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PLATES I-XV

JULY 31, 1907

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DISTRIBUTION OF THE SUBCUTANEOUS VESSELS  
IN THE HEAD REGION OF THE GANOIDS,  
POLYODON AND LEPISOSTEUS.

BY

WM. F. ALLEN.

(FROM THE STANFORD MARINE LABORATORY, PACIFIC GROVE, CALIF.)

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<sup>William Fitch</sup>  
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## I. INTRODUCTION.

*Material.*—The Ganoids used for this problem consisted of *Polyodon spathula* (spoon-bill cat), *Lepisosteus tristæchus* (alligator gar), *Lepisosteus osseus* (spike-bill gar), and *Lepisosteus platostomus* (duck-bill gar), which are the most common Ganoids found on the mud bars and in the sloughs of the Ohio and Mississippi rivers about Cairo, Illinois. The fish were mostly taken through seining by moonlight; for it is at night that they leave the channels to do their feeding on the bars. *L. tristæchus* is by far the largest of the *Lepisosteidae* and I at first hoped to use it as a type for the RHOMBOGANOIDEA, but found it necessary to give it up for the following reasons: *L. tristæchus* could only be obtained during the fall of the year. Other things being equal it was always able to force its way through the seine, and the large specimens were found too massive to inject and pickle conveniently. Consequently most of the injections and dissections were made on *L. osseus*, which differed from *L. platostomus* in no important detail, but which was found to be more suitable for these investigations.

Most of the dissections were made during what spare time I had, while engaged in somewhat similar work for Mr. E. P. Allis, Jr., at Cairo, Illinois, and the work was continued when called by him to the Stanford Marine Laboratory at Pacific Grove, California.

*Method of Procedure.*—As in my previous studies Hoyer's lead chromate gelatin mass and a Berlin blue gelatin mass were the injecting media used. Ordinarily the blood vessels were first injected with the blue mass, and the subcutaneous vessels were afterward filled with the yellow. Instead of making my own soluble blue as formerly, I found that what is sold by druggists as Tiernan's soluble Prussian blue was equally satisfactory and involved far less labor. Since all that is necessary is to add 200 c.c. of concentrated Prussian blue solution, preferably hot, to a hot solution of 25 gr. of gelatin that had been expanded in 100 c.c. of water.

In nearly every case the head was severed from the body a short distance behind the shoulder girdle, the intestine cut at the rectum, and the viscera pulled out with the head. With



*Polyodon* this was a very simple matter; while with the Lepisosteidæ which have such a bulwark of armor it was necessary first carefully to remove entirely two or three rows of scales a little back from the shoulder girdle. Great care should be exercised in this operation for the delicate longitudinal lymphatic trunks are very firmly attached to the scales by connective tissue. When this is completed the body can be severed as easily as *Polyodon*. Usually the blood vessels of *Polyodon* were first injected from the cut aorta, but with the Lepisosteidæ this was not deemed necessary. With the Lepisosteidæ the cut ends of the dorsal, ventral, and one of the lateral lymphatic trunks were first plugged with cotton, and the injection was made from the remaining lateral trunk. Since no dorsal and ventral lymphatic trunks were found in this region in *Polyodon* it was only necessary to stop up one of the lateral trunks and inject from the other. After the cephalic sinus and its posterior connections had been worked out in *Polyodon* it was found that a more satisfactory injection of the cephalic trunks could be obtained by injecting the so-called *cephalic lymphatic trunk*, forward, from a point designated by ( $\alpha$ ) in Fig. 1. During the summer months the heat was so intense at Cairo that the gelatin injecting mass in the vessels would not solidify unless the head was first placed in a bath of ice water. When once the mass was hard and the specimen placed in formalin it was found that no amount of summer temperature would liquefy it.

All the injected microscopic preparations were hardened in formalin, run up the alcohols, and mounted in xylol-balsam. The material for sectioning was fixed in Tellyesniczky's potassium bichromate-acetic mixture, imbedded in paraffin, cut 6 to 10  $\mu$  thick, stained in either Heidenhain's iron hæmatoxylin or Hansen's hæmatoxylin plus 2 per cent. glacial acetic acid,<sup>1</sup> and counterstained in a concentrated alcoholic solution of orange G plus a small per cent. of acid fuchsin.

<sup>1</sup> The object of adding the 2 per cent. glacial acetic to Hansen's solution was to do away with the precipitate which is always formed. The sections thus stained are red, but rapidly turn to a brilliant blue when placed in tap water that is alkaline. Formerly hæmalum was used for a simple hæmatoxylin stain, but my experience has been that the product as sold commercially varied so much that it could not be relied upon, and that Hansen's solution was superior to the strongest hæmalum.

*History.*— Since looking up the literature for my recent paper on the lymphatics of *Scorpaenichthys*<sup>1</sup> several very interesting papers by Neuville,<sup>2</sup> Vialleton,<sup>3</sup> and Jossifoo<sup>4</sup> have been received.

Ever since the subcutaneous vessels have been studied there has been a merry war on as to whether they were lymphatics or veins, but so far as I am aware this controversy has been confined to the Selachians. No one to my knowledge has described these vessels in the Teleostomi as veins. In the Cyclostomi Müller (15,<sup>5</sup> p. 18) describes an abdominal lymphatic trunk in *Myxine* as running along beneath the chorda dorsalis, above the aorta. Throughout the body cavity it receives the intercostals and the visceral vessels. Anterior to the body cavity the trunk divides, each fork following the corresponding row of gills. No connection, however, with the venous system was established. Jackson, in his work on the circulation of *Bdellostoma*<sup>6</sup> (p. 35), observed a marked tendency for the injecting mass to escape from the blood vessels to the subdermal lymphatic spaces of the caudal region and the peri-branchial spaces about the gill pouches. Vialleton<sup>7</sup> (pp. 308–318), under the head of *espaces séreux interstitiels*, gives an extended and most interesting account of these peri-branchial spaces in *Petromyzon planeri* and *Ammocetes*. It seems that the older writers, as Robin, Milne-Edwards, Nestler, Vogt and Yung, and Schneider, regarded these spaces as blood cavities on account of their connection with the interior jugular, and the fact that Schneider

<sup>1</sup> "Distribution of the Lymphatics in the Head, and in the Dorsal, Pectoral, and Ventral Fins of *Scorpaenichthys marmoratus*." Proceedings of the Washington Academy of Sciences, VIII, 1906, pp. 41–90.

<sup>2</sup> H. Neuville, "Contribution à l'étude de la vascularisation intestinale chez les Cyclostomes et les Sélachiens." Annales des Sciences naturelles. 1901.

<sup>3</sup> L. Vialleton, "Les lymphatiques du tube digestif de la Torpille (*Torpedo marmorata*)." Archives d'anatomie microscopique. 1902.

<sup>4</sup> S. M. Jossifoo, "Sur les voies principales et les organes de propulsion de la lymphe chez certains Poissons." Arch. d'Anat. Micr. 1906.

<sup>5</sup> All bibliographical numbers in parentheses refer to a list of literature in a previous paper. See footnote 2.

<sup>6</sup> C. M. Jackson, "An Investigation of the Vascular System of *Bdellostoma dombeyi*." Bulletin of University of Cincinnati. No. 5. 1901.

<sup>7</sup> L. Vialleton, "Étude sur le cœur des lamproies." Archives d'anatomie microscopique. 1903.

found blood in these spaces is accounted for by Vialleton as being an entirely abnormal condition, which is brought about by a hemorrhage of the delicate branchial vessels into these cavities, as a result of excitement from capture. As to considering these spaces lymphatic cavities, Vialleton points out that they differ widely from other cavities designated by that name, and throws out a strong warning about the abuse of that term. Since the peri-branchial spaces are only developed in *Petro-myzon* after metamorphosis, Vialleton pronounces these cavities to be a special apparatus adapted to the movements of the respiratory sacs. Neuville (*op. cit.*, p. 54), in opposition to the general opinion, holds that no separate chylous system is to be found in the digestive tract of the Cyclostomes. As a study in comparative anatomy I injected the blood vessels of the Pacific *Bdellostoma* (= *Polistotrema*) and found that the intercostal arteries alternated with the intercostal veins in supplying the septa between two myotomes, there being but one blood vessel for each septum, but for each septum there is an additional intercostal vessel that terminates in an abdominal sinus, which runs parallel with the aorta. This system we take to be lymphatic rather than a separate venous system. No attempt was made to determine how the injecting mass reached this system; whether it passed through venous-lymphatic openings or whether it broke through the delicate walls of the blood-vessels.

Robin (23, pp. 22-30) gives an excellent account of the early work of Monro and Fohmann on the lymphatics of the Selachians. The former, it seems (14), described the chylous vessels of the viscera fairly well, except that he portrayed the common visceral reservoir as continuing along the vena cava (cardinal) in order to empty into the sinus of Monro (precava or ductus Cuvieri); while according to Robin (p. 2) there are two triangular reservoirs, corresponding in position to the two cardinal sinuses, into which they are discharged. Lymphatics are indicated as coming from the pectoral fin, brain, eye, and ear, and the veine jugulaire antérieure (inferior jugular) is regarded as a lymphatic trunk. Monro confused the lateral line canal for a lymphatic trunk, and because he saw the injecting mass

pass out of the pores, concluded that this system also arose from free openings in the digestive tract. Robin states that Fohmann's work on *Torpedo marmorata* (4) contains nothing not found in Monro, and that his failure to inject the blood vessels has resulted in many incorrect relationships. Fohmann designates the common chylous reservoir as the *réservoir de Pecquet*, and finds in the digestive tract many connections between the small veins and the lymphatics. He has not found muscle fibers in these vessels, but considers them as contractile, and, contrary to Monro, claims that they do not possess valves save at the entrance into the veins.

Leydig (12) made a histological study of the lymphatics of the digestive tract of *Raja batis*, and reached the conclusion that the blood vessels are surrounded by chylous vessels. He was the first to describe the tubular bodies, *türbanliche Körper*, that encircle the lymphatic vessels, which Sappey and Mayer have so fully discussed.

Robin (23) after working up this system of vessels in *Torpedo galvanii* and other plagiostomes, firmly declares (pp. 2 and 32) that these subcutaneous vessels are veins, and that the chylous vessels are the only lymphatics possessed by a fish. He also describes (pp. 15-16) lymphatic networks arising from the heart and neighboring trunks, which reach the veins through the intermedian plexus on the œsophagus and liver.

Parker (20, pp. 720-1) describes these subcutaneous vessels in *Mustelus antarcticus* under the head of cutaneous veins, and states that so far as his experience goes that they invariably contain blood. A *dorsal cutaneous vein* is set forth as extending from the tail to some distance in front of the first dorsal fin. Behind the second dorsal it forks; the two branches encircling the fin unite in front in a single trunk, which when the first dorsal is reached subdivides into three branches, two of which encircle the fin to reunite in front while the median one passes ventrad to terminate in the left renal portal. An *anterior ventral cutaneous vein* extends from the pubis to the shoulder girdle. It is located between the skin and the abdominal muscles, and receives a beautiful plexus from the abdominal wall. "Anteriorly the vein trifurcates, the three



branches uniting again in the form of a rhomboid, the lateral angles of which are connected with the lateral veins." Posteriorly it bifurcates and both branches after following along the border of the pubic cartilage pass inward to unite with the iliac veins. The so-called *posterior ventral cutaneous vein* starts from the tail, and forming a loop around the anals, again unite in front of the fin to bifurcate in the cloaca region and empty into the cloaca veins. Parker notes a direct communication of the cloaca veins with the iliac, so that the anterior and posterior veins might be represented as a single trunk forming a loop around the anal fin and the cloaca. Finally the two *lateral cutaneous veins* are described and figured as running along the side of the trunk at the junction of the dorsal and ventral muscles. Posteriorly they unite with the caudal and dorsal cutaneous veins, and anteriorly they terminate in subscapular sinuses, which are discharged into corresponding cardinal sinuses.

Sappey (25) undoubtedly has done the most work of anyone on these subcutaneous vessels, and unquestionably pronounces them as lymphatics in the ray, dogfish (*Squalus*), and in several Teleosts. In these different groups he also takes up in detail the distribution of the blood vessels and the lateral line system. His monograph is illustrated by 12 large lithographic plates. In a ray he finds these subcutaneous vessels arising from the dorsal and ventral surfaces of the body, from the mucous canals, muscles, electrical apparatus, viscera and heart. Most of the lymphatics on the dorsal surface of the body are described and figured (Pl. 5, Fig. 1) as being in communication with the *grand sinus curviligne* (Fig. 1, 5) which lies above the gills, and near its posterior extremity communicates with the ductus of Cuvier from above. Three trunks have their origin from the anterior part of the pectoral fin and empty into this reservoir, which are designated from cephalad to caudad as *le tronc longitudinal* (Fig. 1, 2), *le tronc latéral antérieur*, and *le tronc latéral moyen*. Coming in from the rear or virtually continuous with the sinus curviligne is *le grand sinus longitudinal* (Fig. 1, 18). It extends caudad to the tail, and at the point of opening into the sinus curviligne it receives *le tronc latéral postérieur* (Fig.

1, 13), which drains the posterior part of the pectoral fin. At various intervals communicating branches are received from *le petit sinus longitudinal* (Fig. 1, 24), which runs parallel but median to the grand sinus. In the lumbar region there is a rich network (Fig. 1, 16), which in part empties into le grand sinus longitudinal and in part into its anterior branch le tronc lateral postérieur. Midway between the pectoral and ventral fins a large lateral branch is given off (Fig. 1, 23) to communicate with the veins at the articulation of the ventral fin, *les veines extrapelviennes*. This communicating trunk also receives the rich network from the ventral fin. Two lymphatic vessels are said to have their source from the snout region and flow toward the eye (Fig. 1, 1). The outer one passes behind the eye and empties into the internal jugular or a branch; while the inner one terminates in like manner mesad of the eye.

In brief, the subcutaneous vessels from the ventral surface of the body are set forth as follows: In the anterior part of the pectoral, laterad of the mouth, four vessels unite in a common trunk (Pl. VI, Fig. 1, 6), which passes dorsal to discharge itself into the anterior end of the sinus curviligne. Two of these vessels arise from the anterior part of the pectoral and are designated as *le tronc antérieur* (Fig. 1, 2) and *le tronc moyen* (Fig. 1, 9); while the other two come from the median portion of the body and are named *le tronc céphalique* (Fig. 1, 1) and *le tronc thoracique* (Fig. 1, 8). The former takes its origin from the snout region and the latter from the region immediately behind the mouth. *Le tronc postérieur* (Fig. 1, 15) collects the lymph from the posterior part of the pectoral and from the abdomen; it pierces the muscular wall to unite with the common vein of the pectoral fin. Sappey states that the abdominal plexus is remarkable for the fact that it not only anastomoses with the networks of the ventral and anal fins, but in addition there are numerous communications with the blood capillaries. The rich network of the anal unites in a great number of vessels that connect with those of the cloaca and intestine, and without a definite course disappear in the veins of the caudal fin.

According to Sappey the chylous vessels terminate in the ductus Curveri through a right and left trunk (Pl. VII, Fig. 5, 7), the openings being guarded by valves.

Sappey (p. 32) describes a lace-like lymphatic network arising from the heart, especially from the ventricle and bulbus, which is collected by two trunks (Pl. II, Fig. 3, 3) that terminate in the sinus of Curver. It should be noted that these two vessels correspond identically with what Parker (20, p. 720) describes and figures (Pl. 34, Fig. 4, Cor. V.) as the coronary veins.

In the rays Sappey finds numerous muscular bands encircling the lymphatics, not only of the viscera as described by Leydig, but also in all parts of the body. Aside from the digestive tract he figures them from the subcutaneous and intermuscular vessels of pectoral, from the abdominal and thoracic networks, and from the networks of the ventral fin and lumbar regions. When he first discovered them in 1870 he supposed that they were characteristic of the lymphatics of all fish, but later found them only in the rays. Sappey attributes a double rôle to these so-called lymphatic hearts, by contracting they would cause a peristaltic movement in these vessels, and to a certain extent would also take the place of valves.

After considering the lateral line system and the blood vessels of *Squalus* Sappey takes up (pp. 37-40 and Pl. X) the distribution of the lymphatic system. On each side of the body he finds two lateral lymphatic trunks, superior and inferior in position. The former (Fig. 3, 2) extends from the tail to the head, a little below the lateral line. In the tail region it forms a sort of fibrous sinus that empties into the caudal vein; while anteriorly it ends with the inferior trunk in a sinus or confluent (Fig. 1, 25), which opens into the precava, near its origin. The inferior lateral trunk (Fig. 3, 11) is a subcutaneous vessel, traversing in a median line from the tail to the head, where it blends with the superior trunk in forming a single vessel, which terminates in the cephalic sinus mentioned above. It should not be confounded with the corresponding vein, which is more profundus, being distinctly submuscular. Sappey states that the inferior trunk is sometimes absent. A median dorsal trunk

(Fig. 1, 15, and Fig. 3, 4), has its origin in the tail region. In passing cephalad it trifurcates when the dorsal fins are reached, the two outer branches receive the superficial networks and the median one the dorsal and ventral branches (Fig. 3, 8 and 9). In front of the fin these branches unite in a common trunk, which upon reaching the cranium bifurcates, each fork making a curve behind the eye to empty into the internal jugular. A median abdominal trunk extends from the ventral fin to the clavicle, where it bends to discharge itself into the sinus of Cuvier. Sometimes, according to Sappey, it bifurcates, and each fork terminates in the corresponding ductus of Cuvier. These six trunks are connected by a series of vessels into which a network of capillaries are discharged. A series of intercostals (Fig. 3, 13 and 14), connect the ventral with the inferior and superior trunks, and an irregular series, further apart, connect the dorsal with the two superior trunks. The chylous vessels as in the ray open into the ductus of Cuvier.

Sappey found lymphatic glands in the walls of the digestive tract and on the hearts of the ray, dogfish and sturgeon.

Mayer (18) in a most extensive monograph on the peculiarities of the organs of circulation in Selachians describes these subcutaneous vessels in *Squatina*, *Torpedo*, and *Raja* as veins. On pp. 339 and 340 he states that when a young *Scyllium canicula* is placed in an aquarium, that the *vena postica* of all the vertical fins are plainly visible. If the fish is excited the blood rapidly disappears from these veins, but returns again after a brief rest. With the ordinary swimming back and forth the blood is said to remain in the fins. Sometimes no fluid flowed out of the lateral vein after cutting it; consequently Mayer reasons because a trunk is bloodless it does not necessarily follow that it is a lymphatic vessel. According to Mayer (pp. 366-7 and 9) the subcutaneous veins do not carry pure blood, but rather a mixture of blood, a few small discs, many leucocytes, intermixed with a fluid resembling chyle; while the intestinal veins commonly contain blood, but at stated times chyle. Mayer has injected the sheaths surrounding the intestinal blood vessels and finds the chylous system of vessels as observed by Robin. On p. 368 he severely criticises Sappey for not being

able to let go of the idea that a fish must have a lymphatic system; while he himself is so impressed with the uselessness of such a system to a fish, that it almost appears to him as if it would be hateful in the eyes of the Lord for a fish to possess a lymphatic system. One might equally well apply the same line of reasoning to mammals.

With *Raja clavata* Mayer found the lymphatic hearts of Leydig and Sappey, or as he calls them *sphincters*, very abundant; while with their close relatives they were often absent. He also found them encircling arteries, and hence for these reasons was not willing to attribute the importance to them that Sappey did.

In the trunk region, in addition to the caudal vein and its intercostal branches, Mayer notes (pp. 316-337) not fewer than four longitudinal veins that have no counterpart in the arterial system. They are homologous to the dorsal, ventral, and lateral cutaneous veins of Parker and the corresponding lymphatic trunks of Sappey. In addition to the descriptions given these vessels by these authors, Mayer finds that the laterals not only terminate cephalad in subscapular reservoirs that empty into the cardinal sinuses, but continue cephalad to the orbit, where they send off anastomosing cross branches that also unite with the dorsal vein. Caudad the dorsal vein empties into a lateral and they, at the origin of the tail, unite with the ventrals, which are here paired, and shortly bend dorsad to culminate in the caudal vein. The two forks of the dorsal that encircle the dorsal fins are designated by Mayer as *venæ circulares*, which are said to receive two large branches from each fin. One or two *vena postica* come from the posterior part of the fin, and a *vena profunda* arises from the musculature of the fin. They unite in a small reservoir at the base of the fin, which communicates with the *vena circularis*. All of the orifices in the reservoir are said to be guarded by valves. Also all of the venous openings into the caudal vein are likewise protected by valves. Certain blood cavities were found in the hæmal canal, which may correspond to the hæmal lymphatic trunk of the bony fishes.

