# 30. Notes on the Circulatory System of Elasmobranchs. I. The Venous System of the Dogfish (*Scyllium canicula*).

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(Plates I., II. * & Text-figures 1–4.)

Index.



## I. Introduction.

The foundation of our modern knowledge of the circulatory ystem of Elasmobranchs was laid by T. J. Parker in his work on the venous system of the skate (*Raia nasuta*, **9**), and extended by his masterly description of the blood-vessels of *Mustelus antarcticus*, in 1886 (**10**). This latter provides a full account of the researches prior to that date, and also a full bibliography.

Since that date only two papers have dealt with the subject. Rand and Ulrich have discussed the posterior connections of the lateral vein in the skate in 1905 (**14**), and Diamare the splanchnic arteries and veins in *Scyllium catulus* and *Torpedo marmorata* (**2**).

Since Balfour's account (**1**) the general development of the venous system in Elasmobranchs has been referred to by a number of authors, including Hoffmann (**5**), Rabl (**11** & **12**), and Hochstetter (**3** & **4**), and the development of the head veins by Grosser (**2** *a*), so that it is only necessary here to refer quite briefly to the stage in a late embryo so as to indicate the order in which the veins in the adult are described.

Although many dogfish have been dissected, there is no complete account of the venous system. The descriptions given in the text-books for the most part appear to be based upon T. J. Parker's work already referred to, and are not altogether

* For explanation of the Plates see pp. 454, 455.

satisfactory. Although the general disposition of the main vessels in *Mustelus antarcticus* is somewhat similar to that in *Scyllium canicula*, the two species differ considerably in detail in the veins and, as might be expected from the modification of form undergone by the skates, the veins of these are markedly different from those in the dogfish. In view of this and of the fact that *Scyllium* is frequently used as a type in the laboratory, the venous system of the latter appears worthy of description.

An account of the arteries, on the other hand, is not so necessary, as they do not vary nearly so markedly from those described in other Elasmobranchs as do the veins and, moreover, they are much more satisfactorily dealt with in text-books.

The animals were investigated by means of injection and series of transverse sections through embryos of 37 and 56 mm. length, and serial sections through a frozen adult were also examined in order to check certain points. The injection-fluids used were the gelatine mass, recommended by Tandler (**15**) for the finer details, and the starch mass advised by Kingsley (**6**) for the larger vessels. In a previous communication on the blood-vessels of the grass-snake (**7**) I recommended using a mixture of the solid matter that settles to the bottom of the starch mixture with about twice its volume of gelatine, and I have now found that an almost identical mixture was suggested for the blood-vessels of the skate some time previously by Rand (**13**).

Perhaps the most striking feature of the venous system of *Scyllium* is the dilatation of the vessels to form sinuses. These sinuses render the injection of the system as a whole impractical, and the indefinite nature of their walls makes it extremely difficult to trace their exact course and extent with certainty or to locate the points of entry of the smaller tributaries.

For the sake of ready reference the names of the vessels adopted by Parker have been used as far as possible, and wherever alteration has been made Parker's terminology is also given.

## II. Development.

The pre-cardiac part of the venous system at a fairly late stage of development is represented by the anterior cardinal vein. This is morphologically composed of two sections: from the ear back to the ductus Cuvieri it is the persistent anterior cardinal, but the front part of this vessel has been replaced by the lateral cephalic vein. It is convenient, however, to speak of the whole trunk in the adult as the anterior cardinal sinus. In the adult an inferior jugular vein is developed on each side in addition to the foregoing sinus.

In the post-cardiac portion two distinct systems are to be recognised: first, the posterior cardinal veins, and second, the sub-intestinal vein. The posterior end of the first forms a loop around the growing mesonephroi, and later the median portions of the two loops fuse to constitute the inter-renal section of the

definitive posterior cardinal sinuses. The second divides into two parts—an anterior which gives rise to the hepatic portal vein, and a posterior which acquires a connection with the outer side of the kidney loop and forms the renal-portal vein.

Text-figure 1

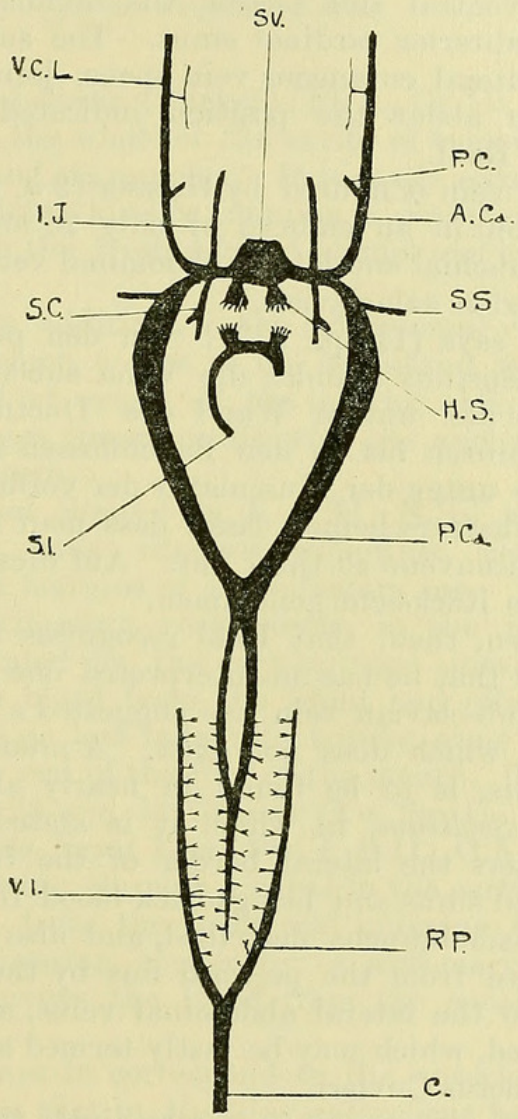



Diagram of the vessels in a fairly late embryo of *Scyllium canicula*.

V.C.L. Vena capitis lateralis. S.I. Sub-intestinal vein. V.I. Inter-renal vein.

For explanation of other lettering see p. 454.

Adopted and modified from Rabl (11).

