

VII.—*Some Peculiarities of the Blood-Vascular System of the Porbeagle Shark*
(*Lamna Cornubica*).

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[PLATES 9 AND 10.]

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Before the middle of last century, owing very largely to the prevalence of injection as a method of research, the coarse anatomy of the blood vascular system drew to itself a considerable measure of attention. Amongst the peculiarities of the system that more than others aroused interest and speculation during this period, were certain meshworks of arteries and veins that formed localised plexuses or retia of fine anastomosing vessels. These retia are found upon vessels supplying many different regions of the body, and occur somewhat haphazard, in genera belonging to practically all the leading groups of Vertebrates. A good summary of their distribution will be found in MILNE EDWARDS' 'Leçons sur la Physiologie,' vol. 3, 1858; it is sufficient here to point out that their structure and composition is far from being similar in all cases (MÜLLER, 17, p. 275); and that, although there is noticeable a tendency to their formation in aquatic air-breathing animals, both birds and mammals, their occurrence depends neither on blood relationship nor on a universal similarity of habit, for they are to be found in creatures of such different mode of life as fish, birds, ungulates, cetacea, edentates and lemurs.

It is a remarkable fact that in spite of the curiosity that these structures originally aroused, little attention appears to have been bestowed upon them for the last fifty or sixty years. This lapse of interest may no doubt be attributed to the predominant importance assumed in more recent times by purely morphological anatomy, although

when looked at from a physiological standpoint, there is no question that these vascular adaptations are of very considerable interest and deserve more study than they have hitherto received.

Among the retiform modifications of the vascular system that have been described, one of the most remarkable is a large paired spongy mass of intermingled meshworks of arteries and veins interposed between the liver and the pericardium of the Porbeagle Shark (*Lamna cornubica*).

This rete was discovered by JOHANNES MÜLLER and described by him in one of the sections of his memoir, "Anatomie der Myxinoiden" (17, p. 271). His description and the diagram by which it is illustrated give a very fair presentation of the outstanding structural facts, but, owing in part to the somewhat mutilated condition of his material, the account is defective and does not show with sufficient fulness the relation of the rete to the organs of circulation as a whole, or give a true picture of the extent to which the rest of the blood-vascular system has been modified by its presence.

In a previous chapter of the same monograph (17, p. 238), MÜLLER draws attention to another peculiarity of the arterial system of *Lamna*, namely, an extraordinary contortion of the carotid arteries within the orbit. This modification, which is shared also by certain other sharks, was further described briefly in a species of *Lamna* by TROIS (24), and again by VIRCHOW (26), but so far as I have been able to ascertain, the above references include all that is known of the highly modified vascular system of this genus.

In view of this comparative lack of information, and in the hope that a fuller study of the modified condition of the vascular system of this shark may re-excite interest in blood retia, and possibly help towards an explanation of their use, I propose to give below a description of the blood-vessels with particular reference to the retia that occur in different parts of the body, and to the modifying influence they evidently have had upon the rest of the vascular system.

Through the kindness of the Director of the Marine Biological Association I have had the opportunity during the past eighteen months of examining four male specimens of *Lamna cornubica*, ranging from three to five feet in length.

In these I have examined the distribution and structure of the arteries and veins both by injection and with the microscope.

In outline what I find is this (fig. 1):—

1. The ground plan of the vascular system resembles in the main that typical of other sharks, but the relative importance of its different parts is profoundly altered.

2. Practically the whole of the blood destined for the alimentary canal and gonads comes, not from the dorsal aorta, but from the ventral ends of the branchial vessels by way of the lateral hypobranchial connectives and the pericardial arteries (fig. 1, *pc.a.*), traversing on its way to the viscera the supra-hepatic retia (fig. 1, *s.hep.r.*) discovered by MÜLLER.

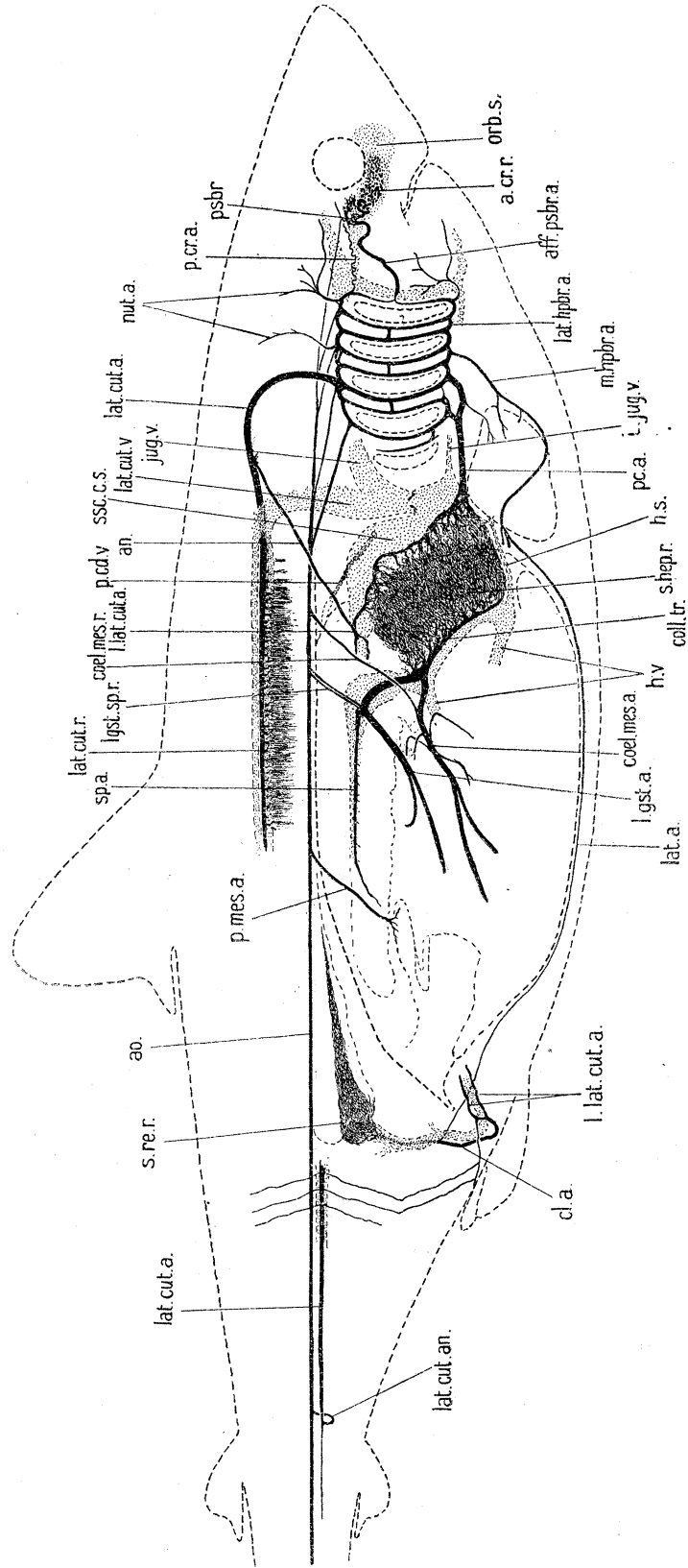


FIG. 1.—Diagram of chief blood vessels of *Lamna cornubica*, from the right side; arteries, black; veins, dotted.

3. The trunk muscles and paired fins receive their chief blood supply from superficial arteries, namely, the lateral cutaneous (fig. 1, *lat.cut.a.*) (an artery derived from one of the dorsal nutritive vessels of the gill pouches), the median hypobranchial and lateral arteries, and a pair of lower lateral cutaneous arteries (fig. 1, *l.lat.cut.a.*). In connection with the lateral cutaneous vessels is a rete of simple construction (fig. 1, *lat.cut.r.*).

4. The cloacal branches of the lower lateral cutaneous arteries and veins (fig. 1, *cl.a.*) form an extensive loose-meshed rete beneath the hinder parts of the kidneys (fig. 1, *s.re.r.*). Through this rete arterial blood is brought to the kidney and venous blood returned to the heart. The posterior cardinals (fig. 1, *p.cd.v.*) are almost entirely absent.

5. In consequence of the altered path of the chief part of the blood supply to the viscera and trunk, the normal source of supply (the aorta and its branches) is much reduced and shows marked signs of atrophy.

6. The carotid arteries, as noted by MÜLLER and VIRCHOW, are enlarged, elaborately coiled, and break up to form dense retia of anastomosing vessels (fig. 2, *a.* and *p.cr.r.*) before giving off normal branches of distribution.

Having thus briefly indicated the chief points to which attention will be drawn, I will now enter more fully into the details of the arrangement and structure of the different vessels, dividing the description for convenience into the following sections:—

1. The dorsal derivatives of the efferent branchial vessels (carotids, epibranchial arteries and aorta, dorsal nutritive arteries of the gill-pouches and the lateral cutaneous artery).
2. The lower lateral cutaneous arteries and sub-renal rete.
3. The ventral derivatives of the efferent branchial vessels (coronary and pericardial arteries).
4. The supra-hepatic retia and visceral arteries.
5. The venous system.

The condition of the blood vascular system in *Mustelus antarcticus*, fully described by PARKER (19), has been taken to represent the normal and is used throughout for purposes of comparison unless otherwise stated. When necessary, the individual fish examined are referred to as A, B, C and D. Of these B was the largest, measuring rather more than five feet in length, D, the smallest, measuring three feet, and the other two, of which in each case I had only the anterior half, intermediate in size.

1. *The dorsal derivatives of the efferent branchial vessels.*

(a) *The carotid arteries* (fig. 2, *a.* and *p.cr.a.*).—Opposite the hyomandibular-hyoid articulation the first efferent branchial becomes much attenuated and is slightly drawn forward across the outer surface of the joint to form a cusp, from the apex of which arises the afferent artery of the pseudobranch (fig. 2, *aff.psbr.a.*).

This artery at its origin is quite small (not more than 1 mm. in diameter in specimen

B), but as it passes forwards to the outer surface of the hyomandibular cartilage, it increases rapidly in size, becoming within a very short distance of its origin at least four times its original diameter (fig. 2, *aff.psbr.a.*); it passes forward towards the spiracular pocket in open sinuous curves and upon the anterior face of the pocket, above the reduced

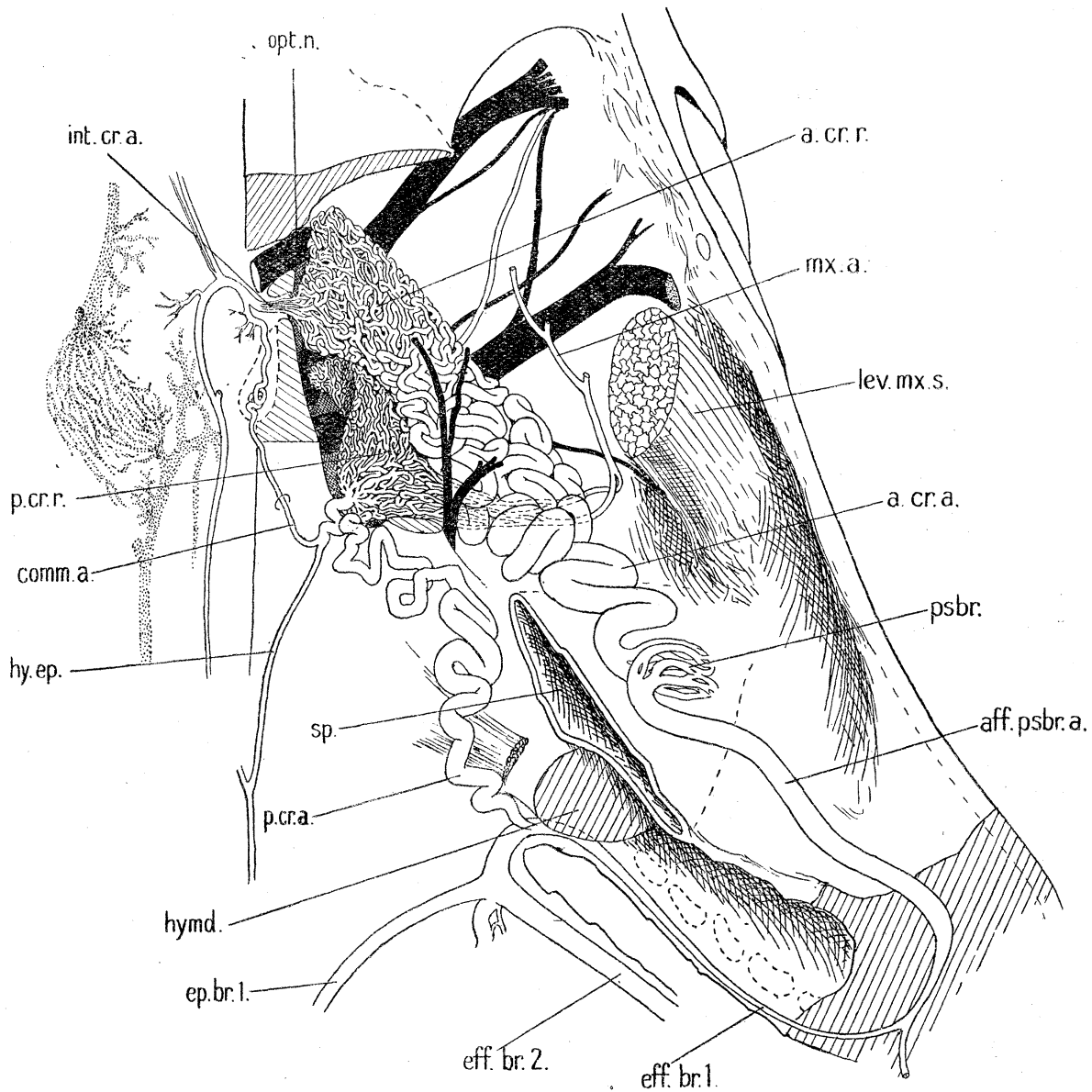


FIG. 2.—Left side of cranium of *Lamna cornubica* dissected from the ventral aspect to show the carotid arteries. On the left the cranial cavity is shown (displaced), as though seen from the mesial plane; nerves black; arteries, white; veins, dotted.

pseudobranch, forms a rete of a few big loops (fig. 2, *psbr.*). These loops, which number five or six, reunite to form the efferent pseudobranch artery or anterior carotid, which continues forward diagonally across the floor of the orbit to the cranial wall in the normal position.

At first this artery (fig. 2, *a.cr.a.*) is, if anything, of larger diameter than the afferent vessel, and is contorted and closely coiled. As it proceeds it becomes gradually smaller and smaller, branching and anastomosing to form a solid cylindrical mass of tangled vessels, about the size and shape of a thumb, extending forward to the cranial wall below and behind the optic foramen.

This rete gives origin to two branches; the arteria ophthalmica magna (a small vessel, for the supply of the eyeball, that arises from the dorsal aspect of the rete by the combination of several drawn-out meshes), and a cerebral branch (internal carotid) represented by a bundle of minute vessels given off from the apex of the rete and penetrating the cranial wall close behind the optic foramen. Within the cranium these vessels lie embedded in the dura mater, and shortly unite with the commissural branch of the posterior carotid (fig. 2, *comm.a.*) to form cerebral arteries of the normal type.

The posterior carotid artery (fig. 2, *p.cr.a.*) arises as usual from the upper loop of the first efferent branchial vessel. Like the afferent pseudobranch artery, it is at its origin small, but rapidly increases considerably in size. It passes forwards in close sinuous coils across the ventral surface of the cranio-hyomandibular articulation to a fenestra of moderate size in the cartilaginous floor of the orbit, and here divides into two. Of these two divisions, the inner again subdivides to form hyoidean epibranchial and cranial commissural branches. The latter, after penetrating the cranial wall, and before uniting in the usual way with the cranial branch of the anterior carotid, forms within a cavity in the dura matter underlying the pituitary a small knot of convolutions.

The outer division, which constitutes the main trunk of the posterior carotid (= external carotid (ALLIS), orbital artery (CARAZZI)), enters the orbit and immediately breaks up into a plexus of innumerable fine vessels (fig. 2, *p.cr.r.*) forming a close-meshed rete wedged in between the rete of the anterior carotid and the cranial wall, and extending forward to the roots of the ocular muscles. The meshes of this rete, near its posterior end, are drawn out laterally dorsal to the anterior carotid and coalesce to form the maxillary artery (fig. 2, *mx.a.*); from its anterior parts are given off by a similar method of origin small vessels to the rostrum and ocular muscles.

These two remarkable carotid retia lie in an ample space (fig. 3, p. 215), bounded externally by the palato-quadrata cartilage, on its mesial and ventral sides by the basal plate and lateral walls of the cranium, and dorsally by the ocular muscles.

Around the arteries and attaching their coils and meshes together, is a web of delicate areolar tissue (Plate 9, fig. 1) that opens out towards the anterior extremity of the retia into wide trabeculated spaces, which form below and in front of the ocular complex a capacious cistern occupied by venous blood. This cavity, which represents the orbital sinus, is connected with the jugular vein by a system of irregular channels, that for the most part accompany the posterior carotid and pass with it through the sub-orbital fenestra in the basal plate of the skull and across the cranio-hyomandibular articulation.

The space between the palato-quadrata and the skull, within which the post-ocular

portion of the venous plexus lies, is filled in around the plexus by a mass of soft gelatinous connective tissue (Plate 9, fig. 1, *g.t.*).

The walls of the carotid vessels and of the retia in connection with them are thick and extremely elastic. They consist mainly of fibrous tissue (the adventitia), the muscular "media" being relatively quite thin.

In the vessels that compose the retia (Plate 9, fig. 2) the elastica interna is more clearly defined than in the main carotid trunks, and forms, particularly in the rete

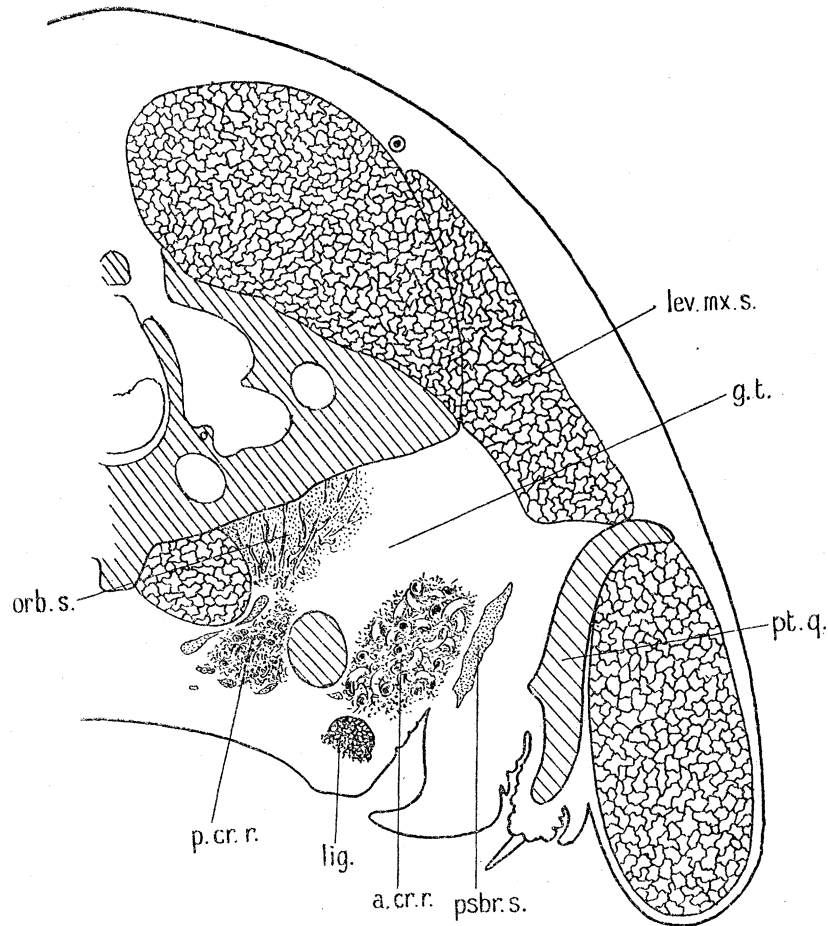


FIG. 3.—Transverse section through the right half of the head of *Lamna cornubica*, showing the position of the retes upon the anterior and external carotid arteries. The section is taken behind the eye, just posterior to the connection between the venous spaces around the retes and the orbital sinus.

on the posterior carotid, a strong elastic lining to the vessels immediately external to the endothelium. The media contains scarcely any elastic tissue; it is a thin even layer of pure muscle, except in the main trunk of the anterior carotid, where it shows a strong admixture of fibrous tissue and varies in thickness in different parts of the circumference of the vessel forming irregular projections into the lumen. Similar but more pronounced projections were observed in the carotids of *Alopias*, but in this case the thickenings appeared to be formed by a local increase of the intima and to

contain a considerable proportion of longitudinal muscle fibres. Whether these projections have a physiological significance or are indications of some general modification of the vessel wall, perhaps of a pathological nature similar to the endarteritis nodosa (THOMA, 22) that commonly occurs in vessels abnormally contorted, and through which there has been a prolonged slowing of the blood-stream, I cannot say ; but it is interesting to note that in certain Teleostean Fishes somewhat similar prominences, possibly of a valvular nature, have been described in many of the arteries (LAGUESSE, 14). Similar local thickenings of the intima, which act probably as regulators of the blood supply, have been described by KRIS (12A) in the arteries of the human penis, and like swellings are stated by KÖLLIKER (Handbuch der Gewebelehre Aufl. 6, Bd. 3, 1902, p. 652) to occur normally in various contorted vessels, such as those of the bulbus urethræ, of the ovaries, and of the placenta.

The fibrous adventitia is very thick and is permeated throughout by an elaborate and strong network of elastic tissue, in which the larger fibres run for the most part parallel to the length of the vessel.

This elastic network spreads from the adventitia into the trabeculæ of connective tissue that bind the coils and meshes of the rete together, and is present also, though of a more delicate character, throughout the soft gelatinous tissue within which the retia are embedded.

The earliest mention that I can find of this curious contortion and enlargement of the carotid arteries in *Lamna* occurs in a paper by ESCHRICHT & MÜLLER in 1835 (9, p. 22). They noted that the floor of the orbit was occupied by a tissue of convoluted tubes, but owing to the mutilated condition of their material, were unable to trace the connection of these "tubes" with the rest of the circulatory system.

Later, MÜLLER, in the chapter of his memoir on the Anatomy of the Myxinoids dealing with the pseudobranch of fishes, goes more fully into the matter, and states (17, p. 238) that in several allied sharks (*Carcharias*, *Lamna*, *Alopias*, and *Zygæna*) in which the spiracle is closed or opens to the surface by only a minute orifice, and the pseudobranch is much reduced and is associated with a rete composed of a few large open loops offering a comparatively uninterrupted passage between the afferent pseudobranch artery and the anterior carotid, the anterior carotid is contorted, forming a rete of many convolutions within the orbit.

Later, TROIS published two short papers on the carotids of *Oxyrhina (Lamna) spallanzanii* (24) and *Alopias vulpes* (23), but his material was too fragmentary to allow him to give anything like a complete description.

In 1890 VIRCHOW (26) contributed further to the subject, laying stress upon the replacement of the capillary circulation in the gill-like pseudobranch of the Notidanidæ by a system of open continuous loops in the reduced pseudobranch of other sharks, by which a freer passage is set up between the afferent pseudobranch artery and the anterior carotid.

He also draws attention to the contortion of both the anterior and posterior carotids

in *Carcharias* and *Lamna*, and records for the first time a fact of probably some considerable importance, namely, the marked increase both in the width of the convoluted vessels and in the thickness of their walls. This, as I have described above, was very noticeable in both the anterior and posterior carotids of *Lamna*, and appears to vary in degree in other sharks according to the amount of contortion of the vessels.

