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De Ryke

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by

WILLIS DE RYKE

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I. INTRODUCTION

1. Purpose and Scope

During the progress of evolution among the vertebrates, for some unknown reason the renal portal system has been discarded. We find it present in a typical form in fishes, Amphibia, snakes, lizards and possibly some Chelonia. In birds it is considerably modified, if present at all, and is apparently entirely absent in mammals. Whatever may have been the advantage or disadvantage of the renal portal system, the change has been made and doubtless the transition lies somewhere in the Reptilia, probably the Chelonia. Its presence in a typical form in turtles has been doubted although many eminent workers in the fields of comparative anatomy and embryology have strongly suspected that the adult Chelonia, or at least some species of them, possess a true renal portal system.

The study of the veins associated with the kidneys of the turtle *Chrysemys marginata belli* (Gray) and their development was undertaken to ascertain the presence or absence of a renal portal system in the adult of this species, to trace its development if present and the development of certain veins closely related to the kidneys and which would probably be involved in the embryological formation of such a system. It was also desirable to compare to some extent the development in this form with that of certain other related forms.

The solution to the problem of presence or absence of the renal portal system in the adult lay in the study of the adult system of veins related to the kidney and a determination of the presence or absence of a capillary network within the adult kidney which permits the passage of blood on its way from the body capillaries to the heart.

The embryological study involved the development of the vertebral veins, posterior cardinals, renal advehens anterior, renal advehens posterior, subcardinals, extreme posterior region of the postcava and the venous network of the kidney.

I wish here to acknowledge my indebtedness and express my thanks to Dr. Frank A. Stromsten for his constant assistance, advice, and criticism and to Prof. Gilbert L. Houser for his many helpful suggestions and provision of adequate laboratory facilities to carry on this work.

2. Historical

A comparatively small amount of work has been done in tracing the detailed development of the venous system of the turtle. It is especially striking that such an important and interesting question as the presence or absence of a renal portal system and its development as found in Chelonia should have remained uninvestigated. The most noteworthy attempts by the early workers to trace the development of the venous system of Chelonia were those by Agassiz, ('57) and Rathke, ('48). Perhaps the reason for these early workers not having investigated this system is due to the scarcity of material or what is more probable, the lack of the modern methods of technique.

A much greater amount of work has been done on the development of the venous systems of Selachians, Amphibians, snakes and lizards. For these extensive contributions we are indebted to Goette, Hochstetter, Hoffmann and Rathke. The condition as found in cyclostomes has been described by Rathke, Retzius and Johannes Müller. The presence of a renal portal system in fishes was first discovered by Jacobsen, one of the pioneer investigators. He found various expressions of the renal portal system which he could classify into three forms as follows: (1) The veins of the skin and body region discharge into the kidney while the caudal vein does not branch into the kidney but discharges into the right cardinal vein. (2) Similar to the first except that the caudal vein branches in the kidney. (3) A modification of the former two in that the caudal vein or another vein unites with the portal vein of the liver. Hyrtl recorded the condition as found in bony fishes and especially that of *Lepidosiren paradoxa.*

The principal work on the development of the veins in Selachians has been done by Balfour, Hochstetter and Hoffmann. Hoffmann in his work "Zur Entwicklungsgeschichte des Venensystems bei den Selachiern" gives an account of the development of the venæ omphalo-mesentericæ, vena subintestinalis and venæ cardinales. He finds that the beginnings of the posterior cardinal veins are closely bound to the anlage of the mesonephros and in early stages

are comparatively free from anastomoses with each other but later freely anastomose. In an embryo of 20 mm. the posterior cardinals have already formed and begun to anastomose with the vena subintestinalis caudalis producing a renal portal system. Balfour records the vena subintestinalis as appearing ventral to the alimentary tract, being the first large venous trunk to form in Selachian embryos and terminating shortly before the end of the tail. It bifurcates at the cloaca, uniting again anteriorly. The anterior part then atrophies, the posterior part remaining and becoming the caudal vein. As soon as the cardinal veins appear the caudal vein unites with them. This is accomplished by the degeneration of the anterior portion of the anal ring and the union of the two posterior portions with the posterior cardinal veins on either side. The anastomosing branches between the caudal vein and the posterior cardinal veins pass through the mesonephros and eventually break up into a capillary network and a renal portal system is established. According to Hochstetter the development of the renal portal system in Selachians is as described by Balfour.

The development of the renal portal system in an Amphibian has been traced by Goette in *Bombinator igneus*. According to his description the posterior cardinal veins which open anteriorly into the duct of Cuvier unite posteriorly with the caudal vein. At this union the iliac veins join the system. In the meantime the mesonephros has developed in the region of the union. The cardinal veins fuse close to the mesonephros and the posterior portion forms a part of the postcava. The anterior part of the postcava develops independently. This is followed by the atrophy of the anterior region of the mesonephros and the posterior cardinals. The veins which first opened into the posterior cardinals now lose their connections and form the renal advehentes. The iliac veins become connected with a newly developed vein, the abdominal, and in this manner have connection with the postcava through Jacobsen's vein and with the anterior abdominal vein through the epigastric vein. In this manner a renal portal system is laid down.

Probably the most valuable work touching on the renal portal system of reptiles has been done by Bojanus, Jourdain, Nicolai, Hochstetter, Hoffmann, Rathke and Stromsten.

Jourdain ('59) in describing the renal portal system of the kidney of an adult Ophidian details its arrangement as follows. After picking up the important vessels, mesenteric vein and cloacal

veins as well as a vein from the tail, the renal portal vein proceeds, accompanied mediad by the ureter and laterad by the vas deferens or oviduct, in a circuitous manner over the kidney. In its course it picks up small veins from the ureter and vas deferens (oviduct), a vein parietalis anterior and a varying number of intercostal-spinalis veins. Each of these veins runs along the edge of the kidney accompanied by the ureter which is on the inside. Their branches are numerous and disappear for the most part in the notches between the small lobes branching out like dendrites between the canals of the kidney. The advehent veins of the kidney branch and become smaller and smaller until they finally lose themselves in the forward part of the kidney. From the anastomosis of the efferent veins, a system, the renal revehent arises which courses anteriorly from the kidney along with the one from the opposite side and unites with the postcava.

Rathke contributed to our knowledge of the venous system of *Tropidonotus natrix* ('39), the crocodile ('66) and the turtle ('48). His account of the development of the venous system of the natter contains a very good description of the posterior venous system development, a resumé of which follows. In the development of the natter the caudal vein is divided early and each branch unites with the posterior cardinal. The postcava is developed as a branch of the common stem of the right omphalo-mesenteric vein and the right vertebral vein lying in the caval mesentery and proceeding along the dorsal wall on the median side of the mesonephros. The mesonephroi then begin to separate from the body wall and degenerate from anterior to posterior. This results in the formation of the vertebral veins which are formed from the anastomoses between the segmental veins on both sides of the vertebral columns. These vertebral veins later atrophy in the posterior region and practically disappear leaving little or no trace. With the separation of the mesonephroi from the dorsal body wall they begin to degenerate, and the cardinal veins to atrophy anteriorly losing their connection with the jugulars.