According to Rabl (**11**), quoted also by Hochstetter (**4**), the sub-clavian vein is described and figured as opening into the posterior cardinal sinus, whereas in *Scyllium*, in *Mustelus*, and in the skates, this vein opens into the ductus Cuvieri, and in the two former it opens into the ductus between the point of entry of the anterior cardinal sinus and the sinus

venosus. In the adult *Scyllium* and *Mustelus* the vessel opening into the posterior cardinal vein in the position of that described by Rabl as the "sub-clavian" is really the sub-scapular.

In an embryo of 56 mm. it is quite easy to trace the relations of these two vessels, which are found to be the same as in the adult. The sub-clavian vein, formed by the union of the brachial and lateral abdominal veins, opens into the sinus venosus on its ventral side nearer the middle line than the opening of the anterior cardinal sinus. The sub-scapular vein, into which the lateral cutaneous vein opens, joins the posterior cardinal vein in about the position indicated by the "sub-clavian" vein of Rabl.

A sub-clavian vein is figured by Grosser (2 *a*, p. 184, fig. 4) in the same position in an embryo of only 26 mm., although its relation to the brachial and lateral abdominal veins is not shown, nor is it identified as sub-clavian.

Rabl himself says (11, p. 233): "In den proximalen Theil des Cardinalvenensinus mündet die Vena subclavia ein. Ausserdem tritt in die untere Wand des Ductus Cuvieri eine Vene, die nach hinten bis zu den Bauchflossen zu verfolgen ist, und deren Lage unter der Musculatur der vorderen Bauchwand es nicht zweifelhafterscheinen lässt, dass man es hier mit der Parietal-oder Seitenvene zu thun hat. Auf diese Vene habe ich im Schema keine Rücksicht genommen."

It will be seen, then, that Rabl recognises two veins, but I venture to think that he has misinterpreted one of them and in calling it the sub-clavian vein has suggested a connection with the pectoral fin which does not exist. A muddle, probably resulting from this, is to be found in nearly all the text-book descriptions of *Scyllium*, in which it is stated that the sub-clavian vein enters the lateral border of the front end of the posterior cardinal sinus and brings back blood from the pectoral fin. In all Elasmobranchs described, and also in *Scyllium*, the blood is returned from the pectoral fins by the brachial veins. These open into the lateral abdominal veins, and the common trunks so formed, which may be justly termed sub-clavian veins, open into the ductus Cuvieri.

For descriptive purposes it is easy to divide the venous system according to its derivation from the embryonic condition just described into pre-cardiac vessels, post-cardinal vessels, and sub-intestinal vessels, to which must be added the lateral veins, the coronary veins, and the cutaneous veins.

## III. The Pre-Cardiac Vessels.

1. *The Orbital Sinus.*
   1. i. The Nasal Sinus.
   1. ii. The Orbito-Nasal Vein.
   1. iii. The Anterior Cerebral Vein.
   1. iv. The Inter-Orbital Vein.

2. *The Post-Orbital Sinus.*

3. *The Anterior Cardinal Sinus.*

3. i. The Hyoidean Sinus.
3. ii. The Posterior Cerebral Vein.
3. iii. The Myelonal Veins.
3. iv. The Nutrient Branchial Veins.

4. *The Inferior Jugular Sinus.*

1. *The Orbital Sinus* (Parker) [Pl. I., Or.] is a large irregular sinus occupying the whole of the cavity of the orbit not occupied by the eyeball and its muscles. It is easily recognised as a blood sinus, for it almost always contains a considerable amount of clotted blood in the freshly-killed animal and even in preserved specimens.

It receives, in addition to the orbito-nasal vein, the anterior cerebral vein, which enters it on its lateral wall a little way behind the point of origin of the inferior oblique muscle. The two orbital sinuses communicate with one another by means of an inter-orbital vein.

1. i. *The Nasal Sinus* [Pls. I. & II., N.S.] is a well-marked crescent-shaped sinus situated somewhat ventrally on the inner and hinder margins of the olfactory sac. The two sinuses, although approximating very closely in the middle line, are completely separated by the cartilaginous inter-nasal septum. They collect the blood from the snout and olfactory sacs by a number of more or less indefinite trunks, some of which come from the anterior end of the roof of the mouth. They are figured in an embryo of 26 mm. by Grosser (2 *a*, fig. 4).

1. ii. *The Orbito-Nasal Vein* [Pls. I. & II., O.N.] is a small but distinct vein passing through a canal in the cartilage separating the olfactory sac from the orbit and entering the latter at its lower, inner, anterior corner by a well-marked orbito-nasal foramen. It conveys the blood from the nasal to the orbital sinus.

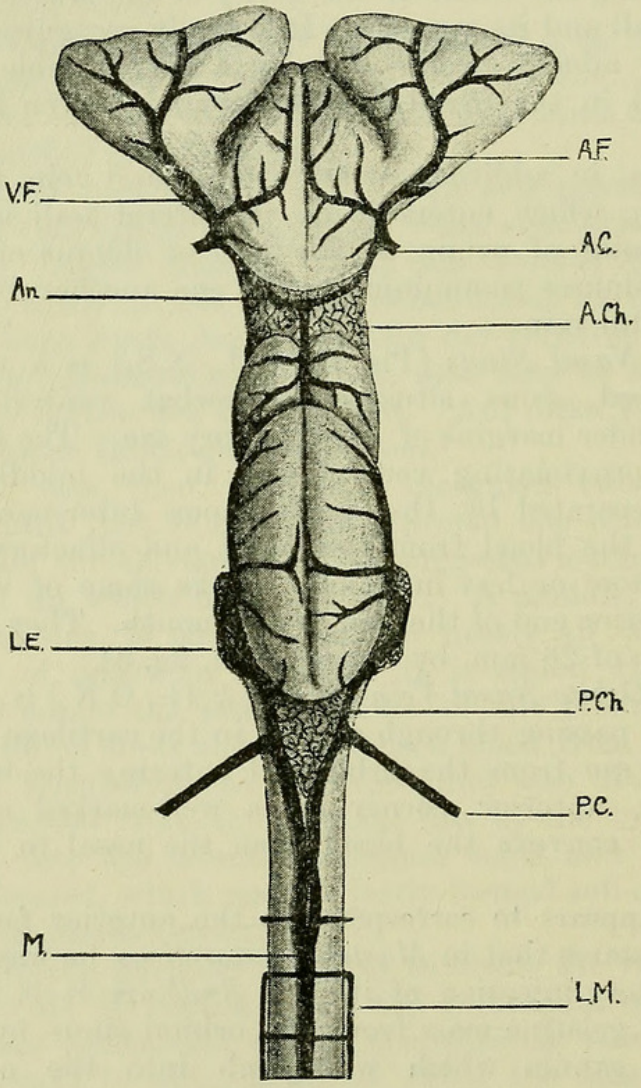
This vein appears to correspond to the anterior facial vein of Parker, who states that in *Mustelus antarcticus* he was unable to get a satisfactory injection of it. In *Scyllium* it is fairly easy to inject with gelatine mass from the orbital sinus by means of a pancreatic canula which will jamb into the orbito-nasal foramen.

