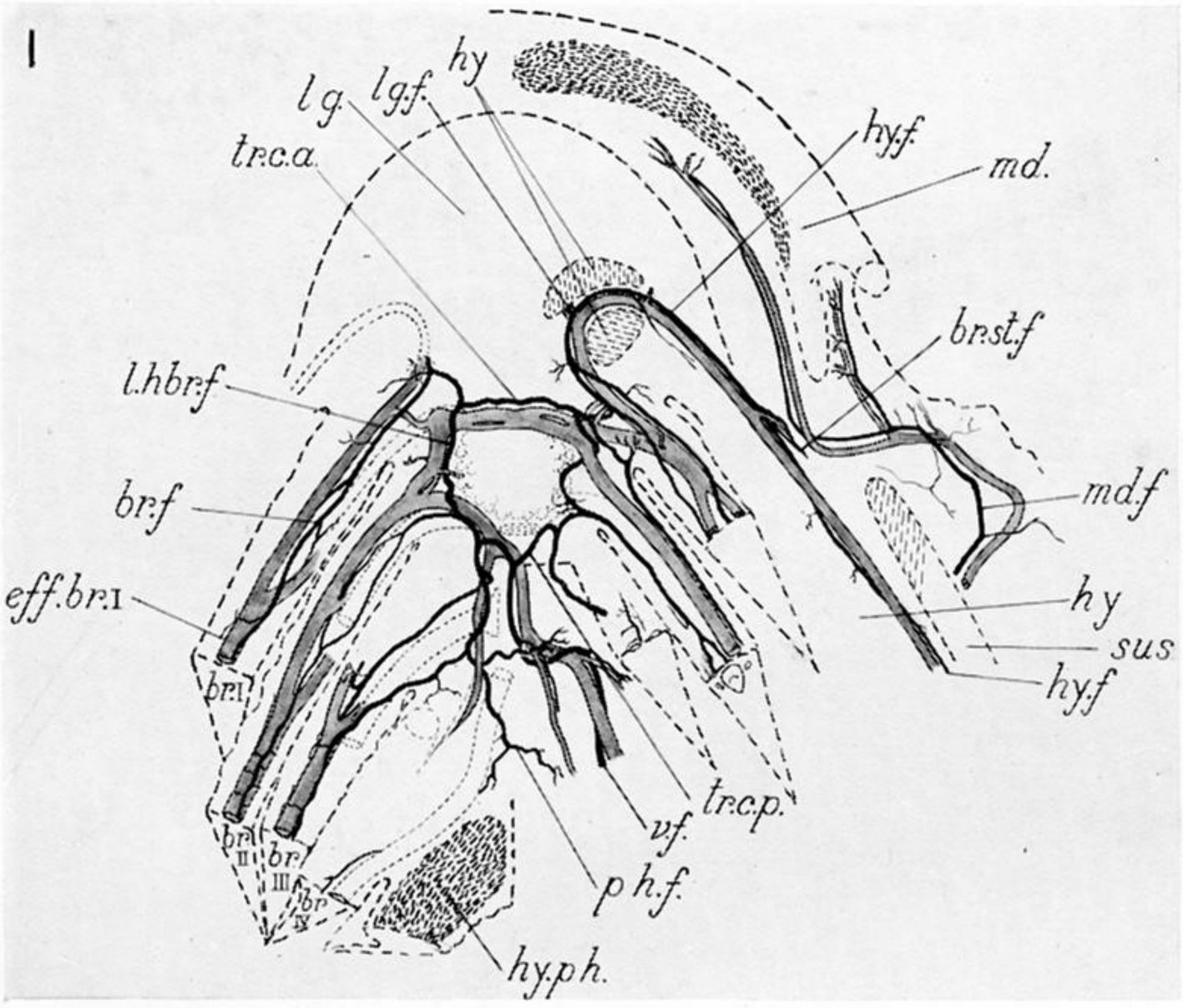

21
f.v.
pl.
·1mm.

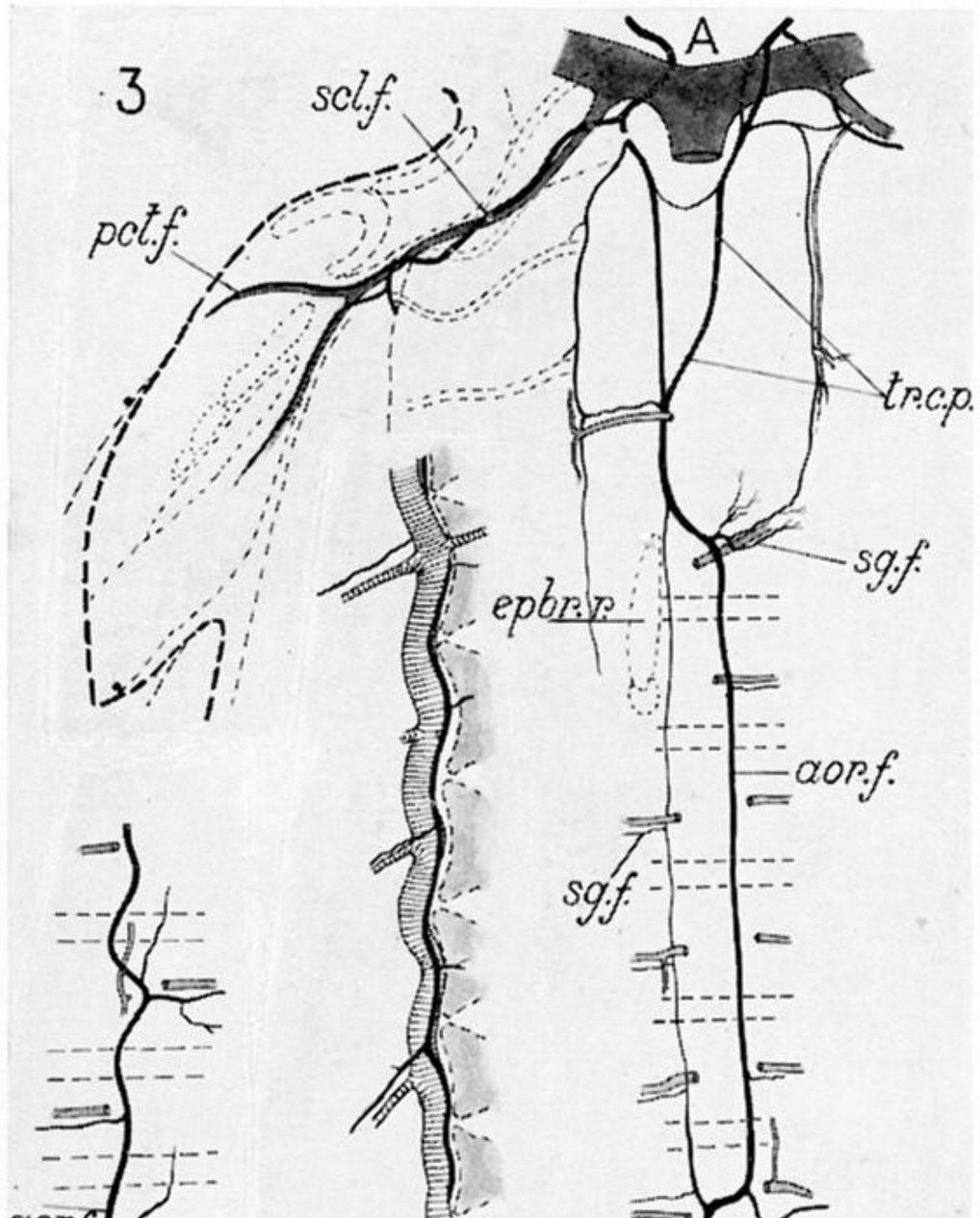
f.v.
22
lph.
·1mm.

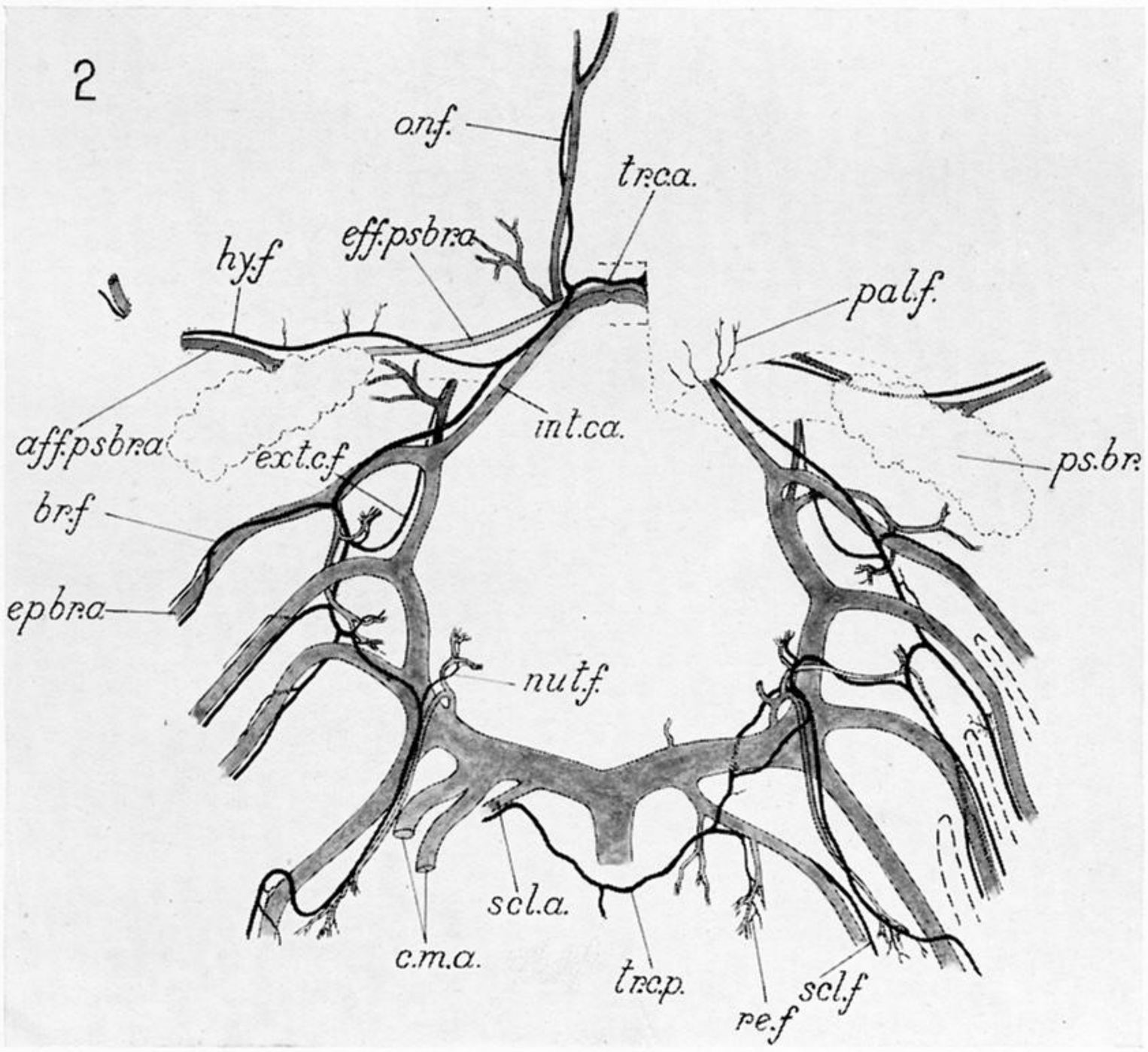

f.v.
23
·1mm.


fv
24
cn
lph
·1mm.