The caudal vein with its two branches and the posterior cardinals with their tributaries comprise the advehent system. The vena cava and its two large branches comprise the revehent system.

Hochstetter ('93) studied the development of several species of lizards giving a splendid account of the development of *Lacerta agilis* and *Lacerta viridis*. According to his observations on the

development of *Lacerta agilis*, in a stage where the intestine is closed to a point where the liver is well developed, the posterior cardinals are already well developed, being clearly marked in the posterior region of the mesonephros but broken up into blood sinuses which lie between the mesonephric tubules in the anterior region. At some points the posterior cardinals appear to be ventral, at others lateral and in the posterior region clearly dorsal to the mesonephroi. These veins also receive blood from the segmental veins. With the increase in compactness of the mesonephroi the veins change their relations.

With the growth of the tail region the caudal vein becomes of importance. It enlarges and bifurcates dorsally and anteriorly to the blind end of the intestine, the two branches running along the median sides of the mesonephroi. These two veins anastomose with each other anterior to the omphalo-mesenteric artery and connect freely with the venous network of the mesonephroi.

With the formation of the postcava by the union of the omphalo-mesenteric veins with the unpaired portion of these veins the branches of the caudal vein lose their connections and unite with the posterior cardinals. A degeneration of the anterior end of the mesonephroi and the atrophy of the anterior portion of the posterior cardinals now make the rest of the posterior cardinals and the caudal vein and its branches the afferent veins of the mesonephroi.

The mesonephroi now begin to separate anteriorly from the dorsal body wall. This process continues posteriorly. The postcava bifurcates and runs between the mesonephric bodies receiving several branches. The postcava and its branches then comprise the revehent system of the mesonephroi.

While this is taking place the venous network of the anterior end of the mesonephros becomes disconnected from the duct of Cuvier and becomes connected to a row of segmental, anastomosing veins which have gradually developed as a result of the separation of the mesonephroi from the dorsal body wall. The chains of anastomosing vessels become larger as the mesonephroi degenerate and lie on either side of the vertebral column ventral to the rib anlagen. With the degeneration of the anterior portion of the mesonephroi the number of connecting veins decreases until only a few of them at the posterior end of the mesonephroi remain. The chains of veins form longitudinal anastomoses and also anastomose with each other.

The embryological development in the other forms, including *Lacerta viridis* on which Jourdain had worked, was found in general to parallel that of *Lacerta agilis*, the difference being in minute details of development.

The latest work of consequence on the development of the posterior portion of the venous system of a reptile is that of Stromsten ('05). He traced the development of the veins in the posterior region of the turtle *Kinosternon pennsylvanicum*. His studies included the development of the hepatic portal system and to a considerable extent the development of the umbilicals, abdominals and the larger veins involved in the development of the renal portal system.

According to Stromsten, the posterior cardinals and subcardinals are already formed in the youngest embryo studied, an embryo of 7.4 mm. crown rump measurement. The posterior cardinals extend from the caudal termination of the mesonephric ducts along the entire length of the mesonephroi. At the caudal termination of the mesonephric ducts the posterior cardinals receive a number of small branches from the tail region, the last dorsal intersegmental branch and a stout anastomosing branch from the subcardinal of the same side. The portion of the posterior cardinals between the cranial end of the mesonephros and the sinus venosus is broken up into two or three vessels.

In a 7.4 mm. embryo the subcardinals are formed and connect with the posterior cardinals by numerous anastomoses but do not connect with each other. With growth the two branches of the caudal vein unite with the subcardinal veins, establishing a renal portal system. With continued development, the forking caudal vein loses its connection with the subcardinals and unites with the posterior cardinals. The postcava develops and the course of the blood is reversed in the portal system of the mesonephroi.

The posterior vertebral veins are fused dorso-segmental branches of the posterior cardinals and lie dorsal to the rib anlage.

The anterior and posterior renal advehent veins of the kidneys represent the remains of the posterior cardinals.

3. Material and Methods

Adults

Ample material for the study of this problem was found in the region of Lake Okoboji located in the northwestern part of the State of Iowa. I was quite fortunate to find that a laying ground

for *Chrysemys marginata belli* (Gray) was conveniently adjacent to the grounds of the Lakeside Laboratory on Miller's Bay. The turtles swarmed up the sloping gravel bank usually between the hours of four to eight of an evening to lay their eggs, making a splendid opportunity for observations, recording the time of laying and marking the nests.

Before proceeding with the study of the embryonic changes involved in the developing venous system the adult venous systems of about twenty-five turtles were studied, special attention being given to the veins related to the kidneys. That the blood vessels might be in as expanded condition as possible and better injections assured the animals were killed with a concentrated solution of chloral hydrate.

The injection media used most successfully were a yellow starch paste mass and a colored gelatin mass. The yellow starch mass was prepared according to Guyer.[1] A carmine gelatin injection mass was prepared according to Walker's variation as given by Guyer,[2] and also a blue gelatin injection mass as given by Guyer.[3] The setting of the gelatin during the process of injection was prevented by adding a small amount of potassium iodide. The injection masses were forced into the vessels by means of a metal syringe or by the gravity method, both of which were quite adequate. Immediately after injection the specimens were plunged into a ten per cent formalin solution, thus coagulating the gelatin.

The necessity for determining the arrangement of the veins within the kidney is quite obvious. The small size of the veins entering or leaving the kidney makes it impossible to remove the kidney and inject. For this reason it was necessary to inject a large portion of the venous system at sufficiently high pressure to guarantee the filling of the vessels of the kidney.

Injections of yellow starch paste were made and dissection carried out as far as possible under the binocular microscope. This method however had its limits in that the relations of the smaller and more numerous vessels were lost through the necessary destruction of some of them during dissection.

In order to preserve these smaller vessels a less mechanical method was sought. The first attempts were by means of an injection of

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[1]Guyer—Animal Micrology, p. 92.
[2]Guyer—Animal Micrology, p. 83.
[3]Guyer—Animal Micrology, p. 84.

ozokerite wax. The greatest difficulty encountered here was that a temperature sufficiently high to keep the wax in a liquid condition had to be maintained. The metal syringe, the wax, and the specimen had to be at this temperature to prevent the hardening before complete injection. This difficulty was overcome by placing the specimen and apparatus in water at the temperature of the melting point of the wax. With rapid operation the injection could be made but by no means was success achieved at all trials.

These injected specimens were then cooled and the kidneys with their projecting blood vessels removed from the turtle. Some of them were then placed in artificial gastric juice and kept in an incubator until the digestion of the tissue was complete. Another method used for eliminating the tissue was that of corrosion to be discussed presently. Wax casts resulted which were very good for study but the difficulty of their preservation and their delicacy made it desirable to have a method whereby permanency might be gained.