VIRCHOW also makes the statement that convolution is restricted not to particular vessels, but to all the vessels within a certain area, becoming less marked as the limits of this area are approached. This to some extent is true. Convolution is strongest and most pronounced upon vessels within the space between the cranium, palato-quadrate and eyeball, but does not affect all vessels within this area, being confined, except rarely (*cf. Alopias*), to the main trunks of the vessels without involving the branches of distribution.

I have myself been able to examine some of the species in which contortion of the carotid arteries has been recorded, and find that a series of steps can be traced in the progress of the modification, connecting the normal type, in which the arteries pass directly to their various distributions, with the elaborate plexus-formation in *Lamna*, the species which, so far as I have observed, shows this remarkable condition of the arteries to a far more pronounced degree than any other.

Carotid arteries of the normal type were found in various common species of sharks (*Scyllium*, *Acanthias*, *Mustelus*, *Galeus*), but in a large example of *Galeus*, measuring five feet in length, a condition was found that suggests a first step in the process of elongation and convolution.

In this particular fish (fig. 4, p. 218) the artery most affected was the anterior carotid—the artery, it should be noted, that undergoes the greatest modification in *Lamna* and the other species in which convolution of the carotids is most marked.

The afferent pseudobranch artery passed to the anterior face of the spiracle without loops or sinuous curves. Above the reduced pseudobranch it formed a plexus of about 10 simple loops which reunited in the usual way to form the anterior carotid. From the pseudobranch the carotid crossed the floor of the orbit to a foramen in the cranial wall behind the exit of the optic nerve in an irregular series of sinuous curves, giving off from the most anterior of these loops the A. ophthalmica magna to the eyeball. This branch was straight, except for the bends necessary to enable it to pass round intervening structures. The main trunk of the carotid, after a further loop, entered the skull.

The posterior carotid differed from the normal only in a slight suggestion of contortion here and there, particularly upon its cranial branch, and showed no increase in size after its origin from the first efferent branchial.

Without an examination of a series of specimens of different ages, it cannot be determined whether the condition shown by this particular fish is an individual variation or an accompaniment of age and increase in size, but in any case it serves to indicate what probably was the first stage in the elongation and contortion of the carotid arteries.

A condition very similar to that just described, but slightly more pronounced, is characteristic of the Hammerhead (*Zygæna*).

MÜLLER (17, p. 238), as stated above, mentions this shark as one of those in which

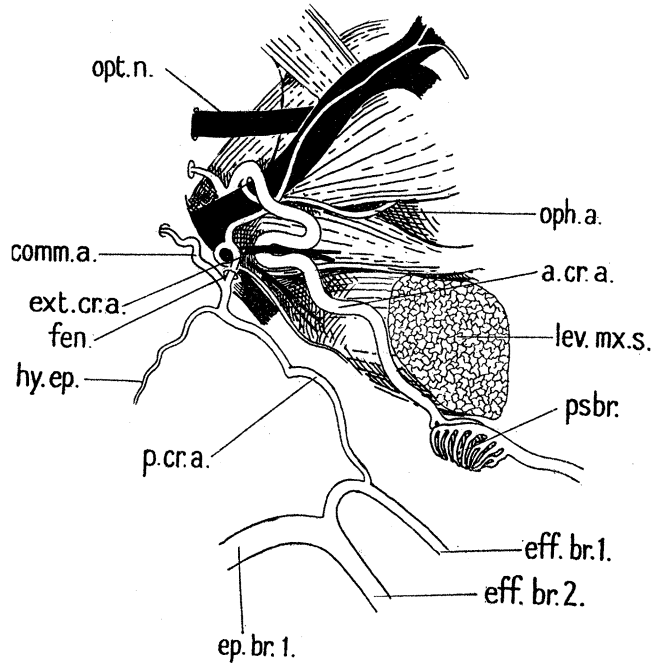


FIG. 4.—The floor of the orbit of *Galeus vulgaris*, seen from below, showing the carotid arteries of the left side.

the carotid arteries showed contortion, and a figure of the arteries in question is given by HYRTL (12, Tf. III, fig. 3) who also states that both the “common carotid” (= posterior carotid) and “ramus anastomoticus” (= anterior carotid) form definite tangles, which in the former case involve the main stem and the cranial and orbital branches.

In a small specimen (head breadth 140 mm.) which I was able to examine,* the arteries were very similar to those described by HYRTL, though the contortion of the vessels was somewhat less pronounced (fig. 5, p. 219). The chief looping occurred upon the main trunk and cranial branch of the anterior carotid and upon the cranial branch of the posterior carotid. It should be noticed in comparison with the specimen of *Galeus* just described, that looping or sinuosity affected also to some extent the afferent pseudobranch artery and the extra-orbital part of the trunk of the posterior carotid. No increase in size could be noticed in the arteries after their origin from the first efferent branchial.

So far as I was able to observe in so small a specimen, the posterior carotid gave off no hyoid epibranchial branch. The main trunk of the vessel passed, as in HYRTL'S

* “Mus. R. Coll. Surgeons,” ‘Physiol. Series,’ No. 940-001.

figure, into the orbit before dividing, and then separated into cranial and external carotid branches only.

A curious condition, evidently of somewhat the same character as that shown in

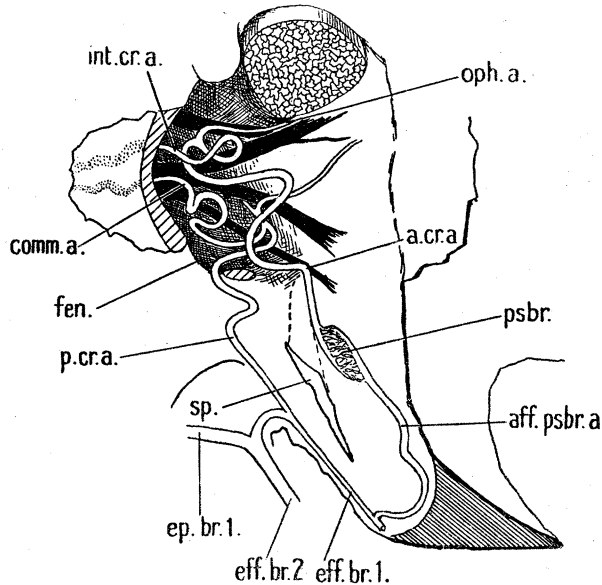


FIG. 5.—The floor of the left orbit of *Zygæna*, seen from below, showing the carotid arteries.

Zygæna, is presented by the carotid circulation in the Basking Shark (*Selache maxima*). The arteries have been described by CARAZZI (6, p. 93), and from his description appear to combine sinuosity of the anterior carotid, such as that present in *Zygæna*, with the formation of close convoluted tangles upon some of the carotid branches similar to those to be seen in *Alopecias* (see below).

CARAZZI'S description may be summarised as follows:—

The afferent pseudobranch artery is not appreciably enlarged after its origin from the first efferent branchial. Upon the spiracular pouch it forms a relatively complex network composed of some ten loops and their subdivisions. The anterior carotid given off from this pseudobranch rete is remarkable for the thickness of its walls and is looped backwards and forwards in a series of short zigzags as it passes across the floor of the orbit. Upon approaching the cranial wall it lessens very considerably in diameter, and enters the cranium in the usual way to supply the brain; but before doing so it gives off a slender branch (1.5 mm. in diameter and 200 mm. in length) which is tightly coiled up to form a spherical tangle about 15 mm. in diameter. This vessel ends blindly; its origin naturally led CARAZZI to expect it to be the A. ophthalmica magna, but he satisfied himself that it was not, and that it did in reality end blindly, forming an offshoot or kind of coiled reservoir attached to the stem of the anterior carotid, and thus, it would seem, presenting a structure of a kind hitherto unknown in the vascular system.

The posterior carotid shows little modification from the normal, except for the

development upon its orbital branch of a small convoluted tangle, and for the fact that it, and not the anterior carotid, gives origin to the *A. ophthalmica magna*.

A further stage in the elaboration of the carotid circulation is presented by the Blue Shark (*Carcharias glaucus*).

As previously mentioned, MÜLLER and VIRCHOW (17, 26) briefly notice the condition of the carotids in this species and point out that the anterior carotid is greatly increased in length and coiled together within the orbit.

From the dissection of two specimens of this fish (one a fragment, the other an individual five feet in length) I am able to confirm the above statement and add further details (fig. 6).

The first efferent branchial, at the point opposite the hyomandibulo-hyoid articulation at which it gives origin to the afferent pseudobranch artery, becomes relatively very small, as it did in *Lamna*, measuring when flattened 1.5 mm. in diameter. The afferent pseudobranch artery at its origin is of about the same size, but rapidly increases to a width of 3.5 mm. as it passes forward to the outer surface of the lower end of the hyomandibular cartilage. Between its origin and the pseudobranch it makes a single, marked, sinuous loop in front of the hyomandibulo-hyoid joint, but otherwise is comparatively straight. The pseudobranch plexus consists of from 8-10 loops.

The anterior carotid, formed by the reunion of the loops of this plexus, passes without convolution into the orbit, but once within the orbit is thrown into a tangle of contorted coils, that lie within a trabeculated venous space above the basal plate of the cranium and extend forward to a point slightly in advance of the optic nerve.

The anterior loop of the coil is reflected back, and after giving off, from its dorsal aspect, the *Arteria ophthalmica magna* (fig. 6, *oph.a.*), enters the cranial wall a short distance behind the optic foramen.

Throughout the extent of the coil the artery continues of large diameter, but lessens in size as it passes through the cranial wall. The ophthalmic branch is relatively small and passes to the eyeball without convolution.

The posterior carotid (fig. 6, *p.cr.a.*) shows some slight and gradual increase in size after its origin from the dorsal bend of the first efferent branchial, but the increase is in no way to be compared with that of the afferent pseudobranch artery. Its main trunk, and to a less degree the three branches into which it divides, are contorted by a series of short zigzag loops; a certain amount of sinuosity may also be observed in the basal parts of the branches given off from the external carotid (fig. 6, *ext.cr.a.*). The modification of the artery as a whole is, however, much less than that of the anterior carotid.

In the Fox Shark (*Alopias vulpes*), one of the *Lamnidae*, the carotid system approaches the extreme degree of elaboration observed in *Lamna*, but is without the formation, as in that genus, of true plexuses by the branching and anastomosis of its several components. In fact, the arrangement of the vessels is similar to that just described in *Carcharias*, but far more complicated.

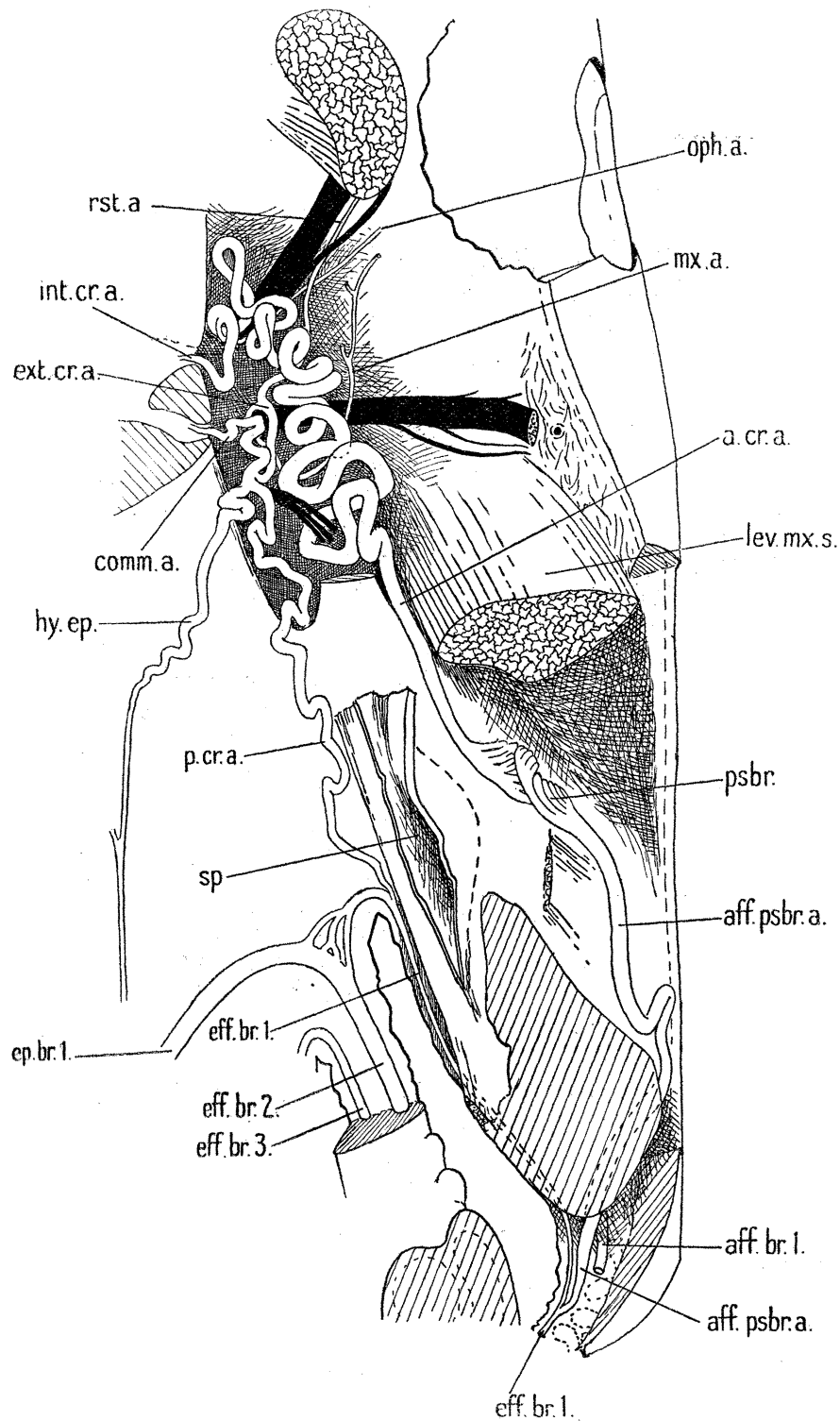


FIG. 6.—Dissection of carotid arteries of left side of *Carcharias glaucus*, seen from below.

The material at my disposal* was somewhat mutilated and did not include the root of the afferent pseudobranch artery, so that it cannot be stated with certainty whether this vessel increased in size after its origin or not. The cut end, which could not have been far removed from the point of origin, was of large diameter (fig. 7, *aff.psbr.a.*), as in *Carcharias* or *Lamna*, but, on the other hand, the first efferent branchial

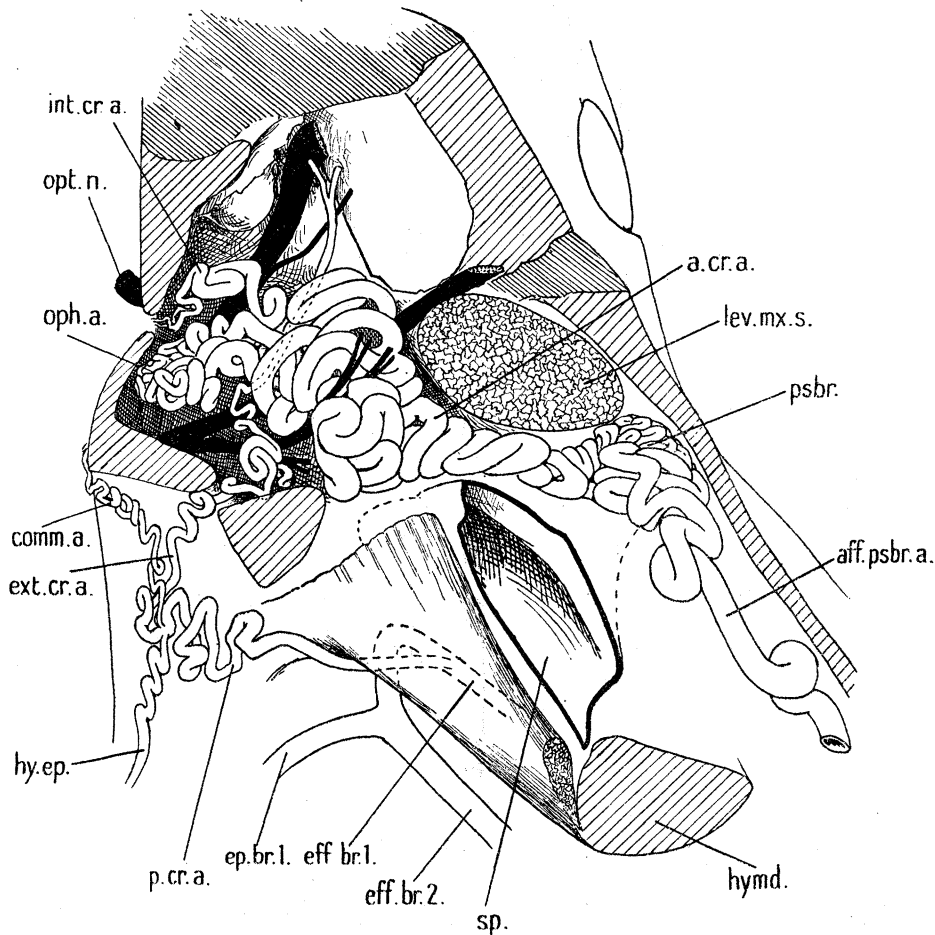


FIG. 7.—Dissection of carotid arteries of left side of *Alopias vulpes*, from below.

was far larger than the same vessel in those species, so that it is probable that the origin of the afferent pseudobranch artery was also large, and that there was no great increase in the size of the vessel after it had left the first efferent branchial.

From its origin opposite the hyomandibulo-hyoid articulation the artery passes to the anterior surface of the spiracular pouch in a few tight coils. Upon the pouch it divides: in the first instance into a couple of branches, which then sub-divide into a number of smaller vessels which are coiled and matted together, forming a large bun-shaped tangle (fig. 7, *psbr.*). When disentangled, this mass of contorted vessels was found to consist of twelve or more long loops, reflected, as in the case of other less

* "Mus. R. Coll. Surgeons," 'Physiol. Ser.,' No. A940A.

elaborate pseudobranch retia, at their attachment to the wall of the spiracular pouch above the rudimentary pseudobranch, and reuniting to form the anterior carotid. The reunion was similar in character to the subdivision, the smaller vessels uniting to form two main branches, which finally joined to constitute the main trunk of the artery.

The loops were very extensively convoluted and showed in a few places small anastomotic branches ; but except for their great length they did not differ essentially from the loops that normally constitute the vascular body of the pseudobranch when this organ is in a reduced condition.

Upon leaving the pseudobranch plexus, the anterior carotid passes across the floor of the orbit towards the optic foramen in tight and very elaborate coils. At about the middle of its course it divides. One branch, or rather the direct continuation of the vessel (fig. 7, *int.cr.a.*), passes forward in complex coils as far as the optic nerve, and becoming smaller enters the cranium through a foramen situated behind that of the optic nerve. An inch or so before reaching the cranial wall it gives off a small branch that enters the cranium at a lower level than the main vessel.

The second of the two original branches is the *A. ophthalmica magna*. From its origin it passes mesially towards the cranial wall ventral to the trigeminal complex and presents an extreme degree of contortion, forming a thimble-shaped, tightly wound labyrinth of convolutions (fig. 7, *oph. a.*). Near the cranial wall it is reflected outwards, passing amongst the ocular muscles to its distribution in the eyeball. This labyrinth is in no sense a plexus, but is composed of one continuous vessel, which when disentangled measures no less than 25 times the distance in a direct line from its point of origin to the cranial wall. The increase in length in the cranial branch of the anterior carotid, though considerable, is less marked than this, being but seven times the direct distance between the point of origin of the vessel and its entry into the cranial wall.

The posterior carotid is as usual smaller than the anterior, but is strongly contorted both in its main trunk and branches. The trunk shows little if any increase in size after its origin. After reaching the floor of the cranium it is folded upon itself in several fairly extensive loops, and divides into the three usual branches, each of which is also folded in tight zigzags. The star-shaped labyrinth formed by these contorted vessels upon the floor of the cranium is enclosed in a wide venous space, connected posteriorly with the head of the jugular vein and merging anteriorly through the suborbital fenestra with the great orbital sinus within which lie the coils of the anterior carotid and of the external carotid branch of the posterior carotid.

After passing through the suborbital fenestra the external carotid divides into two main branches, both of which are highly convoluted. One of these ultimately passes forward dorsal to the anterior carotid for the supply of the jaws ; the other runs upwards behind the eyeball, forming a tangle of small vessels upon the orbital membrane. Its terminal branches were not seen, but probably they supplied the ocular muscles and possibly some of the muscles of mastication.

(b) *The epibranchial system and aorta.*—The efferent branchial arteries form, as is usual, a succession of complete loops (fig. 1, p. 211) encircling each gill pouch, and are united together across each branchial arch near its middle by a series of short longitudinal connectives.

In addition to these mesial connectives between the successive loops, which apparently are common to the efferent branchial system of all sharks, another series is present in *Lamna* between their dorsal extremities (fig. 8, below), forming a relatively capacious longitudinal channel into which a large proportion of the blood passing upwards from the gills is received.

So far as I can ascertain, such a dorsal connection between the efferent vessels is rare among sharks, the only other genus besides *Lamna* in which I have met with any record of its presence being *Chlamydoselachus*, where a similar chain of connectives is described and figured by ALLIS (1, p. 513), though whether the arrangement is constant in this primitive shark may be open to doubt in view of the entirely different account of its efferent branchial vessels given previously by AYERS (3).

In *Lamna* this condition is evidently of an adaptive nature to allow an ample flow of blood to the great lateral cutaneous artery (to be described below), though from its occurrence in the adult of the most primitive living Elasmobranch (*Chlamydoselachus*) it would seem to have originated rather in the retention, for physiological reasons, of a common evolutionary stage than as a secondary adaptation.

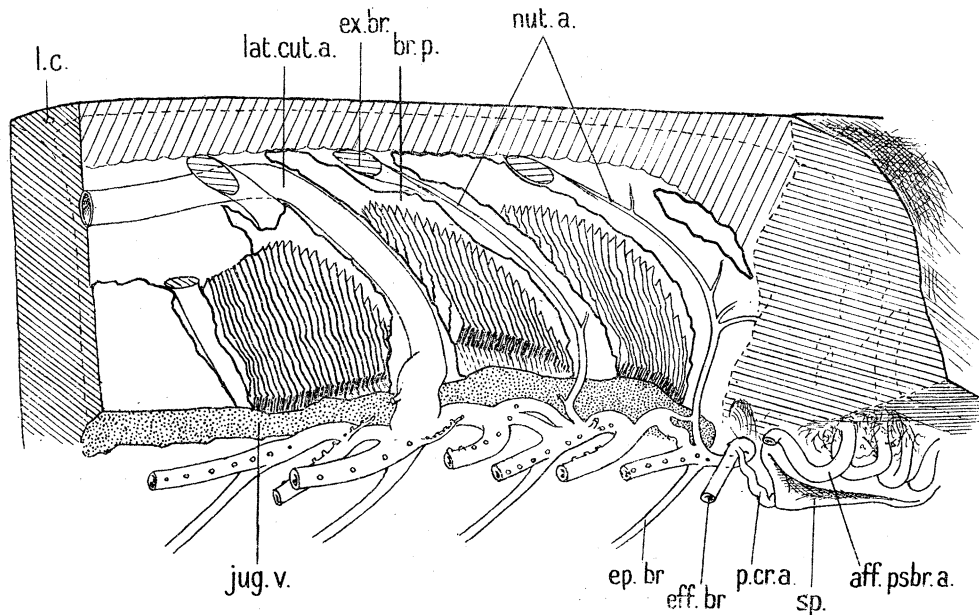


FIG. 8.—Deep lateral dissection of right branchial region of *Lamna cornubica*, showing the dorsal nutritive arteries of the gill pouches and the commencement of the lateral cutaneous artery.