25
fv
lph
·1mm







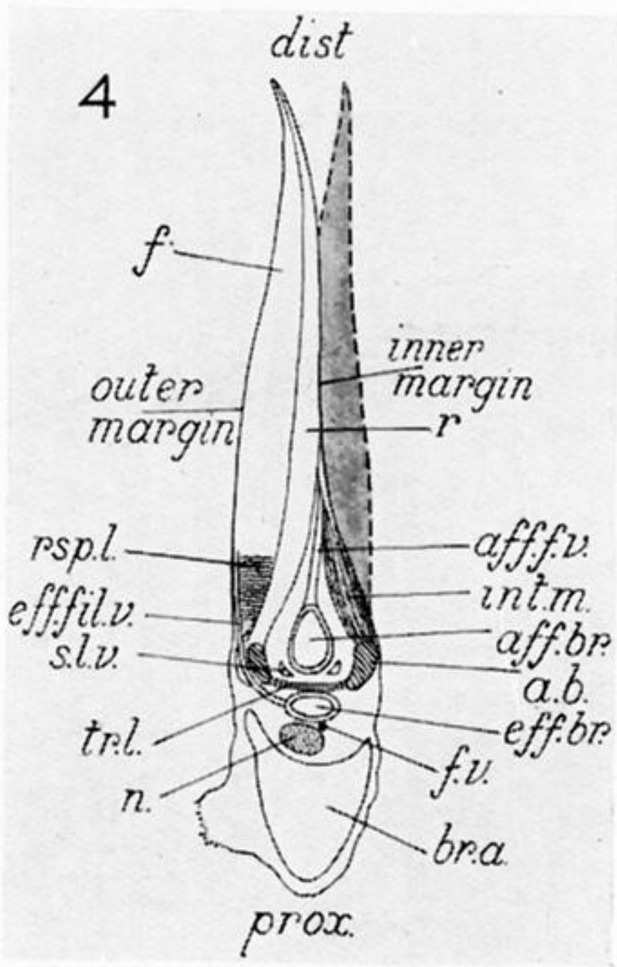


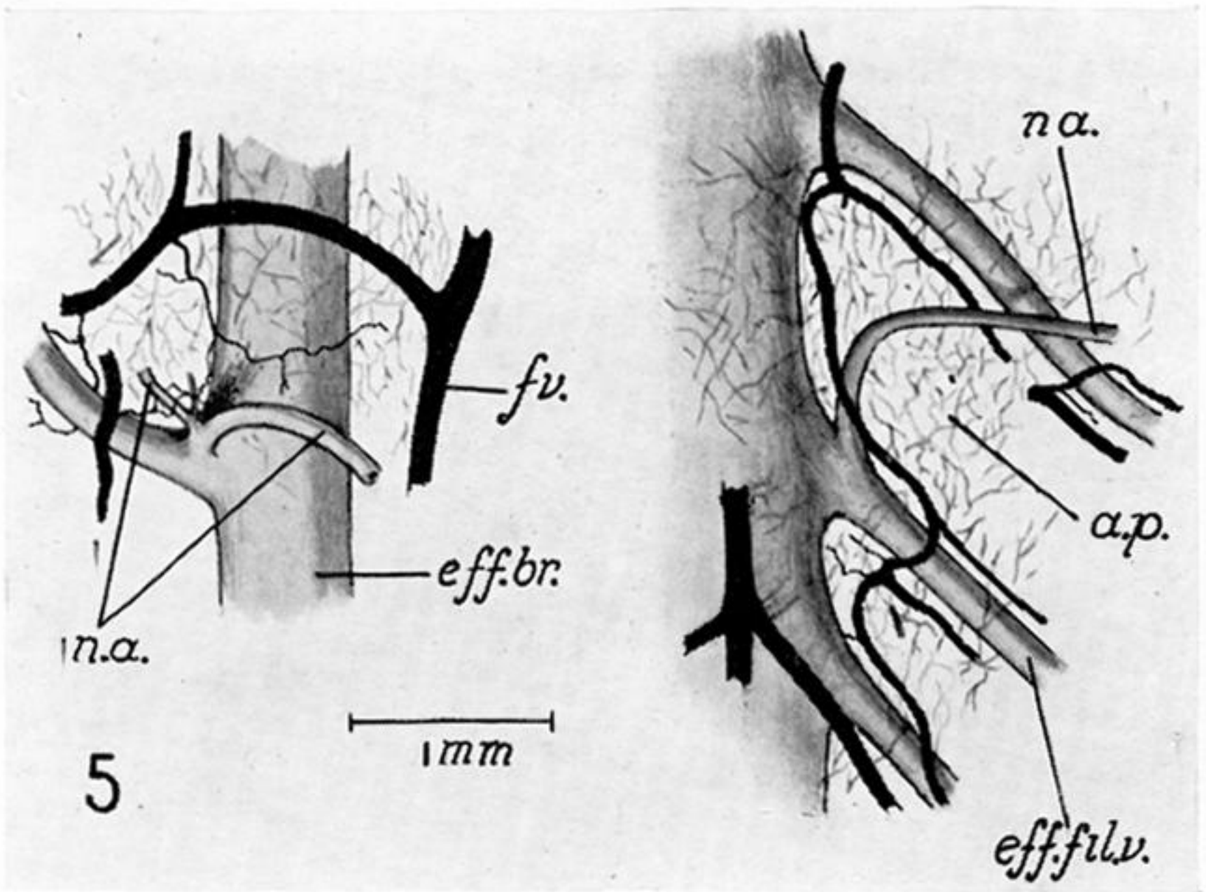
PLATE 84.

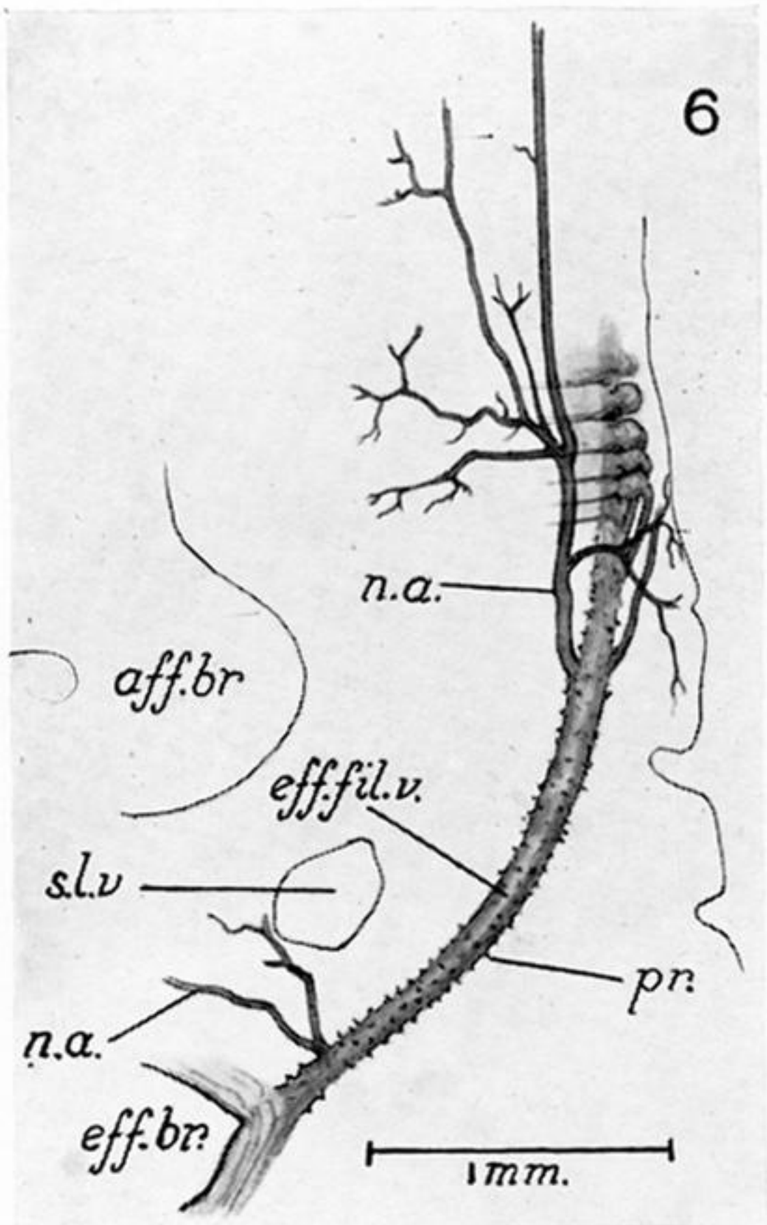
FIG. 1.—The floor of the mouth, dissected from the dorsal aspect to show the main "fine" vessels (black) and the efferent branchial and hypobranchial arteries (grey). On the right side the fourth gill and inferior pharyngeal have been removed to show the ventral artery and "fine" vessel (*v.f.*), running ventrally towards the pelvic fins.