1. iii. *The Anterior Cerebral Vein* (Parker) [Text-fig. 2, A.C.] is formed by the union of three factors at the posterior dorso-lateral border of the diencephalon, whence it passes directly outwards through a foramen in the cranial wall and empties itself into the orbital sinus. The anterior factor is itself composed of two smaller tributaries, one of which starts on the ventral surface of the olfactory lobe and passes forwards and then upwards to the dorsal surface. Here it runs backwards to

the main trunk, just before joining which it receives the other tributary coming from the prosencephalon.

The ventral factor collects blood from the lower surface of the prosencephalon and diencephalon as far back as the optic chiasma and passes dorsally into the main vein. The third factor is a posterior one that passes behind the edge of the prosencephalon to anastomose with its fellow. In the middle line this vessel receives a vein from the optic lobes and a large number of smaller ones from the anterior choroid plexus roofing the third ventricle.

Text-figure 2.




Sketch of the dorsal side of the brain of *Scyllium canicula*, showing the arrangement of the anterior and posterior cerebral veins.

For explanation of lettering see p. 454.

1. iv. *The Inter-Orbital Vein* [Pls. I & II., I.O.] is a small but well-marked vein running from one orbit to the other in a canal in the basi-cranial cartilage, and it enters the orbit towards its posterior end just in front of and slightly below the large

foramen through which the sixth and main branches of the fifth and seventh cranial nerves leave the cranium. It is situated directly under a well-marked ridge in the floor of the cranial cavity immediately behind the pituitary body.

2. *The Post-Orbital Sinus* [Pls. I. & II., P.O.] is a moderate-sized vessel placing the orbital sinus in communication with the anterior cardinal sinus. It passes backwards from the posterior external part of the orbit around the auditory capsule dorsally to the spiracle. Its path around the capsule is indicated by a well-marked groove, the post-orbital groove, which is to be found between the ridge formed by the horizontal semi-circular canal and the smooth surface for the articulation of the hyomandibular cartilage.

3. *The Anterior Cardinal Sinus* * (Jugular Vein, Parker) [Pls. I. & II., A.C.] is a very large and irregular sinus running along the internal dorsal ends of the gill-clefts. It starts close behind the spiracle at the anterior end of the first gill-cleft and runs to a point a short way behind the fifth gill-cleft. At its front end it receives the post-orbital sinus. The two anterior cardinal sinuses are situated at about the same depth below the dorsal surface of the animal as the vertebral column, with which they are approximately parallel. The pharyngeo-branchial cartilages project into the floor of the sinuses, forming well-marked ridges which possess membranous flaps. The sinuses are readily exposed from the dorsal side of the fish when making a dissection of the cranial nerves, and, indeed, the branchial branches of the tenth cranial nerves pass freely through their cavities, while the visceral branches of the same are partially embedded in their mesial walls. Just behind the fifth gill-cleft the anterior cardinal sinus narrows down considerably, and passing ventrally opens into the posterior cardinal sinus by an opening provided with a valve (*vide* footnote, p. 444).

The anterior cardinal sinus receives small tributaries from the dorsal ends of the gill-bars and from the surrounding musculature, but their position is extremely difficult to ascertain owing to the indefiniteness and irregularity of the walls of the sinus. At its front end the anterior cardinal sinus receives the posterior cerebral vein and the hyoidean sinus.

3. i. *The Hyoidean Sinus* (Parker) [Pls. I. & II., H.] is a moderate-sized vessel situated in front of the first gill-cleft and running parallel with it from the dorsal to the ventral side of the fish. It lies in a shallow groove on the external side of the hyomandibular cartilage, and at its dorsal end enters the anterior cardinal sinus near the point where the latter receives the post-orbital sinus. The ventral end joins the inferior jugular sinus at the level of the posterior end of the thyroid gland.

The hyoidean sinus doubtless receives the blood from the tissues surrounding it, but it is extremely difficult to make out

* This name is used because, as Parker points out, the vein is not in any way homologous with the jugular vein of higher animals.

any definite tributaries corresponding to the nutrient branchial veins and the posterior facial vein described by Parker in *Mustelus*.

3. ii. *The Posterior Cerebral Vein* * (Parker) [Text-fig. 2, P.C.] commences at the anterior end of the cerebellum and passes backwards along its side. Towards the posterior end of the cerebellum, after receiving a well-marked tributary coming from its mid-dorsal region, it runs out laterally over the sac-like lateral dilatation of the posterior choroid plexus. Here it drains a remarkable venous network, a kind of rete mirabile, composed of quite well-marked veins. Its path now lies along the lateral border of the median portion of the posterior choroid plexus, from which it receives numerous tributaries, and just before the calamus scriptorius it passes out through the cranium closely apposed to the dorsal surface of the tenth cranial nerve. It parts company with this nerve outside the cranium and apparently passes through the muscles to the front end of the anterior cardinal sinus, but it is difficult to follow. The fine veins from the membranous labyrinth appear to open into the posterior cerebral vein at its inner end. Parker describes and figures the veins not as passing through the cranial wall but as running backwards to unite and form the myelonal vein.

Grosser has figured this vein in an embryo of *Scyllium* 26 mm. long (2 *a*, fig. 4), but does not call attention to it in the text. In dealing with *Triton* and *Salamandrina*, however, he mentions this vein as leaving the skull with the vagus nerve, and points out that it is of general occurrence in many of the higher groups, a fact also noted by Gaupp. It was readily made out in the sections of embryos of 37 and 56 mm. length that were examined.