In seeking a permanent injection mass celloidin was tried and found to be a fairly successful method but somewhat expensive as many failures of injection were unavoidable.

The method finally adopted and the most successful one was that of injecting a colored liquid celluloid. This injection fluid is prepared as follows. Sheet celluloid secured from discarded automobile curtains is thoroughly washed and cut into small pieces. About twenty grams of this is dissolved in 100 cc. of acetone and allowed to stand for twenty-four hours. Fifteen grams of camphor is then dissolved in this solution. This is then used as a stock solution and must be kept air tight. Before using this liquid as an injection medium it is thinned by the addition of acetone carrying a coloring agent. The size of the vessels to be injected determines the viscosity of the injection medium to be employed. The liquid was thinned to almost a watery viscosity when it was desired to inject capillaries. A large number of coloring agents were tried, the most satisfactory of which were found to be crystal violet, brilliant green and alkanet, all soluble in acetone.

This injection fluid on coming in contact with water forms a hard cast and does not readily break. With an increase in the percentage of camphor it may be made to take on the nature of rubber. This medium then produced the desirable characteristics since it is not brittle and stands considerable rough handling.

The turtles were killed by chloral hydrate and the plastron carefully removed. Injection was then made through the left abdominal vein after tying off the right, through the postcava, or through the left aortic arch after tying off the right. Not only single injections were carried out but double and triple injections of the colors were resorted to in all possible combinations.

After injection the specimens were immediately placed in cold water where they remained for twelve hours. This permitted the casts to become hard. The kidneys were then carefully removed with their protruding injected vessels and placed in artificial gastric or pancreatic juice in a suitable warming oven, or more commonly and with equal success they were subjected to the action of concentrated muriatic acid for twelve to eighteen hours. It was then possible to wash out in water the corroded tissue. This was accomplished by admitting a gentle flow down a stirring rod from an open tap or by carefully using a pipette, both of which methods proved satisfactory. For the extremely fine structure this method was slightly altered. After a large portion of the kidney substance had been corroded and washed out the kidneys were permitted to remain in the water for days until disintegration had taken place and the tissue practically removed itself from the meshwork of minute blood vessels. This method produced very beautiful casts, accurate to the minutest detail and of such a permanent nature that they could be studied without damage to them.

In addition to the study of the casts, the finer vascular structure of the kidney was studied by means of serial sections. These serial sections were made of the kidneys of fifteen specimens which had been injected under high pressure with a carmine gelatin mass or an aqueous solution of Berlin blue. Also a specimen just hatched was serially sectioned in the region of the kidneys, stained in borax carmine and mounted for study.

Embryos

Two entire summers were given over chiefly to securing material for the embryological study. No difficulty was encountered in locating the nests or securing eggs. The laying season was found to extend from the middle of June to about the twenty-fifth of July. The laying usually takes place between the hours of four to eight in the afternoon, the number of eggs in a clutch varying from five to fifteen and averaging about eleven.

During the summer of 1923 ninety-six nests of the painted turtle

Chrysemys marginata belli were located and during the summer of 1924 about fifty nests of the same species were located. From these eggs I was able to secure about twelve hundred embryos.

The desire for embryos of as many gradations in size as possible led to two plans for securing them. The first was to stake and record the nest at the time of laying and remove the entire clutch when embryos of this particular age were desired. The second was to stake nests through fifteen successive days of laying and remove two or three eggs from each nest every fifteen days. However no exact method for securing a graded series is possible owing to the fact that different conditions such as kind of soil, depth eggs were laid, amount of sunshine and shade alter the incubation period. Not only is this true of each nest but it is true of each egg in the nest, so it is possible to find a single clutch having embryos at various stages of development. Three pairs of twins were found during this period and it was quite interesting to find in each case that one of the twins had outgrown the other and in one case the larger was at least twelve times the size of the smaller.

The small embryos adhere closely to the shell making their removal somewhat difficult. It was found much more expedient to locate the minute embryo with a hand lens and cut around it through the shell, placing the entire piece, shell and embryo, in the fixing fluid. The embryo could then be easily separated from the shell after reaching the alcohols. The larger embryos could of course be easily removed from the shell and fixed.

Fixation was made in Bouin's picro-formol fluid or in chrom-aceto-formalin mixture. The length of time of fixation ranged from one hour to four hours, depending upon the size of the embryos. Just before using, two volumes of this mixture are added to one volume of formalin.

BOUIN'S PICRO-FORMOL

Picric acid, saturated aqueous solution	75 parts
Formalin	25 parts
Acetic acid (glacial)	5 parts

CHROM-ACETO-FORMALIN MIXTURE

Chromic acid, 1 per cent solution	16 parts
Glacial acetic acid	1 part

These two fixing fluids were found to have a double advantage. They were excellent in fixing the tissues and in addition, the glacial acetic acid attacked and destroyed the greater part of the eggshell.

The embryos were then passed through the graded alcohols until seventy per cent was reached where they remained until they could be stained and sectioned.

The process of staining and sectioning was done at the State University of Iowa. A series of embryos was selected for sectioning. Each embryo was drawn by the camera lucida and the magnification recorded in order that reference might be obtained and measurements made. Some of the embryos were then stained *in toto* with borax carmine, passed through the graded alcohols, cleared in xylol, embedded in paraffin, sectioned and mounted. The majority of the embryos were passed through the graded alcohols, cleared in xylol, embedded in paraffin, sectioned, mounted, stained in Delafield's hemotoxylin and counterstained with Grubler's Orange G. acidulated slightly with acetic acid. In sectioning the embryos those from 1.2 mm. crown rump measurement to 16 mm. crown rump measurement were cut 20 microns. Those from 8 mm. to 12 mm. carapace length measurement were cut 20 microns. Those from 12 mm. to 14 mm. carapace length measurement were cut 25 microns and one with a 22 mm. carapace was cut 50 microns.

That the study of the sections might be supplemented by the study of injected embryos approximately one hundred embryos ranging in size from the earliest stages of development to the adult were injected with various fluids. The greatest difficulty encountered in this technique was to find an injection fluid whose viscosity was low enough to permit the complete injection of the finer vessels of the embryo and still not leave the vessels and penetrate the tissues. Certainly the most logical form of an injection fluid for this purpose would be some colloid solution or perhaps a celluloid injection. The latter was tried numerous times and in many degrees of concentration, but the fluid invariably hardened before complete injection of the finer capillaries. Considerable time was spent in search of a suitable colloid solution. Among the large number tried it was found the best results could be obtained by using Higgin's Black India Ink, an aqueous solution of Berlin blue or alkanet.