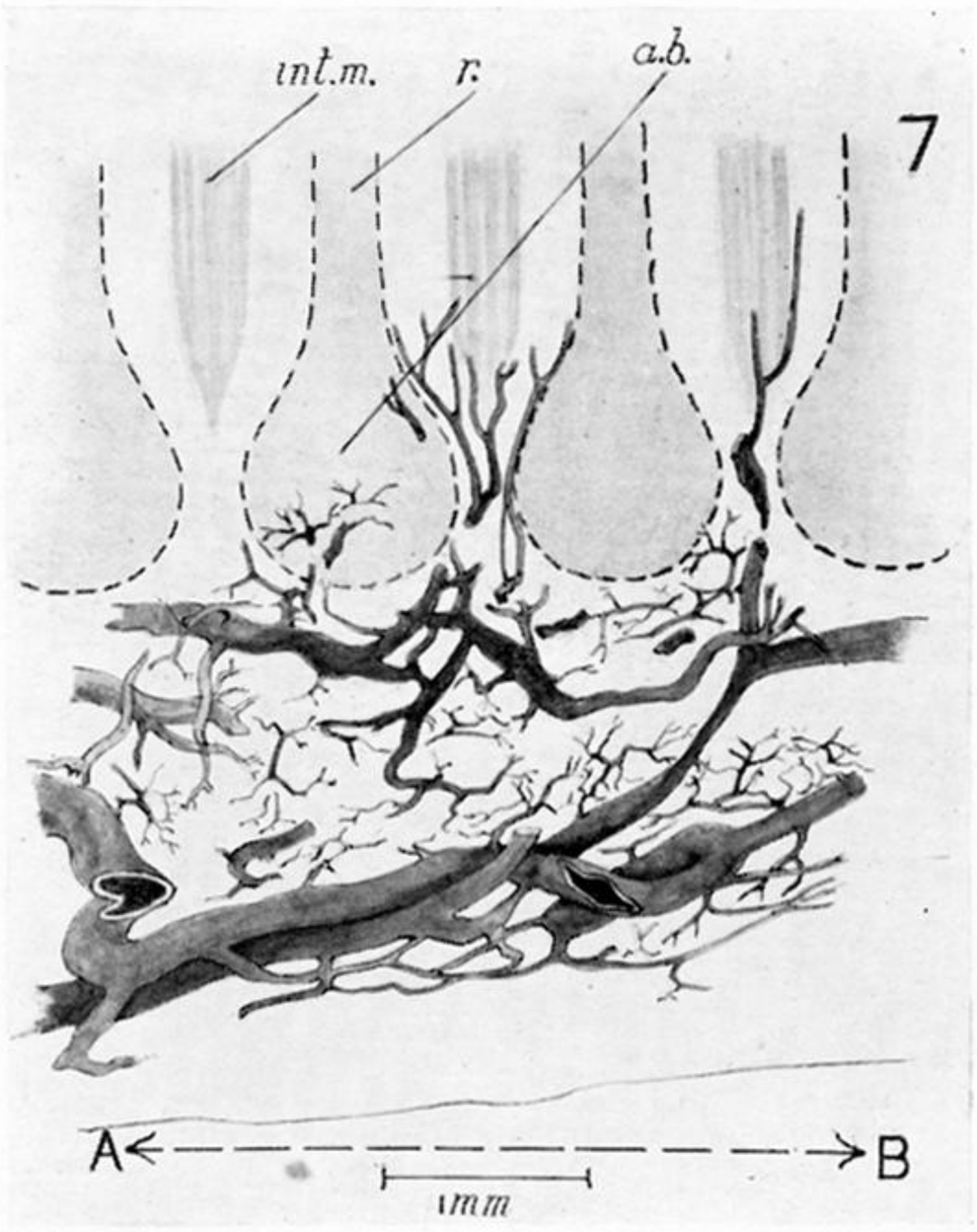
FIG. 2.—The circulus cephalicus with its main factors and branches (grey) and the larger components of the "fine" system that accompany them (black).

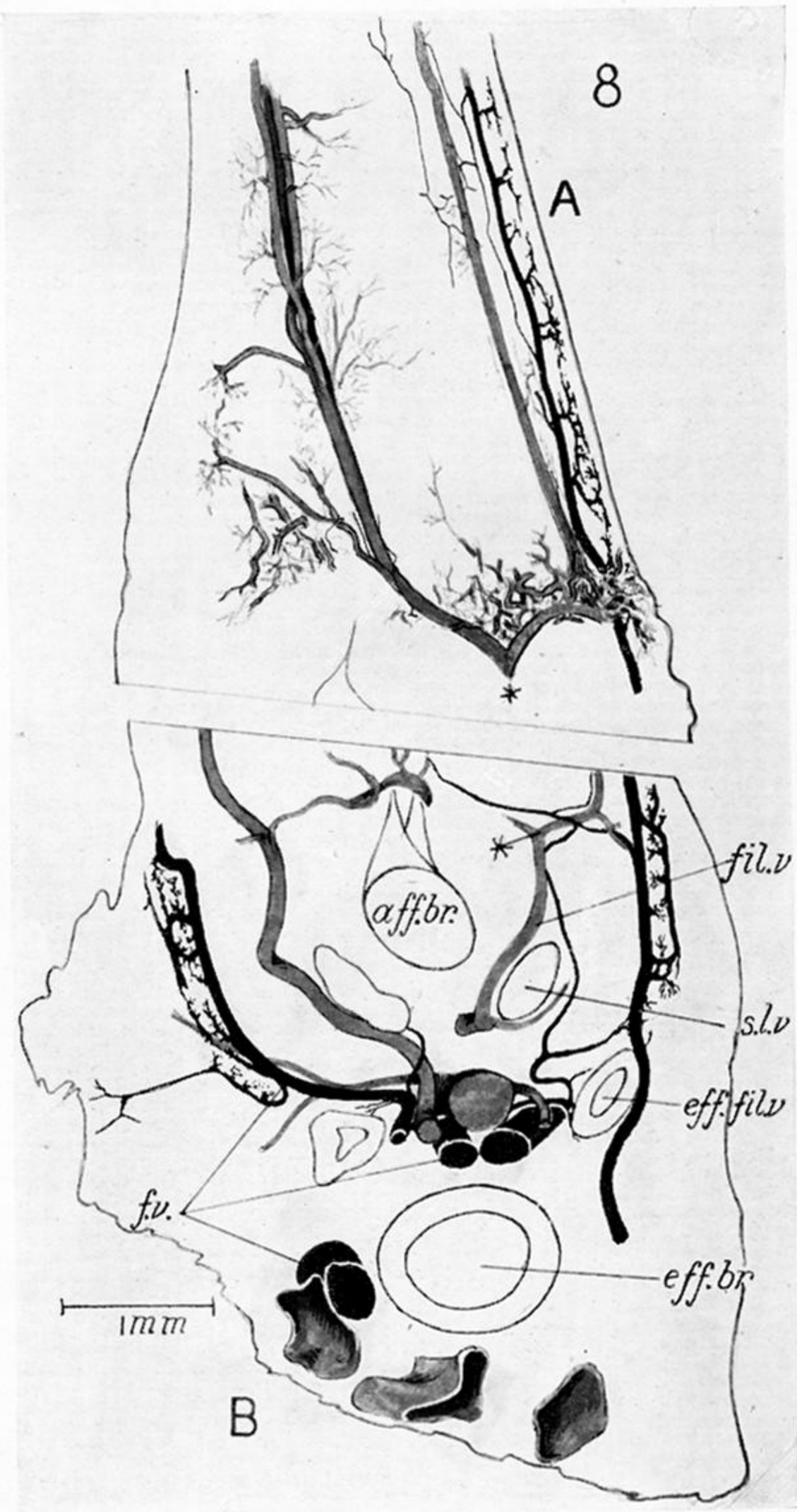
FIG. 3.—Diagram of the branches of the "fine" vessel system to the pectoral fin and along the aorta; arteries, grey; "fine" vessels, black. A. and B, from the circulus cephalicus to the second hæmal spine; C in the tail. Caudal artery, cross hatched.

FIG. 4.—Diagram of cross-section of gill to illustrate the orientation of its different parts and the terms used.









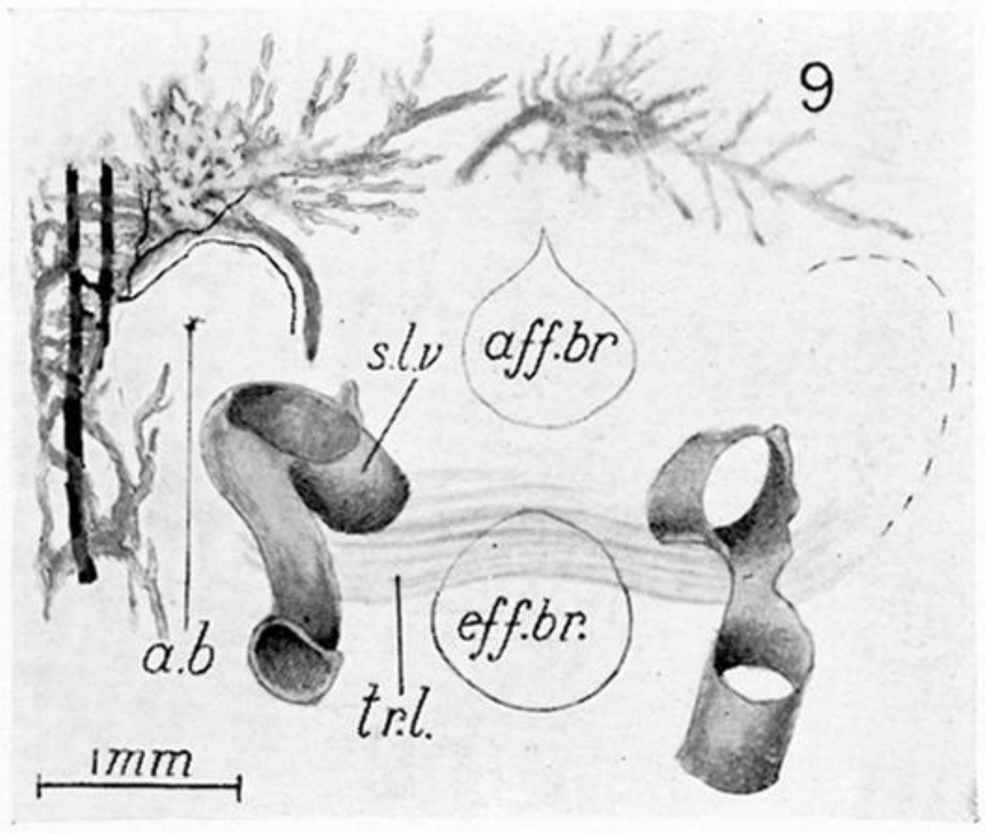


PLATE 85.