Neuville (*op. cit.*) studied in detail the blood vascular supply of the viscera in *Petromyzon marinus* and in numerous Selachians.



In the beginning of his paper he gives a most complete historical sketch of all the work done on the circulatory and lymphatic systems of fishes, and contends that all the vessels found in the digestive tracts of the Cyclostomes and Selachians are either arteries or veins and that a separate chylous system does not exist. He, however, finds a double venous system on the digestive tract of *Acanthias vulgaris*; one of which is the portal system, and the other system, which is figured on p. 92, he recognizes as corresponding to the descriptions of the chylous system as given by Robin and the older authors. Nevertheless he considers them as veins for the following reasons: First, on p. 90, he has found the *sinus stomacal* (Cisterne de Pecquet of Fohmann) to be full of blood. Second, on p. 94, he finds that upon injecting this system that the entire portal system is immediately filled. According to Neuville the system of absorption is entirely carried on by the veins in these groups, and with the Cyclostomes he finds the arrangement of the veins less complex than in the Selachians, which is in accord with their less complicated digestive tract.

A year later Vialleton (*op. cit.*) takes up the same problem from the standpoint of the digestive tract of *Torpedo*, and claims that Neuville was too hasty in his conclusions. In reply to the two objections raised by Neuville as to this system of vessels being veins rather than chylous, Vialleton says (p. 382) in answer to the first that it is not strange to find blood in a lymphatic trunk. As regards the second he states (p. 383) that Neuville much less than Mayer has not attempted a microscopical study of these vessels, that since he has not seen the connections of the superficial canals with the veins he does not know but that they may be only artifacts, and further declares that a histological investigation revealed the fact that these communications were found to be caused by the rupture of the venous wall, which is a contact wall between these two systems. Vialleton found (pp. 452-3) that there were distinct superficial and profundus lymphatic networks in the digestive tract of *Torpedo*, which could readily be told from the venous capillaries on account of the form of its network, its regular caliber, and greater volume. By injecting the lymphatics of the intestine

with blue and the veins with a nitrate of silver solution it was conclusively proved from a histological standpoint that these two systems were always distinct, often running side by side and entwining, but never anastomosing.

Like Neuville, Vialleton included only the viscera in his studies and devoted the first part of his work to a most excellent account of the history of the lymphatics of fishes. In reviewing Sappey's memoir (p. 392) he stated that the numerous anastomosing of the subcutaneous lymphatics with the veins, and the origin of certain lymphatic twigs from veins leads one to believe that the vessels described by Sappey as lymphatics are veins. It should be remembered, however, that Sappey used mercury for his injecting mass; hence it would not be surprising if these connections of the minute lymphatics with the veins, reported by Sappey (p. 24) in the abdominal region, are artifacts formed by the extravasations of the injecting mass.

Hopkins' most excellent paper on *Amia* (8) is to my knowledge the only work that has appeared on the Ganoids.

He finds that each lateral lymphatic trunk terminates anteriorly, in front of the pectoral arch, in a cephalic sinus, which extends from the clavicle into the base of the cranium, where it could be traced to a point opposite the orbit. About 1 cm. cephalad of the clavicle there is a valve, which closes an opening that leads ventrad into the jugular vein. Posteriorly each lateral trunk ends in a caudal sinus, which is located under the last vertebræ. Each sinus has a cephalic connection with the caudal vein, the orifice being guarded by a valve, and there are said to be at least two communications with its fellow sinus. The dorsal lymphatic trunk terminates anteriorly in the cephalic sinus, and posteriorly into one of the laterals after the latter bends to enter the caudal sinus. Hopkins is not positive whether this trunk bifurcates posteriorly with each fork terminating in one of the laterals or not, but thinks that it does. According to the writer the ventral trunk begins in the tail and communicates through a cross vessel with the lateral (Fig. 11, *t*). It collects the lymph from the anal and the ventrals, and in the neighborhood of the heart it forks, the two branches merging into the pericardial sinus, which discharges itself into

the cephalic sinus a little behind the jugular opening. A large pectoral sinus is said to lie at the base of the pectoral fin, which sends off branches to the lateral trunk and one to the pericardial sinus. The termination of the chylous system is in the ductus of Cuvier, on either side of the heart.

On p. 369 Hopkins states that: "In a specimen killed by pithing, the cephalic lymph sinus was exposed while the heart was still beating; the veins were gorged with blood but the lymph sinus appeared perfectly clear and transparent, and at no time was blood found in the lateral vessels. In several instances a clear fluid was seen to run out of the lateral vessel, when cut, in a fresh specimen."

Were not constant reference to this paper to occur in the text a far more complete report of it should be given here.

The latest work bearing on this subject is by Jossifoo (*op. cit.*). He takes up in detail the lymphatics in *Conger* and *Anguilla*. The main ducts of *Conger* (pp. 414-420) follow the vertebral column from the tail to the skull. In the caudal region the principal trunk (*L. Caud*, in Pl. 12) lies in the hæmal canal, directly below the caudal vein. When the thorax is reached it divides, forming the two *perivertebral lymphatic trunks* (*R.* and *L.Pr.S.*), which continue cephalad along the sides of the vertebral column. At the level of the fifteenth and sixteenth vertebræ the right trunk receives the lacteal canals (*D.Ch.*) from the viscera, and upon reaching the fourth vertebra a transverse vessel of considerable size (*La.*) connects the two trunks. At the base of the cranium each perivertebral trunk empties into a *cephalic sinus* (*S.C.*), which communicates with the jugular as it leaves the skull, and both the orifices of the vein and the lymphatic trunk are said to be guarded by semilunar valves. This sinus is so situated between the superior maxilla and the temporal bone that the act of respiration must necessarily dilate and contract it. In *Anguilla* the author (p. 418) states that upon injecting the perivertebral trunks one invariably fills the *branchial lymphatic sinuses*, situated outside the vertebral column between the gills. These sinuses communicate with the perivertebral trunks and serve as reservoirs to the lymphatic vessels arising from the mucosa of the branchial arches. A pulsating

lymphatic heart was found in the tail of *Anguilla*, but its connections with the lymphatic system were not made clear. A specimen of *Anguilla* was said to have lived several days in an aquarium after its tail had been cut off, without seeming to suffer from the operation.

From what we know of the development of the lymphatics in mammals<sup>1</sup> it would not be surprising to find in the embryos of the lower forms, if not in the adults also, even closer relationships between these two systems. For example, it might be possible to find a vessel that functioned both as a vein and a lymphatic trunk, and, again, an homologous vessel or system of vessels might exist, which functioned as veins in the more generalized forms, but which had their exact counterpart in lymphatic canals in the higher or more specialized forms. It is very evident from the above discussion that the last word has not been said on this subject. What is most needed is not more generalizations, but more anatomical and embryological data on many different groups, and especially in the Cyclosoemes. It is not therefore my intention to make what might be considered a dogmatic statement as to whether these subcutaneous vessels in the Ganoids are veins or lymphatics. The chief aim will be to give an accurate description of the distribution of these vessels. They will, however, be described as lymphatics because the balance of evidence (such as size and arrangement of capillaries, and the fact that except in the branchial region the main ducts in the head region always accompany venous trunks), seems to warrant this view. Yet, on the contrary, it must be admitted that if these vessels are termed lymphatics in the branchial region no corresponding nutrient branchial veins were found; further,

<sup>1</sup>In an especially interesting paper Miss Sabin (27) found a stage in the embryo pig that about corresponded with the lymphatic system of the adult frog. Here there were two cervical hearts or sacs that received the lymph from the neck region and emptied into the cardinal vein at its junction with the subclavian, the opening being guarded by a valve. Similar posterior hearts were found to discharge themselves in the common vein formed by the union of the sciatic with the femoral, and their orifices were likewise said to be protected by valves. It was not until considerable later that the thoracic duct and the right lymphatic duct were formed from the anterior heart. To begin with, the lymphatic system of the pig is said to have its origin from two blind ducts that arise from the cardinal at its junction with the subclavian.

the branchial trunks were always filled with red corpuscles, and unquestionably terminated in and apparently formed the principal supply for the so-called inferior jugular vein.

## II. DISTRIBUTION OF THE SUBCUTANEOUS VESSELS IN POLYODON.

The distribution of the subcutaneous vessels in the head region of *Polyodon*, which is a cartilaginous Ganoid, and *Lepisosteus*, a bony Ganoid, admits of so little comparison, that it seems advisable to consider this system of vessels separately in each case, rather than to take them up together in a comparative way. In the former these vessels, in some respects, agree more closely with the Selachians, while in the latter they are more like the Teleosts.

### 1. *Cephalic Sinuses and their Connections.*

What has been designated as the *cephalic sinuses* (Fig. 1, *Ceph.S.*) in *Polyodon* are two rectangular-shaped reservoirs, which are symmetrically placed on either side of the body, directly mesad of the supra-clavicles, and only a little below the level of the post-temporals. In the specimen from which Fig. 1 was drawn their dimensions were about 40 by 18 mm. With the exception of the posterior-ventral corner, each corner of a cephalic sinus has an orifice. The trunk leading into the posterior dorsal opening is the *lateral lymphatic trunk* (Fig. 1, *L.L.T.*). In the thoracic region the lateral trunks were the only subcutaneous vessels found; though both dorsal and ventral trunks were observed farther caudad. Very singular in *Polyodon* the lateral trunks have an extremely small diameter, but little, if any, greater than the lateral line canals. Fortunately, however, they increase in caliber upon approaching the cephalic sinuses; otherwise it would be impossible to inject them, except with a very fine hypodermic needle. What are represented as the *cephalic lymphatic trunks* (Fig. 1, *Ceph.L.T.*) terminate in the anterior dorsal corners of these sinuses, and in one way or another these great canals drain the entire head region. The openings from the anterior ventral corners lead into papillæ (Fig. 1, *V*), which discharge themselves ventrad into the jugulars; either at the angles of their great bends in front of the pectoral arches, or a little below.



So far as could be ascertained by dissections and injections no valves were found at the entrance of either the lateral or cephalic trunks in the cephalic sinus, or at the opening of the latter into the jugular vein, but as none of these orifices was large a histological study might have revealed their presence. Still, however, when the blood vessels were injected with a blue mass, the cephalic lymphatic trunks were invariably filled from either the lymphatic sinus or the inferior jugular connections or through both, and when the blue was allowed partially to solidify before the lateral trunk was injected with the yellow; it was found, upon dissection, that the yellow had forced back the blue a short distance in both the jugular and in the cephalic trunk, but none of it had reached the inferior jugular, showing conclusively that if there were valves at the entrance of the cephalic trunk opening into the cephalic sinus that after death, at least, they are unable to repel an injecting mass, when only a slight pressure is applied.

It will be readily noted that the cephalic sinus of *Polyodon* corresponds exactly in position to a similar reservoir described by Vogt (1, pp. 137-8) in the salmon, but its shape and mode of communications are very different. With the salmon this sinus is said to empty into the ductus of Cuvier, and in addition to receiving the lateral trunk it collects three mucous canals, as they are called, from the head region. The first of these canals is represented as arising at the origin of the temporal (pterotic) crest from two branches coming from the facial region. The second of these canals is portrayed (Pl. L, Fig. 1, 63) as having its source from six branches; one large and one small vessel coming from each of the first three branchial arches. The smaller branch is said to have its origin from the filaments; while the larger branch is a more superficial trunk, that continues ventrad along the surface of the arch to anastomose with the vein of Duvernoy (inferior jugular). The third canal comes from a common reservoir situated near the fourth vertebra, which is described as receiving a trunk from the fourth branchial arch, and one from the median part of the body that also collects the chylous duct.

Hopkins' cephalic sinus in *Amia* (8, p. 371 and Fig. 10, b)

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is located a little further cephalad than the similar reservoir in *Polyodon*, being situated entirely in front of the pectoral arch. The writer observed that this sinus continued cephalad in the cranium to a point about opposite the orbit. As in *Polyodon* it is discharged into the jugular, but the orifice is said to be guarded by a valve opening into the vein. No cephalic trunks were represented as emptying into the cephalic sinus, but in addition to the lateral trunk a fork of the dorsal is said to have its termination in each.

*Cephalic lymphatic trunk* (Figs. 1, 2 and 3, *Ceph.L.T.*). — This is the largest and undoubtedly one of the most important of the lymphatic canals in *Polyodon*. In a 70-pound specimen it had a length of 12 cm., extending from the base of the skull to the pectoral arch, and connecting the so-called *hyo-opercularis sinus* (Figs. 1, 2 and 3, *Hyo.O.S.*) with the cephalic sinus. Its caliber if anything exceeded the jugular vein, but posteriorly it rapidly tapers down into a papilla preparatory to emptying into the cephalic sinus. In position it follows along directly above the jugular vein, about midway between the pterotic crest and the gills. The cephalic trunk is strictly a superficial canal, being separated from the branchial cavity by a thick skin that bears numerous leaf-like papilla; it is surrounded by a tough connective tissue, and cephalad a gland-like body, which I take to be the thymus, lies between it and the skin. The integument of this whole region contains a typical lymphatic network (Fig. 1, *L.N.(1)*), which is collected mesad by larger vessels that apparently discharge themselves into the dorsal end of the hyo-opercularis sinus rather than into this trunk. When the hyo-opercularis sinus is reached the cephalic trunk bifurcates: the dorsal fork communicates with the hyo-opercularis sinus from the rear and behind (Figs. 1 and 2, *C.L.T.O.*), while the ventral fork runs parallel, but mesad, of the hyo-opercularis sinus for a short distance. In this region the ventral fork receives at least two branches coming up along the inner surface of the branchial levator and the pharyngo-clavicularis muscles. Corresponding venous trunks (Fig. 1) followed the course of these lymphatic branches and terminated in the jugular. Frequently as is shown in Fig. 1 a valve is

found in the hyo-opercularis fork of the cephalic trunk, at its junction with the ventral fork, which opens towards the cephalic sinus, but from its size one would not expect it capable of entirely closing the opening. A little posterior to the division of the cephalic canal a combined trunk formed from the fusion of the last three branchial lymphatic vessels (Fig. 1, *X*) is received from below, which will be described in detail later on under the head of the branchial lymphatic trunks.

What is termed the *pericardial lymphatic trunk* (Fig. 1, *Per.L.T.*) corresponds somewhat in position to the pericardial sinus of *Lepisosteus* and the Teleosts, without presenting anything like a sinus-like appearance. It is simply a canal running along in front of the pectoral arch in the connective tissue that surrounds the precava. Immediately after crossing the communicating vessel of the cephalic sinus with the jugular it makes a dorsal curve to culminate in the cephalic trunk, near its union with the cephalic sinus.

In several different specimens of *Polyodon* blood was removed with a pipette from the jugular and injected into a vial containing alcohol; likewise some fluid from the cephalic lymphatic trunk was placed in a second vial containing alcohol. Upon settling, the corpuscles from the vein had a distinct brown or reddish color; while those from the cephalic trunk were practically colorless. Microscopic sections of the two trunks reveal the walls to be structurally about the same. (Compare Fig. 22 with 23.) Both are composed mainly of fibrous connective tissue, with scattering smooth muscle fibers; and both have numerous papilla (*P*), which extend some little distance into the trunk and may to some extent function as valves. The greatest difference between these two vessels is in relation to their contents. The cephalic canal is filled with leucocytes and a few scattering red corpuscles, while in the jugular the red corpuscles greatly predominate; there being, however, in the latter a greater proportion of white corpuscles than would be found in the mesenteric or inferior jugular veins. With the cephalic trunk in the region covered by the field of Fig. 22 the red corpuscles were to the white as 8 is to 153; while with the jugular in the area covered by Fig. 23 the ratio of red to white was 36 to

19. Directly laterad of the cephalic canal, in this region, there is a gland-like body, the thymus, which is completely filled with leucocytes, and in places one can see them transuding through the walls of the lymphatic duct.

As regards its mode of origin, position, and point of termination the cephalic sinus of *Polyodon* corresponds somewhat with the second trunk described by Vogt in the salmon as emptying into the common reservoir (1, pp. 137-8 and Pl. L, Fig. 1, 63). Its position is also similar to Sappey's *sinus curviligne* in the skate (25, p. 20, and Pl. 5, Fig. 1, 5).

*Hyo-opercularis sinus* (Figs. 1, 2, and 3, *Hyo.O.S.*).—The sinus so designated is but little if any greater in diameter than the cephalic trunk; it is situated rather obliquely at the base of the skull, and is distinctly a superficial duct, which at one point crosses laterad of the jugular. Its length is apparently about the same in a 25-pound specimen as in a 70-pound one. Dorsad it receives a short vessel that collects the rich network (Fig. 1, *L.N.(1)*) from the skin and connective tissue in the region of the cephalic trunk. Its mode of connection or termination in the cephalic trunk has already been described. In one way or another it receives both forks of the *first branchial lymphatic trunk* (Figs. 1, 2, and 3, *Br.L.T.(1')* and *(1'')*), which will be referred to in detail later on under the head of the branchial lymphatics. Laterad and ventrad it receives, or virtually is continuous with, the so-called *hyo-opercularis lymphatic trunk*, and, as shown in Fig. 1, a valve is often present at the junction of the two.

Tracing this important canal (Figs. 1, 2, 3, and 4, *Hyo.O.L.T.*) backward, it was found immediately before making a sharp curve caudad in order to pass along the outer surface of the retractor hyomandibularis muscle, a little above the hyomandibular, that it was joined by a significant *facial lymphatic trunk* (Figs. 1, 2, and 3, *F.L.T.*). Throughout its entire course the hyo-opercularis is distinctly a superficial canal, lying directly beneath the skin; it has its beginning from the hyoid arch and the opercle, and collects a network (Fig. 1, *L.N.(3)*) from the membranes and connective tissue of hyomandibular and its retractor muscle; this network communicates below

with what is designated as the *anterior facial lymphatic trunk* (Fig. 1, *F.L.T.*(1)). A cut through the spiracle region near the termination of hyo-opercularis trunk in the sinus shows that this canal is accompanied, more profoundly, by a corresponding hyo-opercularis artery and vein. All of these vessels are enclosed in a fatty connective tissue, and even in uninjected specimens they are readily distinguishable. The lymphatic trunk is the most superficial and has by far the greatest caliber; no distinct walls were visible to the eye, and it appeared to be simply a regular cavity in the connective tissue, that increased in density in the neighborhood of the canal. A little mesad comes the vein, having visible walls, but with a caliber hardly half that of the lymphatic trunk. The artery, which is by far the smallest of the three, is some little deeper, and is characterized by very thick and well-defined walls. A short distance behind the anterior bend the hyo-opercularis trunk receives a large dorsal branch (Fig. 4, *Hyo.O.L.T.*(1)), which takes its origin from the outer dorsal surface of the retractor hyomandibularis muscle. At this point the hyo-opercularis artery and vein follow the hyomandibular rather than the lymphatic trunk; yet each sends off a superficial branch (Fig. 4, *Hyo.O.A.*(1) and *Hyo.O.V.*(1)) that crosses mesad of the lymphatic trunk, and which separates into two branches that follow the main hyo-opercularis lymphatic trunk and its dorsal branch. So that in this region, each lymphatic canal is accompanied by an artery and a vein.

Figures 24 to 26 represent microscopic sections of the hyo-opercularis lymphatic trunk, artery and vein. Except for the papilla, Fig. 24, *P.*, in the lymphatic trunk, there is but little difference between the structure of the lymphatic trunk and the vein, and both resemble the jugular and the cephalic lymphatic canal. When the hyo-opercularis lymphatic trunk was slit in a living specimen it was found to be practically empty, and sections show it to be almost destitute of corpuscles. Fig. 24 is taken from a very favorable section, and some of the few corpuscles portrayed here may have been shaken out from the meshes of the walls during the process of staining, but as the section stands it shows that the white corpuscles far exceed the



red, the ratio being 28 to 2. Fig. 26 represents the corpuscles as also being very scarce in the vein, but here the red predominate, the ratio being 9 to 2; while in the artery the corpuscles are abundant, the ratio of red to white being as 36 is to 8, which, however, is a striking number of white corpuscles for an artery. In the artery the three tunics are very thick and well differentiated.