3. iii. *The Myelonal Veins* (Parker) [Text-fig. 2, M.]. Two well-marked myelonal veins are present, a dorsal and a ventral.

The dorsal myelonal vein runs the length of the spinal cord, and at the anterior end forks just behind the calamus scriptorius. The two limbs of the fork run into the posterior cerebral vein just as it is leaving the cranial cavity. Parker describes this vessel as forming a rhomboidal plexus in each vertebral segment, but although the anterior end of the vein may be more or less double for a short way behind the point where it divides, there is no sign of this arrangement in *Scyllium*. Segmental veins are given off, and these often tend to form a lateral vessel on each side of the cord by anastomosing in a longitudinal direction; it appears to be very irregular, however.

The ventral myelonal vein is formed by the union of two

* This vein and the anterior cerebral are very difficult to inject, as it is almost impossible to insert even a hypodermic needle into them. However, I found that they could be made distinct in the following way. After the anterior cardinal vessels of a freshly killed fish have been quite filled with injection mass and plugged, the cranium is dissected away so as to expose as much of the brain as possible. A fixing fluid, corrosive formol, is slowly injected into the dorsal aorta until the cranial arteries begin to get colourless and the veins distended with blood. If the anterior end of the fish in this condition is placed in 5 per cent. formalin overnight, it will be found that the blood in the veins has coagulated and become dark in colour.

branches. Each commences by the side of the lobi inferiores just behind the optic chiasma and passes backwards, draining the saccus vasculosus, to unite behind the pituitary body to form a median vessel. This runs the length of the spinal cord, giving off small segmental branches.

3. iv. *The Nutrient Branchial Veins* (Parker) are a series of four indistinct vessels on each side which bring back the blood from the four holobranchs. Their anatomical relations do not appear to be so constant and cannot be made out so definitely as in *Mustelus*.

4. *The Inferior Jugular Sinus* (Parker) [Pls. I. & II., I.J.] is a moderate-sized, indefinite vessel situated below the floor of the mouth. It commences as a small vein shortly behind the symphysis of the lower jaw and passes backwards to the level of the hinder end of the thyroid gland, where it receives the hyoidean sinus and also anastomoses with its fellow. This anterier segment may perhaps correspond with the mandibular vein described by Parker. The anastomosis between the two inferior jugulars takes the form of an extremely irregular trunk passing along the base of the thyroid gland (around which blood-clots are frequently to be found) and bathing the innominate arteries. From this point the jugular sinus widens out considerably and runs along the internal sides of the ventral ends of the gill-clefts, bathing the proximal parts of the afferent branchial arteries, back to the wall of the pericardium. Here it narrows and passes along the wall to open into the proximal part of the ductus Cuvieri by an opening common to it and the sub-clavian vein.

## IV. The Post-Cardinal Vessels.

*The Posterior Cardinal Sinus.*

1. *The Renal Veins.*
2. *The Genital Sinus.*
   - A. The Ovarian Sinus.
   - B. The Spermatic Vein.
     - 2. i. The Intestino-Mesenteric Vein.
3. *The Anterior Parietal Veins.*
4. *The Anterior Oviducal Sinus.*
5. *The Sub-scapular Sinus.*
6. *The Spinal and Œsophageal Veins.*

*The Posterior Cardinal Sinus* (Parker) [Pls. I. & II., P.Ca.] originates between the kidneys, where the two posterior cardinal sinuses are united to form a median vessel. At the anterior end of the kidneys the right and left sinuses are usually separated by a partition passing from the dorsal to the ventral wall in the

middle line. Each cardinal sinus runs forwards as a fairly narrow vessel to a point just in front of the anterior mesenteric artery and then commences to widen out. At the anterior end the two sinuses occupy the whole of the region dorsal to the œsophagus right up to the pericardio-peritoneal septum and outwards to the sides of the body. The condition of the septum between the sinuses at the front end varies greatly in different specimens. It may be practically absent, represented only by a few strands, it may be well developed with perforations, or most frequently it is in a condition between these two extremes. The posterior cardinal receives the renal veins, the genital sinus, the anterior parietal veins, the anterior oviducal sinus in the female, the sub-scapular sinus, the veins from the spinal cord, and at its front end the anterior cardinal sinus and the ductus Cuvieri open into it *.

*The Renal Veins* (Parker) are represented by a series of efferent vessels leaving the kidneys. They do not appear as separate vessels outside that organ, as the wall of the posterior cardinal sinus is in contact with the mesial border of the kidney.

2. *The Genital Sinuses* differ in the two sexes and will be dealt with separately.

A. *The Ovarian Sinus* is a large trunk composed of numerous irregular factors and runs in the mesovarium dorsal to the ovary from its posterior end. A very similar but smaller vein is formed at the anterior end of the ovary, and the two unite in the first third of that body and pass dorsally into the posterior cardinal sinus in the region where the anterior mesenteric and lienogastric arteries are given off from the dorsal aorta. Just before entering the posterior cardinal sinus it swells out somewhat and receives the intestino-mesenteric vein.

B. *The Spermatic Vein* (Parker) [Pl. I., R.S.] is subject to a considerable amount of variation, and often each testis possesses two separate veins. The posterior drains the hinder two-thirds of the testis and, passing dorsally through the mesorchium, joins its fellow of the opposite side to form a common genital sinus which opens into the posterior cardinal sinus. The intestino-mesenteric vein often joins the right spermatic vein just before it unites with the left. The anterior spermatic vein drains the front portion of the testis, in front of which it joins with its fellow and opens into the posterior cardinal sinus. Sometimes, perhaps more generally, this anterior spermatic vein is simply a factor of the posterior one, which is always the main vein.

* It is stated that developmentally the anterior and posterior cardinal veins open separately on the anterior and posterior sides of the ductus Cuvieri respectively. That this description. given by Hoffmann (5), Hochstetter (3), Balfour (1), and others, is the correct one can easily be verified by reference to a series of sections of an embryo of *S. canicula*. In the adult, however, the actual *anatomical* relations are different, possibly because of the dilatation of the veins to form sinuses, and we find that the anterior cardinal sinus opens into the posterior cardinal sinus by an aperture guarded by a valve, and the ductus Cuvieri projects as a short tube into the posterior cardinal sinus, opening therein by an oval aperture.