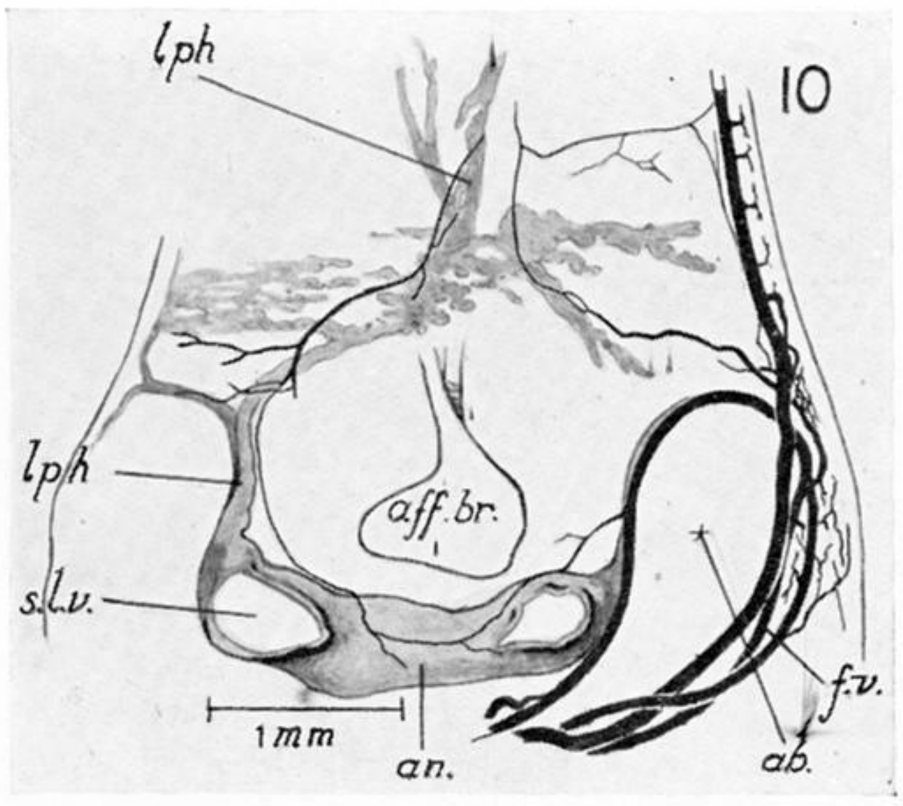
FIG. 5.—Two drawings, from microphotographs, of segments of the efferent branchial artery, showing origin of nutrient arteries from the roots of efferent filamentary vessels.

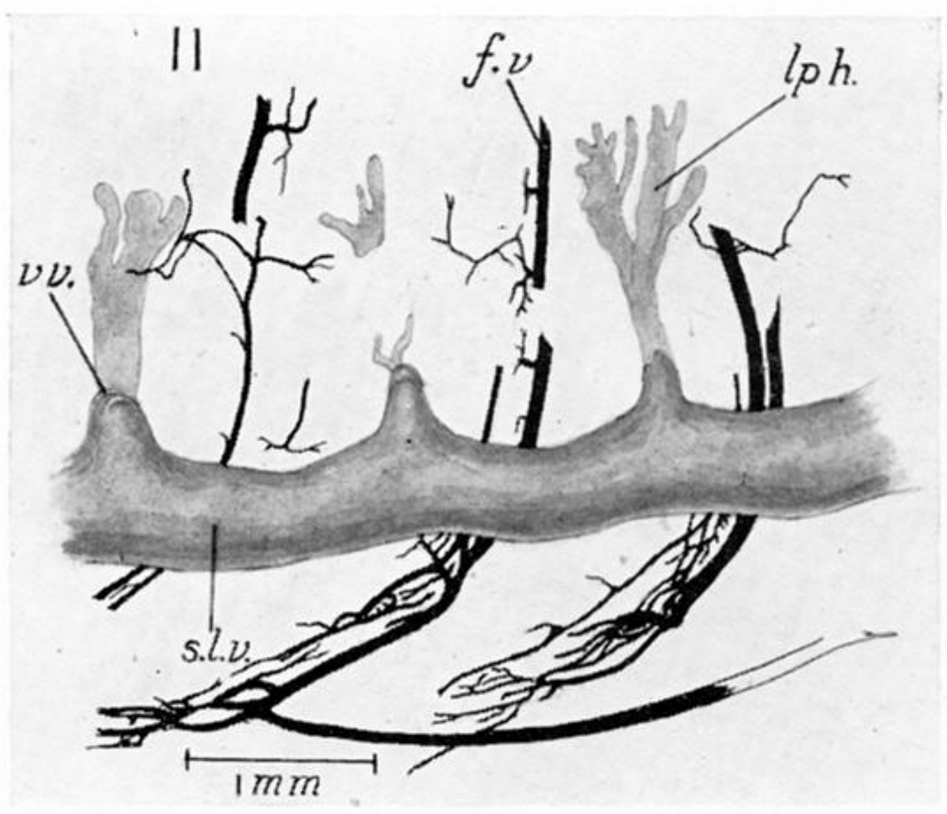
FIG. 6.—Drawing, from microphotograph, of efferent filamentary vessel, showing nutrient arteries of the filament and spine-like processes in basal parts of the artery.

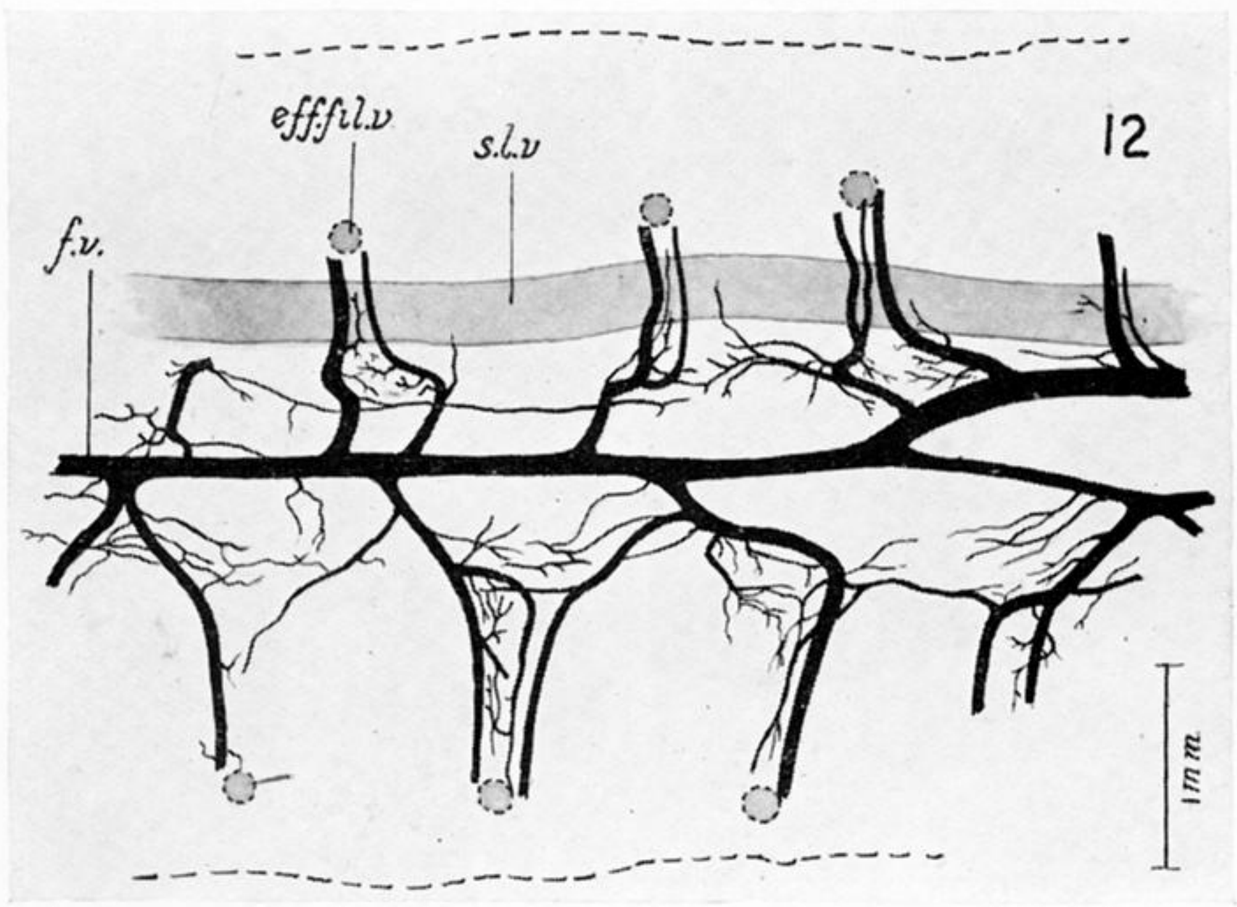
FIG. 7.—Drawing, from microphotograph, of venous plexus within concavity of branchial arch. A-B: long axis of arch.

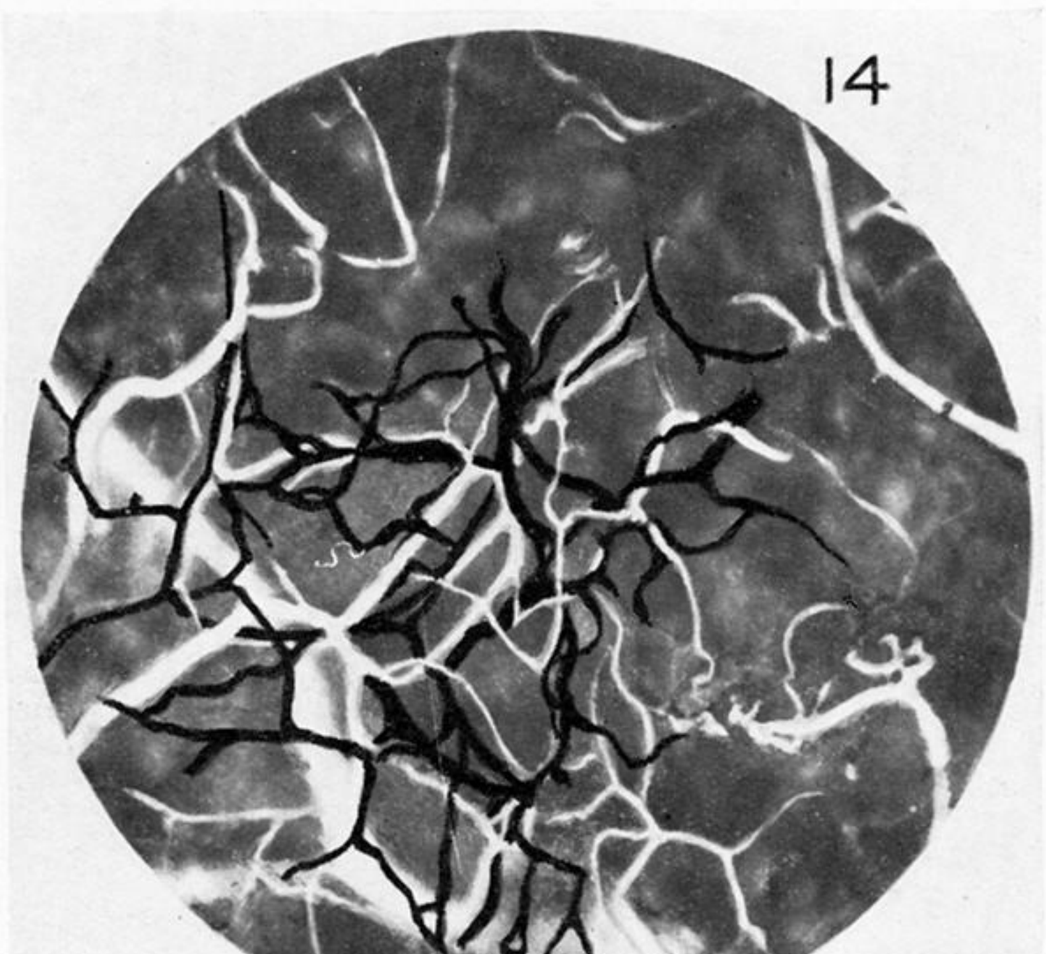
FIG. 8.—Drawings, from microphotographs. A. Basal part of filament, showing the venous factors. B. Transverse section of arch, showing venous plexus and main filamentary factors. Veins: grey; "fine" vessels: black. * Corresponding point in figs. A and B.