*Facial Lymphatic Trunks.*—In *Polyodon* there are two such canals, on either side of the body, which for convenience sake have been designated as the *facial lymphatic trunks* and the *anterior facial lymphatic trunks*.

The latter trunks (Fig. 1, *F.L.T.*(1)) take their origin from the adipose tissue of the paddle, in front of the nasal sac. They are distinctly subdermal vessels, being situated some little distance above the orbito-nasal arteries and veins. When the level of the posterior border of the nasal sac is reached, each trunk bends outward and downward, to pass backward, superficially, along the surface of the adductor mandibulæ muscles. In the region of the spiracle it lies immediately in front of the facialis artery, and receives a rich network from above (Fig. 1, *L.N.*(2)), that passes over the facialis artery, nerve, and vein, to communicate above with the principal facialis trunk. Frequently vessels are received, which collect the network arising from the connective tissue that envelops the adductor mandibulæ muscles; these branches ordinarily accompany and often nearly encircle corresponding blood vessels. As previously stated in the neighborhood of the posterior extremity of the premaxilla, branches are received, that have their source from a rich network above (Fig. 1, *L.N.*(3)), which passes over the hyomandibular and its retractor muscle to communicate with similar branches that end in the hyo-opercularis lymphatic trunk.

In connection with the anterior facial lymphatic trunk it was just noted that the main *facial lymphatic trunk* (Figs. 1, 2, and 3, *F.L.T.*) gathered a rich network in the region of the spiracle that came from the facialis vein, nerve, and artery, and was also in communication with the anterior facial trunk. The lymphatic canal thus formed follows up along the dorsal surface

of the facialis vein, and when the external carotid artery (Fig. 1, *E.Car.A.*) is reached, passes mesad with it in crossing under the external jugular vein (Fig. 1, *E.J.V.*), and then continues caudad a short distance, still mesad of the artery. From here on, instead of passing ventrad and mesad with the external carotid, it continues caudad on practically the same level, directly mesad of the external jugular and above the hyo-opercularis artery.<sup>1</sup> In this locality, which is about opposite the auditory capsule and a little above the spiracle, the facial trunk collects a very rich network from the surface of the external jugular and the hyo-opercularis artery. In company with the hyo-opercularis vein (Fig. 1, *Hyo.O.V.*) this trunk bends outward at right angles. In Fig. 1 it passes between the external jugular and the hyo-opercularis artery, following for a short distance below and in front of the hyo-opercularis vein, and then bends at right angles, crossing under the vein to terminate in the hyo-opercularis lymphatic trunk, at the point where it becomes the hyo-opercularis sinus. In Fig. 2 the facial lymphatic trunk after crossing under the external jugular, followed below the hyo-opercularis vein for a very short distance, before curving, to culminate in the hyo-opercularis trunk; while in Fig. 3, which is from the right side of the same specimen as Fig. 2, the facial trunk after coming out from under the external jugular, nearly encircles the hyo-opercularis vein, before emptying into the hyo-opercularis trunk.

## 2. *Branchial Lymphatics (Nutrient Branchial Veins?)*

These vessels present the most difficult proposition found in *Polyodon*; both in regard to tracing out their distribution, and in determining whether they are veins or lymphatics, or a common system that may function for both. In brief, each branchial arch possesses two main canals; one of which travels along the outer and inner surface of the arch; while the other is for the most part confined to the filaments, following along between the two rows or hemibranchs, with the efferent branchial artery,

<sup>1</sup> This artery (Fig. 1, *Hyo.O.A.*) is a large branch of the external carotid, that for a short distance runs caudad with the external jugular, before bearing off obliquely to the hyoidean region.

but distad of it. The latter is undoubtedly the principal trunk, for it often receives the former, and it is collected above by either the hyo-opercularis sinus or the cephalic trunk, and below by the inferior jugular. Considerable variation, however, is shown in both the dorsal and ventral endings, and as many deviations are to be found on the opposite sides of the same specimen as on the same sides of different specimens. Both the branchial trunks and the branchial arch trunks are connected by a very coarse network of capillaries, which are distinctly lymphatic in the character of their meshes. Transverse sections through the branchial trunk disclosed it to be full of red corpuscles, but at no point was a definite peripheral connection between a nutrient branchial artery established; although at several places hypothetical communications might occur.

The distribution of these branchial canals is practically the same for the first three arches; hence a description of the first arch of a 70-pound *Polyodon*, as shown by Fig. 17 will answer for all. As stated above the main *branchial lymphatic trunk* (*nutrient branchial vein?*) (*Br.L.T.*) travels in the connective tissue, midway between the two rows of filaments, parallel with, but distad of, the efferent branchial artery. For every pair of branchial filaments, a rather large *filament lymphatic trunk* (*nutrient vein?*) (Figs. 17, 18, 19, and 27, *Fil.L.T.*) is received from the connecting tissue lying between the two rows of filaments. A cross-section through these filaments (Fig. 27) reveals the fact that these branches do not lie opposite each pair of filaments as the two corresponding afferent filament arteries do (Figs. 17 and 27, *A.Fil.A.*), but rather about midway in the space separating one pair of filaments from the next, and Fig. 27 represents each of these filament vessels as being about equidistant from four afferent filament arteries. Numerous *transverse filament lymphatic vessels* (*nutrient veins?*) (Figs. 18 and 19, *Tr.F.L.V.*) entwine in various ways with the roots from which the corresponding afferent filament transverse arteries (Fig. 18, *A.F.Tr.A.*) take their origin, and form a very coarse plexus-like network between them. These vessels collect a very rich network from the outer surface of the filament (Fig. 19, *Fil.L.V.*), which in the region of the respiratory septa

have a somewhat rectangular arrangement. Certain twigs traverse the superficial layer of the filament, opposite to and parallel with the spaces separating the septa, and these are connected by transverse branches. This coarse network cannot be confused with the very fine respiratory network (Fig. 18, *Res.N.*); for the latter is more profundus, being confined to planes or septa, which are at right angles to the so-called lymphatic network. With a magnification of 450 diameters (Fig. 18*a*) the meshes of the respiratory network are not as large as the meshes of the lymphatic network as viewed with a magnification of 50 diameters (Fig. 19); hence the caliber of the respiratory capillaries is almost infinitesimal when compared to the lymphatics. After leaving the area of the respiratory septa, which is toward the outer edge of the filament, the lymphatic network assumes a somewhat different character; here, as is shown in the lower part of Fig. 19, the meshes become crowded closer together; while on the outer edge of the filament, in the region of the efferent filament artery, the meshes become elongated in the direction of the artery, which is exactly at right angles to their greatest length in crossing the filament. An examination of the basal portion of the filaments and the membranes overlying the efferent branchial artery with a lens (Fig. 17), or better still a microscopic preparation of this region (Fig. 20), discloses the fact that the lymphatic network of the branchial filaments are continuous with a similar network found on the outer and inner surfaces of the branchial arch (Figs. 17 and 20, *Br.A.L.N.*).

*Branchial Arch Lymphatics (Nutrient Veins?)*. — One of these vessels (Fig. 17, *Br.A.L.T.*) runs along the inner surface of each arch, near its inner margin. It receives numerous radiating branches, which collect an extremely rich network (Fig. 17, *Br.A.L.N.*) that lies in the deeper membranes and connective tissue lining the arch, and which is distinctly lymphatic in the character of its meshes. This trunk also receives large accessory branches that gather a similar network from the other or outer side of the arch. So fine is this network that its meshes cannot be seen without the aid of a lens. At various intervals delicate branches could be traced to the outer membrane, where they collect an extremely minute capillary net-

work; so that each branchial arch would have a minute capillary network overlying and being connected with a more profundus and coarser network. Whether this outer capillary network was also in communication with the branchial arch arteries I am unable to state, any more than to say that no connections were found. A large number of small vessels were received from the gillrakers, the common arrangement being that two minute branches followed along the opposite surfaces of two neighboring gillrakers, collecting a minute network (Fig. 17, *G.R.L.N.*) found in the membrane joining the two, and uniting at the bases of the gillrakers to form a slender twig, which terminates in that portion of the branchial arch lymphatic network, overlying the efferent branchial artery (Fig. 17, *Br.A.L.N.*).

In the specimen from which Fig. 17 was drawn the arterial system was first filled with a blue mass, and afterward the subcutaneous system was injected with the yellow from the cephalic trunk. In certain areas, the minute capillary network found in the outer membrane covering a branchial arch was colored yellow and in other regions blue; similar colored areas were also found in the more profundus network, and in the superficial network of the branchial filaments. Other places also could be found in the more profundus network of the arch and the superficial network of the filaments, which were colored green, showing that the two injecting masses had fused. It does not, however, necessarily follow from the above, that these capillaries are in connection with arterial twigs. For in almost every case when the blood vessels were first injected, the cephalic trunk, the superficial network of the filaments, and the profundus network of the arch were found to be filled; doubtless through either the connection of the jugular with the cephalic sinus or the inferior jugular with the branchial lymphatic trunks, or through both. Since the profundus network of a branchial arch was found to be in communication with the minute superficial network, it is natural to expect that the mass found its way into this network after this manner, rather than through hypothetical arterial connections, which I have never been able to find, either from dissection or a microscopical examination; and upon inject-



ing the cephalic trunk with the yellow mass, it simply pushed back the blue, forming the conditions described above, viz., of certain areas of one color and other regions of a mixture.

Whether these conditions were obtained after this manner or were brought about through the media of peripheral communications with the nutrient arteries, might possibly be settled by removing a branchial arch from a large *Polyodon*, and after securely ligaturing both ends of the arch proper, plug up one end of the so-called branchial lymphatic trunk and inject from the other, but most unfortunately, however, these subcutaneous branchial vessels were not studied with any detail, until after I was removed some 2,000 miles from the source of material. Except for the fact that nutrient arteries were found on the arch, and no nutrient veins were observed, unless the so-called lymphatics function for both veins and lymphatics, I can see no reason for maintaining that hypothetical peripheral connections exist between the nutrient arteries and the so-called branchial lymphatics. Certainly the methods resorted to in this study do not justify it; in fact, the numerous connections with the inferior jugular and the two with the jugulars rather forbid such a view.

A point slightly favoring the hypothesis that the branchial subcutaneous vessels function as veins, is the fact, that a section through a main branchial lymphatic trunk (Fig. 28) always shows a predominance of red corpuscles. The ratio of red to white is 37 to 22, which, however, lacks considerable of being so overwhelming as one would expect to find in a vein. For example in the inferior jugular, into which these vessels terminate ventrad, the ratio of red to white is about 12 to 1 and in the mesenteric vein one has to look some time to find a leucocyte; while in the cephalic trunk, into which these vessels culminate dorsad, the red corpuscles are very scarce, the ratio of white to red being 153 to 8. Hence from purely histological grounds one might infer that the branchial lymphatic trunks discharged themselves mainly into the inferior jugular, but the fact that none of the branchial arch trunks terminates in the inferior jugular, while some of them do empty directly into the cephalic trunk; and the additional observation that the branchial

lymphatic openings into the hyo-opercularis sinus and the cephalic trunk are larger than those into the inferior jugular, barely make this view even tenable.

*Respiratory and Nutrient Branchial Arteries.*—These vessels hold such an intimate relationship with the so-called branchial lymphatic system, and are so different from the similar arteries found in bony fishes, that a brief description of some kind seems to be called for.

With the exception of the last arch, which consists of a single hemibranch, the respiratory system is practically the same for the first three arches; so that the following description, which is taken from the first arch of a 70-pound *Polyodon* will answer for all. The main *afferent* and *efferent branchial arteries* (Fig. 17, *A.Br.A.* and *E.Br.A.*) maintain practically the same positions and connections as in other fishes. An *afferent filament artery* (Fig. 17, *A.Fil.A.*) is given off distad from the main afferent artery, to follow along the inner margin of each filament; its course lies in the connective tissue, close to the filament, and its distribution within the filament is a great deal more complex, than with other fishes that have been studied. At regular intervals (Fig. 18) rather large, but short, cross branches are given off, which are connected in an irregular manner; thus, forming a sort of secondary chain of arteries, from which the so-called *afferent transverse filament arteries* (Fig. 18, *A.F.Tr.A.*) take their origin. The latter vessels follow a nearly parallel course with one another, until near the filament septa, when each separates into from three to six branches, each of which furnishes the venous supply for a respiratory septum. In a 70-pound *Polyodon* the faces of these septa were about .1 mm. apart, which as shown by Figs. 18 and 18a must contain about the finest capillary network that exists. At the outer margin of each septum the respiratory network is collected by a rather short *efferent transverse filament artery* (Fig. 18, *E.F.Tr.A.*), which empties directly into the *efferent filament artery*, and all these vessels (Figs. 17 and 18, *E.Fil.A.*) pass proximad along the outer surface of the filaments, to discharge themselves in, and form, the great efferent branchial arteries (Fig. 17, *E.Br.A.*).

From both the lateral and mesal side of the efferent branchial artery, numerous branches, designated as *nutrient branchial arteries* (Figs. 17 and 20, *N.Br.A.*) arise to supply the membranes and connective tissue, overlying and underlying the efferent branchial artery. Two such branches were sent to the base of each filament. They were found on either side of the efferent filament artery, a little profundus of the lymphatic network, but could not be traced much beyond the base of the filament. Many branches were given off to the gillrakers, and forking to follow the dorsal and ventral surfaces of two adjacent rakers, they break up into a fine network in the membrane connecting them (Fig. 17, *G.R.N.*). Also very fine arterial twigs as *d*, Fig. 20, were frequently seen in the region bordering the filaments, but no connections, not even with the aid of a microscope, could be established with the so-called lymphatic network.

What is designated as the branchial arch artery<sup>1</sup> (Fig. 17, *Br.A.A.*) approaches the arch from the anterior dorsal corner. Shortly before the arch is reached it bifurcates. A large outer fork (*Br.A.A.(1)*) is given off to supply the outer surface of the arch, while the inner fork immediately makes a sharp curve to pass to the cephalic margin of the arch, and continues parallel with the lymphatic trunk. It is, however, a more profundus vessel, traveling for a good part of its length in a muscle overlying the inner surface of the arch. Branches are frequently given off to the muscle and the distal membranes, and they are often accompanied on either side and sometimes nearly surrounded by the so-called lymphatics. The caliber of the branchial arch artery and its branches is, however, only miniature, when compared with the corresponding lymphatic canals.

At this point there arises an apparent inconsistency. In all other parts of the head region in *Polyodon* we have arteries, veins, and lymphatics, running parallel with one another, but in the branchial arch and filaments (not taking the respiratory system into consideration) only arteries and lymphatics have been described. If peripheral connection had been established be-

<sup>1</sup>The source of this artery from the dorsal extremity of the efferent branchial artery has not been worked out as carefully as it should have been.

between these so-called lymphatics and the nutrient arteries, one might claim that these branchial lymphatics are nutrient veins, which receive a network decidedly lymphatic in character, that is continuous from the great trunk passing through the gills to the main trunk of the branchial arch, and which may function both for a venous and a lymphatic system, terminating above in a lymphatic trunk and below in a vein.

Possibly it should be noted here that the fourth or last branchial arch has but one row of filaments, and is therefore a hemibranch. Except for some variation in connection with the efferent branchial artery, which will doubtless be fully noted in a forthcoming paper, by Mr. E. P. Allis on the blood vessels of *Polyodon*, the lymphatics and the blood-vascular systems of the fourth arch correspond very closely to a hemibranch of one of the other arches.

*Dorsal and Ventral Endings of the Branchial Lymphatic Trunks (Nutrient Branchial Veins?)*. — Great variation is shown not only in the dorsal and ventral terminations of these trunks in different specimens, but also on the opposite sides of the same specimen. In tracing out the culmination of these vessels I found it frequently useful to insert a canula into one of these trunks and force water with the aid of a syringe into the trunk; and having previously removed a portion of the sinus or trunk into which it is discharged, note the orifice through which the water was ejected.

Fig. 1 shows the dorsal endings of the branchial lymphatic trunks, as seen from the left side of a 70-pound *Polyodon*, and Figs. 2 and 3 represent the dorsal mode of termination of these trunks on the opposite sides of a 25-pound *Polyodon*. In every case the *first branchial lymphatic trunk* (*Br.L.T.(1)*) bifurcates when about to leave the arch. In Fig. 1 the ventral fork (*Br.L.T.(1')*) continues cephalad in about the same plane until the hyo-opercularis sinus is reached, when it bends dorsad to follow along the mesal surface of the hyo-opercularis sinus for a short distance, and immediately after receiving the dorsal fork (*Br.L.T.(1'')*), the combined trunk opens into the hyo-opercularis sinus through the inner wall (*Br.L.T.(1)O.*). With the specimen from which Figs. 2 and 3 were drawn, both of

these forks opened separately into the hyo-opercularis sinus; the only difference on the two sides being that on the right side (Fig. 3) the openings were further apart. In every case the ventral fork followed along the anterior margin of the first branchial levator muscle, and the dorsal fork traveled along behind the same muscle.

The final dorsal termination of the second, third and fourth branchial lymphatic trunks are so different in these three dissections that a brief description should accompany each, although a far better idea can be obtained by carefully comparing Figs. 1, 2 and 3. In Fig. 1 the third branchial lymphatic trunk unites with the fourth, behind the posterior border of the third and fourth branchial levator muscles, and the common trunk (*Br.L.T.*(3) and (4)) continues dorsad behind the muscle until the jugular is reached, when it receives from in front the second branchial lymphatic trunk (dorsal fork of the second branchial lymphatic trunk?), and the combined trunk ( $x$ ) after crossing over the jugular empties into the cephalic trunk, a short distance behind the hyo-opercularis sinus. In Fig. 2 the fourth branchial lymphatic trunk unites with a rather large branch that comes up from the pharyngo-clavicularis muscle, and very shortly is joined from the rear by the third branchial lymphatic trunk. The course of this common trunk (*Br.L.T.*(3) and (4)) is then obliquely dorsad, following along the inner surface of the second branchial levator muscle; it soon collects the dorsal fork of the second branchial lymphatic trunk, and the combined trunk thus formed ( $x$ ), discharges itself mesad of the hyo-opercularis sinus in the ventral fork of the cephalic trunk. The remaining ventral fork of the second branchial lymphatic trunk (*Br.L.T.*(2)) travels mesad of the first and second branchial levator muscles, and likewise terminates in the ventral fork of the cephalic trunk, a little below trunk ( $x$ ). In Fig. 3 the third branchial lymphatic trunk makes a sharp curve on the outer surface of the arch, where it receives a common trunk, formed from the union of the fourth branchial trunk with a vessel coming from the occipito-clavicularis muscle and the region behind the fourth branchial arch. The dorsal fork of the second branchial lymphatic trunk after traveling along the posterior

edge of the second branchial levator muscle, makes a curve at right angles to pass obliquely ventrad along the inner surface of the second branchial levator muscle, where it shortly bifurcates at right angles, one fork continuing obliquely ventrad terminates in the dorsal arm of the great bend of the combined trunk from the third and fourth arches, while the other fork passes dorso-cephalad for a short distance and receives a large communicating branch from the combined trunk of the third and fourth arches, thus forming trunk ( $x$ ), which, after bending at right angles, passes dorso-caudad to discharge itself in the cephalic trunk, a little behind the hyo-opercularis sinus. As on the opposite side, the ventral fork of the second branchial lymphatic trunk empties into the ventral fork of the cephalic trunk.

Only a few of the so-called lymphatics from the branchial arches have been traced out, and they either terminated in the main branchial trunks or in the ventral fork of the cephalic trunk. In Fig. 3 the trunk from the first arch culminated in the ventral fork of the first branchial trunk, at a point indicated by *Br.A.L.T.(1)*, and the one from the third arch (*Br.A.L.T.(3)*) ended in the ventral fork of the cephalic trunk, directly above the opening of the ventral fork of the second branchial trunk.

Ventrad, the termination of the first two branchial lymphatic trunks in the inferior jugular are practically the same for all the specimens, but considerable variation exists in regard to the endings of the third and fourth trunks, both in different specimens and on the opposite sides of the same specimen.