The individual efferent branchial arteries differ considerably in size, ranging from about 2 mm. to 4.45 mm. in diameter, measured at a point near their dorsal extremities.

Speaking generally, the vessels increase in size from before backwards, the maximum

being attained by the 6th, which lies opposite the origin of the lateral cutaneous artery (fig. 8, *lat.cut.a.*).

From the upper end of the posterior limb of each efferent loop is given off the epibranchial artery which forms the tributary from the corresponding gill pouch to the aorta.

The epibranchial vessels were in every instance relatively very small and differed strikingly both in size and appearance from those of any other species of shark examined. The arteries forming the efferent loops and their connectives are in appearance normal vessels, with large lumen and walls of relatively little thickness, but no sooner does the vessel leave the loop as the epibranchial, than its character completely changes. The walls thicken, the lumen is reduced to minute proportions, and in general appearance the vessel resembles a fibrous cord, similar to the ductus arteriosus of Mammals or any other atrophied vessel.

There is in fact no doubt that the changes apparent in these vessels are of an atrophic nature. Microscopical examination (Plate 9, fig. 3) shows that the lumen is more or less irregular. The elastica interna lies close beneath the endothelium, but is weak, much broken up, and irregular; the media forms the bulk of the wall and consists of a mixture of muscle and fibrous tissue felted together, with the individual fibres and fibre bundles running in all directions, but assuming towards its outer parts a preponderantly circular direction, with the addition close to the adventitia of a number of longitudinal muscle bundles isolated by septa of fibrous tissue. Elastic tissue is poorly developed, and in addition to the elastica interna is represented by a slight and irregular network in the outer parts of the media and in the adventitia.

The mode of reduction shown by these arteries apparently differs in character from that observed in other cases of physiological occlusion. In the ductus arteriosus and umbilical arteries, for instance, the narrowing of the lumen and ultimate closure of the vessel is said (BALLANCE and EDMUNDS, 4, p. 66) to take place by a great proliferation of the intima; the media (which in these reduced arteries of *Lamna* appears to be the coat mainly affected) undergoing progressive diminution.

The condition of atrophy just described was apparent to a marked degree in all the epibranchials of the larger fish (specimens A, B), and the extent of the reduction may be to some extent realised from a comparison between the external diameters of these vessels in B with the corresponding vessels in a specimen of *Galeus* of approximately the same length (5 feet) though of considerably less bulk.

Lamna : epibranchial 1 : 2 mm., 2 : 2 mm., 3 : 2.25 mm., 4 : 3 mm.

Galeus : epibranchial 1 : 5 mm., 2 : 5 mm., 3 : 6 mm., 4 : 5 mm.

But it should be observed that these measurements, being external, do not give a true comparison of the blood-carrying capacity of the vessels, for in *Lamna*, owing to the thickening of the walls, the lumen of the vessel is proportionately far smaller than the measurement of the exterior diameter would lead one to suppose.

The atrophy of the epibranchials was less pronounced in specimen D than in the larger fish, and in this specimen presented a condition of some little interest.

The process of atrophy accompanied by thickening of the walls and reduction of the lumen of the vessel was very apparent in the first three arteries of the series, that is, as far back as the origin of the lateral cutaneous artery; the fourth epibranchial, though small, was of normal structure and in proportion to its size contained a lumen of normal capacity. It would thus seem that in this example the first three gill pouches starve the aorta and divert their chief blood-flow along the dorsal connectives of the efferent branchial loops into the lateral cutaneous artery, and that the aorta depends for its supply mainly upon the posterior gills.

The epibranchial arteries unite, each with its fellow, to form a series of short median trunks that combine in succession from below to make the aorta. This vessel, which normally forms the main channel of supply for the viscera and trunk, shares to a very marked degree in the atrophy noticeable in the epibranchial arteries. This is particularly the case in the larger fish, specimens A and B. In the latter the external diameter of the vessel measured at a short distance behind the entry of the last epibranchial vessels, is only 3 mm., whereas in a *Galeus* of about equal length the aorta at the same level had an external diameter of no less than 10 mm.

The walls of the vessel were most modified in the branchial region, showing thickening and reduction of the lumen similar to that observed in the epibranchial arteries. Behind the entry of the last pair of epibranchials the vessel, though small, was more normal in structure. Its walls were not unduly thickened, though there was a marked development of fibrous tissue in the inner layers of the media, accompanied by irregularity in the direction of the muscle fibres.

Just anterior to the entry of the last pair of epibranchials, the aorta gives off, as usual, the subclaven arteries (fig. 15, *s.cl.a.*). These are, however, extremely small and neither take any share in the supply of the pectoral fins nor form connections with the hypobranchial arteries. Their two main branches of distribution break up respectively in the body wall and upon the anterior ganglion of the sympathetic system.

Between the point of origin of the subclavians and the anterior limit of the body cavity, three vessels arise from the ventral surface of the aorta. These, both by their origin and further connections, are without doubt the usual anterior visceral arteries (the coelio-mesenteric, lieno-gastric, and anterior spermo-mesenteric).

The coelio-mesenteric passes towards the body cavity to the right of the oesophagus (figs. 1 and 15, *coel.mes.r.*) and enters the fold of peritoneum that forms the gastric mesentery. The other two arteries rise a short distance further back (figs. 1 and 15, *l.gst.sp.r.*) close side by side, and run diagonally downwards in the dorsal mesentery to the spermatic venous sinus, bound together within a strong strand of smooth muscle tissue.

All three vessels are relatively very small, as may be realised when they are compared with the same vessels in the specimen of *Galeus* referred to above. In *Lamna* (specimen B) the coelio-mesenteric measures in external diameter 2.5 mm., the lieno-gastric and

anterior spermo-mesenteric 1 mm., while in *Galeus* the diameters of these arteries are respectively 7 mm. and 3 mm.

Apart from their relatively small size, these arteries do not, in most of my sections, show any distinct signs of atrophy. Indications of change such as usually accompanies physiological occlusion (BALLANCE and EDMUNDS, 4) were, however, noticeable in sections taken about half-way along the cœlio-mesenteric root in specimen B. At this level (Plate 9, fig. 4) the intima had undergone marked proliferation, forming a thick band of fibrous tissue between the endothelium and the elastica interna. Otherwise the structure of the artery was normal. (The relation of these vessels to the suprahepatic retia and their ultimate distribution to the viscera are described below.)

Opposite the first dorsal fin the aorta gives off a small posterior spermo-mesenteric artery of normal type (fig. 1, *p.mes.a.*).

Segmental arteries for the muscles of the body-wall arise from the aorta throughout its length. Whether some of these vessels were distributed to the kidneys, as under normal conditions they should be, I cannot say for certain; neither was I able to demonstrate the presence of an iliac artery, and am fairly convinced that that vessel is absent. In any case, as described more fully below, it appears that the bulk, if not the whole, of the arterial blood supply to the kidneys has been transferred from the aorta to the lower lateral cutaneous arteries.

Posterior to the kidneys the aorta proceeds in the usual way to the tail, but on a level with the anterior extremity of the ventral fin is united by a strong anastomosis (fig. 1, *lat.cut.an.*) with the lateral cutaneous artery.

(c) *Dorsal nutritive arteries of gill pouches and lateral cutaneous artery.*—From the dorsal loops of the first three pairs of efferent branchial arteries, opposite the posterior member of each pair, is given off a series of vessels (fig. 8, *nut.a.*) for the supply of the dorsal parts of the constrictor muscles of the gill pouches.

The first of these arteries, which rises opposite the second efferent branchial, sends forward several good-sized branches towards the supra-orbital region of the head for the supply of the tissues in this region and the muscles of the jaws.

The main stem of the artery passes up the anterior reflexion of the second gill pouch along the anterior border of the extrabranchial cartilage and is distributed to the superficial constrictor muscles of the gills. The second artery of the series is given off opposite the fourth efferent branchial and pursues a course along the extrabranchial similar to that of the first. The third artery (fig. 8, *lat.cut.a.*) occupies a similar position between the third and fourth gill pouches, but is of relatively enormous size. It gives off a few small branches to the branchial constrictors, and at the upper angle of the gill chamber passes external to the extrabranchial cartilage and is deflected backwards, assuming, behind the branchial region, a subcutaneous position deep to the lateral canal of the lateral line system. In this position, following the lateral line, the artery runs back the whole length of the body to the root of the tail, and on a level with the anterior margin of the ventral fin is connected by an anastomosis with the aorta.

Towards the hinder end of the branchial region, near the upper limit of the last gill pouch, the artery gave off, in specimens B and D, a branch of moderate size (figs. 1, 10, *an.*), which passed obliquely downwards across the outer surface of the scapula, and at its hinder margin formed a connection with the lower lateral cutaneous artery. This connection will be discussed further in dealing with the latter artery; here it is only necessary to mention that it was present in the two specimens just mentioned, was not looked for or observed in specimen A, and apparently was absent in specimen C. In this latter case it was carefully sought, but was not found, though in place of it upon the outer surface of the scapula and supplying the muscles in this region was a small branch of the lower lateral cutaneous artery.

The importance of this connection between the lateral cutaneous and lower lateral cutaneous arteries lies in the question which will be discussed later, whether it represents a tributary of the supra-hepatic rete, as stated by MÜLLER, or is the original root of the lower lateral cutaneous artery.

In addition to this anastomotic branch, the lateral cutaneous artery gives off in the region of the shoulder several small branches to the neighbouring muscles. As it passes backwards the branches that spring from its deeper surface increase very much in number, and from a point about 3 cm. behind the scapula to the level of the pelvic fins, assume a very peculiar character. Within this area the deep branches form a close-set series of short trunks, not more than 1 mm. in length, each terminating in a brush of fine parallel twigs that run directly inwards between the bundles of the trunk muscles towards the vertebral column.

The components of the arterial brushes are unbranched except towards their final distribution, and lie close side by side, interspersed with corresponding bundles of fine parallel veins, the whole forming a simple rete, differing from those of MÜLLER's unipolar type only in the fact that the individual twigs do not anastomose to form a true plexus.

The vessels that form the arterial component of this rete are of approximately the same size (Plate 9, fig. 5), and retain their diameter for a very considerable distance towards the vertebral column.

In structure (Plate 10, fig. 6) they resemble other arteries of small size, but show an unusually strong and complete *elastica interna*. The media is weak and consists of pure smooth muscle of, at the most, two cells thick; it is surrounded by a fairly deep layer of white fibrous tissue (*adventitia*) which is remarkable for the complete absence of elastic fibres.

The venous spaces are bounded by the *adventitia* of the arteries, lined apparently by a thin pavement endothelium, and are here and there traversed by trabecular strands.

Somewhat similar retia in which the component vessels do not re-collect, as they do in the bipolar type, to form secondary trunks of distribution have been described by ESCHRICHT and MÜLLER (10, p. 325) in the visceral arteries and veins of the Fox Shark (*Alopias*)*, but in this case the vessels form a true rete by anastomosis.

* "Mus. R. Coll. Surgeons," 'Physiol. Series,' No. J. 651, 1.

The area of muscle (fig. 9, p. 231) supplied by this rete is remarkable for a deep red colour, similar to that of the dark muscle band found upon the trunk of the mackerel and many other fishes. As it extends inwards it broadens out and includes the axis of the muscle cones of the central column of trunk muscles. Its deep surface has unusual freedom, being separated from the lateral parts of the vertebral column by a layer of loose connective tissue (fig. 9, s.). A short distance in front of the level of the pelvic fins, near the hinder limit of the rete, the muscle loses its red colour but can still be traced for some inches further back free of the vertebral column, before it finally merges in the ordinary muscles of the tail, and in this part shows a marked development of tendinous strands upon its free surface.

In addition to the deep branches that form the rete just described, the lateral cutaneous artery gives off from its dorsal and ventral surfaces a series of superficial branches that follow the intermuscular septa and anastomose, particularly in the tail and hinder region of the trunk, with corresponding branches of the lower lateral cutaneous artery, forming a superficial oblong-meshed vascular net close beneath the skin.

Slightly in advance of the ventral fin the lateral cutaneous artery forms, as mentioned above, an anastomosis with the aorta by the union of one of its deep branches with a segmental artery. The union, which equals the aorta in size, arches below the central column of the caudal muscles and forms practically the main termination of the lateral cutaneous artery, the direct continuation of the vessel beyond this point being quite minute and breaking up into a few small twigs at the root of the tail.

In no other shark that I have examined are there any arteries comparable to the lateral cutaneous of *Lamna*, nor have I been able to discover any description of such arteries except in MÜLLER'S account of the vascular system of this genus. In his description he refers to them briefly (17, p. 272) as the "great arterial trunks of the muscular lateral wall of the body," and (17, p. 273) as the "*arteriæ thoracicæ* which run superficially beneath the skin" "from which, opposite the commencement of the abdominal cavity, are given off the accessory arteries of the [supra-hepatic] retia" (= my anastomoses between the lateral cutaneous and lower lateral cutaneous arteries).

These *arteriæ thoracicæ* undoubtedly are the lateral cutaneous arteries, but MÜLLER makes no mention of their origin or further distribution and offers no suggestion as to their homologies. It is, however, quite clear from what has been said above of their relation to the dorsal nutritive arteries of the gill pouches that they are members of this series, which have become enormously enlarged and carried beyond the territory to which the branchial nutritive arteries should properly be confined, into the trunk for the supply of a considerable part of the body muscles and particularly of a specialised column of these muscles distinguished by its dark colour and loss of segmental insertion upon the vertebral column.

The use of this new channel for the supply of a large area usually irrigated by branches of the aorta has no doubt been one of the causes of the reduction in size of the latter vessel, which forms so striking a feature in the vascular system of *Lamna*.

The determination of the homology of these important lateral cutaneous arteries with the dorsal nutritive arteries of the gill pouches, led me to enquire how far this latter system of vessels is a common feature of the blood supply of the gill muscles in sharks. A study of the available literature leads me to suppose that dorsal nutritive arteries are unusual. PARKER in his monograph on *Mustelus* (19) makes no mention of them; there is no reference to them in HYRTL's memoir (12); nor, with one exception, in ALLIS's series of papers on the branchial circulation. The exception is the primitive shark *Heptanchus*; in the figure (2, fig. 1) of the branchial arteries of this genus the roots of a series of vessels are shown arising from the upper bend of each efferent branchial loop from the second onwards, in exactly the same position as the dorsal nutritive arteries of *Lamna*, and no doubt homologous with them.

I have myself looked for these vessels in *Scyllium*, *Acanthias*, *Mustelus* and *Carcharias* without success; but in *Galeus* I found one such vessel given off from the upper bend of the third efferent loop and passing within the anterior reflexion of the second and third gill pouches to the dorsal branchial constrictors in a position similar to that occupied by the dorsal nutrient vessels in *Lamna*.

It would thus seem that not only is the lateral cutaneous artery in all probability peculiar to *Lamna*, but that the system of vessels from which it is derived is also of very restricted occurrence, and probably, as indicated by its presence in *Heptanchus*, a primitive condition that in most genera has been supplanted by an extension of the ventral vessels.

2. Lower lateral cutaneous arteries and sub-renal rete.

Some few centimetres below the lateral cutaneous artery there is, close beneath the skin, a double longitudinal artery with a single large vein lying between its two limbs (fig. 1, *l.lat.cut.a.*).

The positions of these vessels relative to the lateral artery and vein at the level of the first dorsal fin are shown in fig. 9. Close to the posterior border of the scapula they lie about half-way up the side of the body, and at this point emerge from a common trunk (fig. 10, *l.lat.cut.r.*), that, as described below, is continuous beneath the scapula with the pericardial artery and the meshes of the supra-hepatic rete.

This common trunk just after its emergence from beneath the scapula is joined by the anastomotic branch of the lateral cutaneous artery mentioned above (fig. 10, *an.*) and possibly receives by it part at least of its blood supply. But there is reason to suppose that this connection, which very probably represents the original root of the lower lateral cutaneous artery, is now of not much importance, and is in process of being supplanted by the trunk that derives from the pericardial artery and supra-hepatic rete. In support of this view it is to be noticed that in one individual at least (specimen C) the connection was absent (p. 228,) and that in another (specimen D) the calibre of the connection was considerably diminished towards the upper part of its extent, suggesting that in this region a natural occlusion of the vessel was in progress.

This suggestion is also borne out by the microscopical structure of the anastomosis

(Plate 9, fig. 6). The walls of the vessel are relatively thick, and as in the case of the ductus arteriosus and other naturally occluding vessels (BALLANCE and EDMUNDS, 4), the greater part of the thickening is due to proliferation of the intima. The elastica interna is divided in places into inner and outer sheets, between which the tissue of the intima forms a deep reticulum of delicate fibrous tissue. Fibrous tissue is also unusually

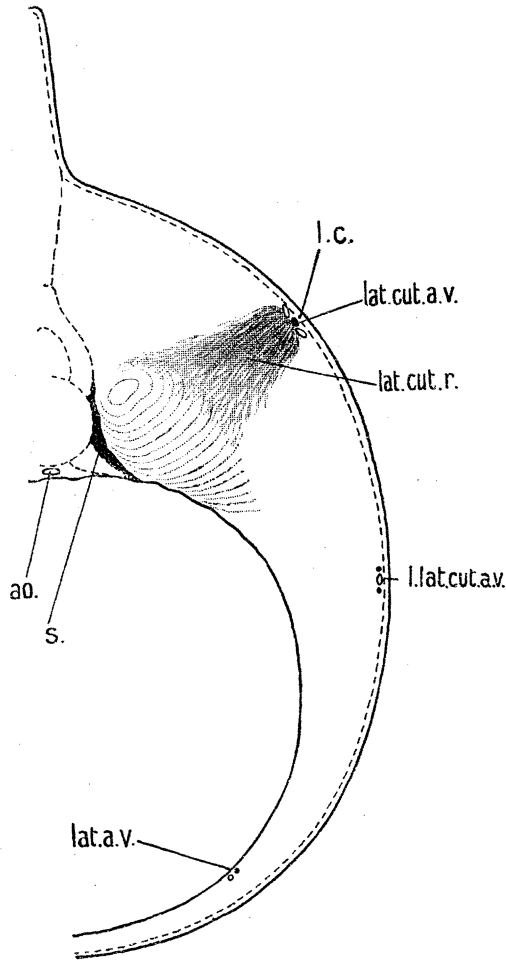


FIG. 9.

FIG. 9.—Transverse section of the trunk of *Lamna cornubica*, at the level of the first dorsal fin, showing the positions of the lateral cutaneous, lower lateral cutaneous, and lateral arteries and veins, and the column of muscle irrigated by the lateral cutaneous rete.

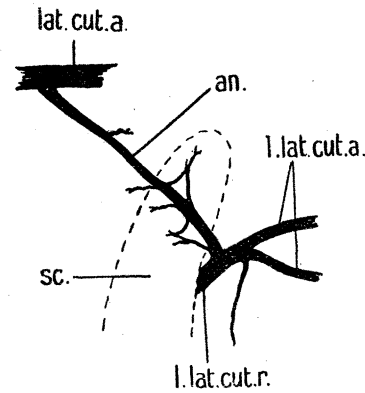


FIG. 10.

FIG. 10.—Diagram of the anastomosis between the lateral cutaneous and lower lateral cutaneous arteries of *Lamna cornubica* (specimen D).

abundant amongst the muscle fibres of the media, but elastic tissue is relatively scarce.

According to MÜLLER (17, p. 272) this anastomosis and the trunk that connects the lower lateral cutaneous artery with the supra-hepatic rete, which he regarded, taken together, as a simple branch of the lateral cutaneous artery, constitute one of the

trunks of supply to the supra-hepatic rete ; he figures it as an unbranched vessel running from the lateral cutaneous artery to the rete, and evidently did not observe its connection with the lower lateral cutaneous artery. This is an important omission, and probably led MÜLLER to the assumption that the flow of blood within this vessel is to the rete, whereas it is almost certainly the other way, from the rete to the lower lateral cutaneous artery. For what MÜLLER takes to be a single vessel is in fact two—(1) a trunk connected at one end with the supra-hepatic rete and the pericardial artery (fig. 15, *l.lat.cut.r.*) and at the other directly continuous with the lower lateral cutaneous artery ; and (2) a branch (the anastomosis) (fig. 10, *an.*) from the lateral cutaneous artery which enters this trunk almost at right angles.

Are we then to consider the branch from the lateral cutaneous artery, or the trunk from the rete, or both, to be the source of blood supply to the lower lateral cutaneous artery ? If the branch from the lateral cutaneous artery is the sole source of supply, blood would flow along it not only to the lower lateral cutaneous artery, but (as MÜLLER thought) to the supra-hepatic rete. Apart from the fact that the branch from the lateral cutaneous artery may be absent (specimen C), the relative size of the various vessels forbids this conclusion ; for the lower lateral cutaneous artery and the rete trunk taken together are four times the diameter of the anastomosis with the lateral cutaneous artery, and the latter obviously could not carry enough blood to supply both. We can thus only conclude that the rete trunk is the main source of blood supply for the lower lateral cutaneous artery, and is thus efferent from the supra-hepatic rete, and not, as supposed by MÜLLER, afferent to it.

How far the anastomotic branch from the lateral cutaneous artery is also a tributary of the lower lateral cutaneous artery is not clear. The angle at which it meets the trunk of the lower lateral cutaneous artery is compatible with the flow being from this vessel, and the same conclusion is suggested by the fact that in specimen C this anastomosis was represented only by a branch of the lower lateral cutaneous artery, and in specimen D was considerably narrower in its mesial parts than at either end, and gave off from its lower half numerous small branches (fig. 10, p. 231), the inclination of which was in many instances away from the lower lateral cutaneous artery.

On the whole it seems probable that the lower lateral cutaneous artery was originally a branch of the lateral cutaneous, which later contracted a connection with the pericardial artery and supra-hepatic rete, and that this connection is now the chief and in some cases the only source of its blood supply, and is in process of supplanting the original root by which the vessel derived from the lateral cutaneous artery.

After leaving the common stem, close behind the scapula, the lower lateral cutaneous artery, now represented by two parallel vessels, runs beneath the skin obliquely downwards and backwards towards the pelvic fins, giving off above and below a series of superficial intermuscular branches. An inch or so above the anterior border of the pelvic fins the ventral inclination of the arteries increases sharply, and the two vessels unite (figs. 1 and 11) external to their companion vein to form a single trunk that passes

inwards and upwards between the fin and the wall of the cloaca (fig. 12, *cl.a.*) towards the posterior extremity of the kidney.

Just anterior to the origin of the single trunk the dorsal arm of the double artery gives off a branch of some size, that runs backwards on the ventro-lateral aspect of the tail and gives off a series of intermuscular segmental branches that unite with corresponding superficial branches of the lateral cutaneous artery.