FIG. 9.—Drawing, from microphotograph, of contents of branchial arch, in cross-section, showing supra-ligamentous vessels passing to proximal surface of ligament, and lymphatic factors at base of filament. Lymphatics: grey; "fine" vessels: black.









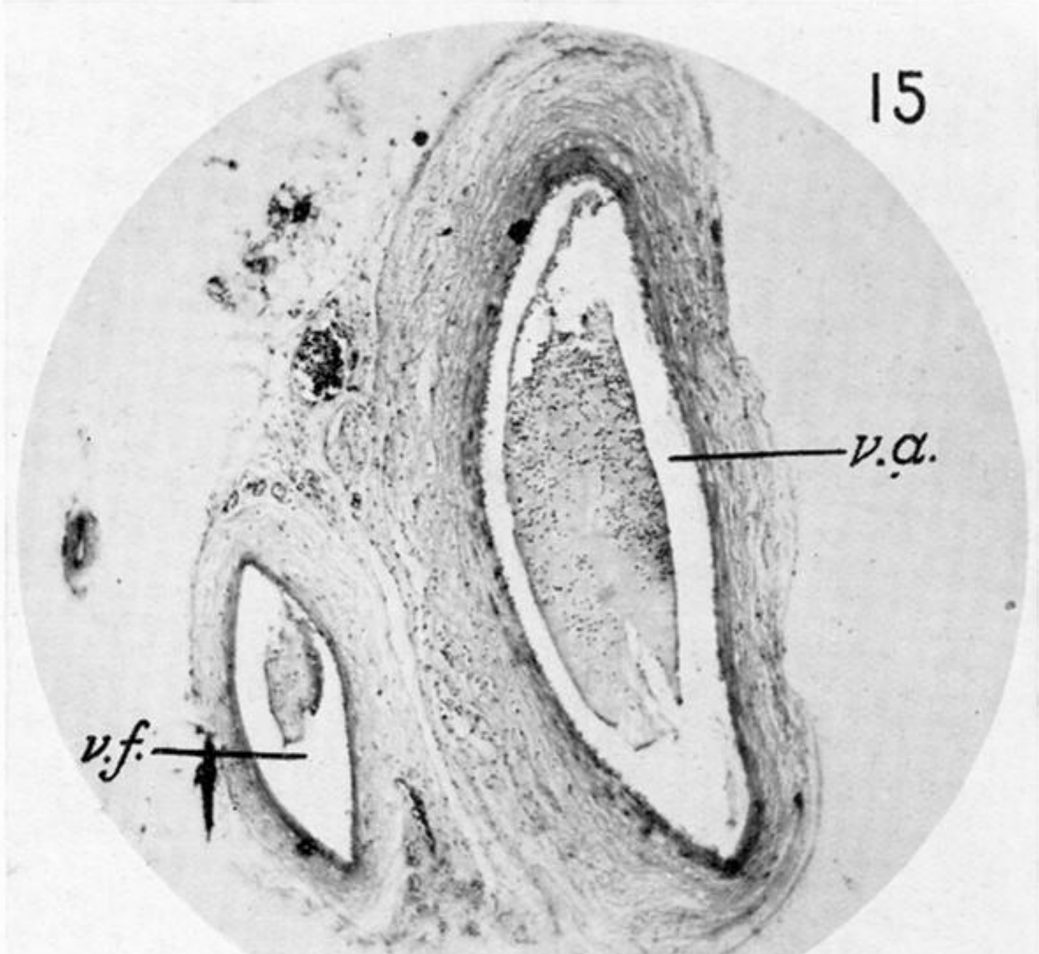


PLATE 86.

FIG. 10.—A figure similar to No. 9, showing connection between the supra-ligamentous vessels and the main filamentary factor. Lymphatics : grey ; " fine " vessels : black.

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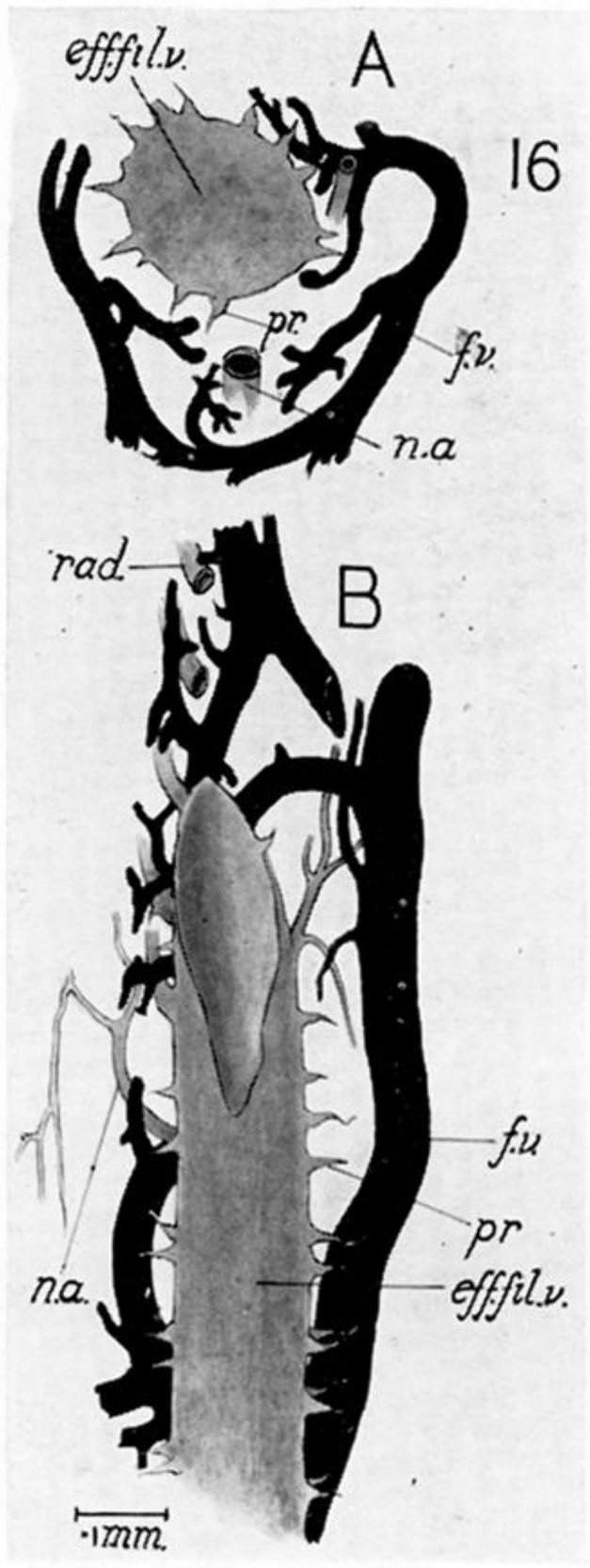