As shown in Fig. 5 the first and second branchial lymphatic trunks (*Br.L.T.(1)* and (2)), in their ventral course, finally get to lie immediately behind their corresponding afferent branchial arteries. When close to the ventral aorta, the second trunk crosses over the ventral surface of the second afferent artery, then passing cephalad, in close proximity to the ventral aorta, it crosses below the second obliquus ventralis muscle to anastomose with the first trunk. Both the first and second branchial trunks communicate above with the inferior jugular. The former connection (Figs. 5, 6 and 7, *Br.L.T.(1) V.O.*) leads up between the sterno-hyoideus tendon and the ventral

aorta, and the first afferent branchial artery and the second obliquus ventralis muscle; so far as could be ascertained it was the first vessel to join the inferior jugular. The latter connection (Figs. 5, 6 and 7, *Br.L.T.(2)V.O.*) passes up between the second obliquus ventralis muscle, ventral aorta, and second afferent branchial artery. In the specimen from which Figs. 5 and 6 were drawn there was a large dorsal opening in the inferior jugular (Fig. 6, *M.O.*), which in front lead into a sinus designated as (*M*) that received two sacs from the rear (*N*). Into the left sac the corresponding fourth branchial lymphatic trunk empties, and the right sac receives a short trunk (Figs. 5 and 6, *S.T.*) that encircles the inferior jugular, and communicates below with a *ventral sinus* (*S*). En route it collects the fourth right branchial trunk (Fig. 5, *Br.L.T.(4)*) from the rear; while the remaining third left branchial trunk (Figs. 5 and 6, *Br.L.T.(3)*) empties directly into the inferior jugular, a little in advance of sinus (*S*).

In the specimen from which Fig. 7 was drawn the third and fourth branchial lymphatic trunks had an entirely different mode of ending from that described above. No dorsal sinus emptied into the inferior jugular, but a *ventral sinus* (Fig. 7, *S*) was present and occupied a similar position as in Fig. 5. Its communicating trunk (*S.T.*) connected directly above with the inferior jugular instead of encircling the right side of the inferior jugular as in Fig. 5. The ventral sinus in Fig. 7, *S*, received the third right branchial trunk in front, and in addition the fourth left branchial trunk from the rear; while the fourth right and the third left branchial trunks terminated directly in the inferior jugular.

The course of the inferior jugular in the branchial region is too irregular and complex to permit of a description. Fig. 6 gives a general idea of its form and its anterior communications. Here it is simply a very thin irregular sinus, conforming to the general arrangement of the branchial arches and the ventral aorta and its branches. In the neighborhood of the union of the third and fourth pair of afferent branchial arteries (Fig. 6, *A.Br.A.(3)* and (4)) it not only surrounds them, but passes dorsad between them.

Like *Acipenser* and *Scaphirhynchus* the ventricle of the heart of *Polyodon* is conspicuous for the amount of lymphoid tissue surrounding it. There is always one large lymphatic gland encircling the anterior part of the ventricle; another smaller one is situated behind it on the lower side of the ventricle, inclosing the greater portion of the posterior end of the ventricle. It is very singular in *Polyodon* that the *coronary artery*, which supplies these glands as well as the heart, comes from the fourth right efferent branchial artery and approaches the heart from the rear. When the ventral side of the sinus venosus is reached it trifurcates. Two of these branches pass cephalad between the auricle and the ventricle, supplying each; while the third follows along the left and ventral border of the ventricle, and gives off branches that traverse between the surface of the ventricle and these glands, supplying each. Corresponding venous branches arise from the anterior and left ventral side of the ventricle, which likewise pass between these glands and the ventricle to terminate in two *longitudinal coronary veins* that travel caudad between the auricle and ventricle. At the posterior apex of the heart these two veins anastomose, forming the *common coronary vein*, which discharges itself into the sinus venosus from below. For the most part the blood-vascular network lies between these glands and the ventricle. In addition to the vascular network described above there is a coarser and more superficial network, decidedly lymphatic in the character of its meshes, which encompasses these glands. This is undoubtedly a lymphatic network, but so far as could be determined it was not collected by any definite lymphatic canal. Consequently it must, as Robin found in *Torpedo* (*op. cit.*, pp. 15 and 16), reach the veins through the œsophagus plexus. One finds upon sectioning this lymphoid tissue surrounding the heart that it somewhat resembles the thymus. It consists of a connective tissue framework which is completely filled with leucocytes. In addition to the numerous blood vessels that traverse it, many lymphatic spaces or sinuses were found which were filled with leucocytes.



### III. DISTRIBUTION OF THE SUBCUTANEOUS VESSELS IN LEPISOSTEUS.

In this genus the subcutaneous vessels of the head, especially the region adjoining the branchial arches and the heart, are far more sinus-like than in *Polyodon* or the Selachians, and in this respect they resemble the Teleosts. The so-called cephalic sinus in *Lepisosteus* occupies a position entirely in front of the branchial arches, which is far cephalad of its position in *Polyodon* or as set forth by Hopkins for *Amia* (*op. cit.*, pp. 371-2), and corresponds about to its position in *Scorpaenichthys* and other bony fishes. Other interesting points such as a communication of a so-called dorsal pericardial sinus with the inferior jugular and separate dorsal and ventral branchial trunks will be described at length later on in the text. Of the three species of *Lepisosteus* that were studied no more variation could be found than in different individuals of the same species.

*Longitudinal Lymphatic Trunks.* — With *Lepisosteus* as in *Amia* and the bony fishes there are four such canals in the thoracic as well as in the abdominal and caudal regions. They are respectively dorsal, ventral, and lateral in position. A transverse section as Fig. 16 shows that they are enveloped in a mass of connective tissue, which is imbedded more or less within the myotomes. To the unaided eye they appear like cavities in this connective tissue. The outer walls of these vessels lie directly below the skin and are frequently ruptured upon removing the horny exoskeleton. Except for their enormous caliber and their different cephalic termination they do not differ materially from the similar canals of *Scorpaenichthys*. The great *lateral lymphatic trunks* (Figs. 8, 9, 11, 12 and 16, *L.L.T.*) upon approaching the thoracic region gradually leave the median lateral line to assume a more and more dorsal position. Accompanying the ramus lateralis vagi each trunk passes beneath its corresponding pectoral arch to culminate in what has been designated as the occipital sinus (Figs. 8, 9, 11 and 12, *Oc.S.*) instead of emptying into the cephalic sinus as in *Polyodon* or *Amia*. The *dorsal lymphatic canal* (Figs. 8, 11, 12 and 16, *D.L.T.*) travels along the median dorsal surface of the trunk, and likewise has a very different ending from what Hopkins

found for *Amia* or from *Scorphaenichthys*. Instead of bifurcating behind the skull and each fork terminating in the cephalic sinus as one might expect, this canal when not far from the posterior end of the skull passes ventrad along the left side of the connective tissue separating the two great lateral muscles, and when the vertebral column is reached it bears off obliquely laterad to cross below the exoccipital portion of the skull and terminates in the anterior part of the left branchial sinus (Figs. 8, 11 and 12, *Br.S.*) from the inner side. In every specimen of *L. tristoechus* and in several of *L. osseus* the *ventral lymphatic trunk* (Figs. 8 and 13, *V.L.T.*) forked at the level of the base of the pectoral fins, and each of these branches, which immediately become sinus-like, continues parallel until the level of the bulbus arteriosus is reached, when they bear off at right angles to pass between the clavicle and pericardium and culminate in the corresponding pericardial sinuses (Figs. 8 and 13, *Per.S.*). In that part of their course which lies between the pectorals and the heart they are separated only by a sheath of tough connective tissue, in which there are at least two connecting orifices. With an equal number of *L. osseus*, as shown in Figs. 14, 15 and 16, the ventral trunk did not fork in the region of the pectorals, but continued cephalad as a single trunk, and when the heart was reached it joined the right pericardial sinus.

As represented in Figs. 14, 15 and 16 the ventral lymphatic trunk is accompanied by a *ventral vein* (*V.V.*), which passes to the left of the heart to discharge itself (Fig. 15) in the left precava a little laterad of the orifice of the hepatic vein. Two *ventral arteries* (Figs. 14 and 16, *V.A.*) also accompanied the lymphatic trunk for a short distance.

Numerous *intermuscular lymphatic vessels* (Figs. 8 and 11, *Intm.L.V.*) were given off from either side of the dorsal trunk, or from above and below in case of the lateral trunk. These vessels traversed superficially on the septa between the myotomes. They doubtless connected the lateral with the dorsal and ventral trunks as in *Scorphaenichthys* and other fishes, but this fact was not established for a certainty in *Lepisosteus*.

*Pericardial Sinuses.* — Each of these sinuses in *Lepisosteus* (Figs. 8-14, *Per.S.*) occupies a like position to a similar sinus

in *Scorpaenichthys* and *Amia*. In *Lepisosteus* it follows along the front and inner surface of the pectoral arch parallel with the precava. Dorsad at about the level of the last branchial arch it communicates with what is designated as the *occipital sinus* (Figs. 8-12, *Oc.S.*), which continues ventrad, mesad of the pericardial sinus, and shortly after receiving the *pectoral sinus* (Figs. 8 and 9, *P.S.*), it again joins the pericardial sinus from the inside through a very large orifice (Figs. 8-10, *Oc.S.O.*). As already stated, in the region of the heart one or both of the pericardial sinuses receive the ventral lymphatic trunk or a fork of it. After which the pericardial sinus proceeds along the lateral surface of the ventricle, just outside the parietal layer of the pericardium, and when the bulbus arteriosus is reached each of the pericardial sinuses has a very large opening (Figs. 8, 9, 13, 14 and 15, *Per.S.O.*), which leads into a large canal that passes mesad and empties into the posterior end of the so-called *dorsal pericardial sinus*. This sinus (Figs. 13 and 15, *D.Per.S.*), which is located directly above the bulbus arteriosus, has the form of an ellipse with its longest axis corresponding with that of the fish. In a 10-pound *L. osseus* its dimensions were 15 by 8 mm. There is always a communication above with the inferior jugular vein. In the specimen from which Fig. 15 was drawn there were two such openings, both of which were located in the posterior half of the sinus, and were guarded by a pair of semi-lunar valves (*D.Per.S.V.*) opening into the vein. In this specimen there was a third aperture in the anterior dorsal wall of this sinus, but it led only into a small blind pocket. This mechanism in *Lepisosteus* recalls a sort of hypothetical connection of the ventral pericardial sinus with a branch of the inferior jugular in *Scorpaenichthys* (*op. cit.*, p. 75). At the points where the connecting branches are given off from the pericardial sinuses to the dorsal pericardial sinus two *anterior pericardial canals* are received (Figs. 13, 14 and 15, *Per.S.(1)*). These doubtless are nothing more than the anterior continuations of the pericardial sinuses, which extend for a short distance along the ventral surface of the parietal layer of the pericardium.

*Occipital Sinus* (Figs. 8-12, *Oc.S.*). — As will be readily

noted, the sinus so designated occupies a somewhat similar position to the cephalic sinus of *Amia*, *Polyodon*, and *Salmo*. It likewise receives the lateral lymphatic trunk and is connected below with the pericardial sinus, but does not communicate directly with the jugular or the precava; hence the term cephalic sinus has been reserved for a sinus located further cephalad, that corresponds in position to a similar sinus in *Scorpaenichthys*, and which terminates directly in the jugular vein. The occipital sinus is therefore a spacious reservoir, situated directly above the epibranchial of the last branchial arch, in front and a little median of the pectoral arch, and immediately behind the last branchial levator muscle. It also lies above and behind what is represented as the *branchial lymphatic sinus* (Figs. 8, 9, 11 and 12, *Br.S.*), from which it is separated by a very thin membrane. A little dorsad and mesad of the fourth epibranchial bone there is an orifice (Figs. 8, 9, 11 and 12, *Br.S.O.*) in the ventral wall of the occipital sinus, which communicates below with the branchial sinus. Laterad and a little below the level of the epibranchial of the fourth arch it is in connection with, or possibly might better be represented as receiving, the pericardial sinus. At this point the occipital sinus passes ventrad along the inner surface of the pericardial sinus for some distance, to again communicate more ventrad with the pericardial sinus (Figs. 8 and 10, *Oc.S.O.*). No special effort has been made to work out in detail the distribution of the lymphatics in the pectoral fin, but nevertheless in all three species of *Lepisosteus* a large *pectoral sinus* (Figs. 8 and 9, *P.S.*) was found at the base of each pectoral fin. With *L. osseus* it collected numerous branches that traveled along the dorsal surfaces of the rays and gathered a network from the adjacent membranes. Only one branch per ray, however, was found in *L. osseus*; whereas in *Scorpaenichthys* each ray possessed two vessels, which collected a network from the adjoining membrane connecting two rays. Upon reaching the anterior proximal part of the fin the pectoral sinus makes a bend at right angles, and after crossing diagonally over the outer surfaces of the superficial and profundus pectoral adductor muscles it again makes a curve at right angles to pass cephalad between the profundus pectoral

adductor muscle and the great lateral trunk muscle, to discharge itself in the occipital sinus.

*Branchial Lymphatic Sinuses* (Fig. 8, 11 and 12, *Br.S.*). — Each of these reservoirs is a cavity of considerable size, which occupies most of the space above the superior pharyngeal region between the auditory capsule and the levator branchial muscles, and is separated from the skull only by the jugular vein. Its posterior depth is double the anterior. This difference in depth is not due to a gradual tapering down of the sinus, but rather to an abrupt rise in the level of the floor a little forward of the center of the sinus; so that this sinus might almost be said to consist of an anterior and a posterior portion. The anterior division lies directly mesad of the first and second branchial levator muscles (Figs. 11 and 12, *L.Br.A.(1)* and (2)). Cephalad it tapers down into a sort of papilla, which curves around these two branchial muscles to unite in front with a papilla from the hyo-opercularis sinus in forming the so-called *cephalic sinus* (Figs. 8, 11 and 12, *Ceph.S.*), which empties into the jugular. Directly mesad of the first branchial levator muscle there is an orifice in the floor of the anterior portion of the branchial sinus (Figs. 11 and 12, *D.Br.L.T.(1)O.*) through which a trunk formed from the union of the first dorsal branchial lymphatic trunk (Figs. 8 and 9, *D.Br.L.T.(1)*) and a fork of the second dorsal branchial lymphatic trunk is discharged. What might be designated as the posterior mesal corner of the left anterior branchial sinus receives the dorsal lymphatic trunk (Figs. 8, 11 and 12, *D.L.T.*). Leaving now the anterior part of the branchial sinus we find that the posterior portion of this sinus extends caudad and ventrad beneath the occipital sinus, and in the neighborhood of the epibranchial of the last branchial arch it communicates above with the occipital sinus (Figs. 8, 9, 11 and 12, *Br.S.O.*). In *L. osseus* there is an opening in the anterior ventro-lateral corner of the posterior part of the branchial sinus (Fig. 12, *D.Br.L.T.(2)O.*) through which one fork of the second dorsal branchial lymphatic trunk is discharged. This orifice is situated almost opposite the space between the second and third branchial levator muscles. There is still another aperture about opposite the fourth branchial levator muscle

(Fig. 12, *D.Br.L.T.(3)O.*) into which the third dorsal branchial lymphatic trunk opens.

In position the branchial lymphatic sinus corresponds somewhat to the so-called hyo-opercularis sinus and the anterior part of the cephalic trunk of *Polyodon*. Its inclination to become separated into two divisions recalls the two branchial sinuses of *Scorpaenichthys* (*op. cit.*, Pls. II and III; Figs. 4 and 5, *Br.L.S.*), which were situated above the epibranchials of the first and second, and the third and fourth arches, respectively, but were some distance laterad of their position in *Lepisosteus*, being located outside the branchial levator muscles, and the space between the branchial levator muscles and the skull in *Scorpaenichthys* was occupied by the anterior continuation of the abdominal sinus and the cranial lymphatic trunk together with the jugular vein. In *Ophiodon* and *Scorpaenichthys* no branchial lymphatic trunks were observed, but in the former nutrient veins were found emptying directly into the jugular.

What is designated as the *hyo-opercularis sinus* in *Lepisosteus* (Fig. 11, *Hyo.O.S.*) is completely drawn on the right side only. It is a reservoir of considerable size situated on the inner side of the operculum, above the gills. So closely does it adhere to the operculum that it is impossible to remove this bone without rupturing its walls. This sinus is very much depressed and conforms to the general curvature of the body. As in *Scorpaenichthys* it may be said to end dorso-cephalad in a papilla, which in *L. tristachus* expands into a distinct sinus immediately laterad and cephalad of the first branchial levator muscle, to which the name *cephalic sinus* has been given.

This sinus (Figs. 8, 11 and 12, *Ceph. S.*) is joined from the inside by the branchial sinus, and directly in front of this point of union the cephalic sinus bends at right angles to pass mesad and discharge itself in the jugular at a point about opposite the cerebellum. With *L. tristachus* the cephalic sinus has much more the appearance of a reservoir than in *L. osseus* (compare Fig. 11 with 12). In the latter it is nothing more than a canal; while even in *L. tristachus* it falls far short of its size in *Scorpaenichthys*, and is somewhat smaller than the corresponding sinus of *Polyodon*.

The positions of the cephalic sinuses and their points of termination in the jugulars are about the same as in *Scorpaenichthys*, but their connections and positions in *Amia*, *Polyodon* and *Salmo* are very different. Hence these somewhat dissimilar sinuses may be only analogous. I take the term *cephalic sinus* to be nothing more than an arbitrary name given to a dorso-cephalic sinus that is in connection with all the subcutaneous vessels and which terminates directly in the jugular vein, or possibly the precava in some species.

*Branchial Lymphatic Trunks (Nutrient Veins?)*.<sup>1</sup>—These vessels in *Lepisosteus* have not been worked out with anything like the detail that they were in *Polyodon*. Each arch possessed a *dorsal* and a *ventral* trunk that traversed between the two rows of filaments, parallel with, but distad of, the afferent branchial artery, and which so far as could be ascertained had no connection with one another. No effort was made to trace out the origin of these vessels from the filaments, and nothing more was attempted than to follow these canals to their ultimate termination. In *Lepisosteus* the branchial arches are round and only miniature when compared with *Polyodon*. They are surrounded by a spare amount of spongy connective tissue, containing only a few corpuscles in its meshes and a small number of blood vessels.

The *first dorsal branchial trunk* (Figs. 8 and 9, *D.Br.-T.(1)*) takes its origin a little above the center of the arch from between the two rows of filaments. Upon leaving the most dorsal pair of filaments it travels along the anterior margin of the first branchial levator muscle, receives a fork (Fig. 8) from the second branchial trunk; then curving to the mesal side of the muscle, penetrates the floor of the anterior part of the branchial sinus, through an opening (Figs. 11 and 12, *Br.L.T.(1)O.*) about opposite the first branchial levator muscle. The *second dorsal branchial trunk* (Figs. 8 and 9, *Br.L.T.(2)*) arises in like manner from the dorsal filaments of the second arch, and after leaving the arch it forks between the

<sup>1</sup>As in the case of the branchial trunks of *Polyodon* the method of forcing water through these trunks and noting the points of its exit was resorted to with advantage in *Lepisosteus*.

second and third branchial levator muscles; the anterior branch continuing on across the outer surface of the second branchial levator muscle, unites with the first branch mesad of the first levator muscles; while the posterior branch passes mesad between the second and third branchial levator muscles to terminate in the anterior ventral corner of the posterior part of the branchial sinus through an orifice designated in Figs. 11 and 12 as *D.Br.L.T.(2)O.* The *third branchial trunk* after leaving its arch curves around the fourth levator muscle to culminate in the floor of the posterior division of the branchial sinus about opposite the fourth branchial levator muscle (Figs. 11 and 12, *D.Br.L.T.(3)O.*); whereas the trunk from the fourth arch discharges itself in an entirely different sinus. Its opening (Figs. 8, 9, 11 and 12, *Br.L.T.(4)O.*) is through the inner wall of that part of the occipital sinus which lies mesad of the pericardial sinus.