The single trunk meanwhile passes dorsal to the pelvic fin to the lip of the cloaca, and at this point gives off or unites with a small artery (fig. 11, *lat.a.*) that runs forward

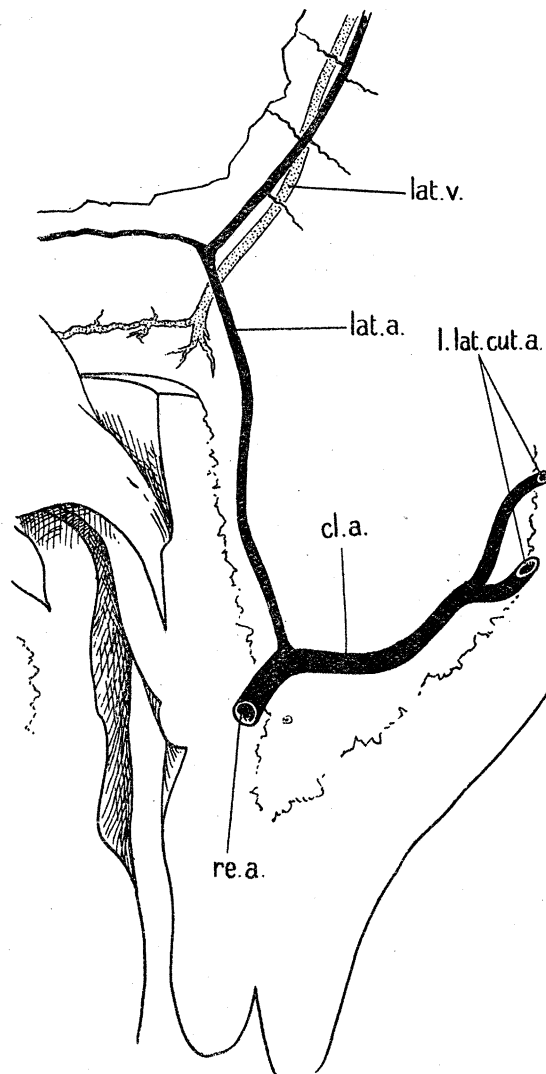


FIG. 11.—The cloacal and pelvic region of *Lamna cornubica*, seen in section from above, showing the connection between the lateral artery and the cloacal trunk of the lower lateral cutaneous artery.

to the dorsal surface of the pubis, is here united with its fellow by a transverse anastomosis, and is continued forward close beneath the peritoneum (fig. 1, *lat.a.*) to the pericardium, to become there continuous with the epicoracoid branch of the median

hypobranchial artery. This small vessel is accompanied by a little vein that rises from a supra-pubic anastomosis, and enters the pericardial diaphragm to open, so far as I could trace it, into the anterior caval sinus.

There seems no doubt that this little artery and vein are the lateral vessels, normal to Elasmobranchs, much reduced in size through the usurpation of the greater part of their function by new superficial vessels (the lower lateral cutaneous), and lying nearer the ventral mid-line than usual (fig. 9, *lat.a.*).

After its union with the lateral artery the cloacal continuation of the lower lateral cutaneous artery runs upwards nearly to the mid dorsal line of the cloacal wall intimately bound up with the branches of the cloacal vein (fig. 12, *cl.a.* and *v.*), and perforates a layer of dense fibrous tissue that separates the hinder end of the kidney from

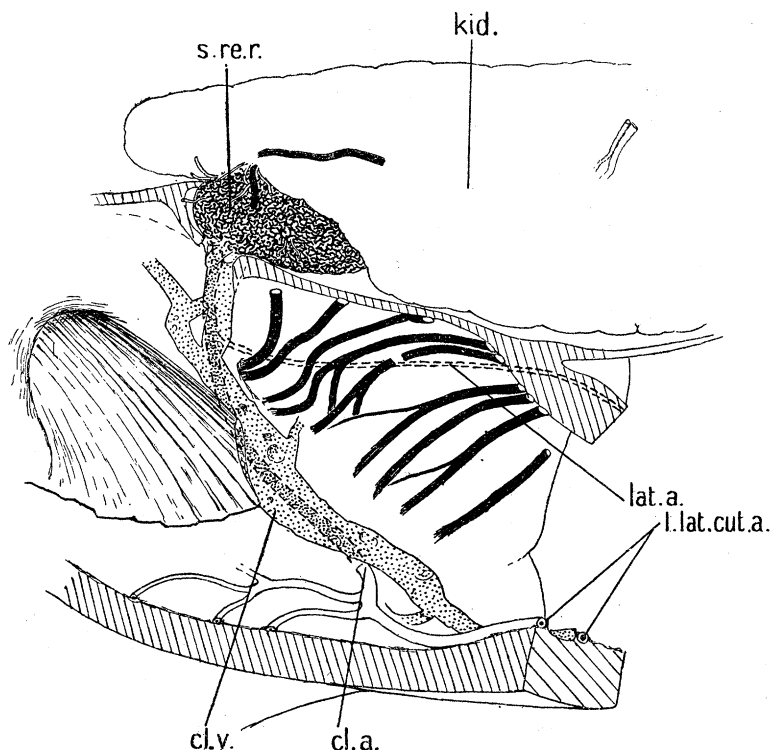


FIG. 12.—The cloacal region and hinder end of the kidney of *Lamna cornubica*, showing the exposed hinder end of the subrenal rete and the blood vessels in connection with it.

the cloaca and the neighbouring muscles. Above this fibrous sheath it breaks up to form a coarse-meshed rete (figs. 12, 13, *s.re.r.*) that extends forward along the ventral surface of the kidney for some considerable distance, decreasing regularly in size as it does so.

The arterial meshwork of the rete consists of vessels of some little size, which are remarkable for the thinness of their walls (Plate 10, fig. 1) and particularly for the small amount of muscular and elastic tissue that they contain. The muscular layer (media) is bounded internally by a definite though delicate *elastica interna*, and externally by

a corresponding but still weaker *elastica externa*. In the adventitia elastic tissue is almost absent.

Interwoven with the arterial network is a corresponding but more capacious system

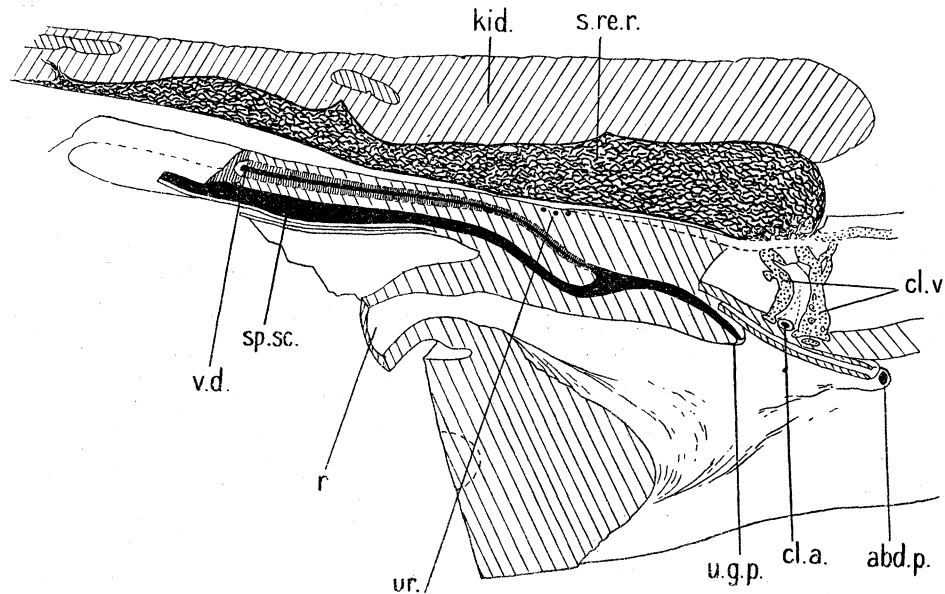


FIG. 13.—The cloaca and hinder end of the kidney of *Lamna cornubica*, in sagittal section, showing position and extent of subrenal rete.

of venous spaces that coalesce posteriorly around the primary branches of the arterial component and pass through the fibrous subrenal sheath to form the main factors of the lower lateral cutaneous vein.

The hinder end of the rete projects below the posterior extremity of the kidney as a rounded prominence (fig. 12, *s.re.r.*), about the size of a walnut (specimen B), and is enveloped by a definite capsule separated from the fibrous subrenal sheath by a layer of loose connective tissue. In continuity with this exposed posterior portion, the rete extends forward upon the concave ventral surface of the kidney for several inches (fig. 13, *s.re.r.*), getting gradually smaller and smaller. At about the level of the first dorsal fin it terminates insensibly in a few vessels spreading forward irregularly upon the ventral surface of the degenerate anterior region of the kidney.

The rete is readily separable from the fibrous sheath that separates the kidney from the vasa deferentia and body cavity, but is closely adherent to the kidney itself, and towards its anterior end is more or less surrounded by it, assuming much the position (fig. 14, *s.re.r.*) normally occupied by the united posterior cardinal veins, which, except at their anterior extremity, are absent. Surrounding and infiltrating the rete is a capsule of fibrous tissue from which strands radiate into the kidney substance carrying with them small arteries and veins.

The ultimate distribution of these vessels was not determined to my complete satisfaction, but in some few instances a small artery was traced to a glomerulus, and I feel

pretty certain (Plate 10, fig. 2) that the glomeruli are in fact supplied in large part, if not entirely, from this source. Whether branches of the aorta also take part in the vascularisation of the kidney, I am not sure; I can only say that I was not able to trace any of the small aortic segmental branches into the substance of the kidney, and am inclined to think that the arterial blood supply has been mainly, if not entirely, transferred from the aorta to the lower lateral cutaneous artery.

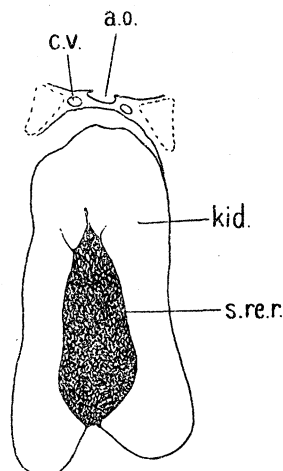


FIG. 14.—Transverse section of the kidney of *Lamna cornubica* (specimen D), showing the position of the sub-renal rete relative to the kidney substance at the level of the anterior end of the cloaca.

From the above it will be seen that the circulation of the trunk and kidneys normally carried on by the aorta, posterior cardinals and lateral vessels, has undergone very profound modification and has been to a large extent transferred from these vessels to a system of subcutaneous arteries and veins and vascular plexuses, with the result that the vessels by which this circulation is usually carried on are much reduced, or even completely lost (e.g., posterior cardinals).

The substituted vessels, with the exception of the lateral cutaneous vein, are apparently peculiar to *Lamna*.

A rete in connection with the kidney is not unknown among Elasmobranchs. CARAZZI (6, p. 89) describes in *Selache maxima* an elaborate network of arteries surrounding the kidney, forming a dense rete upon the surface and penetrating deeply into the renal parenchyma. This rete is formed by the anastomosis of branches of the renal arteries, which rise as usual from the aorta, but in far greater abundance than is commonly the case. There is therefore no morphological comparison between this rete and that described above in *Lamna*, though it is probable that they have a similarity of function.

3. The ventral derivatives of the efferent branchial vessels.

(a) *Coronary and pericardial arteries.*—As in all other sharks, the ventral extremities of each pair of efferent branchial vessels are united to form a complete arterial loop around the corresponding gill pouch. The lower ends of successive loops are likewise joined together in series by a chain of longitudinal connectives, thus giving rise to a paired continuous arterial trunk situated along the floor of the pharynx alongside the ventral aorta above the afferent branchial arteries.

This channel, called by FERGUSON (11) the lateral hypobranchial artery (fig. 15, *lat.hpbr.a.*), extends usually as far back as the fourth branchial loop, and as far as the third is a vessel of large size, measuring, in specimen B, 5 mm. diameter: as large, if not larger, than the corresponding longitudinal connective chain upon the dorsal aspect of the gills. Between the third and fourth loops the connection is small and was in one case (specimen D) absent.

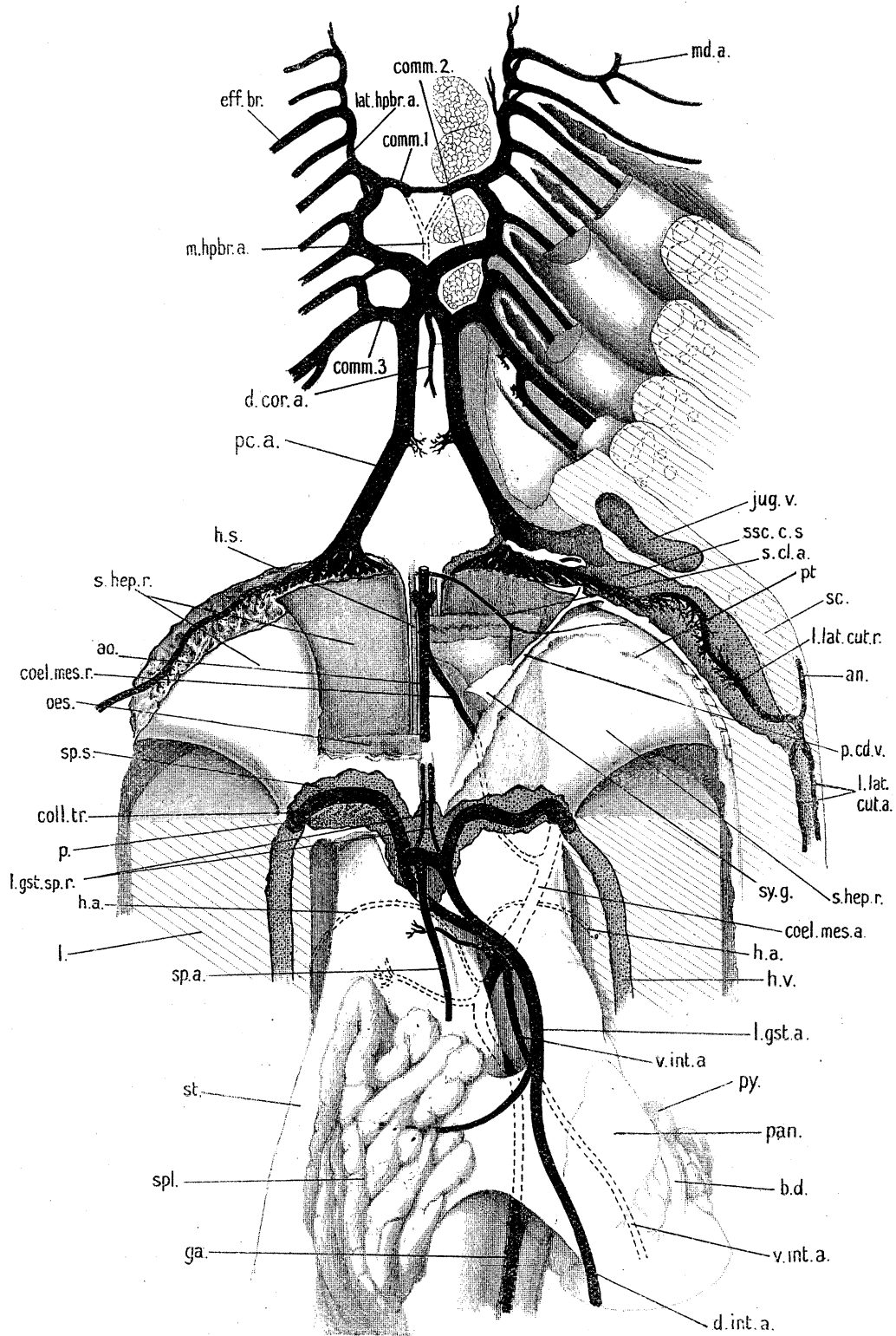


FIG. 15.—The hypobranchial and visceral arteries of *Lamna cornubica* seen from the dorsal aspect. Upon the left side the oesophagus has been cut back further than on the right to expose the supra-hepatic rete; arteries, black; veins, dotted.

The size of this hypobranchial longitudinal trunk and of the lower ends of the efferent vessels that feed it is a matter of some interest, for it is in marked contrast to the condition normally present in other sharks, in which the efferent branchial arteries diminish in size and importance as they approach the ventral surface, and the hypobranchial system is composed of relatively small vessels.

This disparity in the size of the efferent vessels at the two extremities of the gills has been remarked upon by FERGUSON (11, p. 176) and in the various genera that I have dissected was always noticeable though differing in degree. It was very striking, for instance, in *Galeus*, and offers a rough indication of the proportion of the blood carried by the aortic and hypobranchial systems respectively.

The two lateral hypobranchial arteries are connected, as in other sharks, by a series of transverse commissures (fig. 15, *comm.* 1.2.3.), from which arise the median hypobranchial artery and the pericardial arteries.

The first of these commissures (PARKER'S Comm. 3 (19), Plate 34, fig. 2) is given off from the connective between the second and third efferent loops (fig. 15, *comm.* 1). It unites with its fellow below the ventral aorta, as well as by a subsidiary bridge dorsal to it, and supplies in the usual way through the median hypobranchial artery and its branches, the heart, the superficial constrictors of the posterior gill pouches, and the muscles of the ventral body-wall, without, however, making a connection, as it does in *Mustelus* and many other genera, with the subclavian artery.

The second commissure (fig. 15, *comm.* 2) (PARKER'S Comm. 4 (19), Plate 34, fig. 2) arises from the posterior border of the third efferent loop (opposite the 6th efferent artery), and passes to the dorsal aspect of the root of the ventral aorta; here it coalesces with its fellow to form a very short median trunk. At the anterior end of the pericardium this trunk again divides, and after giving off from the bifurcation a dorsal coronary artery, passes backwards as two great longitudinal trunks upon the dorsal wall of the pericardium.

Opposite the posterior border of the fourth efferent loop (*i.e.*, from the 8th efferent artery) is a third commissure (fig. 15, *comm.* 3) (comparable to Comm. VI in *Carcharias*, PARKER and DAVIS (20)) or rather transverse vessel which, passing inwards, almost immediately joins the longitudinal trunk of its own side formed by the re-division of the median confluence of the second commissure.

The two longitudinal trunks, thus reinforced, are of very large size (8 mm. diameter in specimen B). They continue backwards upon the roof of the pericardium to its hinder end, supplying it about midway with several small twigs, and at its posterior outer angle enter an irregular venous space continuous with the subscapular sinus (fig. 15, *ssc.c.s.*).

Each vessel now gives off a number of branches that break up within the trabeculated postero-mesial wall of the subscapulo-cardinal sinus into finer and finer anastomosing twigs that form the arterial component of the great supra-hepatic retia to be described below. The main stem of the vessel passes on upon the postero-mesial wall of the

subscapulo-cardinal sinus, at first diminishing in size and later again enlarging to become continuous with the extremity of the rete-trunk of the lower lateral cutaneous artery. previously mentioned (p. 230).

Throughout its passage through the venous sinus the artery is connected by branches with the meshwork of the rete, and it is not possible to say where these vessels cease to be afferent to the rete and become tributaries of the root of the lower lateral cutaneous artery, though for the reasons stated above in the description of the latter artery (p. 232) there is, I think, no doubt that at some point along its course the vessel receives blood from the rete instead of contributing blood to it.

A comparative study of the hypobranchial system shows that these two great afferent arteries of the supra-hepatic retia are homologous with the pair of small pericardial arteries commonly given off from the hinder of the hypobranchial commissures to the dorsal wall of the pericardium.

These vessels are in ordinary quite insignificant and in fact are seldom mentioned in descriptions of the vascular system. They are briefly referred to by PARKER (19, p. 698, Plate 34, fig. 2) as unilateral and supplying the dorsal wall of the pericardium ; and their roots are apparently indicated in HYRTL's figures of *Mustelus* and *Zygæna* (Tf. 2, fig. 2, Tf. 3, fig. 2), referred to in the former case as epigastric arteries though dorsal to the heart, and in the latter without designation.

A fuller account is given of them in *Mustelus*, *Acanthias* and *Carcharias* by FERGUSON (11). He says, p. 176 :—" From this same sinus [*i.e.*, the dilated termination of the median hypobranchial artery] a small paired artery passes backward on either side of the median line beneath the dorsal portion of the pericardium at the lateral margin of the cartilaginous floor of the pharynx formed by the basi-branchial cartilage ; after anastomosing with its fellow of the opposite side beneath the apex of the cardiac ventricle, it distributes its terminal branches to the wall of the œsophagus and stomach near the cardia."

A description, with excellent figures, of these vessels in *Scyllium* is given by CARAZZI (5), and it is interesting to note that in this genus, in which the vessels are more than ordinarily well-developed, their œsophageal branches form an open and tortuous plexus in the submucosa and ultimately connect with the anterior gastric branches of the coeliac artery.

I have myself found these arteries in all the species I have dissected, and have examined them with care in the hope of finding some indication *external* to the œsophagus of plexus-formation upon them comparable to the supra-hepatic retia in *Lamna*. This hope was not realised, but I find that in all cases the origin and course of the arteries, though subject to irregularity, are essentially similar ; they rise by one or two roots from a bridge of the second commissure that passes dorsal to the base of the ventral aorta, and thence, after in some cases receiving a tributary from the last efferent branchial loop, traverse the whole length of the dorsal wall of the pericardium close to the outer edge of the last basi-branchial cartilage. Where this cartilage begins to narrow posteriorly, the

arteries emerge from beneath it and continue backwards along the œsophagus, as stated by FERGUSON and CARAZZI, within the submucosa, spreading out into a few anastomosing branches from which minute twigs are given off to the mucous membrane.

Although the position of these arteries in the submucosa is not the same as that occupied by the supra-hepatic retia in *Lamna*, which lie completely external to the muscle layers of the œsophagus, the similarity in origin and in relation to the pericardium of the pericardial arteries of sharks and the afferent trunks of the supra-hepatic retia in *Lamna*, shows, I think, quite clearly that these vessels are homologous and that in *Lamna* the pericardial vessels, which normally are insignificant and confined in their distribution to the upper end of the alimentary canal, have become enlarged, to serve (as will be shown below) as the chief source of blood supply for all the abdominal viscera.

In describing these vessels in *Lamna*, MÜLLER makes no comparison between them and any arteries of other sharks, and was apparently not clear as to their nature. He describes them (17, p. 273) as arteriæ intestinales coming both from the left side, from the "circulus arteriosus cephalicus," but was unable to say whether at their origin both were united in a common stem or arose one behind the other. They both, he adds, run dorsal to the pericardium to their respective retia, the artery to the right rete passing diagonally to reach it. From this description, which it must be remembered was made from mutilated material, it appears that MÜLLER thought that these vessels came from the tributaries of the aorta, a view that was expressed more definitely by DUMERIL (8, p. 184), though apparently not from an original observation of his own, but as an elaboration drawn by inference from MÜLLER'S account. He says that the two principal afferent trunks of the supra-hepatic retia "are intestinal arteries, whose origin is here more advanced than in other Plagiostomes, for they rise not from the aorta but from branches given off from arteries which, arising from the branchiæ, carry blood to different organs before forming the aortic trunk. They pass above the pericardium and go one to the right rete and one to the left." Neither of these authors makes any reference to the normal though reduced visceral arteries described above (p. 226) as arising in the usual position from the aorta; and evidently DUMERIL, at any rate, considered that it was these latter vessels, displaced forward, that formed the afferent trunks of the supra-hepatic retia. There is, however, no question that this view is erroneous; the condition that I have described above was exactly the same in all my material and leaves no doubt that the retia are supplied by vessels rising from the hypobranchial system which have anatomically nothing whatever to do with the usual visceral trunks given off from the aorta, but are modified pericardial arteries.

Before pursuing these vessels further, I must refer to the median hypobranchial artery. This vessel, which lies on the ventral surface of the ventral aorta, and gives origin to the ventral coronary and certain other small arteries, was formed in *Lamna* by the union of the first commissural vessels only (PARKER'S Comm. 3 (19), Plate 34, fig. 2) and not, as is more usually the case, by that of the first and second.

Apart from this, its general arrangement was very similar to that depicted by PARKER

for *Mustelus*; as in that genus the posterior epicoracoid branches formed by the bifurcation of its single trunk were of very considerable size, but they formed no anastomosis with the subclavian arteries. After giving off nutrient arteries to the posterior gill pouches and small vessels to the pericardial diaphragm and the pectoral fins, they continued backwards (fig. 1, *lat.a.*) beneath the peritoneum as the lateral arteries, to connect with the lower lateral cutaneous arteries in the region of the cloaca, as described above (fig. 11, *lat.a.*).