2. i. *The Intestino-Mesenteric Vein* [Pl. I., I.M.] is a small but nevertheless well-marked vessel that collects the blood from the right side of the intestine in the region of the spiral valve and runs through the mesentery, from which it receives branches, to open into the genital sinus. In the male it flows into the branch from the right testis shortly before this joins with its fellow in the middle line.

3. *The Anterior Parietal Veins* (ant. spinal veins, Parker) come from the myotomes of the body between the pericardio-peritoneal septum and the anterior end of the kidney and flow into the posterior cardinal sinus.

4. *The Anterior Oviducal Sinus* (ant. ov. vein, Parker) is a large vessel situated around the oviduct in the region of the oviducal gland in the full-grown female. It is a very large sinus, quite separate from the posterior cardinal sinus into which it opens at its anterior end. In the immature female this sinus cannot be detected, but in the adult, and more especially when the oviducal gland appears to be active, it is obvious enough.

5. *The Sub-Scapular Sinus* [Pls. I. & II., S.S.] is a small sinus situated on the dorso-lateral aspect of the dogfish immediately behind the fifth gill-cleft and just ventral to the dorsal end of the scapular cartilage. It joins the posterior cardinal sinus on its dorso-lateral edge towards the anterior end by one or two small openings guarded by a valve. Into it opens the lateral cutaneous vein. As is pointed out above this vessel is generally but incorrectly termed the sub-clavian vein.

6. *The Spinal and Œsophageal Veins.* The veins from the spinal cord in the body region flow into the posterior cardinal sinus. A few small veins from the extreme front end of the œsophagus may also enter this sinus, but the main part of the blood from the œsophagus is collected by a factor of the hepatic portal system.

## V. The Lateral Veins.

*The Sub-Clavian Vein.*

1. *The Lateral Abdominal Vein.*
2. *The Iliac Vein.*
    1. i. The Femoral Vein.
    2. ii. The Cloacal Vein.
3. *The Rectal Vein.*
4. *The Brachial Sinus.*

*The Sub-Clavian Vein* [Pls. I. & II., S.C.]. The condition of this vein in the embryo has already been noted. In the adult it is a short trunk passing from the union of the lateral abdominal vein and brachial sinus dorsally along the edge of the coracoid cartilage, and it flows into the ductus Cuvieri through a common opening with the inferior jugular sinus. Its position justifies it

being termed the sub-clavian vein and, in addition, it is homologous with the similarly named vein in *Rana* *.

1. *The Lateral Abdominal Vein* (Lateral Vein, Parker) [Pls. I. & II., L.A.] is a moderate-sized vessel that runs immediately beneath the peritoneum along the ventro-lateral wall of the body-cavity. It originates as a continuation of the iliac vein on the dorsal side of the pelvic cartilage, across which it anastomoses with its fellow of the other side. Thence it passes forwards in the body-wall to the pericardio-peritoneal septum, in the wall of which it turns very sharply dorsalwards and slightly mesially along the posterior edge of the coracoid cartilage. A short distance along this it unites with the brachial sinus to form the sub-clavian vein.

2. *The Iliac Vein* (Parker) [Pl. I., Il.] is a short vessel formed by the union of the femoral and cloacal veins on the inner side of the basipterygium towards its anterior end. It runs into the lateral abdominal vein on the dorsal surface of the pelvic bar.

2. i. *The Femoral Vein* (Parker) [Pl. I., F.] drains the major part of the pelvic fin and is situated laterally and slightly dorsal to the basipterygium. It passes across the anterior end of this cartilage, which is slightly notched to receive it, to unite with the cloacal vein.

2. ii. *The Cloacal Vein* (Parker) [Pl. I., Cl.] lies on the inner side of the basipterygium, and is formed by the union of factors from the posterior and lateral walls of the cloaca and also from the inner side of the pelvic fin.

It will be noted that the arrangement of the factors of this vein agree more nearly with those described by Parker in *Mustelus* than with those figured by the same author for *Raia nasuta*, and those in *R. erinacea* and *R. lævis* according to Rand and Ulrich (**14**). The additional factors in the skates are doubtless to be correlated with the greater relative size of the pelvic fin. A similar difference is found in the brachial veins; only one such is present on each side in *Scyllium*, while two are found in *R. erinacea* and *R. lævis* and three in *R. nasuta*.

Further similarity with *Mustelus* is shown by the presence of a pelvic anastomosis between the lateral abdominal veins in *Scyllium* but not in the skates.

3. *The Rectal Vein* [Pl. I., Re.] is a small short vessel joining the anastomosis between the lateral abdominal veins in the middle line. Its branches form a fairly rich network of vessels spread over about the last one and a half inches of the rectum and the body-wall ventral to this.

This vessel is not represented in *Mustelus*, where the posterior end of the rectum is drained by a fairly large proximal tributary of the cloacal vein on each side. It more nearly resembles the

* In the tadpole the sub-clavian vein is formed by the union of the musculo-cutaneous, brachial, and the epigastric veins, the latter being homologous with the lateral abdominal veins. In the adult the two epigastrics are reduced to a median vein, the anterior abdominal, which acquires a secondary connection with the hepatic portal vein, though in certain abnormal specimens the primitive connection is retained (8).

condition in *R. erinacea* and *R. lævis*, where paired vessels from the end of the rectum run straight into the lateral abdominal veins.

4. *The Brachial Sinus* (Br. vein, Parker) [Pls. I. & II., B.] collects blood from the pectoral fin and passes along near its posterior edge. It leaves the fin and penetrates the body-muscles to open into the lateral abdominal vein on the posterior edge of the coracoid cartilage.

### *The Cutaneous Veins.*

1. *The Lateral Cutaneous Vein.*
2. *The Posterior Ventral Cutaneous Vein.*

1. *The Lateral Cutaneous Vein* (Parker) [Pls. I. & II., L.C.] originates far back in the tail, and forms a well-marked vessel running to the region of the pectoral fin, in the connective tissue immediately underlying the lateral-line canal. Here it passes inwards and opens into the sub-scapular sinus. Parker describes anastomoses between it and the caudal vein, and such anastomoses can be found in sections of embryos of 56 mm., but I have been unable to inject and display them by ordinary dissection.