After several mechanical devices for injection of the embryos had been tried, it was found that the simplest type was the most successful. This consisted of a small rubber tube with a mouth-piece inserted at one end and a glass canula at the other. In the construction of this apparatus there is but one difficult feature; the

construction of the canula. This is done by drawing out a small glass tube into a hairlike capillary three or four inches long. By placing this under a microscope the point at which the space ceases and the solid glass begins may be determined. With a pair of scissors the tube may be cut at this point leaving a very fine hairlike capillary tube.

In using this mechanism the canula is carefully inserted in the rubber tube and the end dipped into the injecting fluid. The operator then with the mouthpiece in his mouth draws the fluid into the canula. Then while looking through a binocular the canula may be inserted in the heart, the sinus marginalis, the jugular vein, the umbilical vessels or any other clearly discernible vessel. The operator then applies pressure to the fluid, forcing it into the vascular system of the embryo. The canula after once being used must be kept in water to prevent the closure of the tube.

From the injected embryos three series were selected duplicating as nearly as possible the series which had been sectioned. The members of the first series were serially cross sectioned and mounted. Those of the second series were cut into thick longitudinal sections and mounted. The smaller members of the third series were used in whole mounts. By this means it was then possible to obtain a check on the study of the stained cross sections.

II. ADULT RENAL PORTAL SYSTEM

The right and left abdominal veins issue from the liver substance and lie on either side of the ventral median line. They run ventrally for a short distance but soon make a sharp turn in a posterior direction, lie immediately ventral to the peritoneum and course toward the ventral median line. They receive as tributaries during this part of their course, a small gastric vein, a vein from the pectoral muscles and a small vein from the tensor-pleuro-peritoneal muscle. They gradually approach each other in their course diverging again at a point just anterior to the pubis. Slightly posterior and ventral to this they are placed in communication by a transverse vessel lying ventral to the pubis and receiving branches from the obturator externus and pubo-plastinalis. Continuing posteriorly and diverging they angle in a dorsal direction following the curve produced by the pelvic girdle and carapace until they join the external iliac vein of their respective sides. In the latter part of their course they receive tributaries from the obturator

internus muscle, a large branch which anastomoses with the margino-costal vein of the carapace, a vein from the pubo-plastinalis muscle, a branch from the vastus femoras rectus muscle and the femoral vein. The abdominals unite with the circumflex iliac veins of their respective sides to form the external iliac veins.

The ischiadic vein leaves the thigh, passes into the pelvis and unites with the common coccygeal vein to form the circumflex iliac vein.

The circumflex iliac vein courses dorsally, receives the epigastric vein and unites with the abdominal vein of its side to form the external iliac vein.

The external iliac vein makes a sharp turn and courses toward the median line. Reaching the external border of the kidney it passes to the ventral surface where it unites with the renal advehentes.

The posterior renal advehent vein is formed by the union of a number of small branches bringing blood from the muscles of the pelvis, the caudal region and cloaca with its closely related organs. This vein then passes dorsally and anteriorly within the pelvis. Leaving the pelvis and reaching the posterior edge of the kidney it passes over and in close contact with the ventral surface of the kidney where it gives off afferent branches to the kidney and eventually anastomoses with the anterior renal advehent vein at a point where these two unite with the external iliac vein.

The anterior renal advehent vein, as a branch of the vertebral vein arises between the fifth and sixth ribs, receives the fifth intercostal vein and immediately passes to the ventro-lateral surface of the anterior portion of the kidney. As it courses along the surface of the kidney it gives off afferent branches and unites posteriorly with the renal advehent vein at a point where both are joined by the iliac vein.

For convenience of discussion the portions of the anterior and posterior renal advehent veins lying adjacent to the surface of the kidneys will hereafter be spoken of as the renal portal vein.

The vertebral veins arise as a bifurcation of a single vein in the region of the first thoracic vertebra and run posteriorly on either side of the spinal column. In their course they lie dorsal to the ribs and receive the first four intercostal veins and veins from the spinal cord. Between the fifth and sixth ribs the vertebral vein gives off a large branch, the anterior renal advehent vein. Pos-

terior to this branch they diminish considerably in size, give off numerous small branches to the kidneys and continue posteriorly gradually becoming smaller in diameter and eventually ending by receiving a number of minute branches from the extreme caudal region.

The postcava is formed between the kidneys by the union of two short thick veins. These in turn result from an anastomosis of veins leaving the kidney, the latter veins usually numbering three from the left kidney and two from the right, but frequently the reverse is true. The veins returning blood from the ovaries or testes unite with these veins in the region of their entrance into the kidney substance. The postcava leads anteriorly coursing away from the median line toward the duodenal flexure and enters the right dorsal lobe of the liver. Posterior to the kidneys there is no postcava.

The kidneys are a pair of lozenge shaped organs lying in the posterior dorsal curvature of the carapace, one on each side of the spinal column. They present three lobulated surfaces, a curved dorsal surface, a mesial surface and a latero-ventral surface. The surfaces are united with each other by rounded edges of considerable curvature.

The venous tributaries to the postcava arise from the mesial ventral edge of each kidney. These tributaries branch rapidly into smaller veins which enter the kidney substance and embed themselves between the lobules.

Closely adhering to the latero-ventral surface is the renal portal vein joined about midway by the external iliac vein which is partially buried between the kidney lobules. On the side in contact with the kidney the renal portal vein branches profusely, the afferent vessels entering the kidney substance between the lobules.

In an effort to determine the true nature of the connections between the renal portal vein and the postcava a heavy yellow starch paste mass under a constant pressure was injected into the postcava of a large number of specimens. In no case was I able to get the injection mass to pass through the veins of the kidney and appear in the renal portal vein. In another group of specimens the injection was carried out in the opposite direction by injecting into the left abdominal vein after tying off the right and here again I was unable to get the injection mass to pass through the veins of the kidney and enter the postcava. My results from the yellow

starch paste injection agree with those obtained by Lewis ('16) and disagree with those obtained by Robinson ('18) both of whom investigated the condition in the adult of this form.

In other specimens injections of a gelatin mass were carried out in the same manner as that used with the starch paste. The gelatin was colored with carmine or Berlin blue. These fluids never failed to pass through the veins of the kidneys and appear in the opposite vessel.

The results of these injections indicated that the vessels of the kidney are too small to permit the passage of the starch but that vessels do connect the renal portal vein with the postcava and that they are of capillary size.

By means of the celluloid corrosion method celluloid casts were made of the vessels of the kidneys. Some of these were made from single injections while others were made from double injections. In these injections a thin colored celluloid solution was used. In the single injections the fluid was injected into either the renal portal through the abdominal and external iliac or into the postcava. In either case, after corrosion or digestion there remained a cast of the vein with all its branches ultimately breaking up into capillary vessels, quite clearly demonstrating that no connection between the postcava and renal portal vein existed other than of a capillary size. The double injections were made by injecting two colors of thin celluloid, one color through the postcava and the other through the abdominal and external iliac into the renal portal vein. These casts were then carefully examined and dissected beneath the binocular microscope and invariably I was unable to find a single connection larger than capillary size.