My reason for referring to these vessels is that they show a condition the opposite of that found by FERGUSON (11) to occur normally in the genera he dissected. According to his findings, the important vessels for the supply of the limbs and ventral body walls are the subclavians, the posterior (epicoracoid) bifurcation of the hypobranchial being insignificant or even absent, and sometimes forming a small anastomosis with the subclavian and sometimes not.

From this disposition of the vessels FERGUSON concluded that PARKER (19, p. 697) was in error in regarding the hypobranchial arteries as branches of the subclavians, and pointed out that, on the contrary, the whole hypobranchial system must receive its blood from the efferent branchial loops. This conclusion, which was also borne out by CARAZZI'S observations (6) is undoubtedly correct, and is as evident from the arrangement of the vessels in *Lamna* as it was in FERGUSON'S material, although the relative importance of the hypobranchial and subclavian systems in the one case was exactly the opposite of that in the other; in FERGUSON'S genera the subclavians being pre-eminent and in *Lamna* the hypobranchial, but in neither is there any possibility of the flow of blood being from the subclavian to the hypobranchial.

(4) *The supra-hepatic retia and visceral arteries.*

These retia (figs. 1, 15, Plate 10, fig. 3, *s.hep.r.*), which form the most conspicuous peculiarity of the organs of circulation, are two great masses composed of a close mesh-work of intermingled arteries and venous spaces interposed between the liver and the pericardial diaphragm. When seen from below upon opening the abdominal cavity and depressing the anterior projection of the liver lobes, they have the appearance of two swollen columns of soft dull red tissue, attached posteriorly to the forward extremity of the liver and broadening out to the pericardial diaphragm in front. Laterally they present a bluntly-angled margin and are lost above within the dorsal mesentery. In the mid-ventral line the two masses are separated by a shallow longitudinal groove, from which projects the ventral ligament of the liver.

Dissection shows that the retia envelop the ventral and lateral surfaces of the œsophagus posterior to the hinder limit of the pericardium (Plate 10, fig. 3, *s.hep.r.*), being closely adherent to the muscular walls of the œsophagus in front, but separated from them behind by a peritoneal pocket that continues the abdominal cavity forward for a short distance around the œsophagus to the left of the gastric mesentery.

The two masses are quite independent of one another, being separated by a vertical

partition of fibrous tissue continuous below with the ventral ligament of the liver and containing near its dorsal margin the pericardio-abdominal passage and at its ventral border the two true hepatic sinuses (Plate 10, *hs.pc.a.p.*, fig. 1, fig. 15, *hs.*).

The arterial component of each rete is derived, as mentioned above, from the greatly enlarged pericardial artery. The terminal portion of this vessel runs along the antero-lateral face of the rete within a large venous sinus situated beneath the scapula, and gives off during its passage a number of branches that rapidly subdivide and by mutual anastomosis form a rich and very fine lattice-work of minute arterioles (Plate 10, fig. 4), the meshes of which are set in a longitudinal direction, presenting in cross-section very much the fine spongy appearance of a piece of lung. Towards the posterior border of the rete, near its attachment to the liver, the meshwork again opens out, the component arteries combining to form larger and larger vessels which ultimately open into a single large collecting trunk (figs. 1, 15, *coll.tr.*). This trunk lies within a capacious extension of the hepatic sinus and runs at first outwards to the lateral margin of the rete within its attachment to the liver, and then passing into the spermatic sinus (fig. 15, *p.*) is continued beyond the rete nearly to the dorsal middle line of the body. At this point the collecting trunk from each rete receives one of the small lieno-gastric-spermatic arteries (fig. 15, *l.gst.sp.r.*) mentioned above as arising in the usual position from the aorta, and is then reflected posteriorly along the edge of the gastric mesentery to be distributed to the dorsal surface of the stomach and valvular intestine and to the spleen. A connecting bridge unites the two collecting trunks across the dorsal mid-line of the body at their point of backward reflexion, and from it is given off a median spermatic artery (fig. 15, *sp.a.*) that runs backwards in the dorsal parts of the testes within the posterior extension of the spermatic sinus.

The collecting trunk of the right side, as it passes, at the lateral margin of the rete, from the hepatic to the spermatic sinus, gives off a large branch (fig. 15, *cœl.mes.a.*). This vessel runs backwards within the gastric mesentery and at or shortly after its origin is joined by the reduced cœlio-mesenteric artery (fig. 15, *cœl.mes.r.*) given off, as described above, from the aorta. The combined artery continues backwards in the gastric mesentery, giving off branches, much as in *Mustelus*, to the liver, to the dorsal and ventral surfaces of the stomach, and to the ventral surface and spiral valve of the intestine.

It will thus be apparent that the visceral arteries in their plan of distribution are very similar to those of *Mustelus* as described by PARKER, but that instead of receiving their blood solely from the aorta, they derive their chief supply from the pericardial arteries through the supra-hepatic retia, at the same time retaining their original connection with the aorta through much reduced cœlio-mesenteric and lieno-gastric spermatic roots. The relative blood contribution from the two sources can be realised from the following measurements taken from specimen B:—

| | | | | | | |
|--------------------------------------|----|----|----|----|----|-----------------|
| Right collecting trunk of rete | .. | .. | .. | .. | .. | 5 mm. diameter. |
| Left collecting trunk of rete | .. | .. | .. | .. | .. | 6·5 mm. ,, |
| Aortic cœlio-mesenteric root | .. | .. | .. | .. | .. | 1·5 mm. ,, |
| Aortic lieno-gastric spermatic roots | .. | .. | .. | .. | .. | 1 mm. ,, |

The arterial component of each rete is surrounded by a complementary though more open system of venous spaces, which are derived from an extension of the hepatic sinus placed transversely in the attachment of the rete to the liver. This cavity is relatively capacious and lodges the main arterial collecting trunk of the rete; in front it rapidly breaks up amongst the meshes of the arterial component into a system of communicating spaces that gradually get smaller and smaller as the arterial network becomes closer, and towards the anterior end of the rete again opens out amongst the larger arterial tributaries to communicate finally with a great subscapular venous sinus and through it with the ductus Cuvieri and sinus venosus of the heart. Throughout the rete the spaces of the venous component are considerably larger than the arterioles.

In histological structure (Plate 10, fig. 5) the arterioles that compose the bulk of the rete show no marked deviation from that normal to arteries of small size. The nuclei of the endothelium are perhaps less flattened than is usually the case, but the cells of this layer do not suggest an epithelium modified to produce by secretion or otherwise any alteration in the constitution of the blood passing along the vessel.

Beneath the endothelium is a very delicate *elastica interna*, and outside this a media of pure smooth muscle two or three cells thick. The media contains no elastic tissue and is separated by a delicate *elastica externa* from the fibrous and feebly elastic adventitia. The adventitia bounds the lumen of the surrounding venous spaces without the interposition of an epithelium.

The description of these supra-hepatic retia by MÜLLER (17) gives a very clear and excellent picture of their position and general appearance, but is misleading as regards their connection with the rest of the vascular system. Thus, as shown above in discussing the afferent vessels of the retia, MÜLLER was evidently in doubt as to the true origin of these vessels and regarded them as *cœlio-mesenteric* and *lieno-gastric* arteries shifted out of their proper position, and not, as they are in truth, the pericardial arteries. He also included amongst the tributaries of the retia, the vessel that connects the rete with the lateral and lower lateral cutaneous arteries. In this he may have been correct, though I venture to think that the evidence I have brought forward (p. 232) with regard to the mutual relations of these vessels is conclusive that this trunk is efferent from the rete and not afferent to it, and forms the main root of the lower lateral cutaneous artery.

Nor am I able entirely to confirm MÜLLER's statements about the vessels that spring from the retia. His description of them (17, p. 273) is as follows:—

“The arteries which collect the blood from the retia and carry it to the chylopoëtic organs emerge partly from the outer side of the retia, partly from between the two organs. On the outer side many vessels of the anastomotic vascular network unite together to form a great artery which, on each side, passes behind the corresponding liver lobe, thus forming two new *arteriæ intestinales*. The right divides upon reaching the stomach into three branches, one passes down to the right side of the valvular intestine and accompanies it, another is distributed to the ventral surface of the

stomach ; a third passes upwards with the portal vein between the upper part of the two liver lobes and divides into two twigs, one for each lobe of the liver ; at this spot these arteries again form a connection with the rete, so that from this spot the liver receives blood direct from the lower part of the rete as well as from the branch of the right arteria intestinalis secundaria that accompanies the portal vein."

"The left arteria intestinalis secundaria, after emerging from its rete, takes a similar course behind the liver lobe of its side and behind the stomach, and then divides into two branches, one of which supplies the hinder wall of the stomach, the other forming the second or left artery of the valvular intestine."

From this quotation and from the figure attached to his paper, it is evident that, if the facts are as I have stated them to be, MÜLLER was mistaken in his observation of the efferent vessels of the retia in several more or less important particulars. He failed to notice the interesting partially obsolete connection between the aorta and the efferent vessels of the rete representing the original roots of the cœlio-mesenteric and lieno-gastric spermatic arteries. He did not realise the double nature of the lieno-gastric vessels and their symmetrical origin, one from the dorsal flexure of each collecting trunk, but regarded the cœlio-mesenteric trunk as comparable in origin to the lieno-gastric and symmetrical with it, whereas in fact this latter vessel is asymmetrical and has no counterpart given off from the left rete.

After careful examination I am unable to confirm the statement made by MÜLLER that the hepatic arteries draw some of their blood from the rete. These arteries (fig. 15, *h.a.*) rose separately and not by a single trunk, from the main cœlio-mesenteric vessel and curved outwards to either side upon the dorsal surface of each liver lobe, but so far as I was able to see received no such contingent from the posterior mesial parts of each rete as he describes. The blood-vessels of sharks are notoriously prone to form anastomoses, but it is unlikely that such an important connection, if it were normal to the genus, should have been absent in both the individuals I examined on this particular point. We may thus, I think, conclude that whatever may have been the condition in MÜLLER'S specimen, an hepatic supply from the rete is not usual.

5. *The Venous System.*

In the foregoing description of the arteries passing reference has been made to certain of the veins, but a few remarks of a more general nature are necessary to give a coherent picture of the system and of the modifications it has undergone in correspondence with the adaptive changes that have taken place in the rest of the organs of circulation.

In the head region the venous sinuses show comparatively little deviation from the normal. The orbital sinus lies below and in front of the eyeball along the floor of the orbit, forming in its anterior parts a simple reservoir, but becoming more and more broken up further back by trabeculæ which support the coils of the carotid arteries and bind them together in a fairly compact meshwork of connective tissue.

Posteriorly this sinus is in connection with the head of the jugular vein through a

system of small irregular communicating spaces that pass through the suborbital fenestra in the basal plate of the skull and accompany the main trunk of the posterior carotid.

The jugular vein occupies the normal position above the dorsal extremities of the gill slits. Just above its valved entry into the duct of Cuvier it is joined by a large vessel (unrepresented, so far as I know, in other sharks) that runs downwards (fig. 1, *lat.cut.v.*) within the posterior wall of the fifth gill pouch, between the last branchial arch and the scapula, and is continuous above with the lateral cutaneous vein.

The lateral cutaneous vein at its union with this vessel passes external to the main trunk of the lateral cutaneous artery, and from this point backwards is double—one arm lying above and one below the artery. The two veins accompany the artery throughout its course beneath the lateral line to the root of the tail, receiving factors corresponding to the arterial branches and contributing to the rete in the lateral trunk muscles brush-like bundles of veins that run between and parallel to the vessels of the arterial component filling in the interspaces between them. Close below the entry of the jugular vein, the duct of Cuvier receives posteriorly the outlet of a capacious sinus (fig. 15, *ssc.c.s.*) that extends behind the pericardial diaphragm from near the ventral mid-line to the posterior border of the scapula. This sinus occupies the antero-lateral border of the supra-hepatic rete and forms, as previously mentioned, a great trabeculated reservoir through which all the venous blood of the rete passes on its way to the heart.

At the hinder margin of the scapula the sinus narrows and is continuous with a subcutaneous vein that runs between the two arms of the lower lateral cutaneous artery to the pelvic region of the body, receiving throughout its course factors similar to the branches of the artery.

Upon the wall of the cloaca, the main trunk of the vein is resolved into a coarse meshwork of a few large communicating spaces (fig. 12, *cl.v.*), into which below the hinder end of the kidney is received the blood from the venous component of the sub-renal rete.

The homology of these cutaneous veins in *Lamna* is not too clear. Normally upon the lateral body wall there is a single large cutaneous vein underlying the lateral line and opening into the subscapular sinus. This vessel in the late embryo, but apparently not in the adult (MAYER, 15, p. 324), may be represented by two parallel vessels, one beneath the lateral line, the other situated somewhat lower down the body wall, and both uniting before opening into the subscapular sinus.

The position of the vessel that in *Lamna* I have called the lateral cutaneous vein, beneath the lateral canal, suggests that it is homologous with the lateral cutaneous of other sharks, in spite of the fact that it is connected with the jugular system and not, as it should be, if normal, with the subscapular sinus. For it seems more likely that any change that has occurred should be in the mode of connection of the vessel with the central part of the venous system than in its general position upon the body and in its territory of distribution.

But if this vessel is the lateral cutaneous, what is the vessel, called by me the "lower lateral cutaneous," which opens into the extremity of the subscapular sinus as the lateral cutaneous normally does? Is this a new vessel, or a separated branch of the lateral cutaneous, comparable with the ventral branch recorded by MAYER in the embryo? From its connection with the subscapular sinus it seems most probable that it is the latter, and that the upper branch ("lateral cutaneous") has become separated from it at its anterior end and migrated upwards to join the jugular.

With regard to the subscapular reservoir, there is little doubt from its position relative to the scapula that the posterior part, at any rate, is homologous with the normal subscapular sinus, though considerably enlarged owing to its association with the supra-hepatic rete. Its anterior part, however, must be considered, from its relation to both the pericardial diaphragm and ductus Cuvieri, to represent the terminal portion of the posterior cardinal sinus. This suggestion is borne out by the entry into this region of the common subscapular reservoir of a vein which, though minute, can from its anatomical relations be nothing else than the posterior cardinal trunk.

This interesting little vessel (figs. 1, 15, *p.cd.v.*) commences at or shortly behind the first sympathetic ganglion and passes outwards across the dorsal aspect of the œsophagus at the anterior limit of the body-cavity to the mesial wall of the subscapular reservoir and opens into it in front of the level of the scapula by a funnel-shaped mouth.

There can, I think, be no doubt that this small vein is the posterior cardinal in a very much reduced condition, extending back little, if at all, beyond the first sympathetic ganglion. Sections taken further back (fig. 16,) through the soft tissues underlying

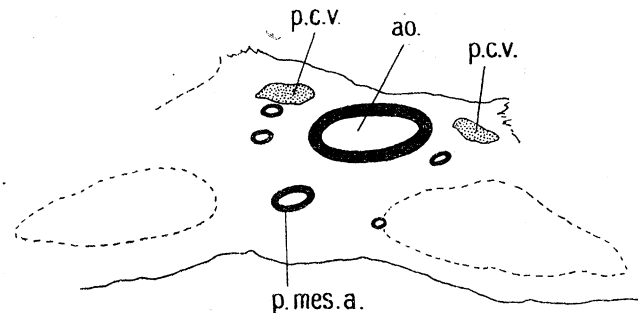


FIG. 16.—Transverse section of the aorta and its surroundings at the level of the first dorsal fin of *Lamna cornubica* (specimen D), showing two small veins that probably are the reduced posterior cardinals.

the spine showed no clear indication of posterior cardinals, which under normal circumstances form so conspicuous a feature throughout the trunk, and it is clear that the posterior cardinal system has to all intents and purposes been eliminated, so far as the trunk circulation is concerned, and its place taken by the sub-renal rete and lower lateral cutaneous veins; the only part of any importance that remains being the extreme anterior portion, which, in combination with its subscapular offshoot, has been enlarged to form the efferent reservoir of the supra-hepatic rete.

The lateral veins have been already described (p. 234) and except for their small

size and loss of connection with the pelvic fins and cloaca, call for no particular comment.

The caudal and hepatic portal veins, so far as I examined them, appeared to be normal.

Each lobe of the liver is drained by two hepatic veins, which pass forward parallel to one another near the dorsal surface of the lobe, one near the ventral (mesial) border, the other (figs. 1, 15, *h.v.*) about half-way up towards the outer border. These two veins open respectively into either end of a capacious cylindrical sinus set transversely across the anterior end of the lobe at the base of the corresponding supra-hepatic rete.

Within this reservoir lies the commencement of the main collecting duct of the arterial component of the rete, and from its anterior surface a labyrinth of spaces passes forward into the rete, occupying all the interstices between the meshes of the arterial network, and constituting the venous component.

At the lateral extremity of the sinus, where it is joined by the outer or more dorsal of the two hepatic veins, a small hole (fig. 15, *p.*) gives passage to the arterial collecting trunk of the rete and forms a connection between the hepatic and spermatic sinuses. From this passage the spermatic sinus (fig. 15, *sp.s.*) extends upwards, beside the œsophagus and across the middle line within the mesentery of the testis, and is prolonged backwards around the spermatic artery.

A connection between the hepatic and spermatic sinuses appears to be unusual in sharks, though common to the rays, and may in *Lamna* be part of a general modification (due to the development of the supra-hepatic retia) by which the blood from the gonads is made to pass through the retia on its way to the heart, and has no doubt been one of the factors responsible for the reduction of the posterior cardinal circulation.

The inner and ventral extremity of each transverse hepatic sinus reaches the attachment of the ventral ligament of the liver and at this point is prolonged forward between the two lobes of the supra-hepatic rete as a narrow tube (fig. 15, *h.s.*) that perforates the pericardial diaphragm and opens into the sinus venosus close beside its fellow by an orifice with valved protuberant lips. These ventral prolongations of the hepatic reservoirs are without doubt, as MÜLLER has already pointed out (17, p. 274), the original hepatic sinuses, presenting a condition comparable to the narrow and separate hepatic veins found in *Centrophorus* and other *Spinacidæ*.

The transverse segment of the sinus, on the other hand, would seem to be a new structure, called forth in relation to the supra-hepatic retia, deflecting the flow of blood from the liver through these organs and supplanting the channels by which it was originally conveyed direct to the heart. The venous meshwork of the retia, if the transverse sinus is a secondary adaptation, can hardly be regarded as representing a stage in the transformation of simple and separate hepatic veins into the single large sinus characteristic of *Scyllium* and other sharks, as suggested by LAFITE DUPONT and NEUVILLE (13, 18).

General Discussion.

From the above description of the anatomy of the main blood vessels of *Lamna* it is apparent that nearly the whole vascular system has undergone extensive alteration from the normal type. The changes observed are closely bound up with the presence of large retiform meshworks of vessels, and it is pretty evident that the development of these retia has been the main, possibly the sole, cause of the whole series of modifications that has taken place.

If this is the case, it is plain that these retia must in some way be of immense value in the general life of the fish, for one cannot conceive that anatomical changes so extensive and so profound could be brought about except for reasons of really fundamental importance. What these reasons are and the precise way in which the retia are an aid to the circulation are problems of some difficulty.

In the introduction to this paper it was pointed out that retia are found in a large number of Vertebrates, but in view of the great diversity in the habits and zoological position of the animals that possess them, there is no reason to assume that their action is necessarily the same in all cases. Fishes, in which respiration is carried on by gills and which in consequence have a mode of circulation essentially different from that of an air-breathing animal, have problems to deal with of a nature other than those that confront, for instance, an aquatic mammal, and although retia may, and in fact do, occur in both it would be unwise to assume that their action in the two cases is necessarily the same.

It seems therefore to be justifiable in discussing the possible use of these organs in *Lamna* to consider them without reference to other non-piscine retia and to be content if a plausible explanation can be suggested of their function in this particular instance.

So far as I have been able to ascertain, little has been written recently on the action of retia.

General opinion, founded chiefly on MÜLLER'S suggestions (17, p. 277), assigns to these structures a mechanical function causing by means of the obstruction they offer to the flow of the blood a local slowing down of the blood stream to the organs they supply.

Such a retardation certainly would occur within a rete both on account of the increase of the vascular capacity within the organ and the extra friction to which the blood stream would be subjected ; but one would expect that upon leaving the rete by vessels of a decreased capacity the stream would again be accelerated to a degree proportionate to the smallness of the vessels of exit. That such an increase in velocity takes place was maintained by VOLKMANN, in a work on "Hæmodynamics," quotations from which are given by MILNE EDWARDS ('Leçons sur la Physiologie,' T. IV, 1859, p. 260).

CARAZZI (6, p. 124) in discussing the use of the carotid tangles in the Carchariidæ lays some stress on the probable moderating influence of the contorted and sinuous arrangement of these vessels upon the blood stream, and suggests that they may act

as a sort of buffer to absorb abrupt changes in the blood pressure, transmitting such changes slowly and gently to the delicate tissues of the eye and brain.

The same author when describing the rete that he discovered upon the kidney of *Selache maxima* (6, p. 89) pursues the same idea, and considers that the rete probably acts as a reservoir into which may be received any excess of blood thrown out of the aorta when the pressure in this vessel is suddenly increased. By this means the actual supply to the kidney would be maintained at an even pressure, and abrupt fluctuations would be avoided.

It will be observed, that in these explanations the rete is regarded essentially as a passive organ, which by the increase in the capacity of its component vessels and their labyrinthine disposition either retards the blood flow (MÜLLER) or maintains it at a comparatively constant, but not necessarily reduced, velocity, and acts as a protection against sudden increases in pressure.

The active properties of the vessels are ignored.

Due consideration was however given to this latter aspect of the question by VOLKMANN in the case of the carotid retia of Ruminants. Observing that the nerve supply to these retia was rich, he inferred that the vessels would be correspondingly active and suggested that the rete not only moderated the blood stream to the brain passively, but exerted an active control over it by suitable expansions and contractions of its component vessels.

From this brief *résumé* of such literature on the function of retia as I have been able to discover, it would seem that the *rôle* of these organs is usually thought to be a mechanical one for the control of the blood supply to particular organs. It is suggested that by their means the blood stream is kept constant, either at a diminished (MÜLLER) or increased (VOLKMANN) velocity, harmful abrupt rises in pressure are neutralised, and (in some cases) suitable variations in the quantity of the supply are actively brought about.

In discussing any question of the circulation in fishes, there are certain peculiarities that must be borne in mind.

1. The systemic circulation differs from that of air-breathing Vertebrates in that the blood pumped from the heart encounters almost at the very outset of its course the heavy resistance of the capillary system of the gills. Thus the pulsations due to the heart-beat are checked and though, under favourable circumstances, they may just be detected beyond the gills in the aorta and visceral arteries (SCHOENLEIN, 21), the pumping action of the heart exerts practically no *direct* pressure upon the general arterial circulation, and the flow of blood in the arteries approximates rather to that in the veins of an air-breathing Vertebrate than to that in the arteries.

2. From experiments carried out by SCHOENLEIN (21) on dogfish and rays it appears that in fishes the blood pressure is extraordinarily low. In the ventral aorta of the torpedo for example, the mean pressure is 22–24 cm. water, in the dogfish somewhat higher. Beyond the gills the pressure is much decreased, being no more than 8 cm.

water in the abdominal aorta of the torpedo, which is slightly less than that in the lateral cutaneous vein. The pressure in the cardinal sinus is practically reduced to zero and in the pericardium there is a negative pressure of — 5 cm. water.