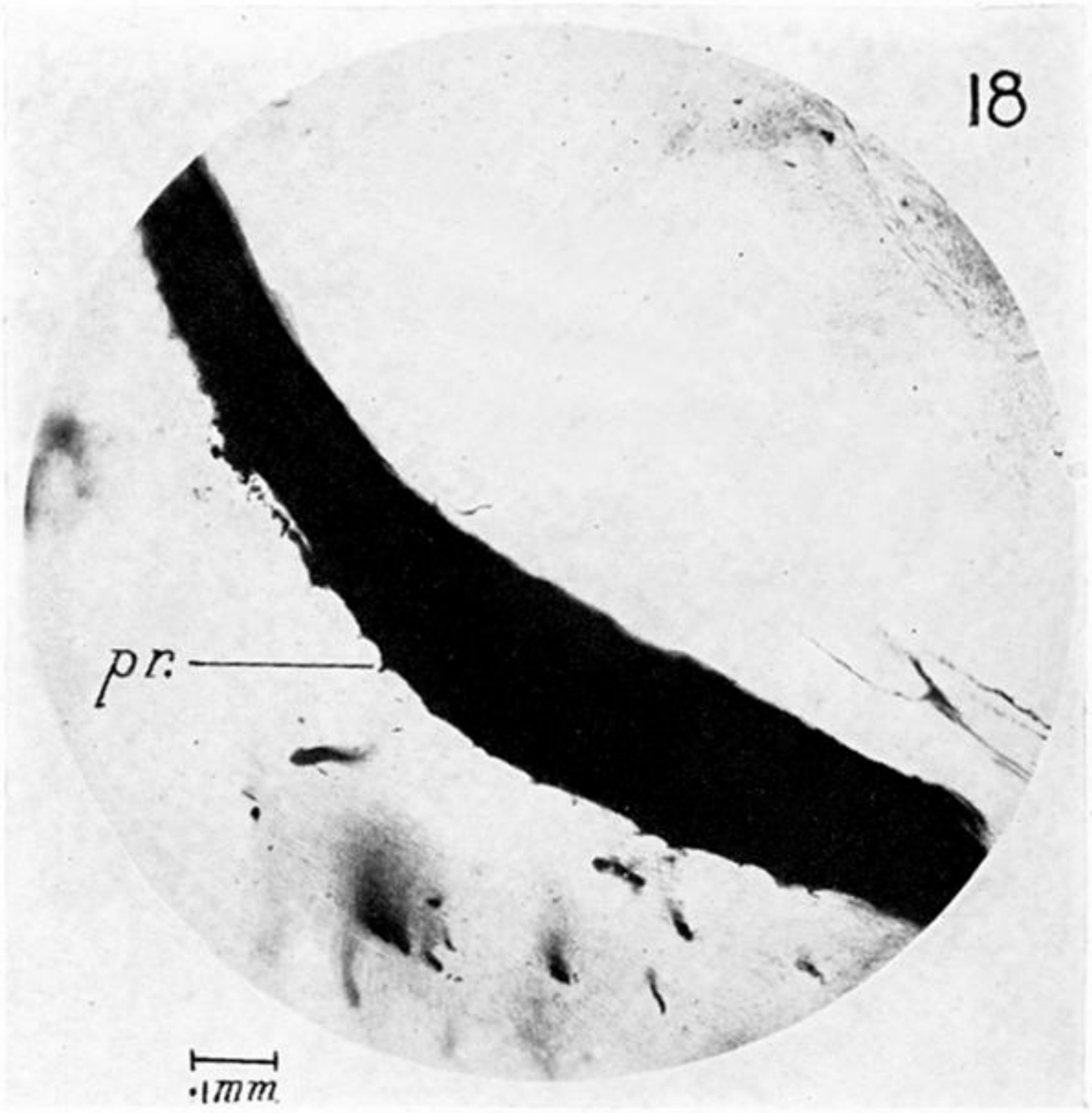

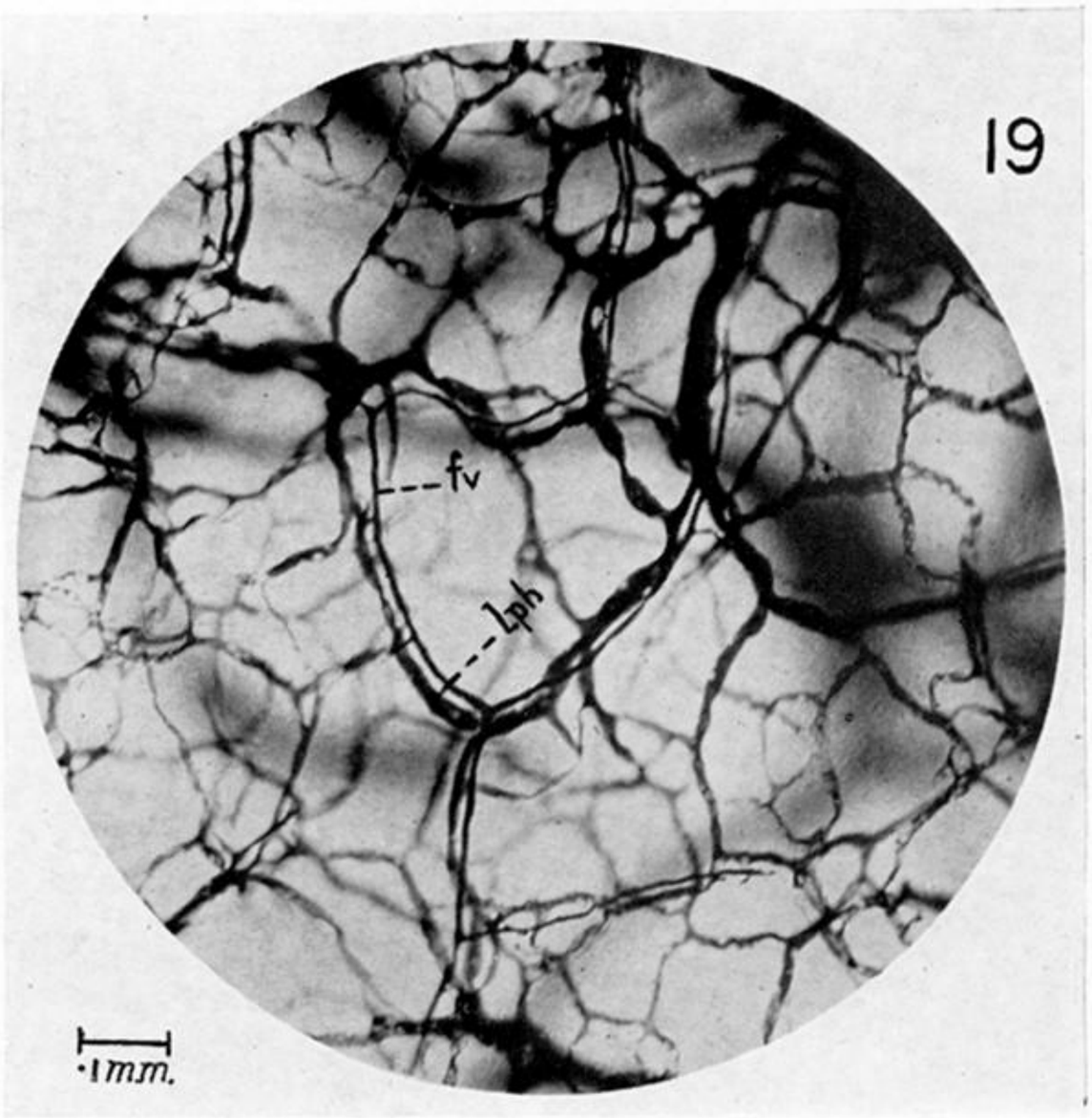

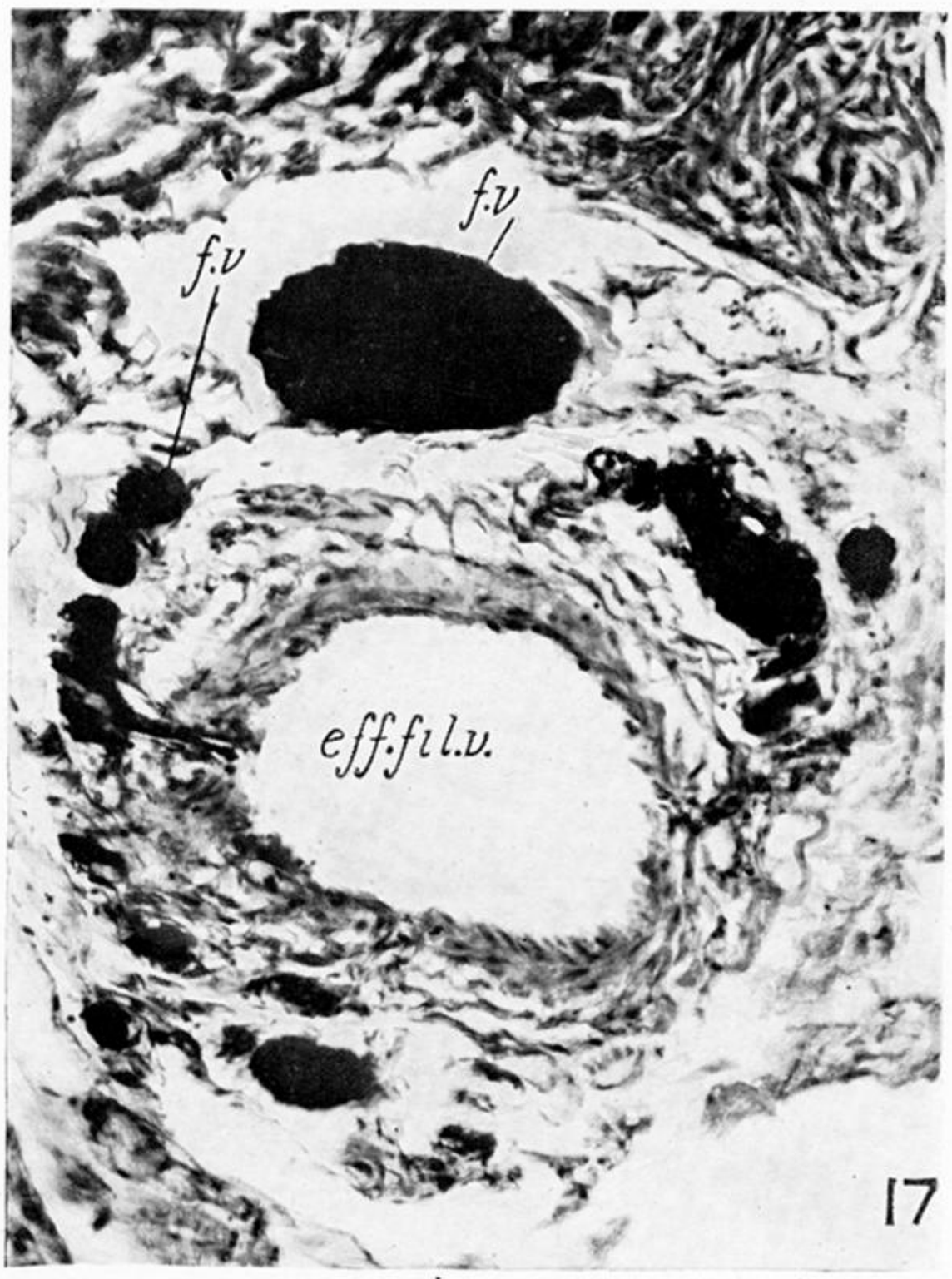

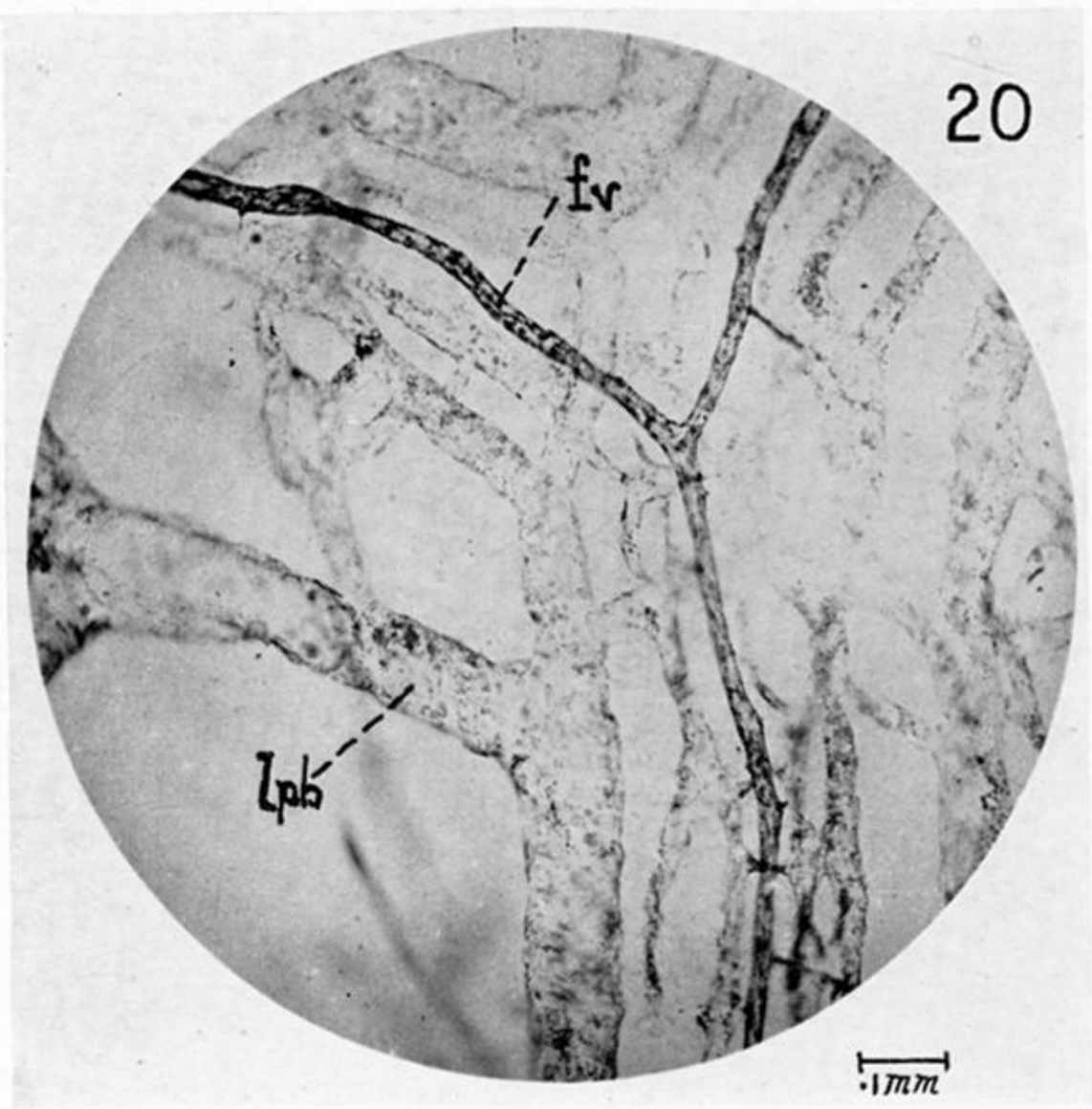

PLATE 87.

FIG. 16.—Basal (non-respiratory) segment of efferent filamentary vessel, showing thorn-like projections from lumen. Arteries : grey ; " fine " vessels : black. A. transverse section. B. longitudinal view.

FIG. 17.—Transverse section through non-respiratory segment of efferent filamentary vessel, showing passage of injection (black) from " fine " vessel plexus to artery.

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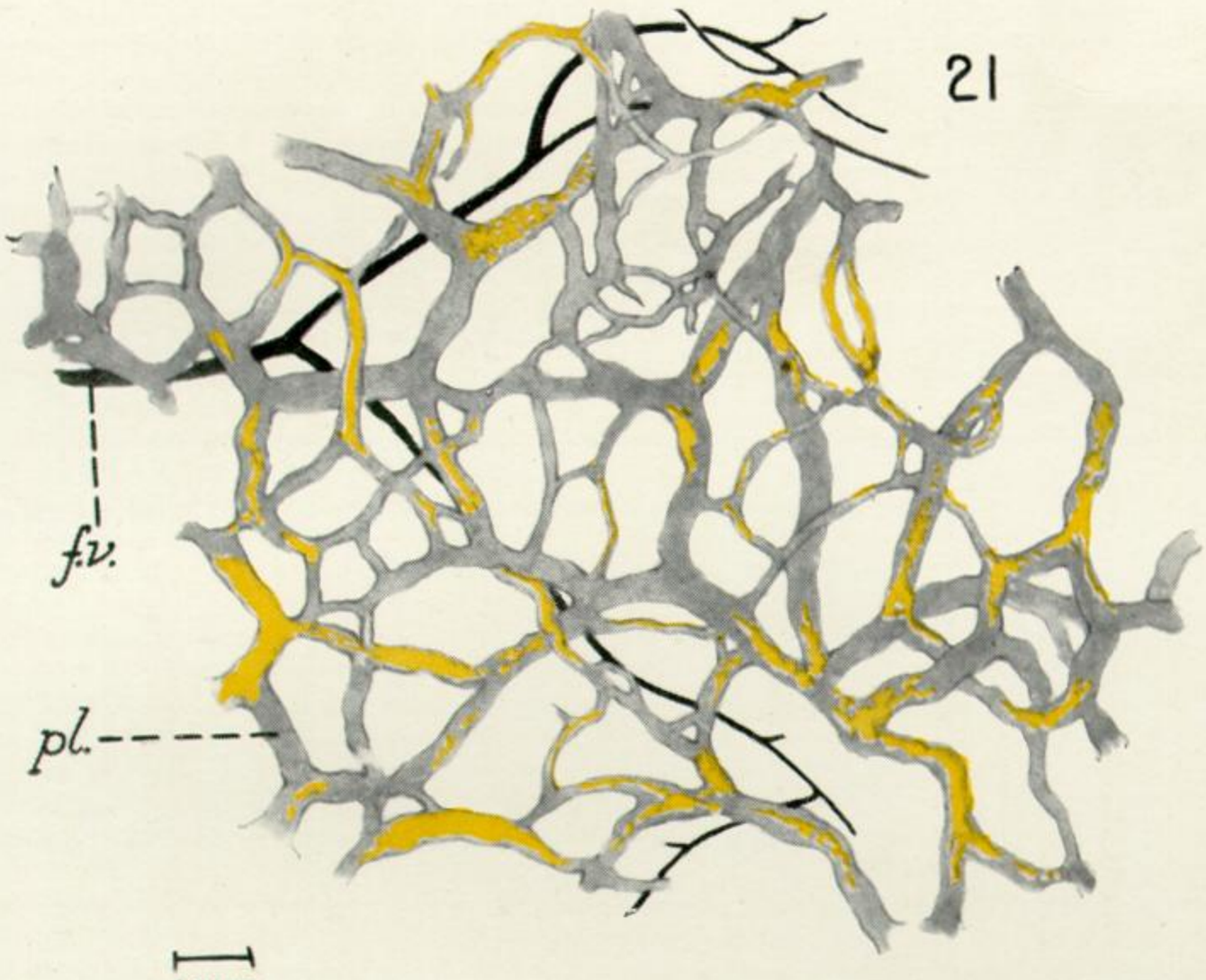