For microscopical examination of the internal vascular structure a number of kidneys were injected with carmine gelatin through the left abdominal vein and an aqueous solution of Berlin blue through the aorta. A study of the serial sections of these injected specimens revealed the fact that no connections larger than capillaries were present between the branches of the renal portal vein and those of the postcava but that a capillary network with its glomeruli connections existed in which the branches of the postcava and renal portal vein ended, thus making a capillary system the only passage for blood between these two large trunks.

III. EMBRYOLOGY

The development of the renal portal system has been followed through a series of serially sectioned embryos of *Chrysemys marginata belli* and this supplemented by a study of injected embryos of the same species. The youngest embryo of the sectioned series measures 1.2 mm. in length and the oldest has a carapace length of 22 mm. The measurements of the younger embryos are crown rump measurements while those of the older embryos are measurements of the length of the carapace. In the present work the measurements referred to will be crown rump measurements unless carapace measurement is specified.

The outlines as shown in Figs. 1 to 6, Plate I, are outlines of the embryos whose reconstructed blood vessels are used for explanation in this work. The following table indicates the outline drawing, the length of the embryo and the reconstructions of its venous system.

OUTLINE FIGURE	LENGTH IN MM.	RECONSTRUCTION FIGURES
1	7	Plate II
2	10	Plate III
3	13	Plate IV
4	8 (carapace)	Plate V
5	12 (carapace)	Plate VI
6	22 (carapace)	Plate VII

The posterior cardinal veins first appear in an embryo of 4 mm. length. At this early stage these vessels open into the duct of Cuvier, continue posteriorly and gradually diminish in diameter. In the anterior portion they lie lateral to the mesonephric duct but shortly swing to a dorso-lateral position. At this time there are also noticeable disconnected venous islands formed ventral and mesial to the mesonephric duct. These islands are to be connected in the future to form the subcardinal veins.

An embryo of 7 mm. length (Plate II) has the posterior cardinal veins well developed anteriorly but posteriorly the vessels gradually reduce their diameter and are entirely wanting as a continuous vein in the extreme posterior region of the mesonephroi. However, the evidence of their future development in this region is indicated by several blood sinuses of considerable size. The posterior limb bud has at this time made its appearance, its drainage being cared for by the external iliac vein (V. E. I. D. and S.) which empties its blood into the posterior cardinal.

The future vertebral veins are also foreshadowed at this early

period by the development along their future path of a number of small blood sinuses.

The subcardinal veins follow rather closely the development of the posterior cardinal veins. Through anastomoses of the blood sinuses of the preceding stage a pair of venous channels or veins has been established. These vessels lie on the median ventral surface and in close relation to the mesonephroi. They eventually unite with each other and with the posterior cardinal veins. Even at this early stage there has been formed a few prominent unions between the posterior cardinals and the subcardinals (Plate II, Pc.Sc.A.). Not only has a connection been established between the larger portions of the veins, but at least one has been formed between two of the small portions which are as yet little more than blood sinuses. These anastomoses do not at this time penetrate the mesonephric substance but lie close upon the surface of that organ.

Anteriorly the posterior cardinals are beginning to show dorsal branches which later pass dorsal to the rib anlagen and usually bifurcate at this point, later becoming connected with each other through intermediate blood sinuses.

An embryo of 10 mm. length shows conditions as represented in Plate III. With the growth of the mesonephroi the posterior cardinal veins have reached a stage of completeness. Their position is dorsal and slightly lateral to the mesonephroi. The dorsal segmental branches of the posterior cardinals are fairly well established. The blood sinuses in the path of the future vertebral veins have by this time increased considerably in size and become more numerous. The subcardinal veins have rapidly developed into a pair of definite blood vessels lying ventral along the mesial edge of the mesonephroi, the right subcardinal vein being continued somewhat more anteriorly than the left.

A complete union of the subcardinal vessels has occurred just posterior to the omphalo-mesenteric artery by three large connections. There has also developed a free anastomosis between the posterior cardinal and the subcardinal vein of its respective side. These connections are for the most part situated on the periphery of the mesonephros, either on the dorso-median surface or the latero-ventral surface but appear to be in closer relation to the mesonephric tubules than in the previous stage. However, many of them do find their way between the tubules of that body.

At this stage in the development we find the caudal vein defi-

nitely laid down. It bifurcates and each branch unites with the posterior portion of the subcardinal vein of its side. This arrangement establishes an embryonic renal portal system, the subclavian veins and caudal branches being the advehent veins while the posterior cardinal veins function as the revehent veins.

With the further development of the mesonephroi, changes take place rapidly. The mesonephroi present a condensed appearance in the posterior region while the anterior portion is apparently beginning to atrophy. The posterior cardinals take up a more lateral position to the mesonephroi and greatly increase in size. The anastomoses between the posterior cardinal veins and the subcardinal veins, and between the two subcardinal veins increase extensively.

When the stage in development as represented by an embryo of 13 mm. length (Plate IV) is reached, the majority of the anastomosing connections no longer lie near the surface but dip deep into the mesonephric body sending venous pockets between the tubules. One of the most important developing structures during this period is the postcaval vein. The posterior portion of this vein develops from the subcardinal veins, chiefly the right. The development as found in this species duplicates that as found by Stromsten ('05) in *Kinosternon pennsylvanicum*.

The formation of the postcava which opens a new channel for the blood to reach the heart is accompanied by an important change in the embryonic renal portal system previously established. This change is completed by the change in position of the two branches of the caudal vein. These branches were previously connected with the posterior ends of the subcardinal veins. Through a shifting of the anastomosing connections between the subcardinals, postcardinals and caudal branches, the connection between the caudal branches and the subcardinal veins is lost and there is a connection established between the caudal branches and the posterior cardinal veins. With this new arrangement the blood is routed differently, the posterior cardinals and the caudal branches becoming the advehent veins while the subcardinal veins and the postcava become the revehent veins.

The anterior portion of the vertebral vein has been completed at this age, being connected to the posterior cardinal vein by the dorsal segmental veins. The posterior region has not yet been formed but the process of development is under way as shown in Plate IV.

Following this stage in development there is a gradual approach toward the condition as found in the adult. The mesonephroi in the anterior region become more and more separated from the dorsal body wall. As development progresses they continue to degenerate in the anterior region while posteriorly they are large and compact.

This anterior degeneration of the mesonephroi is accompanied by the degeneration of the anterior region of the posterior cardinal veins and their dorsal segmental branches. A typical condition at this time is represented by reconstruction figures of Plate V made from an embryo measuring 8 mm. carapace length. The posterior cardinal veins still show the connections anteriorly in the regions of the subclavian vein but instead of a single large connection there are several small ones producing a network between the anterior end of the posterior cardinal vein and the duct of Cuvier. The degeneration process is quite apparent.