All of the so-called *ventral branchial trunks* doubtless terminate in one way or another in the inferior jugular vein. This is certainly true for the first three pairs, but the final ending of the last pair I have never been able satisfactorily to trace out. Each of these ventral branchial trunks has its source from the ventral filaments, and traverses between the two hemibranchs, in company with, but distad of, the afferent branchial artery. The first pair of these vessels discharged themselves through two orifices (Figs. 14 and 15, *V.Br.L.T.(1)O.*) situated in the dorsal walls of the right and left forks of the inferior jugular, directly in front of their corresponding afferent branchial arteries. In the specimen from which Figs. 14 and 15 were drawn, the second right branchial trunk joined the right fork of the inferior jugular exactly in front of the second right afferent branchial artery through an orifice designated as *V.Br.L.T.(2)O.* The precise point of union of the third right trunk was not located, but upon injecting this vessel ventrad with water it was discharged through the opening of the right fork of the inferior jugular into the inferior jugular (Fig. 15, *R.I.J.V.O.*), indicating of course that it came from the inferior jugular. In the dorsal wall of the left fork of the inferior jugular, immediately behind the second left afferent branchial artery, there is



an orifice (Fig. 15, *E.*), which leads cephalad into a pocket through which water is ejected upon injecting either the second or the third left branchial trunks. Neither from dissection nor from the water injection method could the termination of the fourth pair of branchial trunks be located. Undoubtedly, however, they are discharged into the inferior jugular vein.

As shown in Fig. 15 the *inferior jugular vein* in *Lepisosteus* arises in the branchial region from two branches, which unite immediately behind and above the combined trunk formed by the union of the last pair of afferent branchial arteries; the right fork, however, extends caudad for a short distance as a blind sac. Thus formed, the main stem of the inferior jugular (*I. J. V.*), passes caudad above and parallel with the ventral aorta. Dorsad of the bulbus, as already noted, it receives one or more communications from below from the so-called dorsal pericardial sinus; after which it bears off obliquely to the left to discharge itself in the left sinus venosus. It seems in *Lepisosteus* that this sinus is divided, and the opening into the auricle below is from the left side (Fig. 15, *S. Ven. O.*). Both sinuses receive a precava or ductus of Cuvier, but the hepatic and ventral veins, so far as could be ascertained, terminated in the left precava.

#### IV. DEDUCTIONS AND SUMMARY.

From the preceding discussion it would seem that the subcutaneous vessels of the Ganoids occupy a position fairly well between the generalized Selachians and the more specialized Teleosts or Batrachians. There is a vast difference between the character and distribution of these vessels in the *Chondroganoidea* (the cartilaginous ganoids) and in the *Holostei* (the bony ganoids). *Polyodon* as a representative of the former group has non-sinus subcutaneous vessels, which in structure are not very dissimilar to the corresponding veins, and in this respect resemble the subcutaneous vessels of the Selachians, which have been described by many authors as veins. While in *Lepisosteus*, which is one of the bony Ganoids, many of the subcutaneous vessels are thin-walled and decidedly sinus-like; in this respect resembling the conditions as found in the Teleosts and Batrachians.

With the Ganoids, especially in the branchial region, it is a very difficult proposition to determine whether these subcutaneous vessels are lymphatics or veins or a common system that may function for both. For the present, until after the embryology has been studied, and this system has been worked out in the Cyclostomes, it has seemed best to leave it as an open question. These vessels have, however, in this paper been described as lymphatics for the following reasons: In every part of the head, excepting the branchial region, each of the main subcutaneous canals is accompanied by a corresponding artery and vein, and frequently the arterial and venous branches are surrounded on either side by branches of these subcutaneous vessels. They receive a superficial network, which is distinctly lymphatic in the character of its meshes, and which is often continuous with another subcutaneous canal of the same class, and never to my knowledge with a corresponding arterial trunk. Excepting the branchial trunks, as far as could be ascertained, all of the subcutaneous canals contain a predominance of white corpuscles; although in some of the trunks they may be very scarce. If the longitudinal subcutaneous canals of the trunk were considered as veins it would be necessary to treat them as a separate venous system, that had no counterpart in the arterial system. As in the Teleosts the principal arterial trunks of this region are the aorta and the caudal artery which are accompanied by the cardinal and caudal veins. From these vessels are given off or received the neural, hæmal, and the lateral branches, which extend to the skin and fins to supply or collect the blood from the region drained by the superficial longitudinal trunks.

So far as could be determined in the branchial region of the Ganoids there is a nutrient branchial arterial system, but no nutrient venous system was observed unless the so-called branchial lymphatic system functions for both veins and lymphatics. In *Lepisosteus* each arch had a dorsal and ventral branchial trunk, the latter terminating below in the inferior jugular and the former in a branchial sinus, which was in connection with the cephalic and pericardial sinuses. With *Polyodon* but one branchial lymphatic trunk travels between the branchial fila-

ments of an arch. Throughout its course it collects a rather coarse network of capillaries from the filaments, which is in direct communication with what is designated as the branchial arch lymphatic trunk, and further this network on the arch is in connection with a very fine and more superficial network, which so far as could be learned had no connections with the corresponding arteries. These branchial arch trunks terminate dorsad either in the common branchial trunk or in the ventral fork of the cephalic canal, while the main branchial trunks in *Polyodon* discharge themselves ventrad in the inferior jugular and dorsad in the cephalic canal and the hyo-opercularis sinus.

A comparative study of the cephalic sinuses in this group apparently does not throw much light on the phylogeny of the lymphatic system. *Polyodon*, the most primitive member of this series, has a cephalic sinus, which in position and connections resembles a similar reservoir in *Amia* and *Salmo*, while the cephalic sinus of *Lepisosteus* is more closely allied to a like sinus in *Scorpaenichthys* and other Teleosts. This reservoir in *Polyodon* is situated just mesad of the supraclavicle. It receives the great cephalic canal from in front which drains the entire head region, the lateral lymphatic trunk from the rear, and emits itself ventrad into the jugular vein. With *Lepisosteus*, especially *L. osseus*, this reservoir is hardly deserving the term sinus. It is far cephalad of its position in *Polyodon*, and as in *Scorpaenichthys*, lies about opposite the auditory capsule. From the rear it receives the hyo-opercularis and branchial sinuses. The latter is in connection with a series of sinuses that surround the branchial cavity and gather the subcutaneous vessels from the remainder of the body, and about opposite the cerebellum the cephalic sinus discharges itself mesad into the jugular vein.

With *Lepisosteus* the first in the chain of sinuses encircling the branchial cavity to connect anteriorly with the cephalic sinus is the branchial sinus. It lies between the branchial levator muscles and the skull, and collects the first three branchial trunks, the left branchial sinus receiving the dorsal lymphatic trunk. Posteriorly each branchial sinus is in connection with a spacious occipital sinus, which collects the lateral trunk from

the rear. Ventrad the occipital sinus communicates with the pericardial sinus; then passing mesad of the latter it again joins the pericardial sinus from below, after gathering in the pectoral sinus. The course of the pericardial sinus is along the inner and anterior margin of the clavicle, and shortly after receiving the ventral communication of the occipital sinus it is usually joined by a fork of the ventral lymphatic trunk. Occasionally, however, the ventral trunk does not divide, and in that case it empties directly into one or the other pericardial sinuses. Each pericardial sinus then continues cephalad along the side of the ventricle, immediately outside of the parietal layer of the pericardium, and when the bulbus is reached, sends inward a large communicating branch that terminates in the so-called dorsal pericardial sinus. This sinus, which is situated directly above the bulbus arteriosus, has one or two communications above with the inferior jugular, each orifice being guarded by a pair of semilunar valves opening into the vein.

The subcutaneous vessels surrounding the branchial cavity in *Polyodon* take on the form of canals rather than sinuses. Situated obliquely at the base of the skull is the hyo-opercularis sinus, which is formed from the union of the hyo-opercularis and facial trunks. The latter in the main follows the external jugular and its facialis branch, which in the region of the adductor mandibulæ muscles communicates through a lymphatic network with the so-called anterior facial lymphatic trunk. This vessel travels along the surface of these muscles and extends into the snout region. The hyo-opercularis sinus also receives the first branchial trunk, and opens mesad into a very large cephalic canal that runs along the branchial chamber directly above the jugular. The cephalic canal receives a great trunk from below, formed by the union of the second, third and fourth branchial vessels. When the supraclavicle is reached the cephalic canal tapers down into a sort of papilla preparatory to emptying into the cephalic sinus, and at this point it receives from below what is designated as the pericardial trunk. This vessel corresponds only in position to the pericardial sinuses of *Lepisosteus* and other fishes, and in no way is it suggestive of a sinus. In fact no pericardial sinuses were found in the region of the heart.

Strange to say, in *Polyodon* a great mass of lymphoid tissue surrounds the heart, which is supplied by the coronary blood vessels, and from which a lymphatic network arises that evidently reaches the veins through the medium of the œsophagus plexus.

Only in the caudal region of *Polyodon* were dorsal and ventral trunks found. They were present and extremely large in the thoracic region of *Lepisosteus*; while in *Polyodon* all of the subcutaneous vessels of the trunk were very minute.

## EXPLANATION OF THE PLATES

### PLATE I.

Figs. 1 to 17 were drawn to a scale from injected specimens; 18 to 21 are from microscopic preparations of injected material; and 22 to 27 are from sections. In general the arteries are stippled, the veins are cross-barred, and the so-called lymphatic trunks are drawn in outline. A vessel drawn in dotted outline signifies that it passes within or behind a bone, muscle or organ. All outlines for the microscopic drawings were made with a camera lucida and the details were filled in afterward.

FIG. 1. Represents a general lateral dissection of a 70-pound *Polyodon spathula* head as seen from the left side and above. Most of the paddle or spoon, all of the opercle and branchial arches, a part of the shoulder girdle, and the left wall of the brain case were removed so as to best portray the vessels.  $\times \frac{1}{2}$ .









## PLATE II.

FIG. 2. Sketch of the principal trunks of a 25-pound *Polyodon* as seen from the left side.  $\times \frac{3}{4}$ .

Fig. 3. Same view and specimen as above, but seen from the opposite or right side.

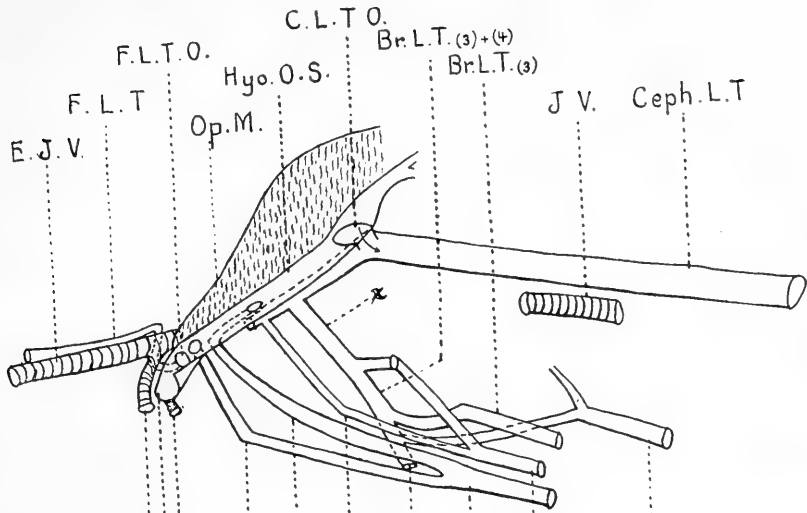


FIG 2.

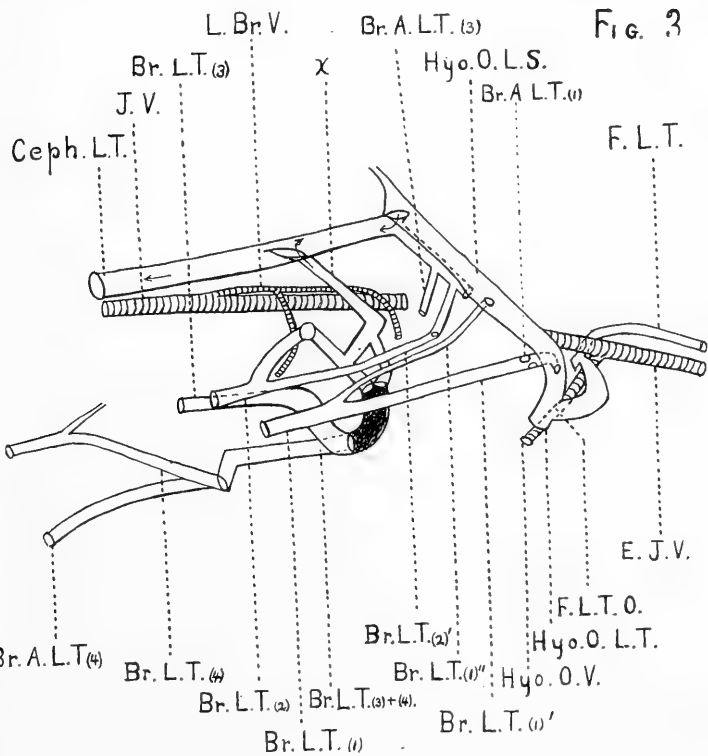
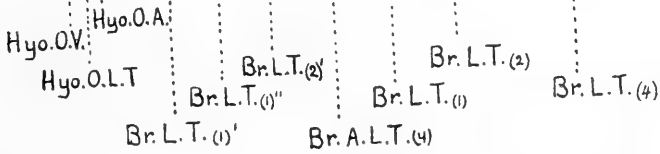


FIG 3





### PLATE III.

FIG. 4. Shows the course of the hyo-opercularis lymphatic trunk and its relations with the corresponding superficial branches of the hyo-opercularis artery and vein, as seen from the right side of a 15-pound *Polyodon*.  $\times \frac{5}{6}$ .

FIG. 5. Ventral view of the termination of the branchial lymphatic trunks (Nutrient branchial veins?) in the inferior jugular. 25-pound *Polyodon*. Natural size.

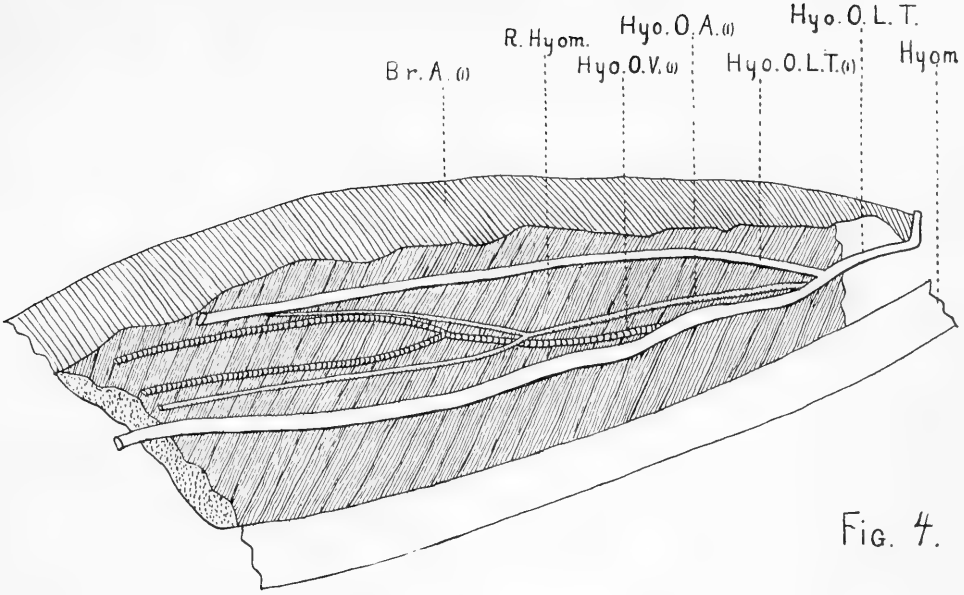


Fig. 5.

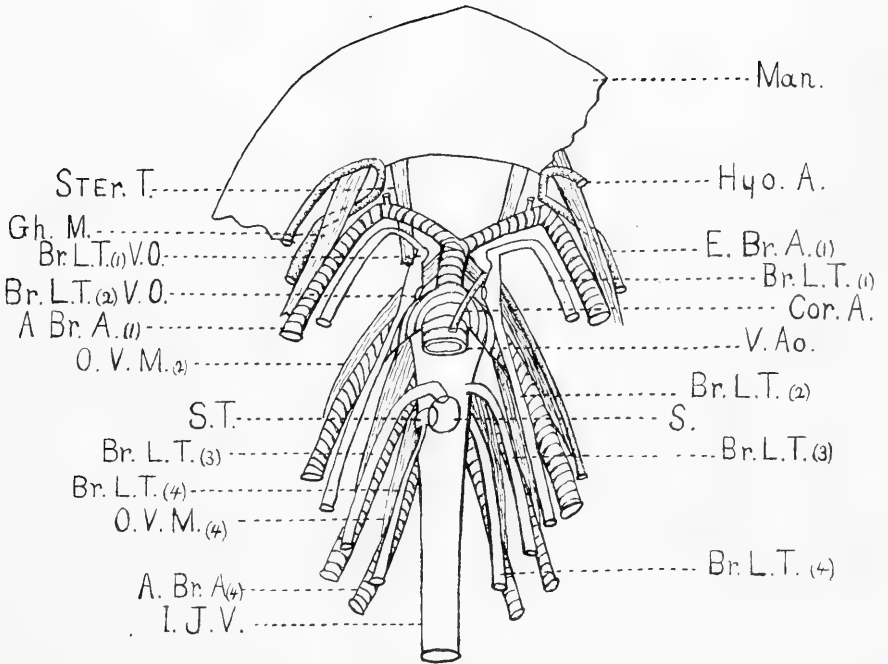








PLATE IV.

FIG. 6. Deeper dissection of the same specimen as above.

FIG. 7. Similar view and dissection as 6 of a 10-pound *Polyodon*. Natural size.

Fig. 6.

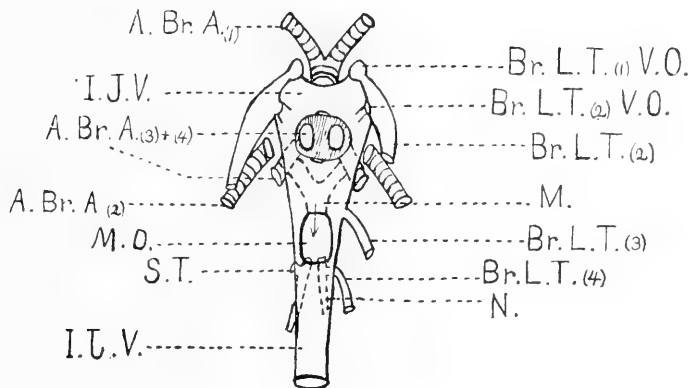
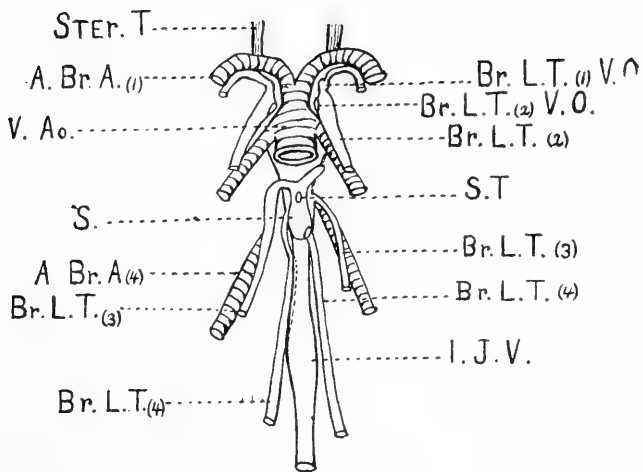


Fig. 7.







## PLATE V.

FIG. 8. Is from a general lateral dissection of a small *Lepisosteus tristachus* as seen from the left side. Most of the opercular and shoulder girdle regions removed.  $\times \frac{4}{5}$ .

FIG. 9. Diagram of the left pericardial sinus and connections from a 10-pound *Lepisosteus osseus*.  $\times \frac{2}{3}$ .

FIG. 10. Same specimen as above, showing opposite or right pericardial sinus.  $\times \frac{2}{3}$ .