It would thus seem that the circulation of fishes is very feeble, and is subject to little variation in pressure from the heart's action, though no doubt local variations may occur, even in the arteries, through the direct pressure of surrounding muscles upon the vessels in accordance with the active movements of the fish.

3. It is stated by WIDAKOWICH (25, p. 648) that the amount of blood in the dogfish, though not so small compared with the body-weight as it is in many fishes, is far from sufficient to fill the great venous sinuses characteristic of the Elasmobranchs.

In this connection some interest attaches to an observation made by MAYER (15, p. 339) on semi-transparent young dogfish. In these young individuals he noticed that the small superficial veins upon the fins, when the fish were quiescent, were dark with blood, but as soon as strong movements of the body took place, the blood in these veins was drawn off and it was only after some 10 to 15 minutes that the equilibrium of the circulation was restored and the vessels became again dark with venous blood. This observation suggests that with sudden activity the reduction in pressure in the larger veins, due to the suction of the heart, increases out of proportion to the rapidity of the arterial flow and draws off blood into the half-empty venous sinuses faster than it can be replaced in the capillaries. If this is a correct interpretation of MAYER'S observation, one may reasonably suppose that a mechanism of any sort calculated to rapidly adjust and preserve the equilibrium between the various parts of the circulatory system irrespective of changes in the general bodily activity would be of distinct advantage and tend to increase the efficiency of the circulation.

Bearing in mind the above statements on the general character of the circulation in fishes, it is evident that the mode of propulsion of the blood is far less efficient than in Terrestrial Vertebrates and the flow in the arteries is in consequence probably sluggish and more or less liable to local interruption from the fluctuating pressure of neighbouring organs and muscles. Adaptations to increase its efficiency might then very well be expected to occur in fishes of special activity where an improved blood supply was called for.

If the retia in *Lamna* are modifications for this purpose, as seems likely, one might hope to find indications of some special life habits to account for the need of them. Such, however, is apparently not the case, for this shark, so far as my information goes (DAY, 7, p. 297), presents no strongly marked peculiarities of habit. It is a pelagic shark of very powerful build and extremely active mode of life, though no more active than other genera in which no retia occur.

Turning now to the structure of the retia themselves, the following particulars are worthy of consideration.

The carotid tangles present in all cases, though to very different degrees, an increase in capacity. At its simplest this is due mainly to a lengthening of the vessel without

an increase in calibre (*Galeus*); in the more specialised cases not only is the vessel enormously lengthened, but it also presents a marked enlargement in girth, and in the most extreme instance (*Lamna*) breaks up to form a close meshwork of smaller anastomosing channels.

It is difficult to estimate the increase in capacity represented by these different modifications, but in *Carcharias*, *Alopias* and *Lamna*, it is evidently very great.

A like increase in capacity is shown by the sub-renal rete and probably also by the trunk rete of the lateral cutaneous artery. In the supra-hepatic, although the ultimate subdivision of the afferent trunk was very minute, an estimate founded (in specimen D) on a comparison of the area of the lumen of the afferent trunk with the sum of the areas of the arterioles in a section through the middle of the rete, shows that the blood-containing area is increased within the rete by at least ten times.

It is thus clear that these retia, with the possible, though not probable, exception of that in connection with the lateral cutaneous artery, are in the nature of reservoirs capable of containing far more blood than that brought to them at any particular moment by their afferent vessels or removed from them by the efferent. They would thus appear to resemble mill-ponds in which a head of water is maintained to render the outflow constant and independent of fluctuations in the inflow.

But apart from this common feature of increased capacity the retia differ from each other in general structure and in the histological details of their components.

The carotids (Plate 9, fig. 2) are comparatively weak in muscle but show a great increase in the thickness of the fibrous adventitia and are particularly remarkable for the richness of their elastic tissue elements; these not only form a close and elaborate network throughout the adventitia, but permeate the surrounding tissues and trabeculae by which the coils and meshes of the rete are bound together. This structure is difficult to interpret. The thickness and elasticity of the outer coats indicate a mechanism to resist and neutralise sudden increases of pressure, as suggested by CARAZZI, although it is difficult to see how such increases could arise, particularly when one considers the extremely restricted origin (fig. 2, p. 213) of the carotids from the efferent branchial vessels, the interposition (in the case of the anterior carotid) of the pseudobranch plexus at the commencement of the artery, and the protected position in which the coils and retia of the carotids lie (fig. 3, p. 215).

In view of the difficulty in imagining how the blood in the carotids can be subject to marked fluctuations in pressure, I am unable to regard the modifications of these vessels as designed to neutralise the shock of sudden pressure increases, and can only explain them as reservoirs for providing a constant and regulated flow of blood to the organs they supply, particularly the brain and internal structures of the eye. Their action would appear to be mainly that of distensible elastic tubes and to depend relatively little upon their muscular properties to judge from the great elaboration of their elastic tissues and the relative weakness of their muscular walls.

The histological structure of the vessels of the subrenal rete is of a very negative

character. Their walls are in fact remarkable only for the relatively slight development of all their constituent elements. It is therefore difficult to suggest any function for this rete, beyond that of a reservoir within which blood can be stored in sufficient quantity to make the supply to the kidney constant and independent of any fluctuations there may be in the flow within the lower lateral cutaneous artery; the flow in this artery would apparently depend largely on the condition of the outflow from the supra-hepatic rete, which, as will be suggested below, is probably of a variable character.

The peculiar arrangement of the deep branches of the lateral cutaneous artery, in a mass of fine parallel vessels of somewhat remarkable structure (Plate 10, fig. 6), seems to be in some way connected with the semi-independence of the column of trunk muscles that they supply. The want of segmental attachments to the vertebral column in the region of the trunk suggests that this muscle column is in a special sense adapted for the lateral movements of the tail, but in what way its actions are correlated with the peculiarities of its blood supply, I am at a loss even to suggest.

The arterioles of the supra-hepatic rete differ considerably from those of the retia hitherto considered. They show a thickish middle layer of pure muscle, a fibrous outer layer of moderate thickness, and a comparatively slight development of elastic tissue (Plate 10, fig. 5). This type of structure, although in no way specialised, indicates an arteriole capable of very considerable powers of contraction and expansion.

It seems likely, therefore, that in action this rete is not so passively automatic as the others probably are, and I am inclined to suggest that it is a reservoir, in which not merely a head of blood is collected to maintain a constant flow to the viscera, but an active reservoir from which a richer supply of blood may be injected into the viscera as required. For this action to take place it is necessary to assume that contraction of the arterioles of the rete should take place progressively from the afferent end of the rete to the efferent, a mode of contraction of which there is certainly no proof, but which, I think, is not in itself improbable. Granted that such contraction of the rete takes place, it is to be observed that the fine meshed structure of the organ, in which the proportion of muscle tissue to the blood carrying capacity is vastly greater than it would be in the case of a single large vessel, renders it eminently suitable for delicately regulated injection.

Contraction of the arterioles of the rete would also have a secondary effect upon the circulation by increasing the size of the venous spaces by which they are surrounded. Thus not only would blood be directly driven to a given part by the contraction of the arterial component, but the return flow of the blood from the part would be eased by an automatic dilatation of the venous component.

Whether the supra-hepatic rete acts in this way or not, it seems clear from its position and relations to surrounding structures that in any case blood must be squeezed from it into the visceral arteries in deglutition. Upon referring to Plate 10, fig. 3, it will be seen that the mass of the rete lies between the œsophagus and a dense non-extensile layer of peritoneum (*pt.*). Close above the œsophagus is the vertebra column.

The dilatation of the œsophagus caused by swallowing food, which in the case of this shark consists of fish of some size, would undoubtedly compress the rete against its peritoneal covering from before backwards, forcing blood from it into the visceral arteries, and thus flooding the stomach and other alimentary viscera preparatory to the processes of digestion.

In making the above suggestions on the possible action of the series of retia that occur in *Lamna*, I do so naturally with very great hesitation, owing to the inadequacy and purely anatomical character of the facts upon which they are based. It seems, however, fairly clear that their main object is, as suggested by CARAZZI and others, to provide a stabilising head of blood, to ensure that a given part should constantly receive the optimum supply. In view of the poor arterial propulsion and low pressure in the arteries of fishes it does not seem likely that they are needed or used to neutralise the shock of sudden increases in pressure, as has generally been assumed; in fact the opposite is more likely the case, to guard against temporary diminution of the supply and consequent local anæmia.

In carrying out the above work I have received much kindly encouragement from my chief, Sir ARTHUR KEITH, for which I wish to thank him cordially. I am also much indebted to Mr. S. STEWARD for preparing the photographs reproduced in the Plates and to Mr. TERZI for help in translating various Italian papers for me.

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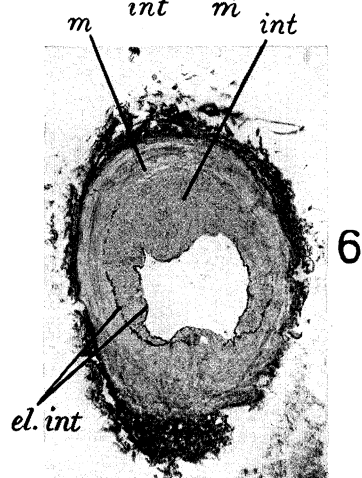
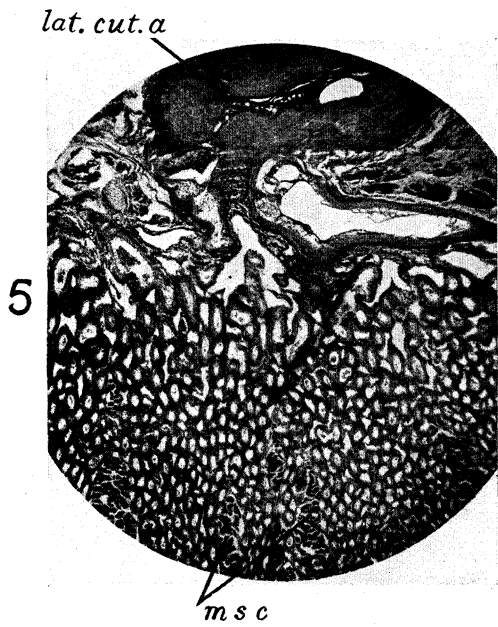
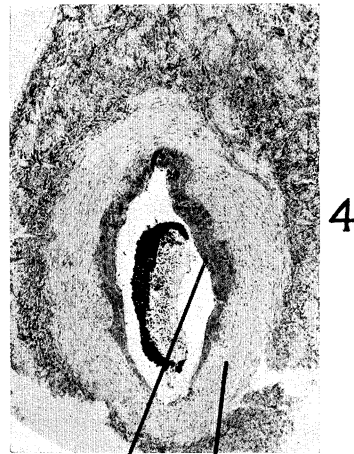
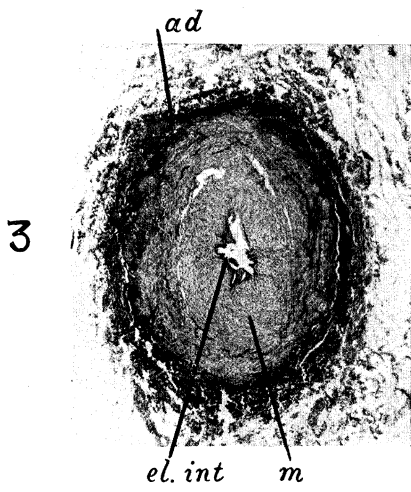
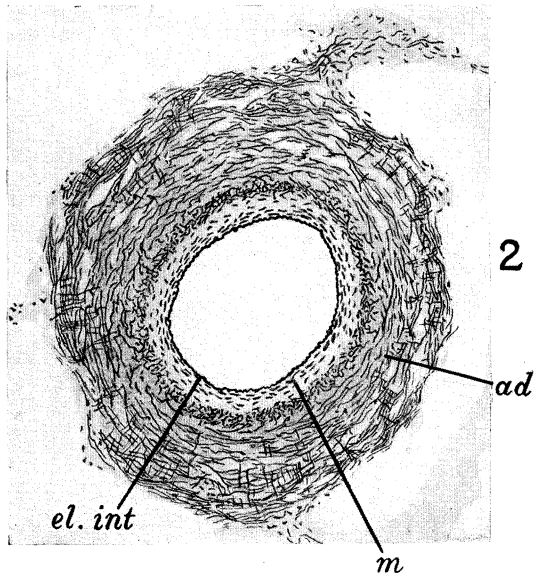
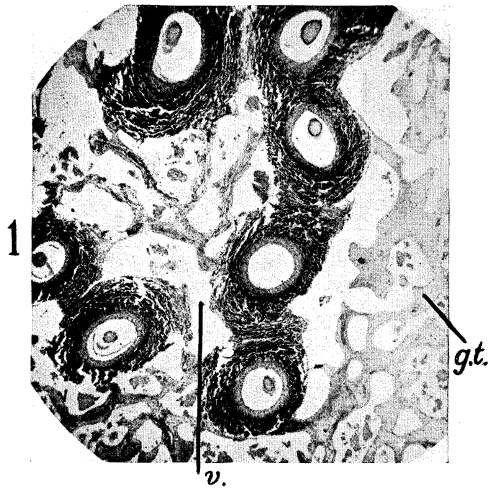
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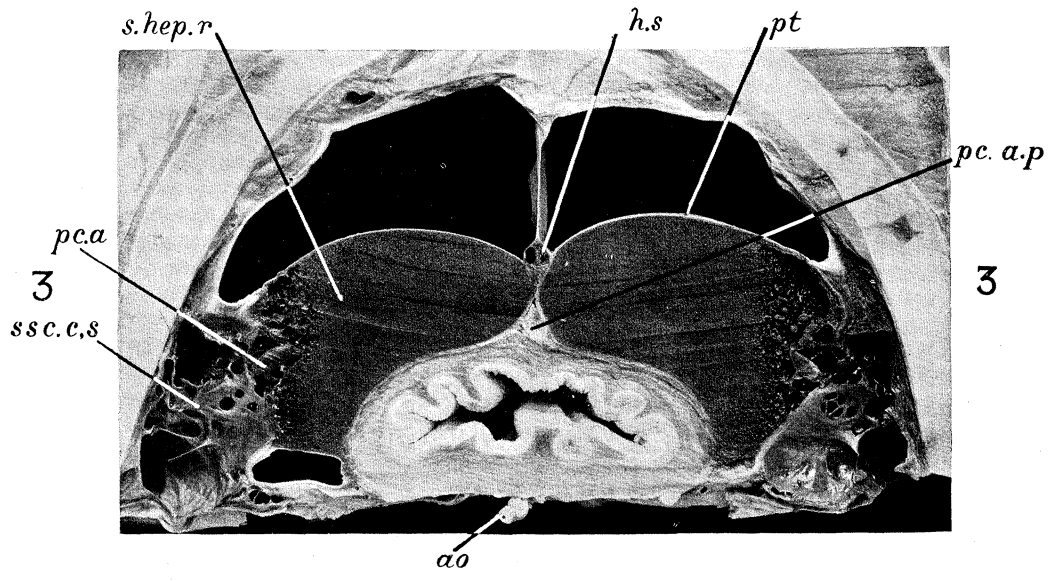
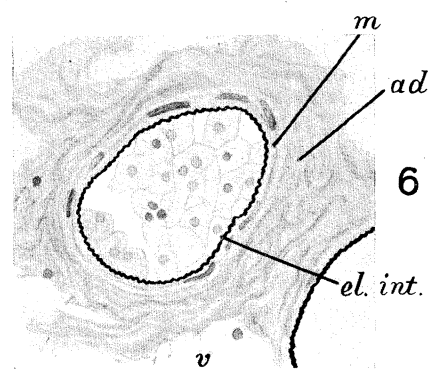
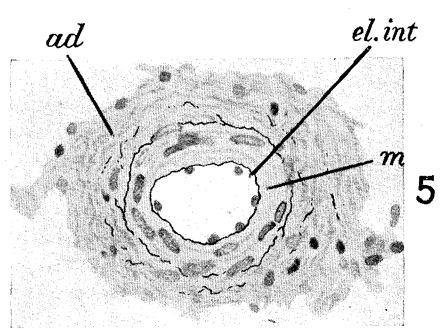
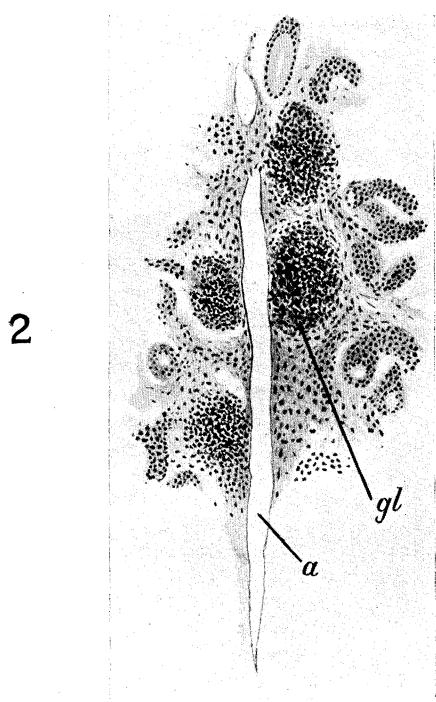
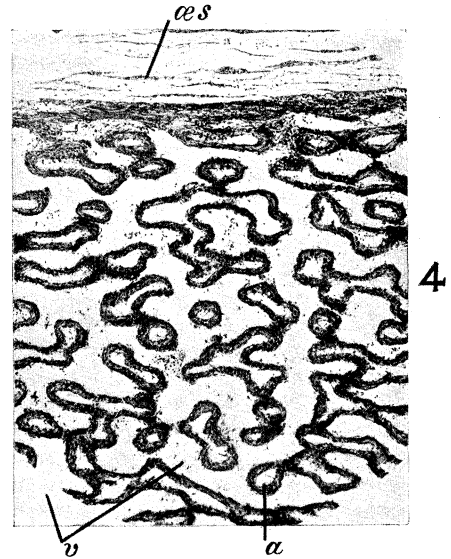
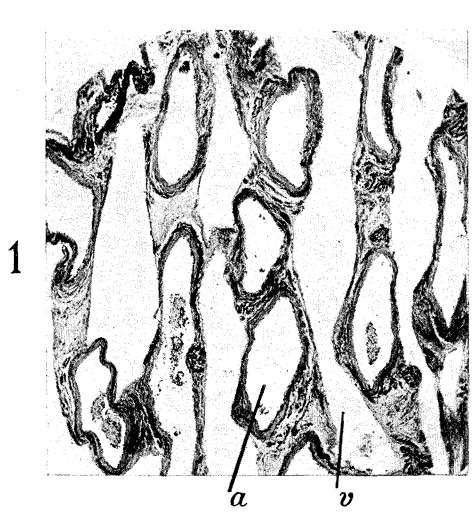
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LIST OF REFERENCE ABBREVIATIONS FOR PLATES AND TEXT-FIGURES.

- a., artery.
 abd.p., abdominal pore.
 a.cr.a., anterior carotid artery.
 a.cr.r., anterior carotid rete.
 ad., adventitia.
 aff.br., afferent branchial artery.
 aff.psbr.a., afferent pseudobranch artery.
 an., anastomosis between lateral cutaneous and lower lateral cutaneous arteries.
 ao., aorta.
 b.d., bile duct.
 br.p., mesial wall of branchial pouch.
 c.v., caudal vein.
 cl.a.,v., cloacal artery and vein.
 coel.mes.a., coelio-mesenteric artery.
 coel.mes.r., coelio-mesenteric aortic root.
 coll.tr., collecting trunk of supra-hepatic rete.
 comm. 1, commissure giving rise to median hypobranchial artery.
 comm. 2, 3, commissures giving rise to pericardial arteries.
 comm. a., commissural branch of posterior carotid artery.
 d.cor.a., dorsal coronary artery.
 d.int.a., dorsal intestinal artery.
 eff.br., efferent branchial arteries.
 ep.br., epibranchial arteries.
 el.int., elastica interna.
 ex.br., extrabranchial cartilage.
 ext.cr.a., external carotid artery.
 fen., suborbital fenestra.
 g.a., gastric artery.
 gl., glomerulus.
 g.t., gelatinous connective tissue.
 h.a., v., hepatic artery and vein.
 h.s., original hepatic sinus.
 hy.ep., hyoidean epibranchial branch of posterior carotid artery.
 hymd., hyomandibular cartilage.
 i.jug.v., inferior jugular vein.
 int., intima.
 int.cr.a., internal carotid artery.
 jug.v., jugular vein.
 kid., kidney.

- l., liver.
- l.c., lateral line canal.
- l.gst.a., lieno-gastric artery.
- l.gst.sp.r., lieno-gastric-spermatic aortic roots.
- l.lat.cut.a., v., lower lateral cutaneous artery and vein.
- l.lat.cut.r., root of lower lateral cutaneous artery from supra-hepatic rete.
- lat.a., v., lateral artery and vein.
- lat.cut.a., v., lateral cutaneous artery and vein.
- lat.cut.an., anastomosis between lateral cutaneous artery and aorta.
- lat.cut.r., lateral cutaneous rete in trunk muscles.
- lat.hpbr.a., lateral hypobranchial connecting chain.
- lev. mx.s., levator maxillæ superioris.
- lig., ligament from hyomandibular cartilage to floor of cranium.
- m., media.
- m.hpbr.a., median hypobranchial artery.
- md.a., mandibular artery.
- msc., muscle columns.
- mx.a., maxillary artery.
- nut.a., dorsal nutritive arteries of gill pouches.
- oes., oesophagus.
- oph.a., ophthalmic artery.
- opt.n., optic nerve.
- orb.s., orbital sinus.
- p., passage between hepatic and spermatic sinuses.
- p.cd.v., posterior cardinal vein.
- p.cr.a., posterior carotid artery.
- p.cr.r., posterior carotid rete.
- p.mes.a., posterior mesenteric artery.
- pan., pancreas.
- pc.a., pericardial artery.
- pc.a.p., pericardio-abdominal passage.
- psbr., pseudobranch rete.
- psbr.s., extension of orbital sinus covering pseudobranch rete.
- pt., cut edge of peritoneum.
- pt.q., palato-quadrate cartilage.
- py., pylorus.
- r., rectum.
- re.a., afferent artery to subrenal rete.
- rst.a., rostral artery.
- s., space between trunk muscle and vertebral column.
- s.cl.a., subclavian artery.





s.hep.r., supra-hepatic rete.
 s.re.r., subrenal rete.
 sc., scapula.
 sp., spiracle.
 sp.a., spermatic artery.
 spl., spleen.
 sp.s., spermatic sinus.
 sp.sc., sperm sac.
 ssc.c.s., subscapulo-cardinal sinus.
 st., stomach.
 sy.g., sympathetic ganglion.
 u.g.p., uro-genital papilla.
 ur., ureters.
 v., venous spaces.
 v.d., vas deferens.
 v.int.a., ventral intestinal artery.

DESCRIPTION OF PLATES.

PLATE 9.

- Fig. 1.—Anterior carotid rete of *Lamna cornubica* trans. sec., $\times 20$.
 Fig. 2.—Component artery of anterior carotid rete of *Lamna cornubica*, showing the abundance of elastic tissue., trans. sec., $\times 60$.
 Fig. 3.—Third epibranchial artery of *Lamna cornubica* (specimen B), trans. sec., $\times 20$.
 Fig. 4.—Aortic root of coelio-mesenteric artery of *Lamna cornubica* (specimen B), trans. sec., $\times 50$.
 Fig. 5.—Rete arising from lateral cutaneous artery of *Lamna cornubica*, transverse to the lateral cutaneous artery. $\times 20$.
 Fig. 6.—Anastomosis between the lateral cutaneous and lower lateral cutaneous arteries of *Lamna cornubica*, trans. sec., $\times 20$.