The degeneration of the anterior dorsal segmental branches is almost complete at this time, severing entirely the anterior portion of the vertebral vein and the anterior portion of the degenerating posterior cardinal vein. Posteriorly, the dorsal segmental branches, which have in the meantime developed, still persist, uniting the vertebral veins to the posterior portions of the posterior cardinals.

The posterior cardinals in the region of the mesonephroi are large and lie laterally within the periphery of these organs sending into the substance of the mesonephroi numerous small branches which anastomose freely with the remainder of the subcardinals or the posterior region of the postcava. This network at this stage is quite complex and represented in Plate V semidiagrammatically. Its character has been determined by a careful study of cross sections and longitudinal sections of injected embryos.

The mesonephros continues to become shorter and thicker due to the degeneration proceeding in the anterior portion. The splitting away from the dorsal body wall proceeds from anterior to posterior. At about this stage the metanephros appears as a dorsal outgrowth from the mesonephric duct, growing anteriorly and maintaining its position dorsally.

A general shortening of the renal portal system is in progress. The posterior cardinal veins lose their slight connection with the duct of Cuvier anteriorly and rapidly undergo degeneration in the anterior region (Plate VI). In the region of the largest por-

tion of the mesonephros and metanephros the posterior cardinal veins lie lateral to these organs and are quite large. Posteriorly these vessels diminish in size forming the posterior renal advehent veins. The postcava has increased in size and the subcardinal anastomosis has not entirely disappeared. The mesonephric plexus has become still more complex and consists of much smaller blood passages than those in the previous stage. The dorsal segmental branches anterior to the fifth rib have all degenerated. Those posterior to the seventh rib have likewise degenerated leaving but two, one between the fifth and sixth ribs and one between the sixth and seventh ribs. The anterior portion of the vertebral vein is now entirely free from the posterior cardinal vein and is considerably larger than that lying posterior to the sixth rib.

The mesonephroi continue to degenerate from anterior to posterior and the metanephroi continue to develop from posterior to anterior, the two becoming about the same size in an embryo of 22 mm. carapace length (Plate VII).

The vertebral veins are completely formed at this time and receive the intercostal veins. The connection between the vertebral veins and the posterior cardinal veins lying between the sixth and seventh ribs as described in the embryo of a twelve millimeter carapace has now disappeared, leaving one large prominent connection between the fifth and sixth ribs.

The posterior cardinal veins have completely degenerated anterior to the mesonephroi and metanephroi. That portion of the posterior cardinal vein lying along the mesonephros becomes embedded between the mesonephros and the metanephros, giving branches to each of them. This is brought about by the fact that the vein lies along the dorsal surface of the mesonephros. The metanephros developing dorsal to the mesonephros gradually assumes a position dorsal to the vein so that the vein lies between the two. In addition to this vein as a blood supply there has resulted at this stage during the process of degeneration of the mesonephros a second and smaller vein, a branch of the embedded vein, which lies posteriorly along the lateral surface of the degenerating mesonephros. This vein I have termed the lateral mesonephric vein. With further development this vein disappears with the mesonephros.

The venous plexus of the metanephroi during this later period of growth is constantly becoming one of finer vessels as is shown by both stained and injected embryos.

Except for the portions of the subcardinal veins which enter into the formation of the posterior portion of the postcaval vein and metanephric venous plexus they entirely disappear. The changes taking place in the further development are not of great consequence. The mesonephros continues to degenerate until it disappears and the metanephros continues to develop until it reaches full size. The renal portal vein maintains its position and appears in the adult on the ventral surface of this organ. The larger veins of the venous plexus of the metanephros continue to be broken up into finer vessels until a complete capillary network exists between the renal portal vein and the posterior terminal branches of the postcaval vein. Thus there is established a true renal portal system, the advehent veins of which are the vertebrals, iliacs, renal portals and posterior advehentes, while the revehent vein is the postcava and its posterior terminal branches.

IV. DISCUSSION

In the embryology of the renal portal system of *Chrysemys marginata belli* there occurs the usual three important periods in structural development. There is a constructive period during which various structures are developed, a period of degeneration equally as important in respect to the final result, and a period of rearrangement and development of the organs functioning in the adult. These periods are not distinctly marked off from each other but one gradually merges into the other as the necessity for the change arises.

Due to the polarity of the embryo the anterior region develops first and remains in advance of the posterior region. Likewise any degeneration occurring originates in the anterior region and proceeds posteriorly.

The early formation of the anterior portion of the posterior cardinal veins seems to be shrouded in considerable doubt. The difficulty of following them during the earliest period of development has led to various ideas as to their origin. The prevailing idea of their origin is that advanced by Hoffmann, that they arise as longitudinal anastomoses between the intersegmental arteries. In view of the fact that I wish to deal with their later development and its influence in the establishment of a renal portal system I shall pass by this early stage of the formation of the anterior portion of these veins.

The studies of the posterior cardinal veins in Elasmobranch

embryos by Hoffmann, Balfour and Hochstetter agree quite closely, in so far as my observations go, with this form of Chelonia. In the Selachians these veins are found in early embryos to be two short veins lying closely beside the mesonephric duct and gradually growing posteriorly until they reach the full length of the mesonephroi. It is in much the same manner that they behave in the turtle. However, here I may add that the term "growth posteriorly" would be a general term since in reality a series of blood sinuses unites to form the posterior cardinal veins, the progress of the unions being from anterior to posterior. In an embryo of 7 mm. length these vessels have not yet been laid down the full length of the mesonephroi, but this condition is attained in an embryo of 10 mm. length.

According to Hochstetter ('88) in Selachians the subintestinal vein plays a conspicuous part in the formation of the renal portal system. In Chelonia another group of vessels is concerned in serving the same purpose as the subintestinal vein in Selachians. The shifting of the caudal vein branches and the posterior cardinal veins establishes a renal portal system in the adult Selachian. While this shifting of the caudal vein branches does occur in the turtles *Chrysemys marginata belli* and *Kinosternon pennsylvanicum*, the same structures are not affected in the Selachians as in the Chelonia. This is due to the fact that in the higher type of vertebrate, a new vessel, the post-cava, has arisen and functions in place of the anterior portions of the posterior cardinal veins which atrophy.

In *Chrysemys marginata belli* we find the Selachian stage of development of the renal portal system at its height when the mesonephroi, posterior cardinal veins, subcardinal veins and the caudal vein with its branches are functioning most efficiently. At this time the fact that a great change is imminent may be discerned by the presence of conspicuous vertebral blood sinuses and the initial formation of the dorsal segmental veins which appear to grow dorsally from the posterior cardinal veins.

For a comparison of the development of the veins of the renal portal system of this species of turtle with those of other Amniota we may turn our attention to the work of Rathke on snakes, Hoffmann and Hochstetter on lizards and Stromsten on turtles.