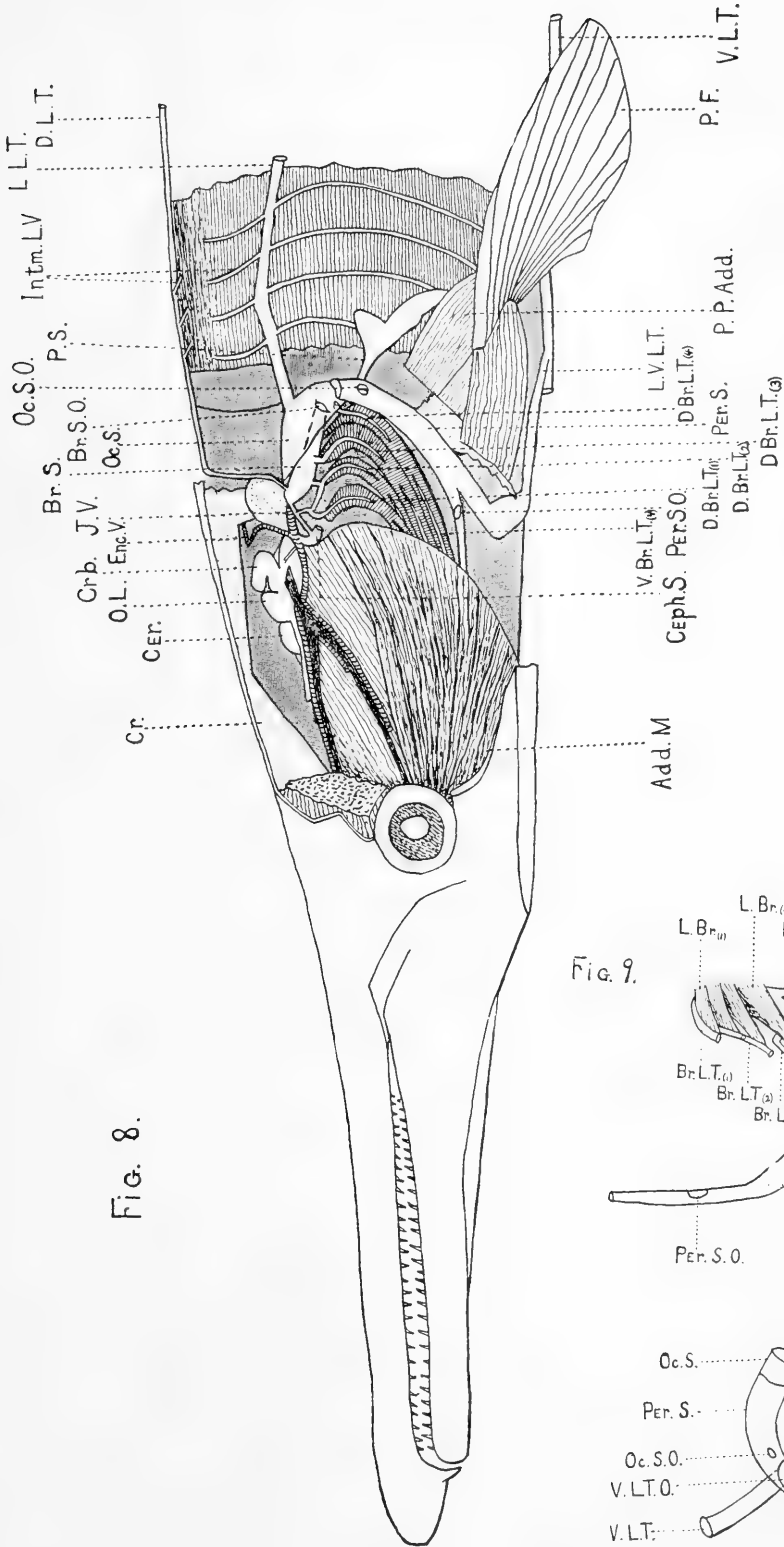


Fig. 8.

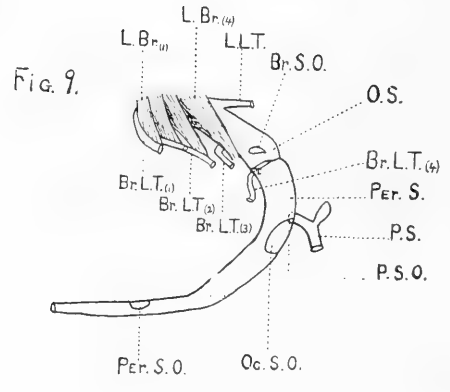


Fig. 9.

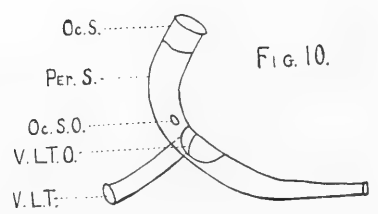


Fig. 10.







## PLATE VI.

FIG. 11. Dorsal view of the same *Lepisosteus tristæchus* as Fig. 8. The dissection on the left side is carried considerably deeper than the right. Shows especially the termination of the cephalic lymphatic trunks in the cephalic sinus, and the communication of the latter with the jugular vein.  $\times \frac{2}{3}$ .

FIG. 12. Similar view to Fig. 11 of a 10-pound *Lepisosteus osseus*. Right side not figured.  $\times \frac{2}{3}$ .

Fig. 11.

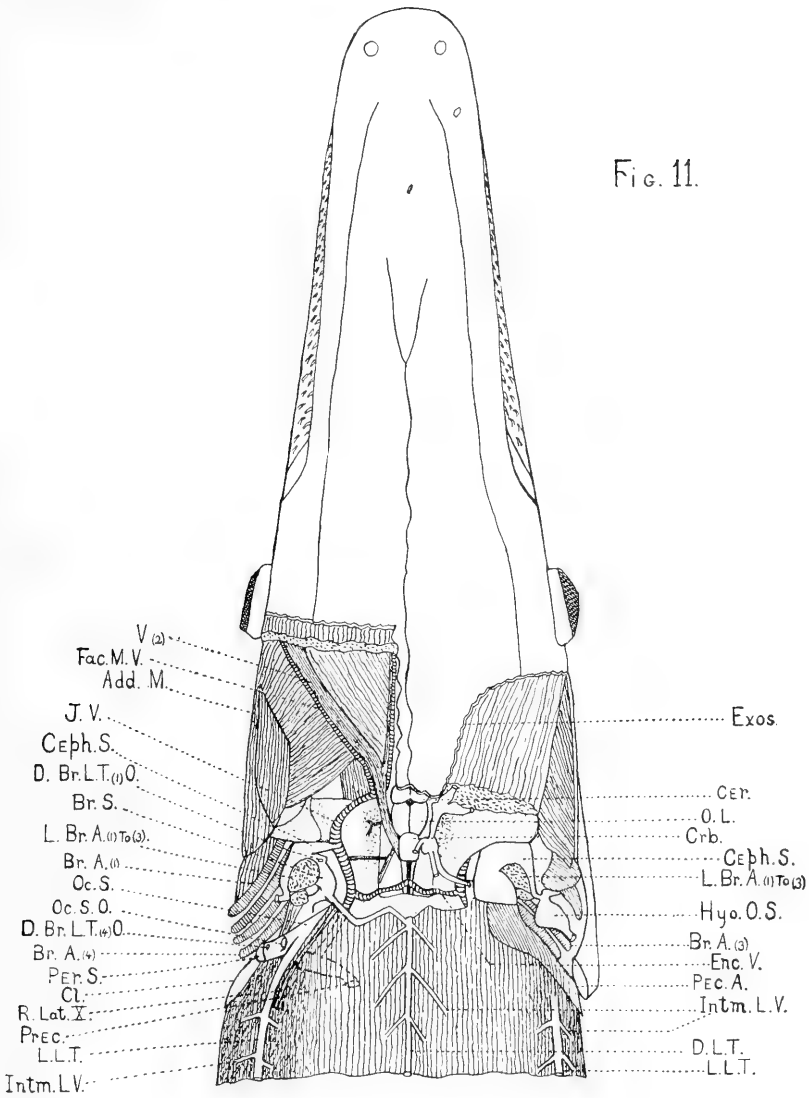
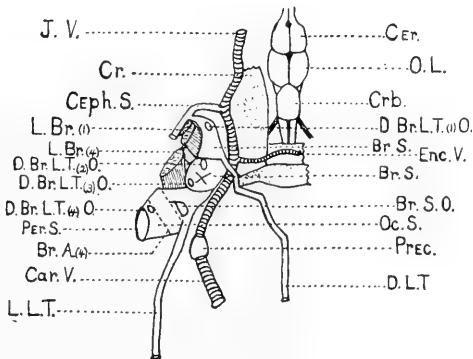


Fig. 12.



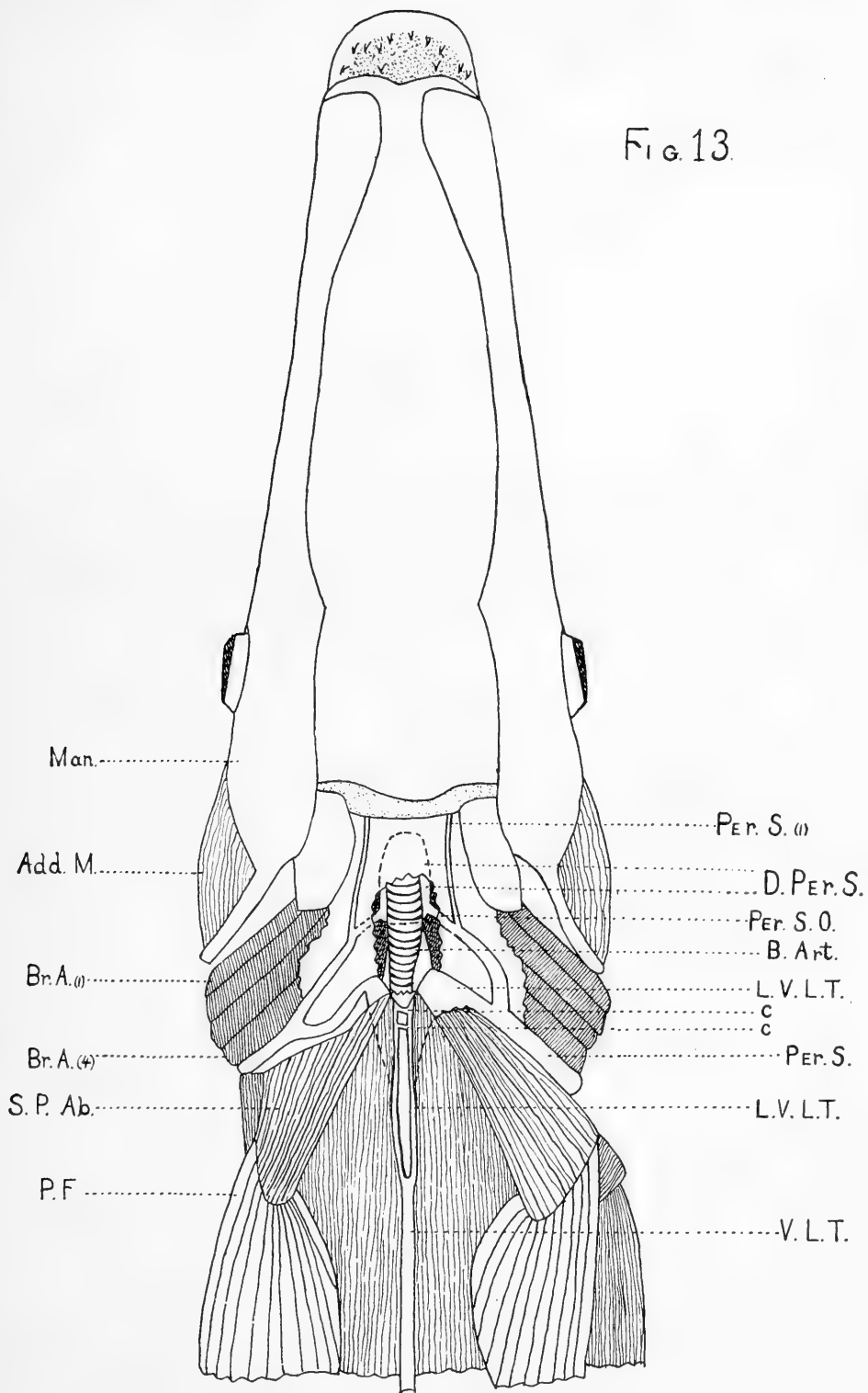




## PLATE VII.

FIG. 13. Ventral view of the same *Lepisosteus tristachus* as Figs. 8 and 11. Shows the termination of the ventral lymphatic trunk in the pericardial sinuses and the union of the latter in a dorsal pericardial sinus, which lies directly above the bulbus arteriosus and communicates with the inferior jugular above.  $\times \frac{3}{4}$ .

FIG. 13.









## PLATE VIII.

FIG. 14. Represents a dissection of a 10-pound *Lepisosteus osseus* in the region of the heart as seen from the ventral side. Ventral walls of the lymphatic sinuses and the right inferior jugular removed to show the union of the ventral lymphatic trunk with the right pericardial sinus, the orifice of the latter which communicates with the dorsal pericardial sinus, and the termination of the two anterior branchial lymphatic trunks (nutrient branchial veins?) in the right fork of the inferior jugular.  $\times \frac{5}{8}$ .

FIG. 15. Is a deeper dissection of the same specimen as 14. Heart, ventral aorta, most of the efferent branchial vessels, and the ventral walls of the lymphatic sinuses and inferior jugular removed to show the points of termination of the branchial lymphatic trunks (nutrient branchial veins?) in the inferior jugular, the pericardial sinuses in the dorsal pericardial sinus, its connections with the inferior jugular above, and finally the discharging of the inferior jugular in the sinus venosus.  $\times \frac{6}{7}$ .

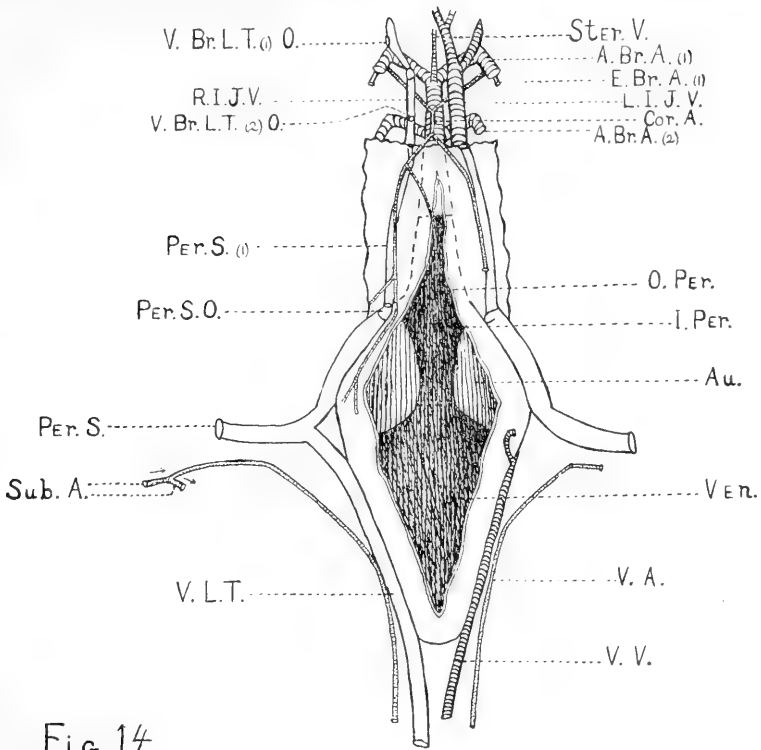


FIG. 14.

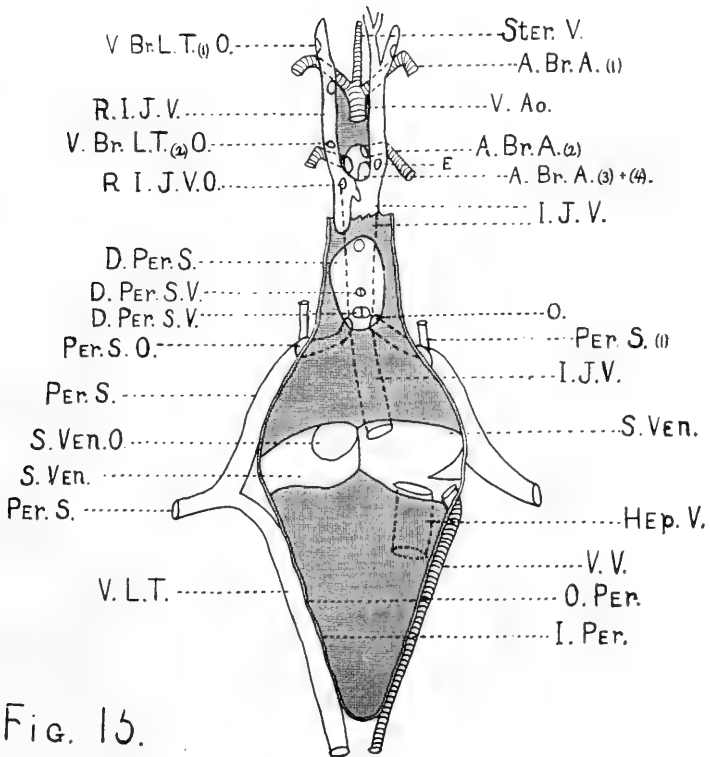


FIG. 15.





## PLATE IX.

FIG. 16. Transverse section through a rather small *Lepisosteus osseus* taken 33 mm. behind the opercle as seen from the rear. Shows the main longitudinal lymphatic trunks in section. Natural size.

FIG. 16a. Transverse through the ventral lymphatic trunk region 20 mm. caudad of Fig. 16 as seen from the rear. Natural size.

FIG. 16b. Transverse section through the ventral lymphatic trunk region 20 mm. cephalad of 16 as seen from the rear. Note the trunk is curving off to the right preparatory to emptying into the right pericardial sinus. Natural size.

FIG. 17. Represents the inner or posterior surface of the first branchial arch of a 70-pound *Polyodon*. Except at the two extremities the gill rakers are cut at their bases so as to best display the branching of the lymphatics (veins?) over the surface of the arch. At one place a few of the inner branchial filaments are removed to show the position of the branchial lymphatic trunk (nutrient branchial vein?) in relation to the afferent and efferent branchial trunks. Preceding this gap the filament lymphatic network (nutrient venous network?) is indicated on the outer surface of several of the filaments.  $\times \frac{1}{2}$ .

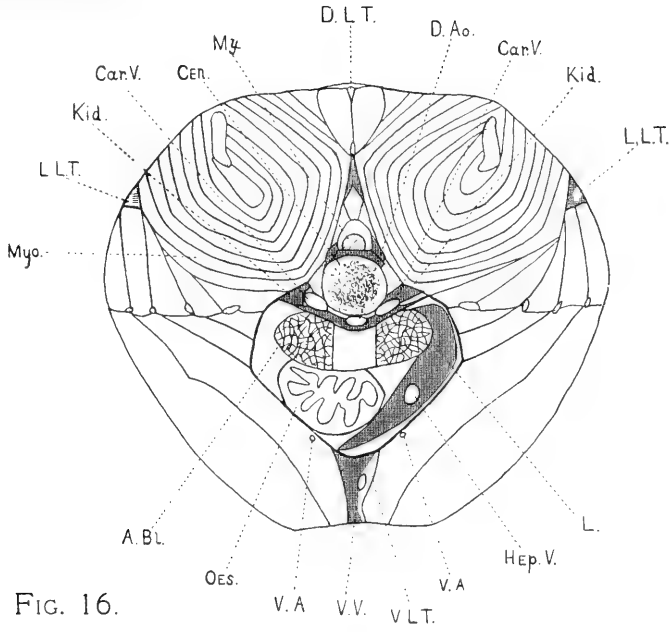


FIG. 16.

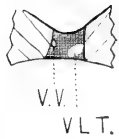


FIG. 16a.

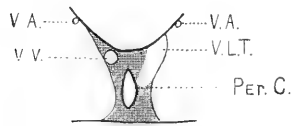


FIG. 16b.