PLATE 10.

- Fig. 1.—Section through the subrenal rete of *Lamna cornubica*, $\times 50$.
 Fig. 2.—Artery given off from the subrenal rete in close proximity to several renal glomeruli, $\times 70$.
 Fig. 3.—Transverse section through the supra-hepatic retia of *Lamna cornubica*, seen from anterior aspect.
 Fig. 4.—Transverse section through centre of the supra-hepatic rete of *Lamna cornubica*, $\times 50$.
 Fig. 5.—Arteriole of supra-hepatic rete of *Lamna cornubica*, trans. sec., $\times 270$.
 Fig. 6.—Arteriole of lateral cutaneous rete of *Lamna cornubica*, trans. sec., $\times 270$.
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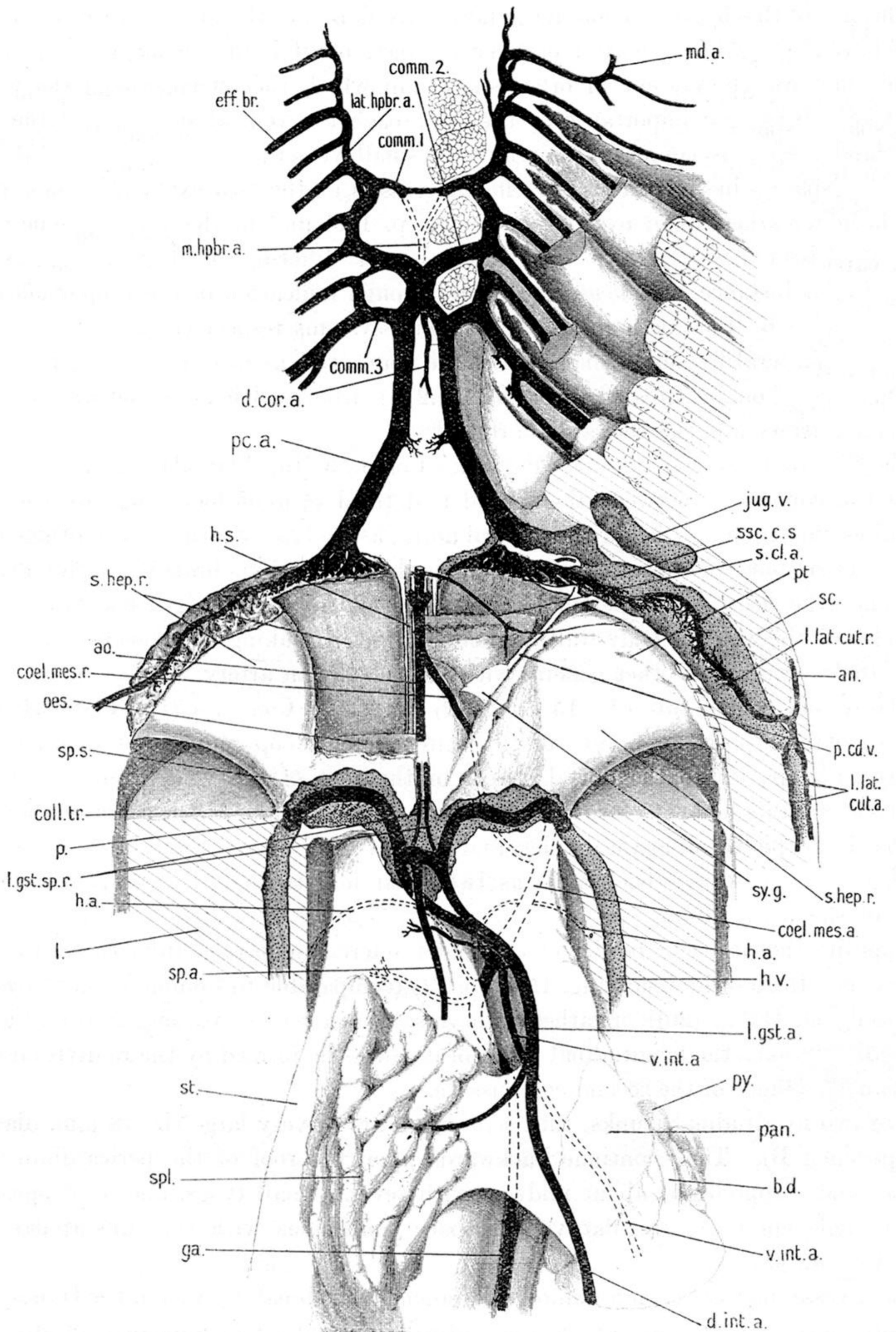


FIG. 15.—The hypobranchial and visceral arteries of *Lamna cornubica* seen from the dorsal aspect. Upon the left side the oesophagus has been cut back further than on the right to expose the supra-hepatic rete; arteries, black; veins, dotted.

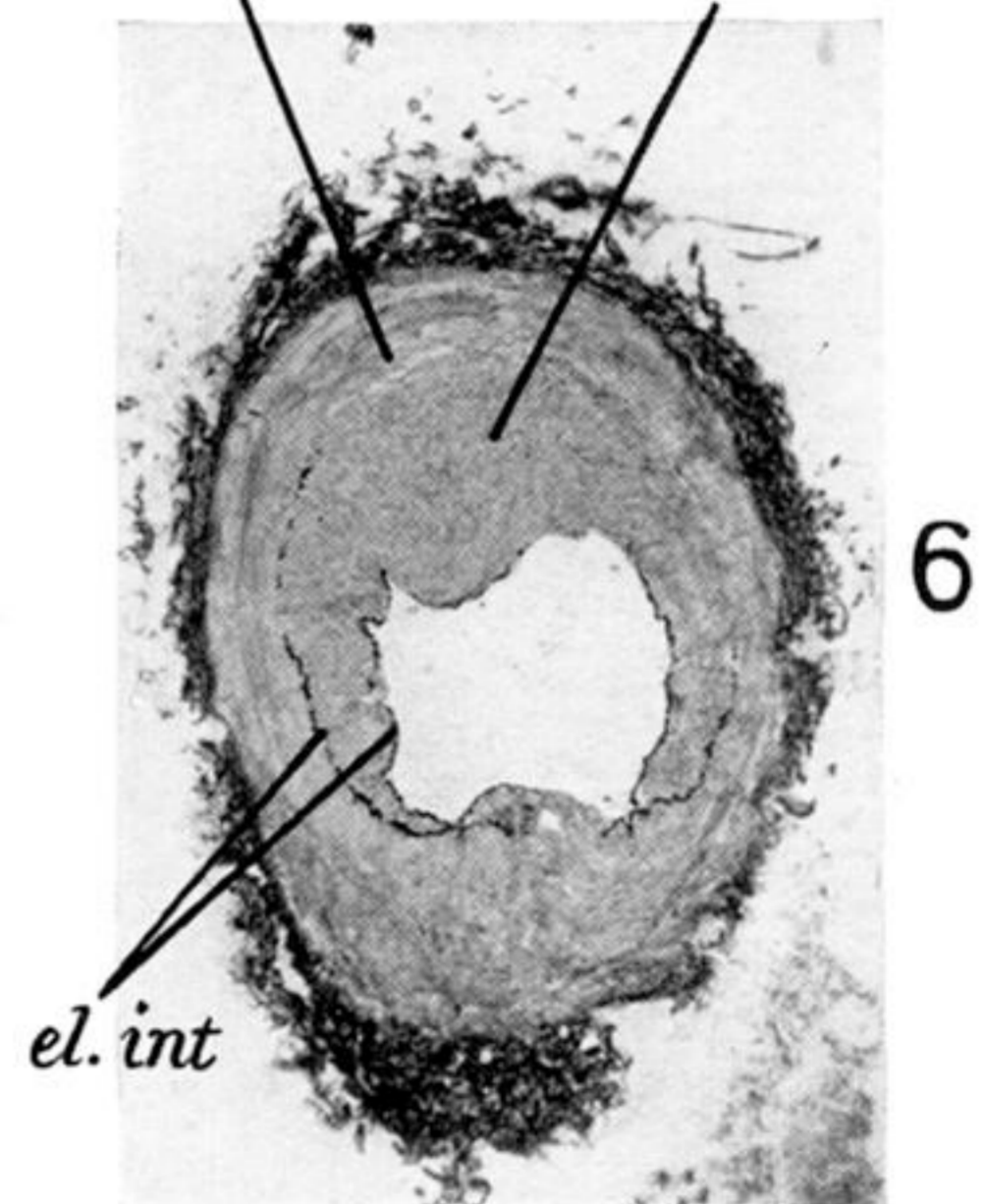
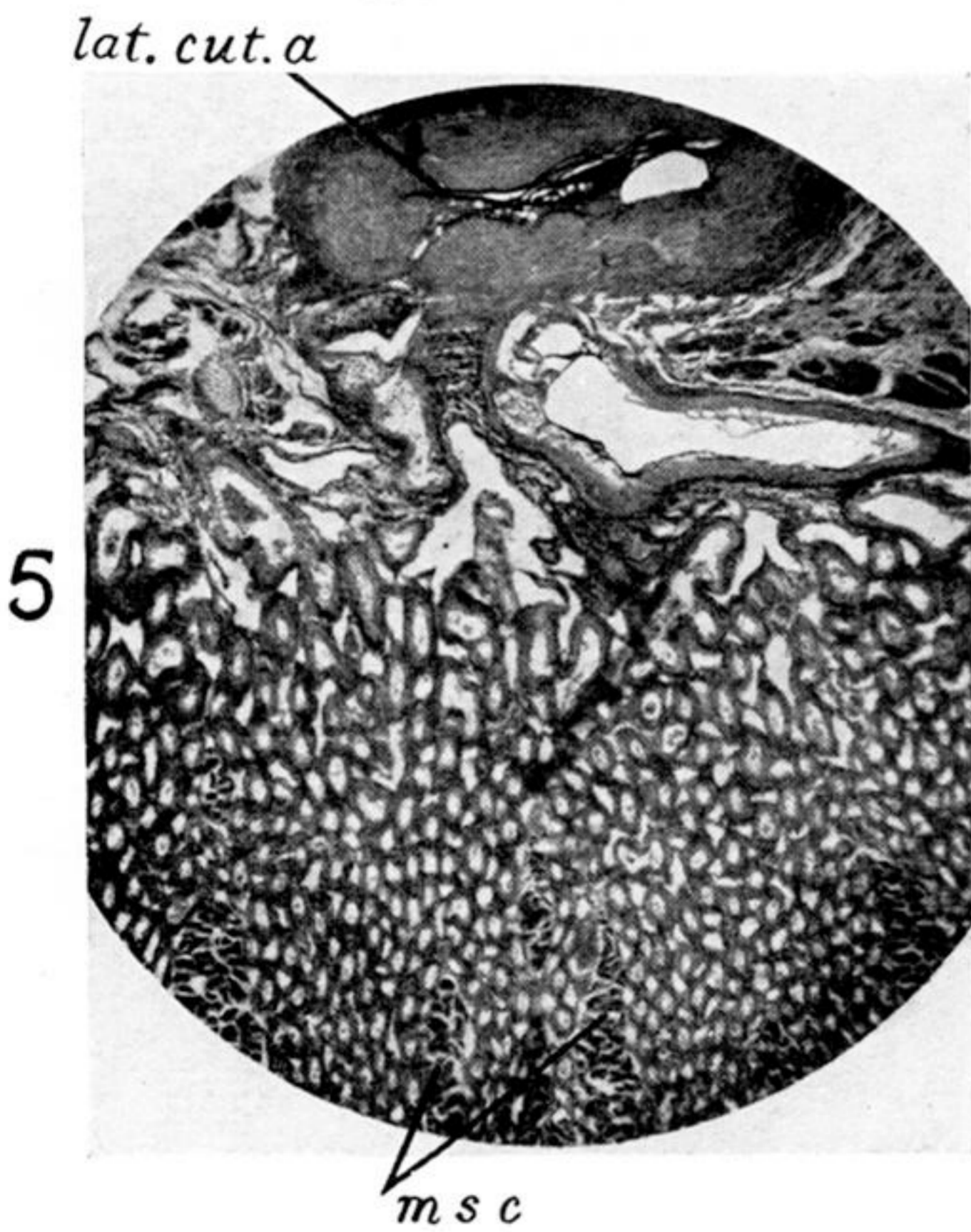
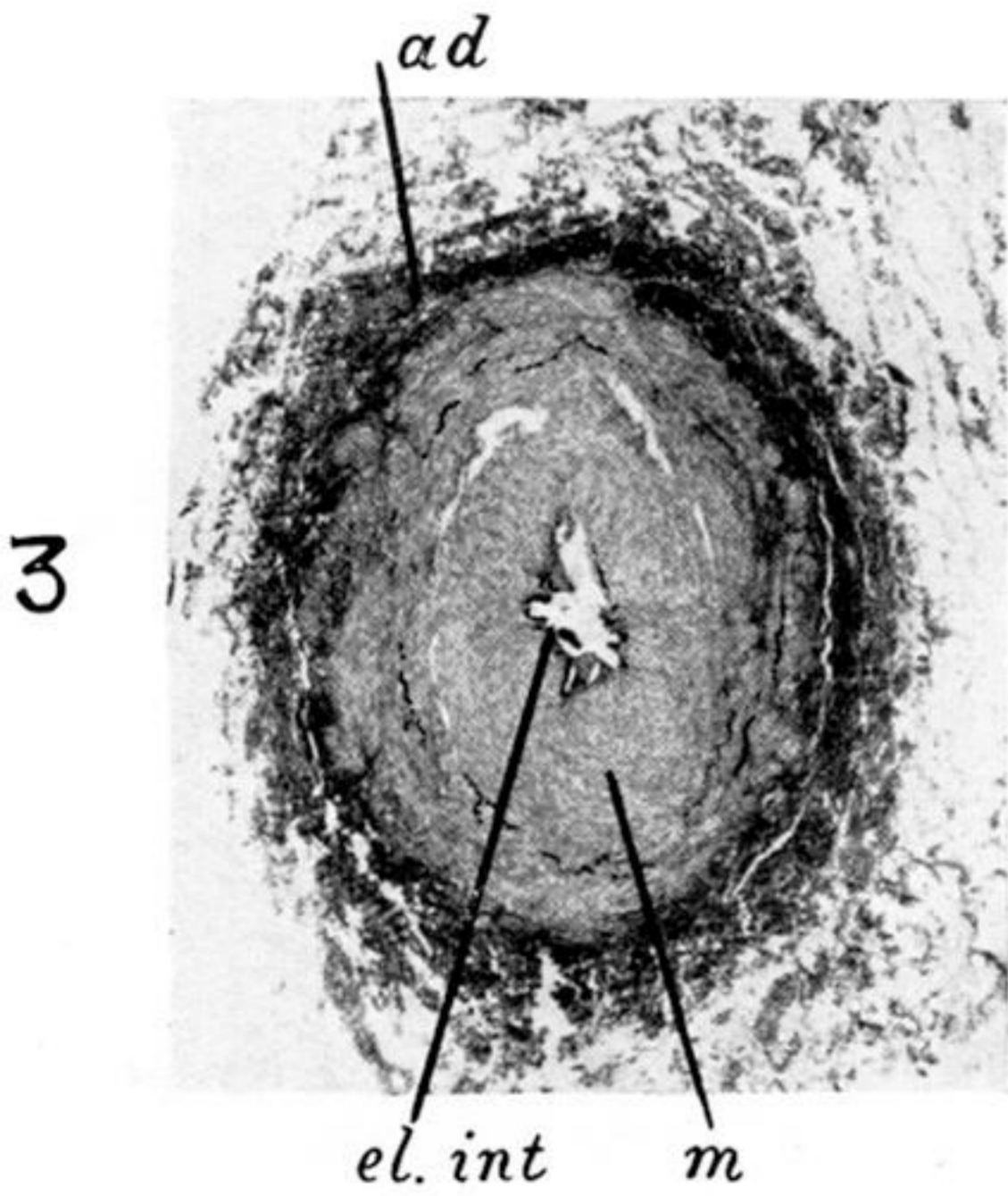
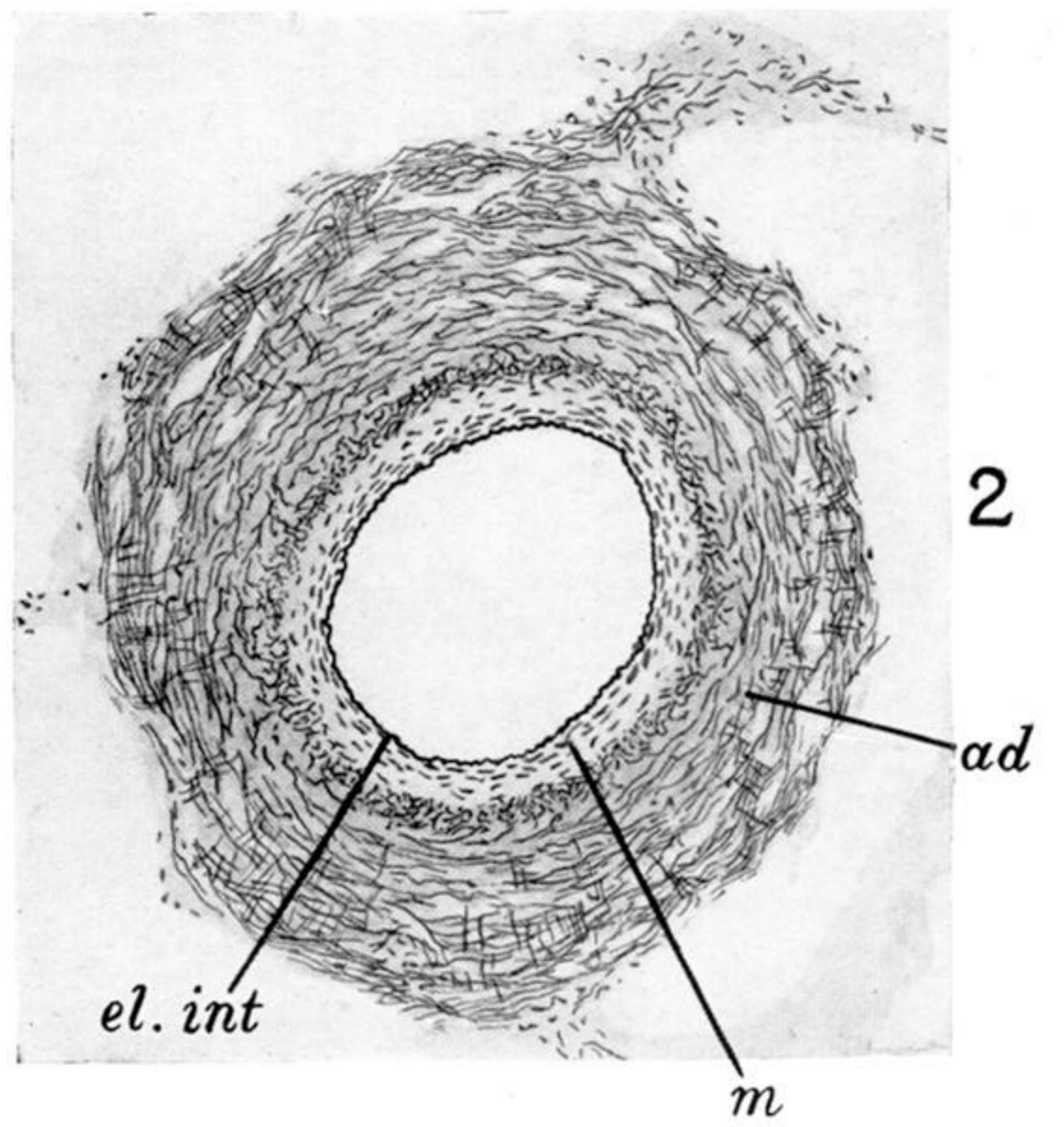
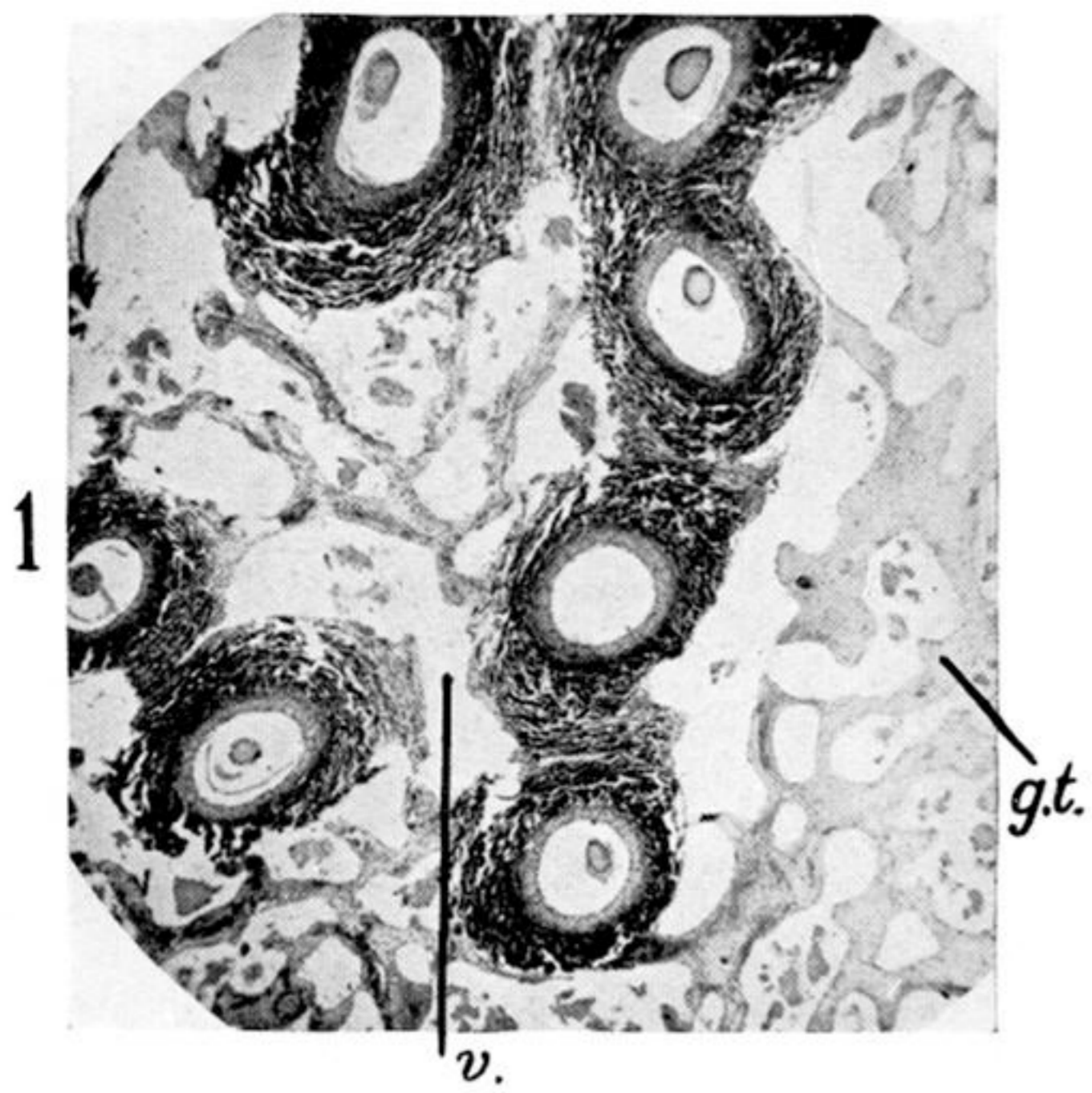


PLATE 9.

Fig. 1.—Anterior carotid rete of *Lamna cornubica* trans. sec., $\times 20$.