The posterior cardinal veins in *Chrysemys marginata* lying on the surface of the mesonephroi in early embryonic stages are apparently in sufficiently close relation to the mesonephric tissues

so that they can efficiently take care of these organs but with an increase in the volume of these bodies the veins must necessarily maintain their close association with the tubules. The surface of the growing mesonephros becomes somewhat rough due to the increase in number and size of the tubules. As a result, the posterior cardinal veins and subcardinal veins closely adhering to the surface become somewhat pocketed and these pockets extend inwardly between the mesonephric tubules. With continued growth of the mesonephroi the pockets increase in size and number and eventually those from the subcardinal unite with those from the posterior cardinal. The earliest unions of the pockets are formed on the dorsal and ventral surfaces of the mesonephroi so that a circulation is established between these two groups of veins. This arrangement is almost identical with that found by Lewis ('02) in the rabbit and probably corresponds with the intertubular vascular spaces of Minot. Later these connections penetrate the organs making a coarse network which with development is broken up into a finer network of capillaries (or sinusoids). The anterior portions of the posterior cardinals, in the region of their union with the duct of Cuvier, while originally large single vessels, break up later into several small venous connections (Plate V). This condition is due to the process of degeneration in this region.

The formation of the vertebral veins in *Chrysemys marginata* begins quite early. In fact there is indication of their formation as early as the 7 mm. stage. This is previous to the complete formation of either the posterior cardinal veins or the subcardinal veins and before a fusion exists between the subcardinals. There is already a chain of blood sinuses laid down in the position to be occupied by the vertebral vein. This early development of venous sinuses in turtles as anlagen for veins corresponds to the development of the posterior cardinals and subcardinals in birds as recorded by Miller ('03). In the early stages of the development of *Chrysemys marginata* the posterior cardinal veins, the subcardinal veins and the vertebral veins all show this primitive type of development. The vertebral vein originates as has been described, by the dorsal segmental branches passing dorsal to the anlagen of the ribs and through anastomoses with intervening blood sinuses. The formation of this vein is a progressive process beginning at the anterior end and proceeding posteriorly. This same method of origin, other than the inclusion of the blood sinuses, has been described by Stromsten ('05) in *Kinosternon pennsylvanicum* and by Kim-

ball ('23) for *Chrysemys marginata belli*. As has already been pointed out by Stromsten, the development of the vertebral veins in turtles differs from the development in the lizards, as recorded by Hochstetter, in that they develop dorsal to the rib anlagen in the former and ventral to them in the latter.

The subcardinals originally laid down as a series of anastomosing venous sinuses are well established in an embryo of 10 mm. length with a strong interanastomosis posterior to the omphalo-mesenteric artery (Plate III). These continue to develop and establish intimate connections between themselves and the posterior cardinal veins so that at the stage of 13 mm. length there exists a very extensive network of connections posterior to the omphalo-mesenteric artery, not only between the posterior cardinal veins and the subcardinal veins, but also between the two subcardinals. Since these connections are posterior to the omphalo-mesenteric artery there is no venous ring formed as described by Hochstetter in the development of *Lacerta agilis*. In regard to the dense network formed here, this agrees favorably with the lizards and with *Kinosternon pennsylvanicum*.

While the previous changes have been taking place, the branches of the caudal vein, through sinusoidal changes have had their connections with the subcardinal veins shifted to the postcardinal veins.

During these developmental stages the postcava has also begun to appear and has assumed a highly developed condition at the time the branches of the caudal vein shift from the subcardinal veins to the posterior cardinal veins. Among the animals possessing this vessel there is considerable variation in the method of its formation. This accounts for the various types of its expression in the adults. Goette in his work on *Bombinator igneus* describes the development of the posterior portion of the postcava as being formed by the union of the posterior cardinal veins which approach each other and fuse in this region. Balfour believes this to be incorrect since the Amniota as described by Rathke and others show no such process. In the lizard, *Lacerta viridis*, as described by Hochstetter, the extreme posterior portion of the postcava is formed from the two branches of the caudal vein and exists in the adult as a bifurcated vessel posteriorly. In *Chrysemys marginata belli* I find the development of its posterior region to wholly corroborate that as given by Stromsten for *Kinosternon pennsylvanicum*, that is, in this region it is formed by the "right subcardinal craniad of the

origin of the omphalo-mesenteric artery and the fused subcardinals caudad of this point.''

When the development has reached this stage the degenerative factor assumes prominence. Previous to the formation of the postcava, the vertebral vein and the shifting of the caudal veins, the blood was carried from the caudal region by the caudal vein and through its branches was poured into the subcardinal veins. It then passed through the venous plexus of the mesonephros into the posterior cardinal veins which carried it anteriorly and discharged it into the ducts of Cuvier.

Now a new condition arises. The functioning of the postcava allows the blood to make a short cut to the heart. As a result of this, the posterior cardinal veins lose their connections with the ducts of Cuvier and degenerate. As found in lizards by Hochstetter this condition is accompanied by the separation of the anterior region of the mesonephroi from the dorsal body wall and the progressive degeneration of the mesonephroi and dorsal segmental veins. The posterior progressive degeneration of the mesonephros is probably aided by the development of the metanephros which appears at about this time (Plate VI). A rapid growth of the limb buds and the consequent relative reduction of the caudal region causes an increase in the size of the iliac vein and a reduction in importance of the posterior vertebral veins. This results in an enlargement of the iliac veins and a reduction in the size of the vertebral veins posterior to the kidneys. This progressive degeneration continues until the only connection remaining between the vertebral vein and the posterior region of the posterior cardinal vein is that as previously described lying between the fifth and sixth ribs. The portion of the posterior cardinal vein which fails to atrophy is that lying along the latero-ventral surface of the kidney and dorsal to the degenerating mesonephros. The lateral mesonephric vein is still present. The vein connecting the undegenerated portion of the posterior cardinal vein with the vertebral vein becomes the anterior renal advehent vein.

With this arrangement the blood flow is reversed. The blood now passes from the vertebral vein, the iliac vein and the caudal veins into the renal portal vein and from here through the venous network of the mesonephros and kidney into the postcava.

Degeneration of the mesonephros continues simultaneously with the growth of the kidneys. With the degeneration of the remain-

ing portion of the mesonephros the lateral mesonephric vein disappears leaving the vein lying ventro-lateral to the kidney as the only persisting part of the posterior cardinal vein. The kidney now takes the place of the mesonephros.

As the foregoing changes take place the venous network of the kidney becomes broken into more minute vessels until only a fine network exists. This network of capillaries (or sinusoids) has been tested as previously stated, by injections, by casts and by serial sections and in every case I find definite capillary connections (or sinusoids) which may be traced between the renal portal vein and branches of the postcava but in no case have I found a connection larger than capillary size.

This arrangement then produces a renal portal system in this form, the blood entering the kidney through the renal portal vein, traversing the capillary plexus of the kidney and leaving by the postcava.