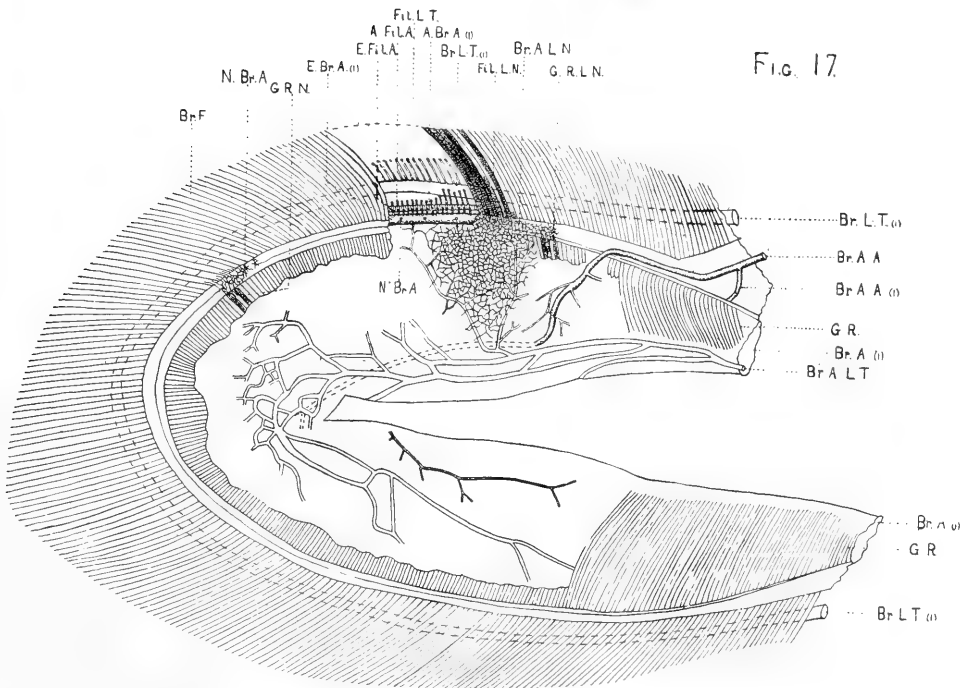


FIG. 17







## PLATE X.

FIG. 18. Microscopic preparation of an injected branchial filament of a 70-pound *Polyodon* as seen from above. The respiratory filament vessels are stippled and the lymphatic network (nutrient filament veins?), which are shown only in part, are drawn in outline.  $\times 50$ . Reduced  $\frac{1}{3}$ .

FIG. 18a. A portion of the filament respiratory network.  $\times 450$ . Reduced  $\frac{1}{3}$ .

FIG. 19. Dorsal view of the lymphatic (nutrient venous?) network of a 70-pound *Polyodon*. This network is superficial to the septa that contains the respiratory network, and for the most part the transverse vessels run parallel to the spaces separating the respiratory septa. Its meshes are more irregular and very much coarser (compare with Fig. 18). A longitudinal filament lymphatic trunk (nutrient filament vein?) receives the network from the two opposite filaments.  $\times 50$ . Reduced  $\frac{2}{3}$ .

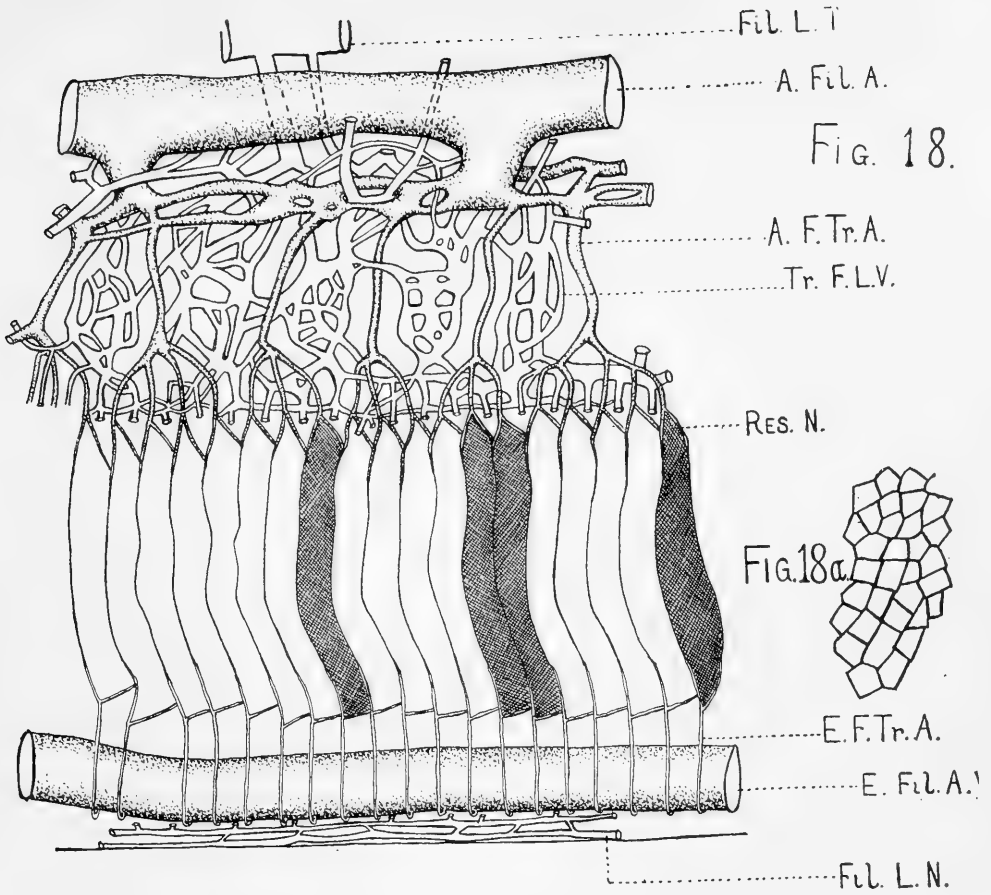


Fig. 18.



Fig. 18a.

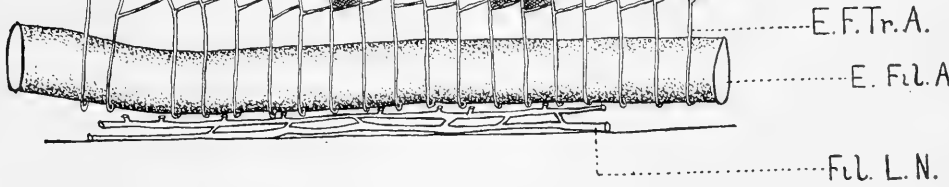
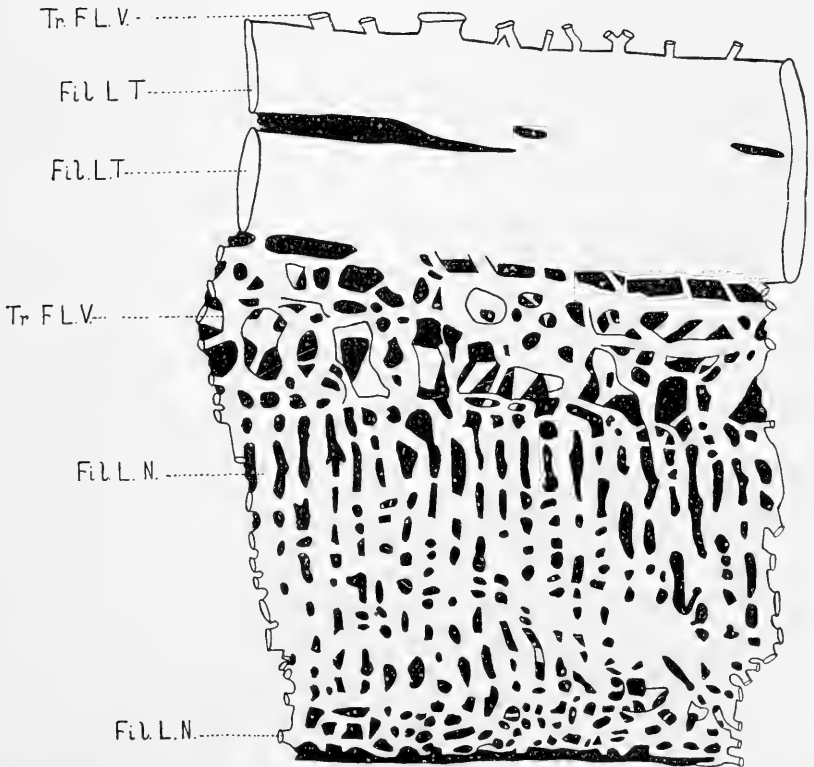


Fig. 19.







## PLATE XI.

FIG. 20. A portion of the outer surface of a branchial arch [of a 70-pound *Polyodon* at the base of two filaments. The main efferent branchial artery, which lies directly below the efferent filament arteries is not figured. The efferent filament and the nutrient arteries are stippled; while the branchial and filament lymphatics (nutrient veins?) are drawn in outline.  $\times 50$ . Reduced  $\frac{1}{2}$ .

FIG. 21. Like Fig. 19, a dorsal view of the same filament taken nearer the basal end of the filament. Introduced to show the character of the so-called lymphatic network on the outer edge of the filament.  $\times 50$ . Reduced  $\frac{1}{3}$ .

Fig. 20.

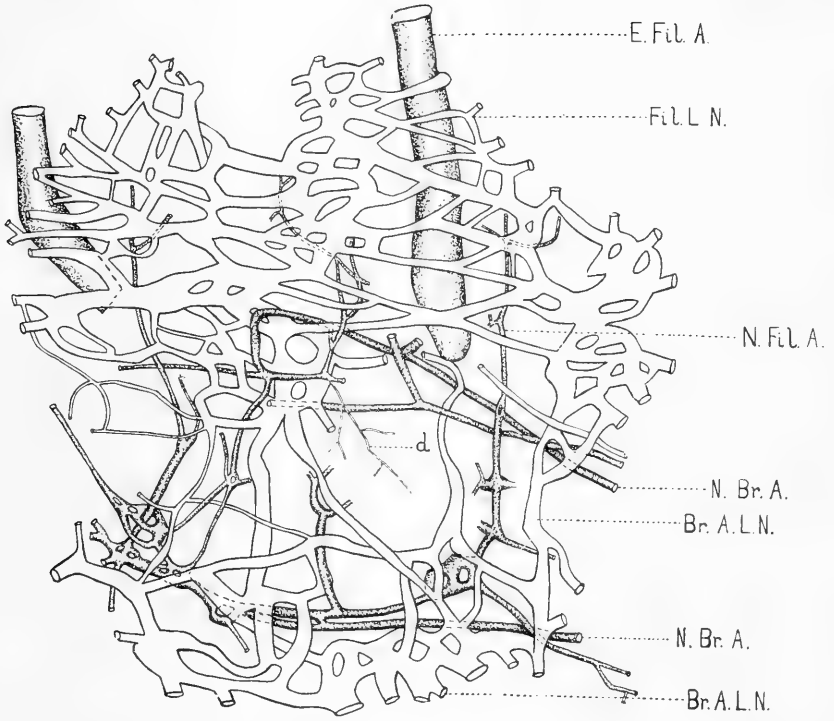
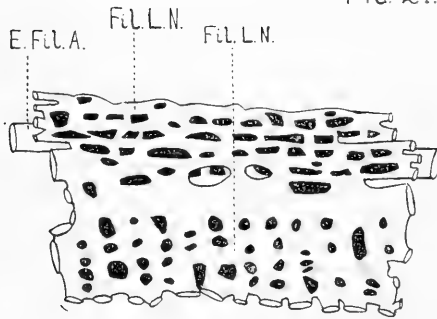


Fig. 21.





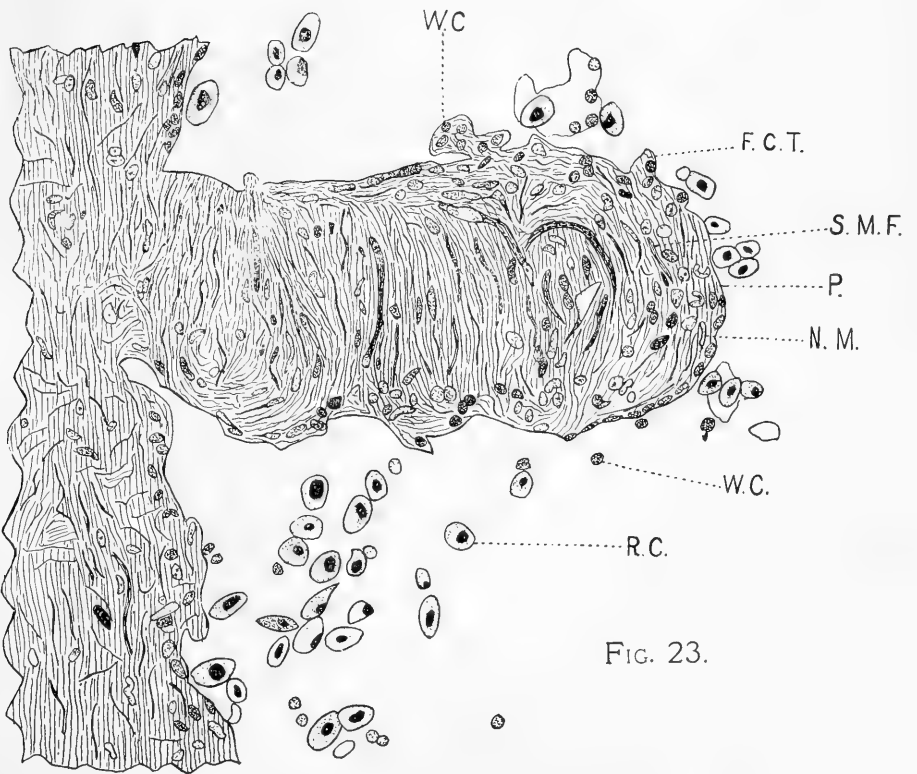
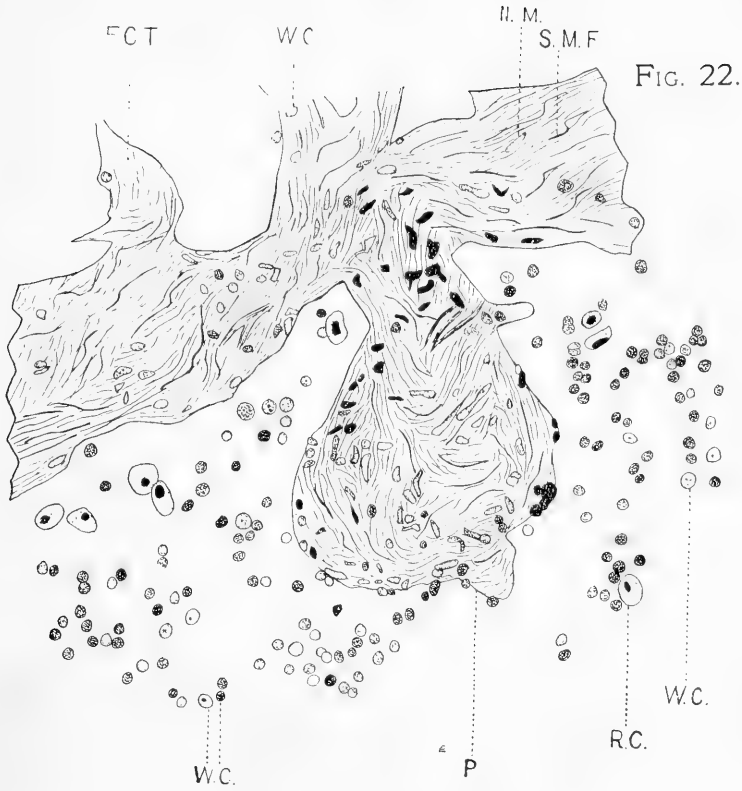




## PLATE XII.

FIG. 22. Portion of a longitudinal section through the so-called cephalic lymphatic trunk of a 15-inch *Polyodon*. Note the papilla and the relative proportion of white corpuscles to red.  $\times 450$ . Reduced  $\frac{3}{8}$ .

FIG. 23. Transverse section through the jugular vein of a 15-inch *Polyodon*. Note papilla here also and that the red corpuscles predominate. Outline surrounding some of the corpuscles denotes plasma boundary.  $\times 450$ . Reduced  $\frac{1}{4}$ .







### PLATE XIII.

FIG. 24. Transverse section through the so-called hyo-opercularis lymphatic trunk of a 15-inch *Polyodon*. The section is taken through a papilla near its surface. In this trunk the white corpuscles, although very scarce, greatly predominate over the red.  $\times 450$ . Reduced  $\frac{2}{7}$ .

FIG. 25. Similar section to 24 through the hyo-opercularis artery.  $\times 450$ . Reduced  $\frac{2}{7}$ .

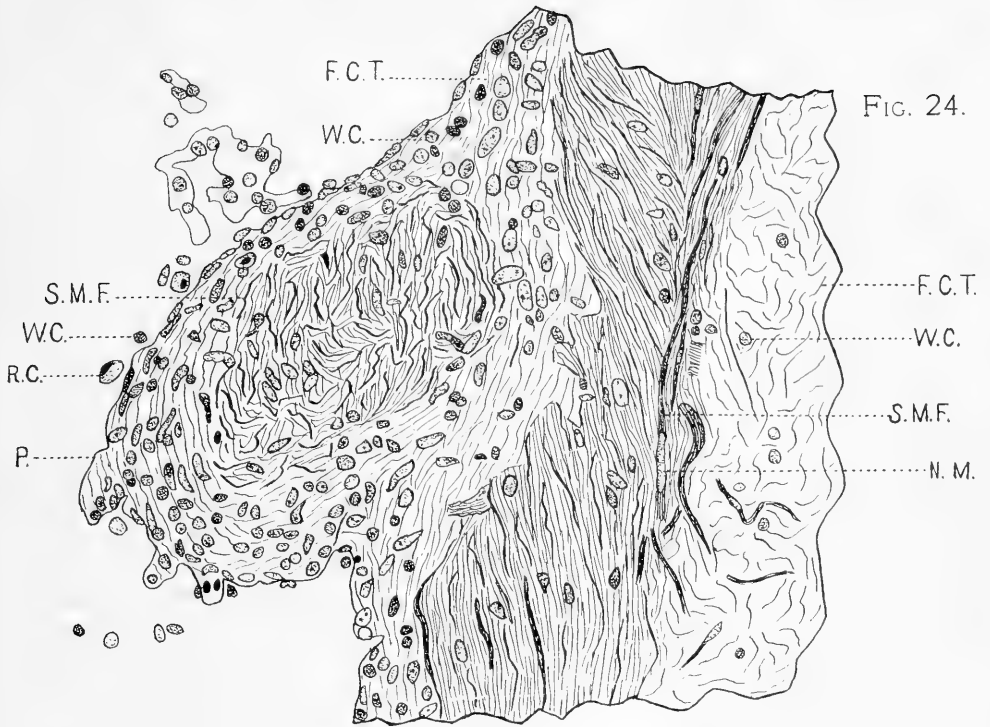


FIG. 24.