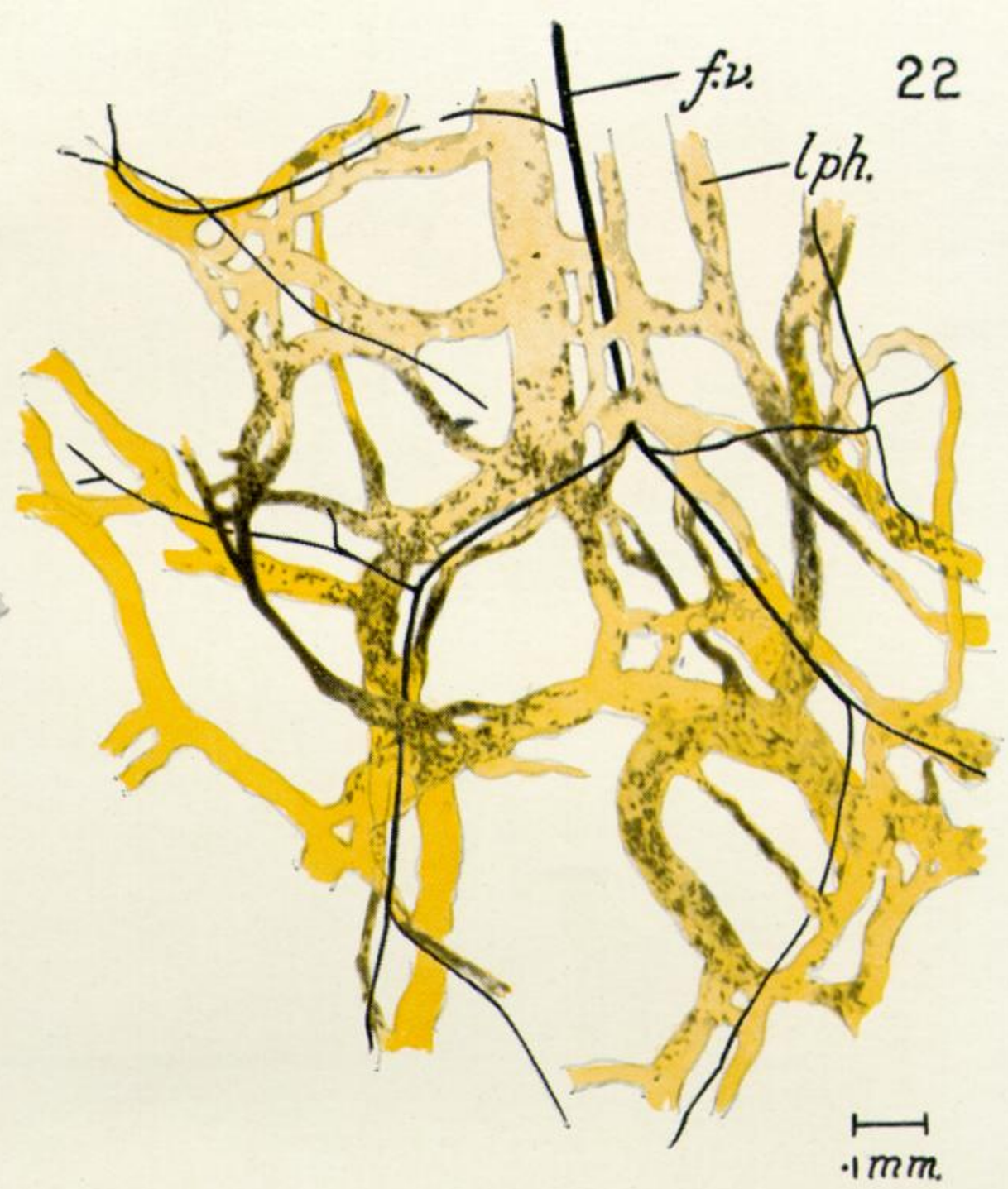

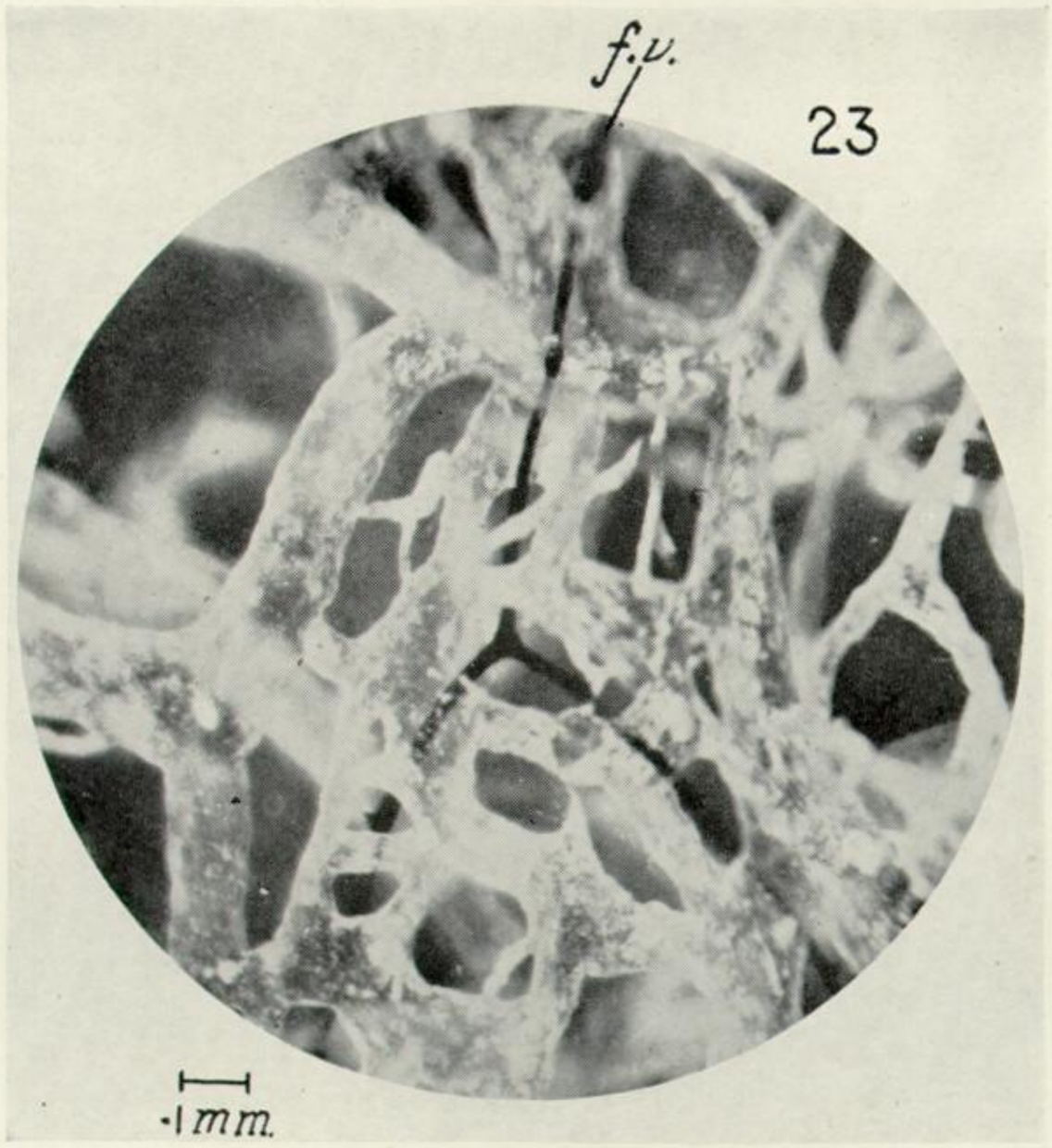

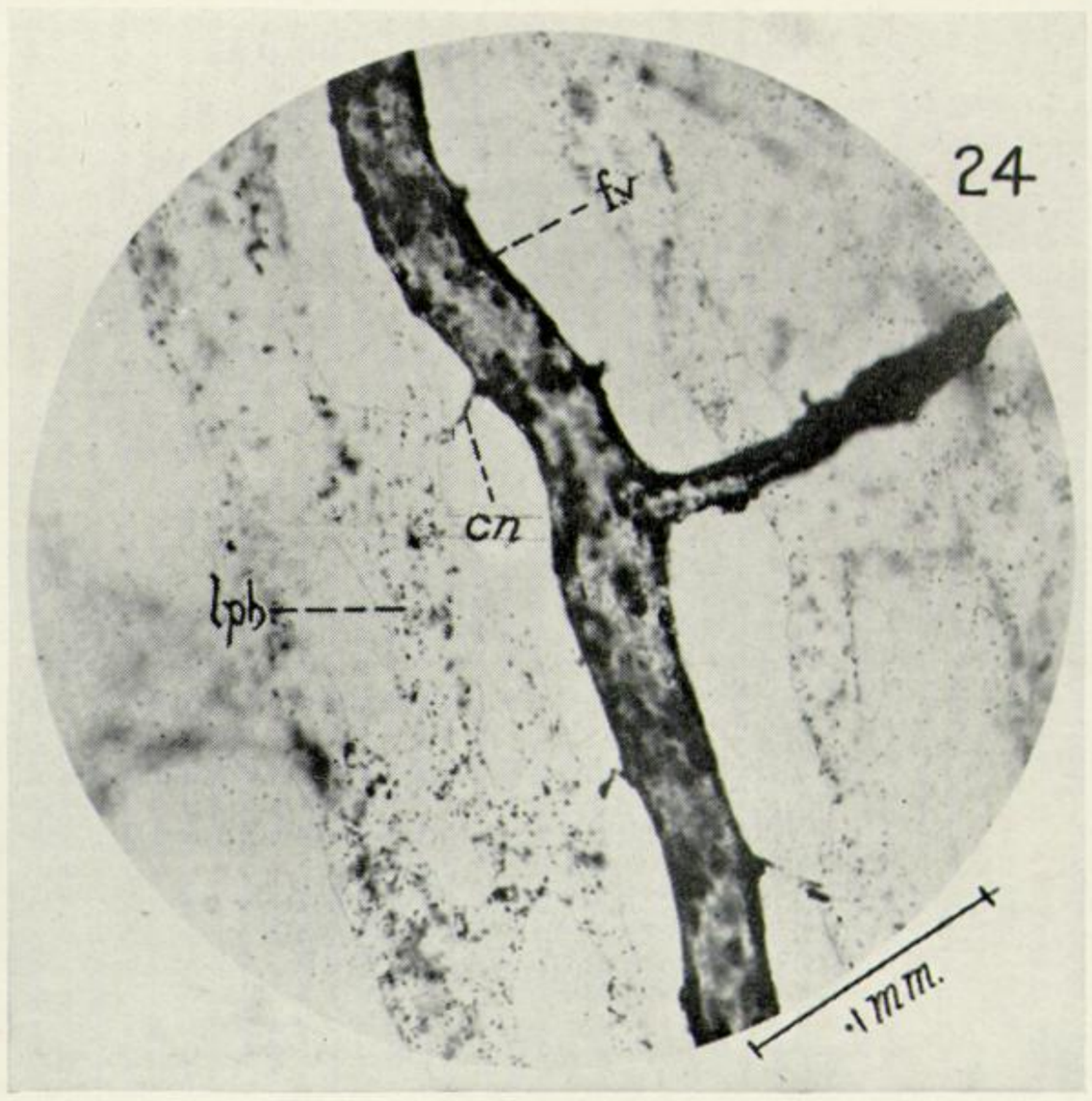

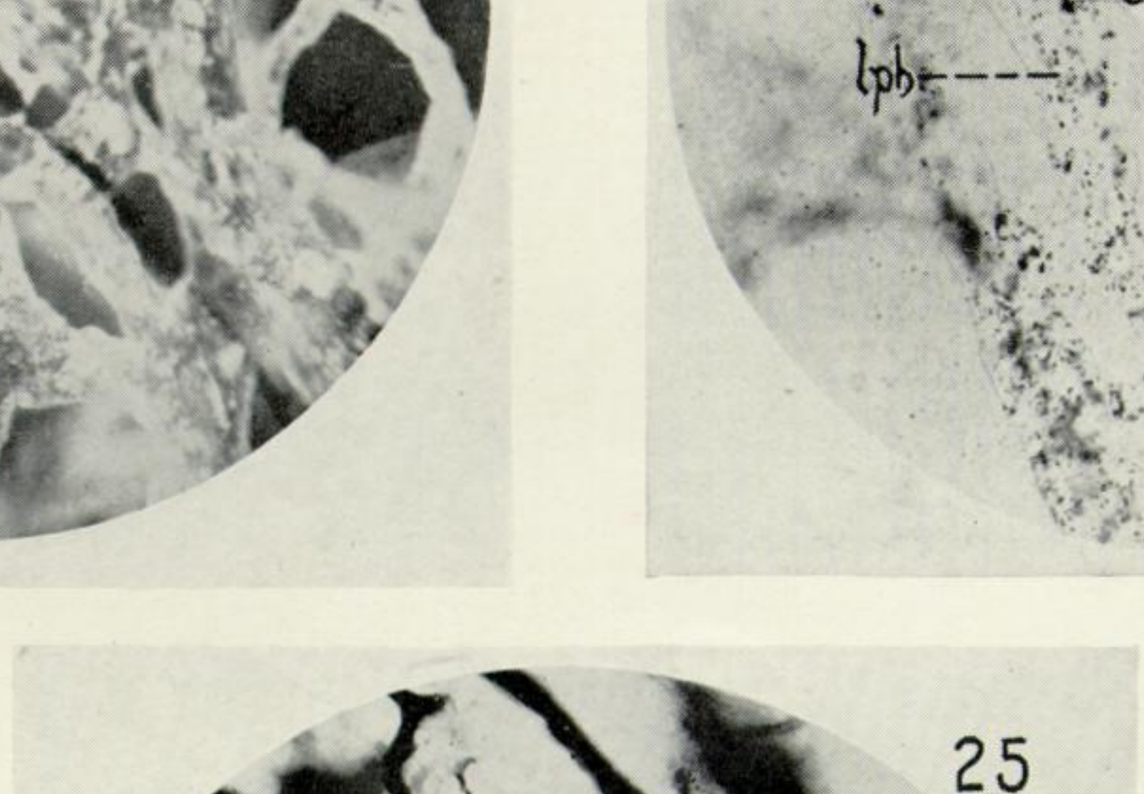

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