2. *The Posterior Ventral Cutaneous Vein* (Parker) can be seen in transverse sections both of embryos and of adult fish. It runs forward embedded in the connective tissue in the mid-ventral line from the tail, forms a loop around the anal fin, and forks in the region of the cloaca. A similar vein is to be found under the cutis in the median line of the abdomen, and this doubtless corresponds to the anterior ventral cutaneous vein of Parker, but the exact relations of its anterior and posterior ends could not be ascertained as it is too small for injection.

Serial sections through embryos of 37 and 56 mm. length have been studied, and the general arrangement of these cutaneous vessels is apparently similar to that in *Mustelus* as described by Parker. They are not dealt with in detail here as they have only been followed in the above sections, and they cannot be studied in the adult by ordinary methods of injection.

The ventral cutaneous veins are too small to inject successfully, even with a hypodermic syringe, and the dorsal cutaneous vein is barely visible to the naked eye.

## VI. The Sub-Intestinal Vessels.

A. The Hepatic Portal Vein.

1. *The Posterior Intestinal Vein.*
2. *The Posterior Lieno-gastric Vein.*
   - 2. i. The Posterior Splenic Vein.
   - 2. ii. The Median Gastric Vein.
3. *The Pancreatic Veins.*

4. *The Gastro-intestinal Vein.*
   - 4. i. The Intra-intestinal Vein.
   - 4. ii. The Anterior Intestinal Vein.
   - 4. iii. The Anterior Lieno-gastric Vein.
5. *The Dorsal Anterior Gastric Vein.*
   - 5. i. The Dorsal Gastric Vein.
   - 5. ii. The Dorsal Œsophageal Vein.
6. *The Ventral Anterior Gastric Vein.*
   - 6. i. The Ventral Gastric Vein.
   - 6. ii. The Ventral Œsophageal Vein.
7. *The Hepatic Veins and Sinuses.*

B. The Renal Portal Veins.

1. *The Caudal Vein.*
2. *The Renal Portal Vein.*
   - 2. i. The Posterior Oviducal Veins.
   - 2. ii. The Posterior Parietal Veins.

## The Hepatic Portal System.

The hepatic portal system consists of a number of large well-marked veins, mostly lying in the gut mesenteries, which convey blood from the whole of the alimentary canal (from œsophagus to rectal gland inclusive) to the liver. In the higher vertebrates all the blood collected from the gut is taken to the liver, but in *Scyllium* there is an exception to this general rule in the presence of an intestino-mesenteric vein. There are marked differences between the component veins of this system in *Mustelus antarcticus*, according to Parker, and in *Scyllium*, and in consequence the nomenclature here adopted is descriptive and does not necessarily imply homology. The system may be conveniently and easily injected from the main trunk near the liver.

A. *The Hepatic Portal Vein* [Pl. II., H.P.] is formed in the pancreas, a short distance from its posterior end, by the confluence of the posterior intestinal and posterior lieno-gastric veins. It runs partially embedded in the right dorsal edge of the pancreas to the anterior end of that body, and receives during this part of its course a number of small tributaries, the pancreatic veins. At the anterior end of the pancreas it is joined by two large veins; one, the dorsal anterior gastric, enters it on the right, and the other, the gastro-intestinal, enters it somewhat ventrally on the left. From this point it runs for a short distance, about 1·5 cm., in the gastro-hepatic omentum before it receives its last large tributary, the ventral anterior gastric vein. It is now an extremely large vein with a diameter, when fully distended, of

about 5 mm., and it quickly divides into two main branches, a right and a left, one feeding each lobe of the liver.

Text-figure 3.

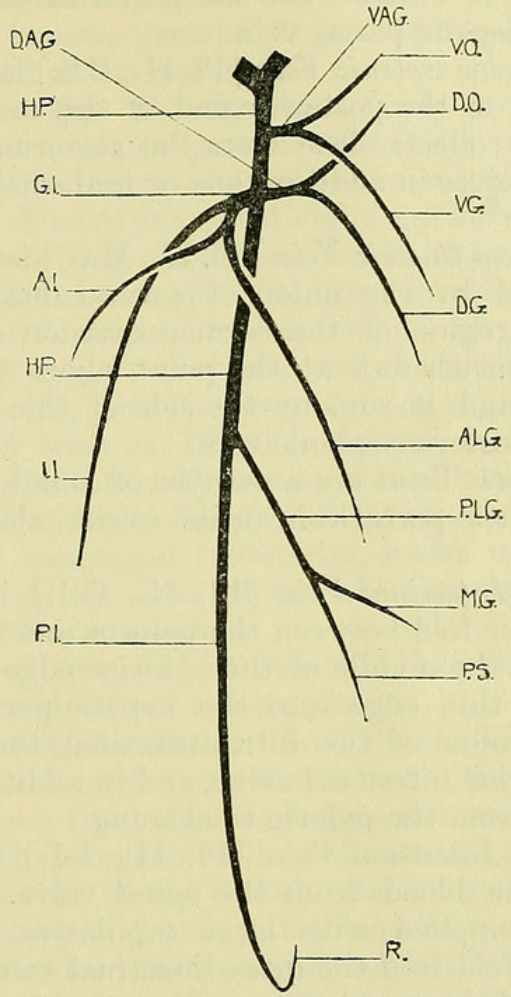



Diagram of the factors of the Hepatic Portal System in *Scyllium canicula*, viewed from the ventral side.

For explanation of lettering see p. 454.

1. *The Posterior Intestinal Vein* [Pl. II., P.I.] commences as a small vein on the ventral side of the rectal gland, and then, turning sharply upon itself, passes along the dorsi-lateral wall of the intestine to a point just posterior to the caudal end of the pancreas. At this place, marked also as the point at which the anterior mesenteric artery reaches the gut-wall, the posterior intestinal vein receives a fairly large factor from the anterior end of the intestine, and then it runs freely to join the posterior lieno-gastric vein in the pancreas. During its course along the intestine the vein receives a number (usually eight) of well-marked paired tributaries, whose position on the outside of the intestine marks the line of insertion of the folds of the spiral valve within.

2. *The Posterior Lieno-gastric Vein* [Pl. II., P.L.G.] is formed dorsally to the gut by the union of the posterior splenic and posterior gastric veins, and it runs from this junction to the posterior end of the pancreas and along the right dorsal edge of this gland, until it unites with the posterior intestinal vein to give rise to the hepatic portal vein.