Fig. 2.—Component artery of anterior carotid rete of *Lamna cornubica*, showing the abundance of elastic tissue., trans. sec., $\times 60$.

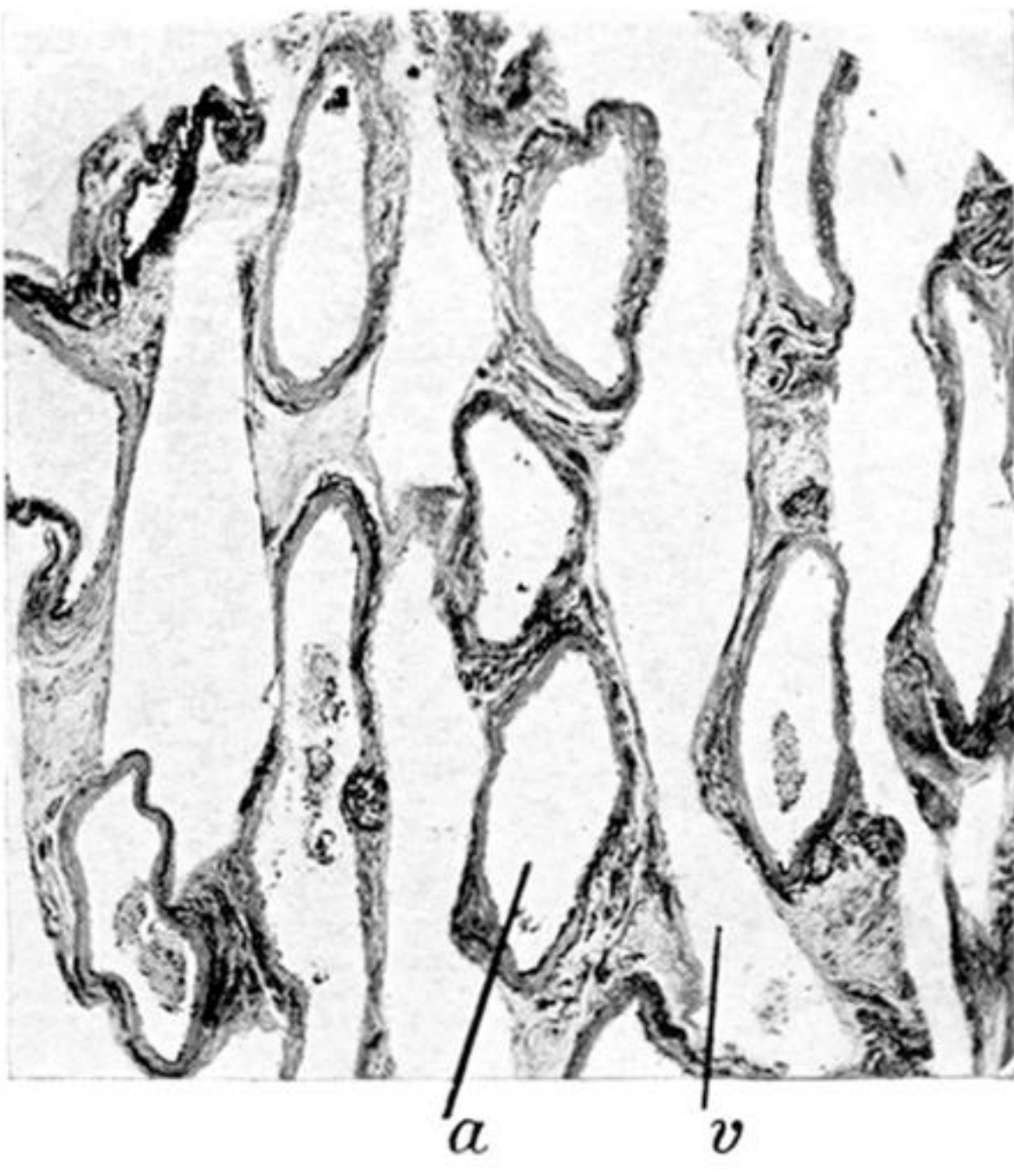
Fig. 3.—Third epibranchial artery of *Lamna cornubica* (specimen B), trans. sec., $\times 20$.

Fig. 4.—Aortic root of coelio-mesenteric artery of *Lamna cornubica* (specimen B), trans. sec., $\times 50$.

Fig. 5.—Rete arising from lateral cutaneous artery of *Lamna cornubica*, transverse to the lateral cutaneous artery. $\times 20$.

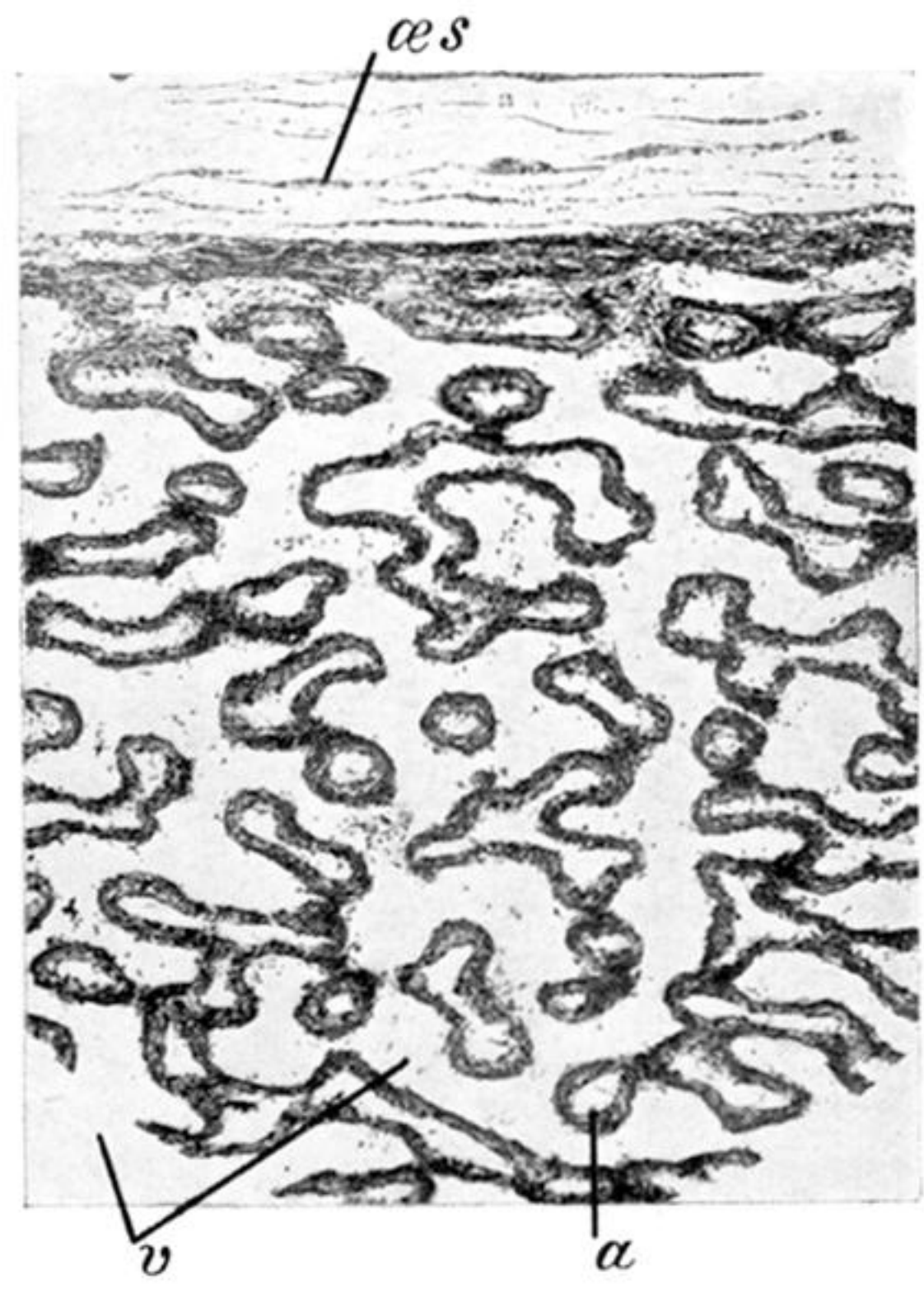
Fig. 6.—Anastomosis between the lateral cutaneous and lower lateral cutaneous arteries of *Lamna cornubica*, trans. sec., $\times 20$.

1



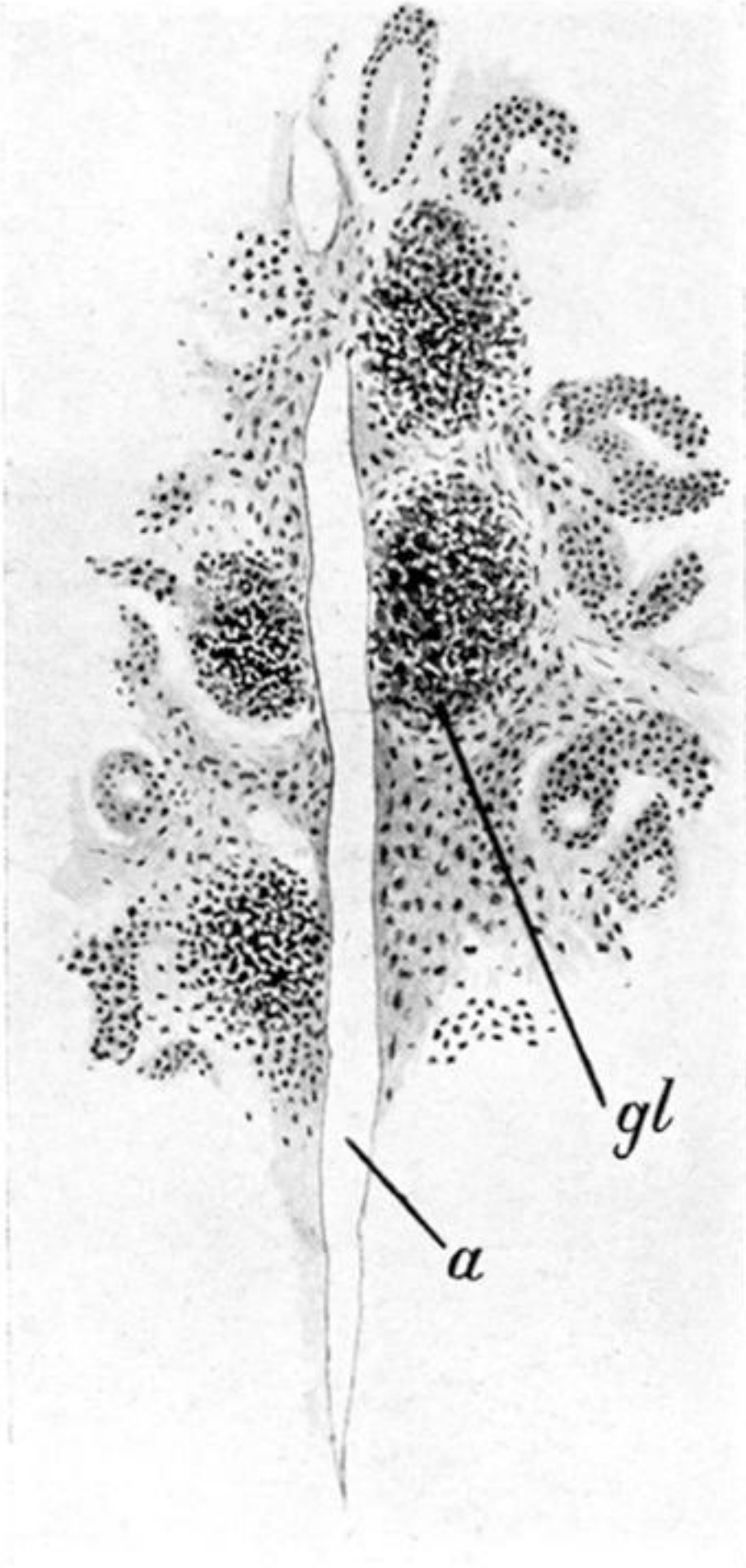
a v

4



v a

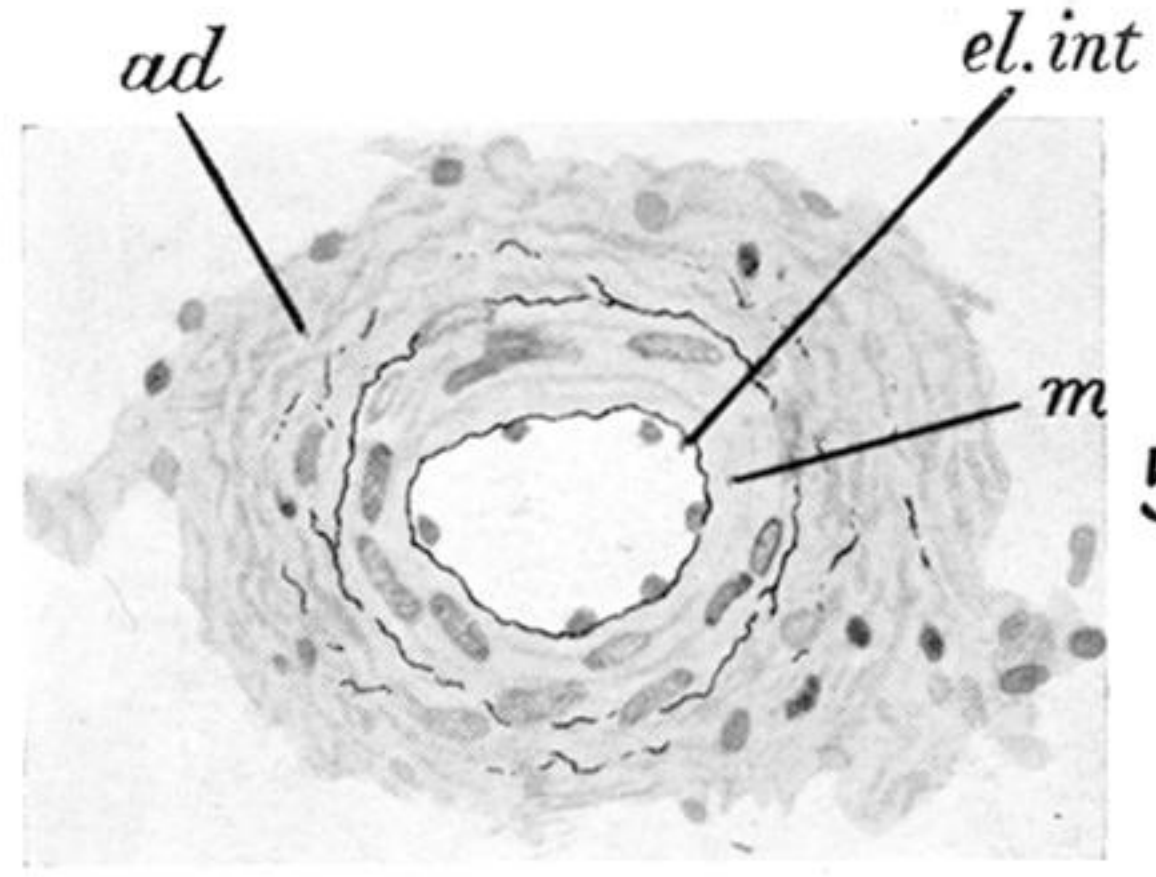
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gl

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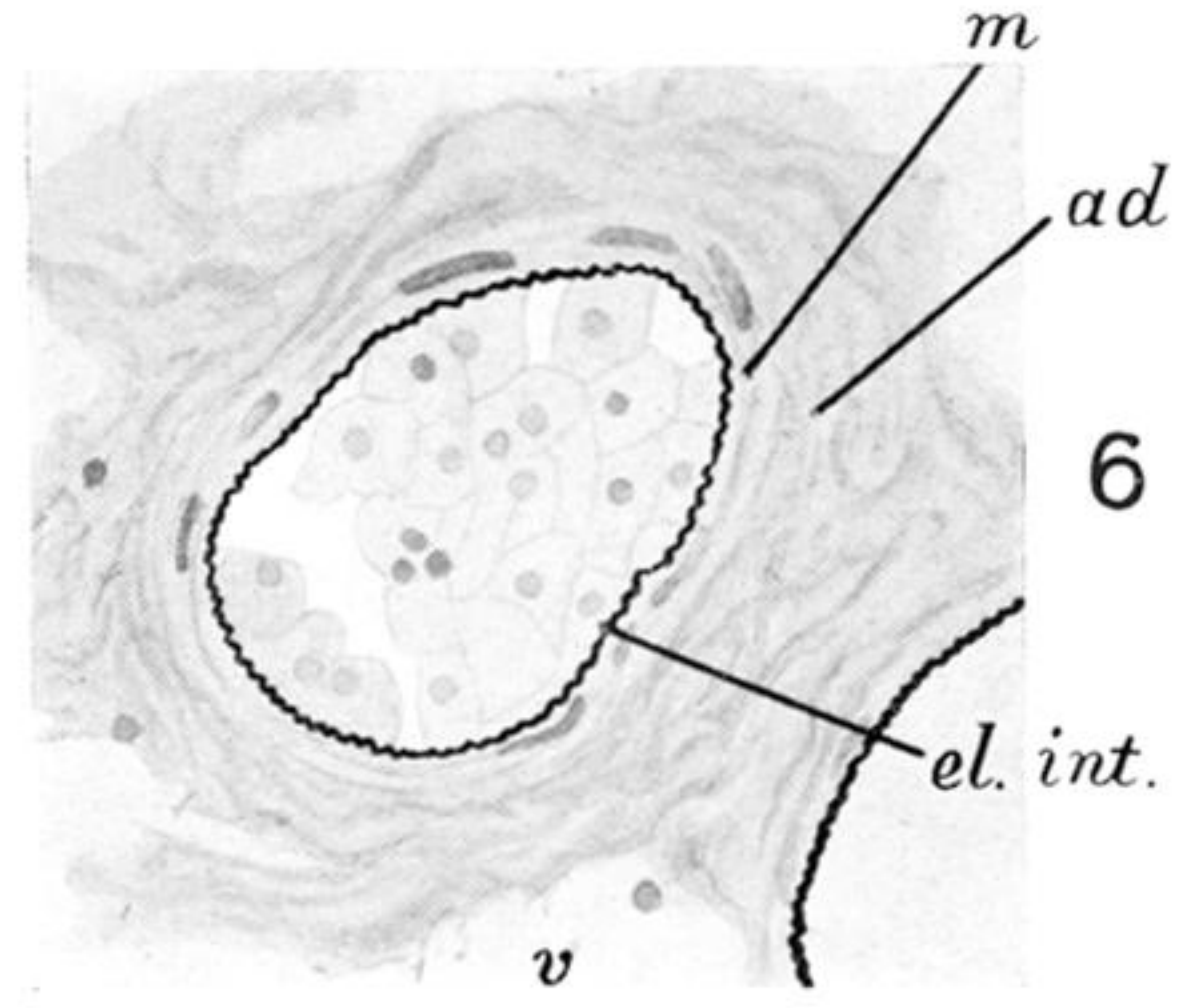
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ad el.int

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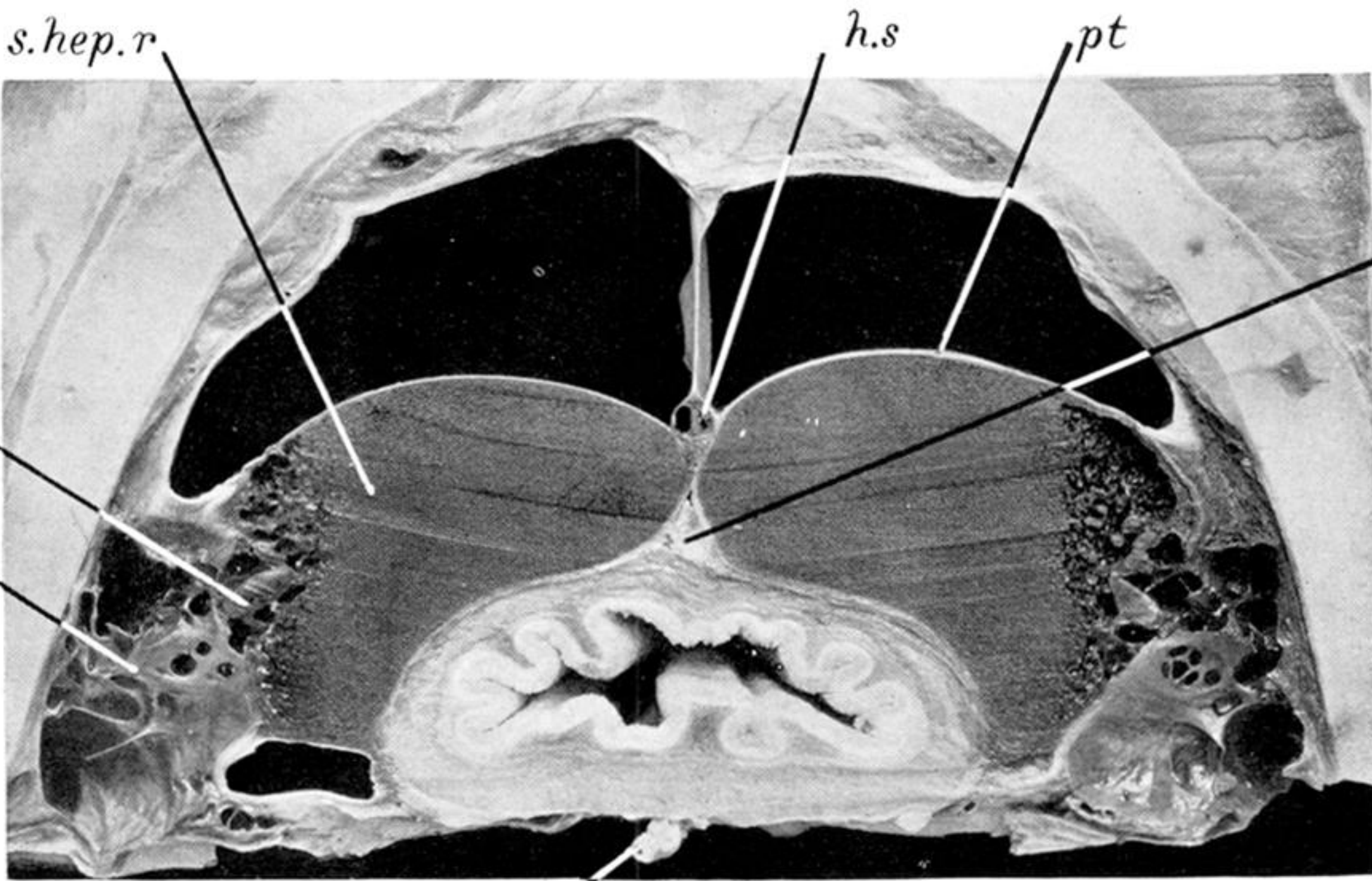
6



el.int.

v

3

p.c.a.
s.s.c.c.s

s.hep.r

h.s

pt

p.c.a.p

a.o

3

PLATE 10.

Fig. 1.—Section through the subrenal rete of *Lamna cornubica*, $\times 50$.

Fig. 2.—Artery given off from the subrenal rete in close proximity to several renal glomeruli, $\times 70$.

Fig. 3.—Transverse section through the supra-hepatic retia of *Lamna cornubica*, seen from anterior aspect.

Fig. 4.—Transverse section through centre of the supra-hepatic rete of *Lamna cornubica*, $\times 50$.

Fig. 5.—Arteriole of supra-hepatic rete of *Lamna cornubica*, trans. sec., $\times 270$.

Fig. 6.—Arteriole of lateral cutaneous rete of *Lamna cornubica*, trans. sec., $\times 270$.