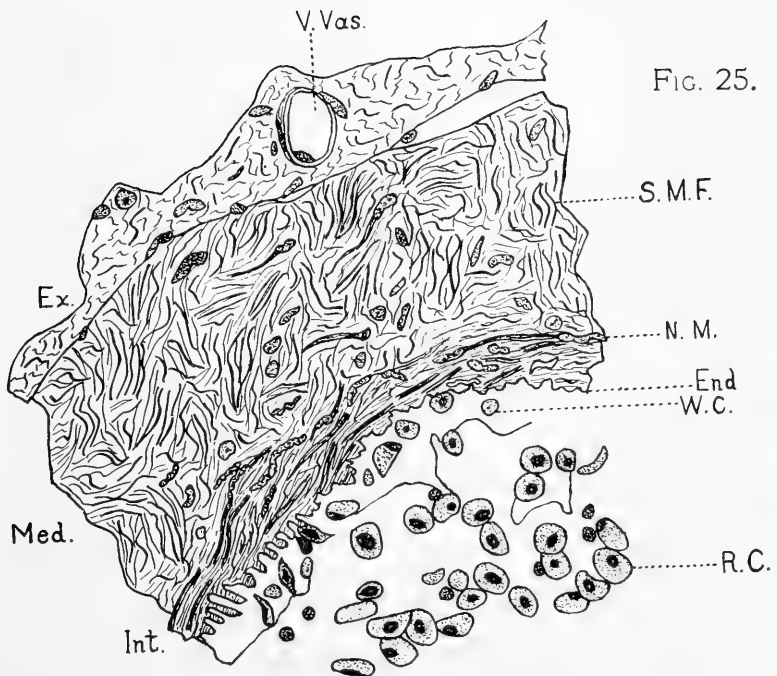
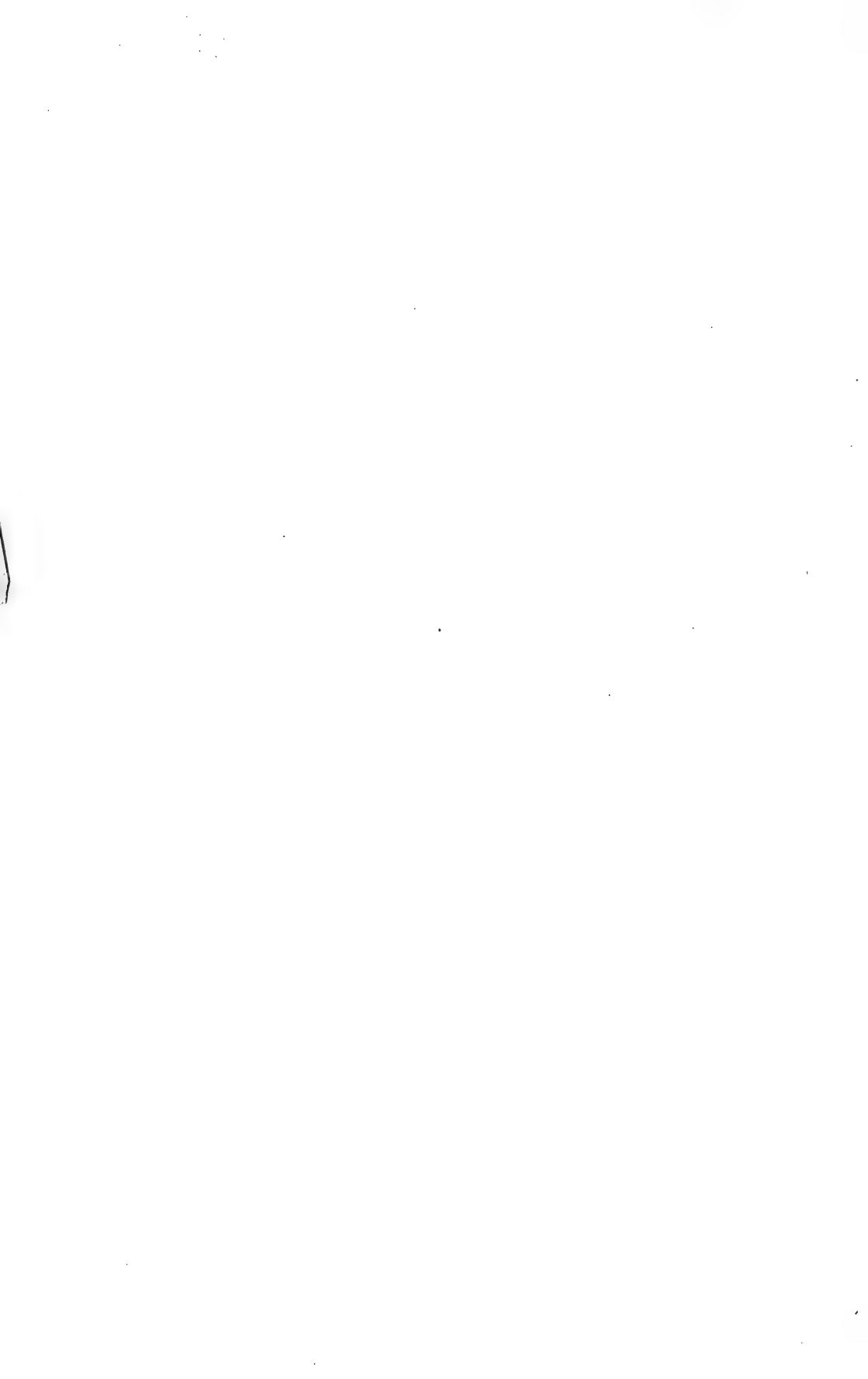


FIG. 25.







## PLATE XIV.

FIG. 26. Similar section to 24 through the hyo-opercularis vein. Structure is very similar to the lymphatic trunk, but the red corpuscles greatly predominate.  $\times 450$ . Reduced  $\frac{1}{3}$ .

FIG. 27. A diagrammatic transverse section through three pairs of branchial filaments of *Polyodon*.

FIG. 26.

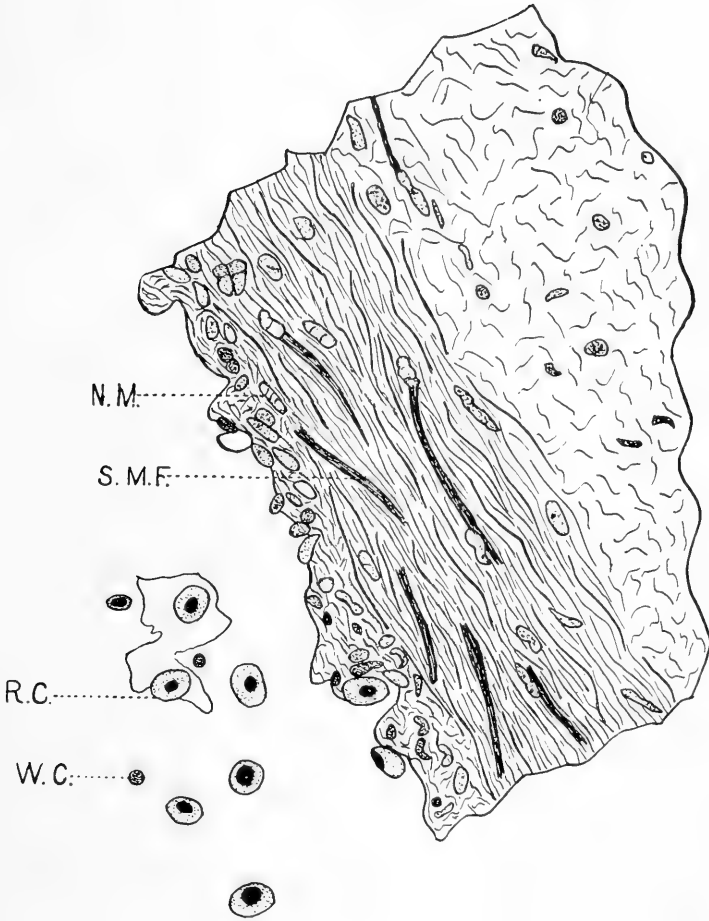
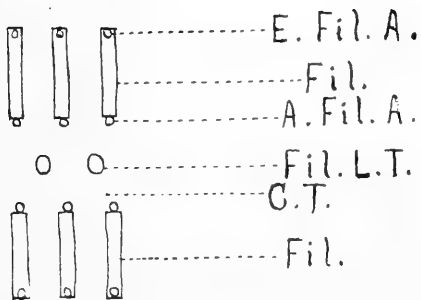


FIG. 27.



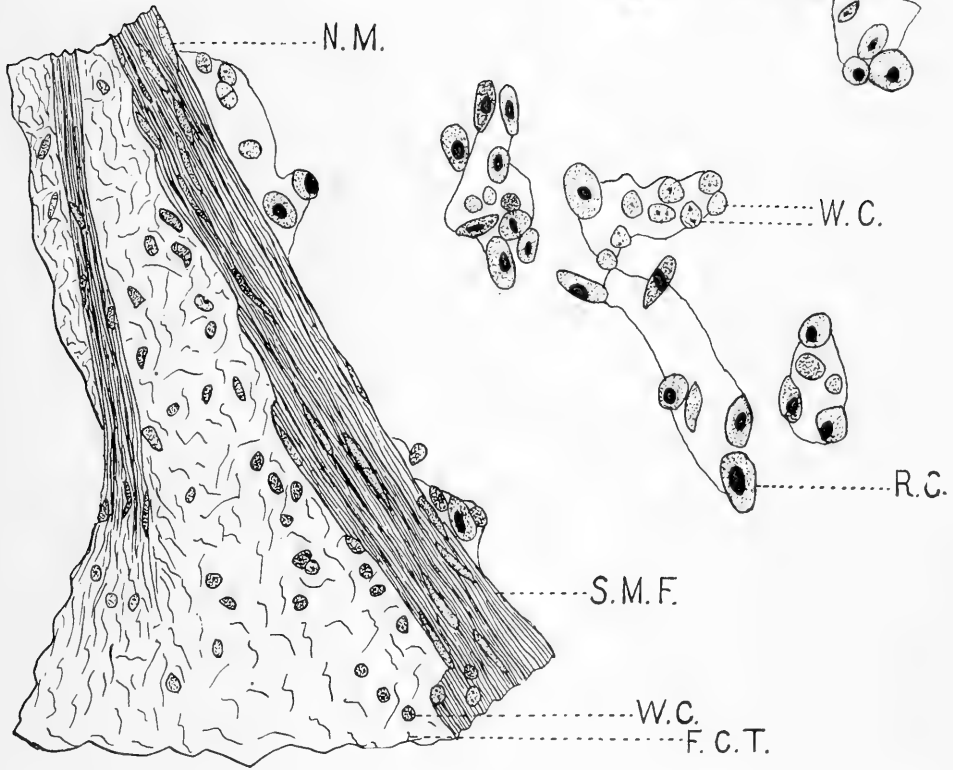




## PLATE XV.

FIG. 28. Is a transverse section through the branchial lymphatic trunk (nutrient branchial vein?) of a 15-inch *Polyodon*. Note the predominance of red corpuscles. In another portion of the section the wall is much thinner.  $\times 450$ . Reduced  $\frac{1}{20}$ .

FIG. 28.







## VI. LIST OF ABBREVIATIONS USED IN THE FIGURES.

- A* or *P* prefixed to an abbreviation signifies anterior or posterior; *R* or *L*, right or left; a series is numbered from cephalad to caudad.
- a.* In Fig. 1 point where injections were made with *Polyodon*.
- A.Bl.* Air-bladder.
- A.Br.A.*(1)-(4). Afferent branchial arteries 1 to 4.
- Add.M.* Adductor mandibulæ muscles.
- A.Fil.A.* Afferent filament arteries.
- A.F.Tr.A.* Afferent filament transverse arteries.
- A.T.* Adipose tissue in brain cavity.
- Au.* Auricle.
- B.Art.* Bulbus arteriosus.
- Br.A.*(1)-(4). Branchial arches 1 to 4.
- Br.A.A.* Branchial arch artery.
- Br.A.A.*(1). Branchial arch artery for outer surface of arch.
- Br.A.L.N.* Branchial arch lymphatic (venous?) network.
- Br.A.L.T.* Branchial arch lymphatic trunk (nutrient branchial vein?).
- Br.F.* Branchial filaments.
- Br.L.T.*(1)-(4). Branchial lymphatic trunks (nutrient branchial veins?)  
1-4.
- Br.L.T.*(3) and (4). Combined trunk formed by the union of the third and fourth branchial lymphatic vessels.
- Br.L.T.*(1'). Ventral fork of the first branchial lymphatic trunk.
- Br.L.T.*(1''). Dorsal fork of the first branchial lymphatic trunk.
- Br.L.T.*(2'). Ventral fork of the second branchial lymphatic trunk.
- Br.L.T.*(1) *O.* Opening of branchial lymphatic trunk (1) into the hyo-opercularis sinus, *Polyodon*.
- Br.L.T.*(1) *V.O.* Opening of the first ventral branchial trunk in the inferior jugular.
- Br.S.* Branchial sinus, *Lepisosteus*.
- Br.S.O.* Branchial sinus opening into the pericardial sinus.
- c.* Communications between the 2 forks of the ventral trunk.
- Car.V.* Cardinal vein.
- Cen.* Centrum.
- Ceph.L.T.* Cephalic lymphatic trunk, *Polyodon*.
- Ceph.S.* Cephalic sinus.
- Cer.* Cerebrum.
- Cl.* Clavicle.
- C.L.T.O.* Cephalic trunk opening into hyo-opercularis sinus in *Polyodon*.
- Cor.A.* Coronary artery.
- Cr.* Cranial wall.
- Cr.b.* Cerebellum.
- C.T.* Connective tissue.
- d.* In Fig. 20 capillary from nutrient branchial artery.
- D.Ao.* Dorsal aorta.

- D.Br.L.T.*(1)-(4). Dorsal branchial lymphatic trunks (nutrient branchial veins?) 1 to 4, *Lepisosteus*.
- D.Br.L.T.*(1)-(4) *O*. Dorsal branchial trunk openings into the branchial and occipital sinuses, *Lepisosteus*.
- D.L.T.* Dorsal lymphatic trunk.
- D.Per.S.* Dorsal pericardial sinus, *Lepisosteus*.
- D.Per.S.V.* Semilunar valves of the dorsal pericardial sinus of *Lepisosteus* opening into the inferior jugular.
- E.Br.A.*(1)-(4). Efferent branchial arteries 1 to 4.
- E.Fil.A.* Efferent filament arteries.
- E.F.Tr.A.* Efferent filament transverse arteries.
- Enc.A.* Encephalic artery.
- Enc.V.* Encephalic vein.
- End.* Endothelium.
- Ex.* Tunica externa (adventitia).
- Exos.* Exoskeleton.
- F.A.* Facialis artery.
- Fac.M.V.* Facialis-mandibularis vein.
- F.C.T.* Fibrous connective tissue.
- Fil.* Filament.
- Fil.L.N.* Filament lymphatic (nutrient venous?) network.
- Fil.L.T.* Filament lymphatic trunk (nutrient filament vein?).
- F.L.T.* Facial lymphatic trunk.
- F.L.T.*(1). Anterior facial lymphatic trunk.
- F.L.T.O.* Facial lymphatic trunk opening into the hyo-opercularis sinus.
- F.V.* Facialis vein.
- Gh.M.* Glossohaly muscle.
- G.R.* Gill rakers.
- G.R.L.N.* Gill raker lymphatic (venous?) network.
- G.R.N.* Gill raker arterial network.
- Hep.V.* Hepatic vein.
- Hyo.A.* Hyoidean artery.
- Hyo.M.* Hyomandibular.
- Hyo.O.A.* Hyo-opercularis artery.
- Hyo.O.A.*(1). Superficial branch of the hyo-opercularis artery.
- Hyo.O.L.T.* Hyo-opercularis lymphatic trunk.
- Hyo.O.L.T.*(1). Dorsal branch of the hyo-opercularis lymphatic trunk.
- Hyo.O.S.* Hyo-opercularis sinus, *Lepisosteus*.
- Hyo.O.V.* Hyo-opercularis vein.
- Hyo.O.V.*(1). Superficial branch of the hyo-opercularis vein.
- I.J.V.* Inferior jugular vein.
- Int.* Tunica intima.
- Intm.L.V.* Intermuscular or transverse lymphatic vessels.
- I.Per.* Visceral or inner layer of the pericardium.
- J.V.* Jugular vein.
- Kid.* Kidney.
- L.* Liver.
- L.Br.*(1)-(4). Branchial levator muscles 1 to 4.
- L.Br.V.* Branchial levator muscle veins.

<i>L.I.J.V.</i>	Left fork of the inferior jugular vein.
<i>L.L.T.</i>	Lateral lymphatic trunk.
<i>L.N.(1).</i>	Lymphatic network on surface of the thymus gland and adjacent region, <i>Polyodon</i> .
<i>L.N.(2).</i>	Lymphatic network overlying the facialis blood vessels, <i>Polyodon</i> .
<i>L.N.(3).</i>	Lymphatic network in hyo-opercularis region of <i>Polyodon</i> .
<i>L.V.L.T.</i>	Left fork of the ventral lymphatic trunk.
<i>M.</i>	Dorsal sinus emptying into the inferior jugular, <i>Polyodon</i> .
<i>Man.</i>	Mandible.
<i>Med.</i>	Tunica media.
<i>M.O.</i>	Orifice of the dorsal sinus opening into the inferior jugular, <i>Polyodon</i> .
<i>My.</i>	Myelon.
<i>Myo.</i>	Myotomes.
<i>N.</i>	Posterior sacs of <i>Polyodon</i> that terminate in the inferior jugular.
<i>N.Br.A.</i>	Nutrient branchial arteries.
<i>N.Fil.A.</i>	Nutrient filament arteries.
<i>N.M.</i>	Nucleus smooth muscle.
<i>N.S.</i>	Nasal sac.
<i>o.</i>	In Fig. 15 orifice of pericardial sinus leading into the dorsal pericardial sinus.
<i>Oc.S.</i>	Occipital sinus, <i>Lepisosteus</i> .
<i>Oc.S.O.</i>	Occipital sinus opening into the pericardial sinus.
<i>Œs.</i>	Œsophagus.
<i>O.L.</i>	Optic lobes.
<i>O.Per.S.</i>	Parietal or outer layer of the pericardium.
<i>Op.M.</i>	M. Opercularis.
<i>O.V.M.(1)-(4).</i>	Obliqui ventrales muscles 1 to 4.
<i>P.</i>	Papilla.
<i>Pec.A.</i>	Pectoral arch.
<i>Per.C.</i>	Pericardial cavity.
<i>Per.L.T.</i>	Pericardial lymphatic trunk, <i>Polyodon</i> .
<i>Per.S.</i>	Pericardial sinus, <i>Lepisosteus</i> .
<i>Per.S.(1).</i>	Anterior continuation of the pericardial sinus.
<i>Per.S.O.</i>	Communications of the pericardial sinuses with the dorsal pericardial sinus.
<i>P.F.</i>	Pectoral fin.
<i>P.P.Add.</i>	Pectoral profundus adductor muscle.
<i>Prec.</i>	Precava.
<i>Prem.</i>	Premaxilla.
<i>P. S.</i>	Pectoral sinus.
<i>P.S.O.</i>	Pectoral sinus emptying into the occipital sinus.
<i>Pt.</i>	Post-temporal.
<i>R.C.</i>	Red corpuscle.
<i>Res.N.</i>	Respiratory network.
<i>R.Hyom.</i>	Retractor hyo-mandibularis muscle.
<i>R.I.J.V.</i>	Right fork of the inferior jugular vein.
<i>R.I.J.V.O.</i>	Right fork of the inferior jugular opening into the inferior jugular.

<i>R.Lat.X.</i>	Ramus lateralis vagi.
<i>S.</i>	A sinus in <i>Polyodon</i> , which lies above the ventral aorta and opens into the inferior jugular above.
<i>S.Cl.</i>	Supra-clavicle.
<i>S.M.F.</i>	Smooth muscle fiber.
<i>S.P.Abd.</i>	Superficial pectoral abductor muscle.
<i>Spir.</i>	Spiracle.
<i>S.T.</i>	Communicating trunk from sinus <i>S</i> to inferior jugular.
<i>Ster.T.</i>	Sterno-hyoideus tendon.
<i>Ster.V.</i>	Sterno-hyoideus vein.
<i>Sub.A.</i>	Subclavian artery.
<i>S.Ven.</i>	Sinus venosus.
<i>S.Ven.O.</i>	Orifice of sinus venosus leading into the auricle.
<i>Tr.F.L.V.</i>	Transverse filament lymphatic vessels (nutrient veins?).
<i>V.</i>	Point where cephalic sinus joins jugular vein.
<i>V.A.</i>	Ventral artery.
<i>V.Ao.</i>	Ventral aorta.
<i>V.Br.L.T.(1)-(4).</i>	Ventral branchial lymphatic trunks (nutrient veins?) 1 to 4, <i>Lepisosteus</i> .
<i>V.Br.L.T.(1)-(4)O.</i>	Ventral branchial trunks opening into the inferior jugular.
<i>Ven.</i>	Ventricle.
<i>V.L.T.</i>	Ventral lymphatic trunk.
<i>V.L.T.O.</i>	Ventral lymphatic trunk opening into the pericardial sinus.
<i>V.V.</i>	Ventral vein.
<i>V. Vas.</i>	Vasa vasorum.
<i>W.C.</i>	White corpuscle or leucocyte.
<i>x.</i>	Combined trunk formed by the union of the third and fourth dorsal branchial trunks with the dorsal fork of the second branchial trunk.
<i>z.</i>	Point of union of the third branchia trunk with the fourth.
<i>I.</i>	Olfactory nerve.
<i>II.</i>	Optic nerve.
<i>V.(2).</i>	Truncus buccalis maxillo-mandibularis.
<i>V and VII.</i>	Trigemino-facial complex.
<i>VIII.</i>	Auditory nerve.
<i>IX.</i>	Glossopharyngeal nerve.
<i>X.</i>	Vagus nerve.



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