2. i. *The Posterior Splenic Vein* [Pl. II., P.S.] is fairly large and situated dorsally to the posterior end of the cardiac division of the stomach. It collects blood from the posterior portion of the spleen, and it receives in addition one or two small branches from the stomach.

2. ii. *The Median Gastric Vein* [Pl. II., M.G.] is also fairly large, and it is formed by the union of several branches from the posterior dorsal region of the cardiac division of the stomach. It leaves the stomach-wall at the point where the lieno-gastric artery joins it, and it runs by the side of this artery until it unites with the posterior splenic vein.

3. *The Pancreatic Veins* are a number of small tributaries that flow into the hepatic-portal vein in its course along the edge of the pancreas.

4. *The Gastro-Intestinal Vein* [Pl. II., G.I.] is a short vein, hidden away in the fold between the pylorus and intestine, which commences about the middle of the anterior edge of the pancreas and runs along this edge into the hepatic-portal vein. It is formed by the union of the intra-intestinal, the anterior lieno-gastric, and anterior intestinal veins, and in addition receives one or two branches from the pyloric thickening.

4. i. *The Intra-Intestinal Vein* [Pl. II., I.I.] is a large vein bringing back the blood from the spiral valve. The valve is extremely well supplied with large capillaries, and numerous branches in each fold feed the intra-intestinal vein which runs in the central core of the spiral valve. It perforates the wall of the intestine at the anterior end of the spiral valve close against the pyloric valve, and it emerges from the intestinal wall in the sharp bend between the intestine and the pyloric thickening, where it quickly unites with the anterior intestinal and anterior lieno-gastric veins.

4. ii. *The Anterior Intestinal Vein* [Pl. II., A.I.] is of moderate size, and originates in the line of insertion of the first fold of the spiral valve in the intestine towards the dorsal side of the latter. It follows the valve round and comes through the intestinal wall on its ventral side close to the anterior lobe of the pancreas. Here it receives one or two branches from the wall of the ventral part of the anterior end of the intestine and runs straight to the pancreas, where it unites with the anterior lieno-gastric vein.

4. iii. *The Anterior Lieno-gastric Vein* [Pl. II., A.L.G.] is situated between the anterior lobe of the spleen and the pyloric division of the stomach, and receives tributaries from both these bodies. It arises near the level of the division between the two parts of the stomach and runs to the beginning of the bend

between the intestine and the stomach, where it branches off to the anterior lobe of the pancreas.

5. *The Dorsal Anterior Gastric Vein* [Pl. II., D.A.G.] is formed by the union of the dorsal gastric and dorsal œsophageal veins, and runs in the mesentery from the dorsal anterior side of the stomach into the hepatic-portal vein just as the latter is leaving the front dorsal end of the pancreas.

Diamare (2) describes and figures a fairly large anastomosis between the dorsal anterior gastric vein (vena gastrica dorsalis anterior) and the median gastric vein (vena gastrica media) in *Scyllium catulus*. I have examined eight specially injected specimens of *S. canicula* and numerous fresh ones, but have been unable to find this anastomosis. A large branch runs forwards to join the dorsal anterior gastric vein, and a smaller one originating near it runs backwards into the median gastric vein (*vide* fig. 1, Pl. II., P), but the two do not anastomose by any well-marked vessel such as Diamare figures, although they are indirectly in communication by means of capillaries.

5. i. *The Dorsal Gastric Vein* [Pl. II., D.G.] is a well-marked vein composed of two main tributaries, which collect the blood from the right and left sides of the anterior two-thirds of the cardiac division of the stomach.

5. ii. *The Dorsal Œsophageal Vein* [Pl. II., D.O.] brings back blood from the dorsal side of the œsophagus.

6. *The Ventral Anterior Gastric Vein* [Pl. II., V.A.G.] is a large trunk receiving one branch from the stomach, the ventral gastric vein, and one branch from the œsophagus, the ventral œsophageal vein. It leaves the stomach-wall on its ventral side, anterior to the point of departure of the dorsal anterior gastric vein, and it runs in the mesentery to flow into the hepatic-portal vein shortly before the latter divides into its right and left branches.

6. i. *The Ventral Gastric Vein* [Pl. II., V.G.] is a conspicuous vessel formed by the confluence of a number of tributaries from the ventral side of the anterior two-thirds of the cardiac division of the stomach.

6. ii. *The Ventral Œsophageal Vein* [Pl. II., V.O.] collects the blood from the ventral side of the œsophagus.

The œsophagus has a very rich plexus of large capillaries similar to that described by Parker (10) in *Mustelus*, save that in *Mustelus* the blood from this plexus is taken to the posterior cardinal sinuses, while in *Scyllium* it goes to the hepatic-portal vein in the manner described above.

7. *The Hepatic Veins and Sinuses* [Pls. I. & II., H.S.]. The hepatic vein is a large thin-walled venous trunk situated at the anterior end of the corresponding lobe of the liver. The two hepatic veins unite just outside the liver to form a large sac, the hepatic sinus, which, when dilated, entirely fills up the space between the ventral body-wall, the œsophagus, the anterior ends of the lobes of the liver, and the pericardio-peritoneal septum.

This sinus is partially divided into two chambers by an incomplete vertical septum formed of interlacing trabeculæ. It passes through the pericardio-peritoneal septum and opens into the sinus venosus, however, by two small circular apertures, one on either side of the middle line, by means of which all the blood brought to the liver by the hepatic-portal vein and the hepatic arteries is returned to the heart.

### B. The Renal Portal Veins.

1. *The Caudal Vein* (Parker) [Pl. I., C.] originates far back in the tail and runs forwards in the hæmal canal ventrally to the caudal artery to a point just posterior and dorsal to the anus. Here it leaves the vertebral column and divides into two large equisized branches, the renal-portal veins. It receives numerous small branches from the myotomes of the tail.

2. *The Renal Portal Vein* (Parker) [Pl. I., R.P.] starts from the bifurcation of the caudal vein and passes forward along the dorsal and dorso-lateral edge of the kidney, to which it sends numerous afferent renal branches. It gradually diminishes in calibre, and dies away towards the anterior extremity of the caudal mesonephros at about the level of the front end of the vesicula seminalis in male. The two renal-portal veins are completely separated in the middle line, and do not communicate directly with the posterior cardinal sinus.

2. i. *The Posterior Oviducal Veins* (Parker) are small veins from the dorso-lateral wall of the posterior portion of the oviduct, and open into the renal portal vein.

2. ii. *The Posterior Parietal Veins* (p.-spinal veins, Parker) arise from the myotomes of the region of the body along the side of the kidney, and open into the renal portal vein on its dorsal side.

### VII. The Coronary Veins (Text-fig. 4).

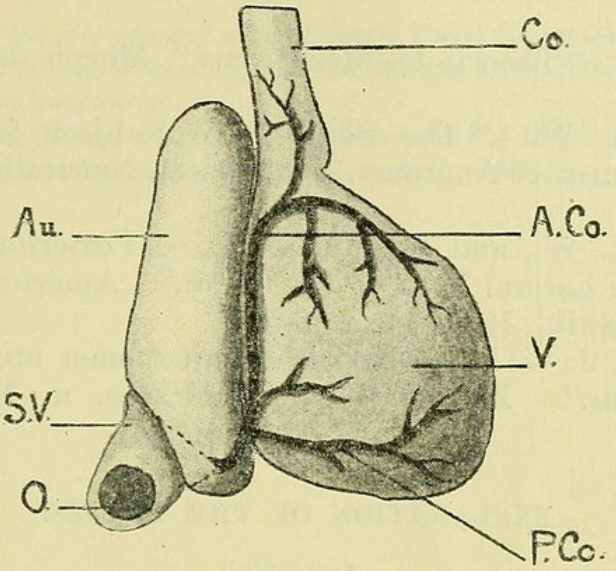
*The Coronary Veins* are situated one on each side of the heart. Each of them is formed at the posterior end of the furrow separating auricle and ventricle, and enters the sinus venosus just behind the corresponding flap of the sinu-auricular valve. The posterior smaller vein collects the blood from the caudal end of the ventricle, while the remaining one collects blood from the anterior part of the ventricle, and, after receiving a well-marked tributary from the conus arteriosus, runs backwards in the groove between auricle and ventricle. Small factors from the auricle probably join the coronary veins, but are difficult of injection.

### VIII. The Ductus Cuvieri.

*The Ductus Cuvieri* (Parker) [Pls. I. & II., D.C.] convey to the heart all the venous blood save that brought by the hepatic veins. Their anatomical relations in the adult have already been briefly noted. The outer end forms a spout-like structure with an oval end projecting into the posterior cardinal sinus. Each passes

inwards almost horizontally on the ventro-lateral sides of the œsophagus through a very conspicuous notch in the posterior border of the fifth cerato-branchial cartilage up to the lateral wall of the pericardium. It is continuous through this with the sinus venosus.

Text-figure 4.




Lateral view of the heart to show the arrangement of the coronary veins.

For explanation of lettering see p. 454.

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## EXPLANATION OF THE PLATES.

*Lettering.*

A.C. Anterior Cerebral Vein.
A.Ca. Anterior Cardinal Sinus.
A.Ch. Anterior Choroid Plexus.
A.Co. Anterior Coronary Vein.
A.F. Anterior Factor of A.C.
A.I. Anterior Intestinal Vein.
A.L.G. Anterior Lieno-gastric Vein.
An. Anastomosis between Posterior factors of A.C.
Au. Auricle.
B. Brachial Vein.
Ba. Basipterygium.
C. Caudal Vein.
Cl. Cloacal Vein.
Co. Conus Arteriosus.
D.A.G. Dorsal Anterior Gastric Vein.
D.C. Ductus Cuvieri.
D.G. Dorsal Gastric Vein.
D.O. Dorsal Œsophageal Vein.
E. Eye.
F. Femoral Vein.
G.I. Gastro-Intestinal Vein.
G.S.2. 2nd Gill-cleft.
H. Hyoidean Sinus.
H.P. Hepatic Portal Vein.
H.S. Hepatic Sinus.
I.I. Intra-Intestinal Vein.
I.J. Inferior Jugular Sinus.
Il. Iliac Vein.
I.M. Intestino-Mesenteric Vein.
I.O. Inter-Orbital Vein.
K. Caudal Mesonephros.
L.A. Lateral Abdominal Vein.
L.C. Lateral Cutaneous Vein.
Le. Lateral expansion of the Posterior Choroid Plexus.
L.M. Lateral Myelonal Vein.
M. Myelonal Vein.
M.G. Median Gastric Vein.
N.S. Nasal Sinus.
O. Opening of the Ductus Cuvieri.
O.C. Olfactory Capsule.
O.N. Orbito-Nasal Vein.
Or. Orbital Sinus.
P.An. Pelvic Anastomosis between the two L.A.
P.C. Posterior Cerebral Vein.
P.Ca. Posterior Cardinal Sinus.
P.Ch. Posterior Choroid Plexus.
Pe. Pectoral Fin.
P.I. Posterior Intestinal Vein.
Pl. Pelvic Fin.
Pl.C. Pelvic Cartilage.
P.L.G. Posterior Lieno-gastric Vein.
P.O. Post-Orbital Sinus.
P.S. Posterior Splenic Vein.
R. Portion of the P.I. on the Rectal Gland.
Re. Rectal Vein.
R.P. Renal Portal Vein.
R.S. Right Spermatic Vein.
S.C. Sub-Clavian Vein.
Sp. Spiracle.
S.S. Sub-Scapular Sinus.
S.V. Sinus Venosus.
T.G. Thyroid Gland.
V. Ventricle.
Va. Valve between A.Ca. and P.Ca.
V.A.G. Ventral Anterior Gastric Vein.
V.F. Ventral factor of A.C.
V.G. Ventral Gastric Vein.
V.O. Ventral Œsophageal Vein.

## Plate I.

Diagram showing the general disposition of the main venous trunks in *Scyllium canicula*. The more dorsally situated vessels are stippled and the more ventral ones black. For the sake of clearness, the ventral cutaneous vein has been omitted.

## Plate II.

Fig. 1. Sketch of the arrangement of the Hepatic Portal factors seen from the dorsal side. The vessels were injected and the gut hardened and removed whole from the body-cavity.

Fig. 2. Diagram of the main vessels of the anterior end of the Dogfish viewed from the side in order to give their dorso-ventral relations.