V. SUMMARY

Previous workers have found a true renal portal system present in adult forms of fishes, Amphibians, lizards and snakes, but absent in birds and mammals. Occasionally suggestions have been made of the possibility of the transitional stages being found in the Chelonian group.

Selachians

The early development of the renal portal system in *Chrysemys marginata belli* is fundamentally the same as the development of the renal portal system in the Selachians. The chief differences are that in Chelonia the postcava is substituted for the anterior portions of the posterior cardinal veins of the Selachians and the subcardinal veins in Chelonia are substituted for the subintestinal vein in Selachians.

The later development in Chelonia carries it far beyond the Selachian stage and agrees to a considerable extent with that as found in other reptiles and Amphibia, although several important differences in development appear.

Amphibia

In Amphibia as described by Goette the posterior portion of the postcava is formed from the fused portions of the posterior cardinal veins while in Chelonia it is formed from the subcardinal veins.

Lizards

In lizards, the records of the earliest stages of development of the posterior cardinal veins and the subcardinal veins describe them as continuous connected blood vessels. The earliest stages of these vessels as observed in *Chrysemys marginata belli* show them to be discontinuous vessels with no connections.

The formation of venous pockets by the posterior cardinal and subcardinal veins is not described for lizards. These venous pockets are quite definite and distinct in this form of Chelonia and enter into the formation of the venous network of the mesonephros and metanephros.

The vertebral veins of the lizards develop ventral to the rib anlagen by anastomosing dorso-segmental branches.

The posterior portion of the postcava in lizards develops through anastomosis with the omphalo-mesenteric ring. In Chelonia, since there is no complete omphalo-mesenteric ring present it develops from a portion of the right subcardinal vein and the anterior region of the fused subcardinal veins.

Snakes

In snakes the posterior portion of the postcava is developed as a bifurcated vessel while in Chelonia it is a single vessel in this region.

The posterior vertebral veins are prominent in the snake embryo and develop ventral to the rib anlagen. They finally disappear, leaving little or no trace in the adult while in Chelonia they remain as definite veins.

Chrysemys marginata belli (Gray)

1. The posterior portions of the posterior cardinal and subcardinal veins are formed by anastomosing blood sinuses.
2. The posterior cardinal and subcardinal veins become pocketed, these pockets lying between the mesonephric tubules.
3. The venous pockets unite to form venous connections between the posterior cardinal and subcardinal veins.
4. The subcardinal veins fuse posterior to the omphalo-mesenteric artery only.
5. The renal portal vein is the persisting portion of the posterior cardinal which lies between the mesonephros and metanephros.
6. The anterior renal advehent vein is the persisting dorso-segmental branch of the posterior cardinal which lies between the fifth and sixth ribs.

7. The vertebral vein develops from anastomosing branches of the dorso-segmental veins and intervening blood sinuses.

8. The connections formed by the union of the venous pockets of the posterior cardinal and subcardinal veins become broken up into a network of capillaries (or sinusoids) which persist and form an intra-renal network in the adult.

9. A true renal portal system is present in the adult form.

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PLATES

EXPLANATION OF PLATES

Plate I. Outline drawings of embryos whose reconstructed veins appear in plates II-VII.

Plate II. Frontal and right lateral reconstructions of the veins of an embryo 7 mm. long. (See Pl. I, Fig. 1).

Plate III. Frontal and right lateral reconstructions of the veins of an embryo 10 mm. long. (See Pl. I, Fig. 2).

Plate IV. Frontal and right lateral reconstruction of the veins of an embryo 13 mm. long. (See Pl. I, Fig. 3).

Plate V. Frontal and right lateral reconstruction of the veins of an embryo 8 mm. carapace length. (See Pl. I, Fig. 4).

Plate VI. Frontal and right lateral reconstruction of the veins of an embryo 12 mm. carapace length. (See Pl. I, Fig. 5).

Plate VII. Frontal and right lateral reconstruction of the veins of an embryo 22 mm. carapace length. (See Pl. I, Fig. 6).

..... Outline of mesonephros.

— - — - — —Outline of metanephros.

Heavy horizontal lines indicate the level of the spinal ganglia.

Ao. Aorta.
Bl.S.Pc. Posterior cardinal blood sinuses.
Bl.S.Sc. Subcardinal blood sinuses.
Bl.S.V. Vertebral blood sinuses.
D.C.D. Ductus Cuvier Dextra.
D.C.S. Ductus Cuvier Sinistra.
D.Seg.Br. Dorso-segmental braneches.
L.A. Longitudinal anastomosis.
M.P. Mesonephric plexus.
Pc.Sc.A. Posterior cardinal and subcardinal anastomosis.
Sc.Sc.A. Subcardinal and subcardinal anastomosis.
V.Ac.D. Vein anterior cardinal dextra.
V.Ac.S. Vein anterior cardinal sinistra
V.C. Postcava.
V.C.A. Postcava anastomosis.
V.Ca.D. Vein caudalis dextra.
V.Ca.S. Vein caudalis sinistra.
V.D.Seg. Vein dorso segmental.
V.Ext.J. Vein external jugular.
V.I.E.D. Vein iliac externa dextra.
V.I.E.S. Vein iliac externa sinistra.
V.Int.J. Vein internal jugular.
V.L.B.D. Vein limb bud dextra.
V.L.B.S. Vein limb bud sinistra.
V.Pc.D. Vein posterior cardinal dextra.
V.Pc.S. Vein posterior cardinal sinistra.
V.R.A.D. Vein revehens anterior dextra.
V.R.A.S. Vein revehens anterior sinistra.
V.R.P.D. Vein renal portal dextra.
V.R.P.S. Vein renal portal sinistra.
V.Sc.D. Vein subcardinal dextra.
V.Sc.S. Vein subcardinal sinistra.
V.Sbc.D. Vein subclavian dextra.
V.V.D. Vein vertebral dextra.
V.V.S. Vein vertebral sinistra.

PLATE I

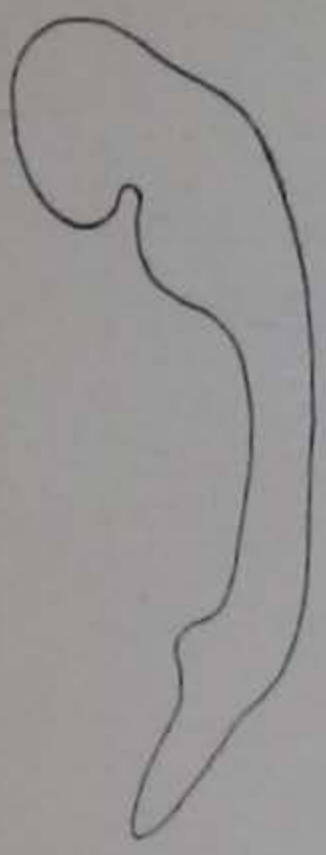


Fig 1

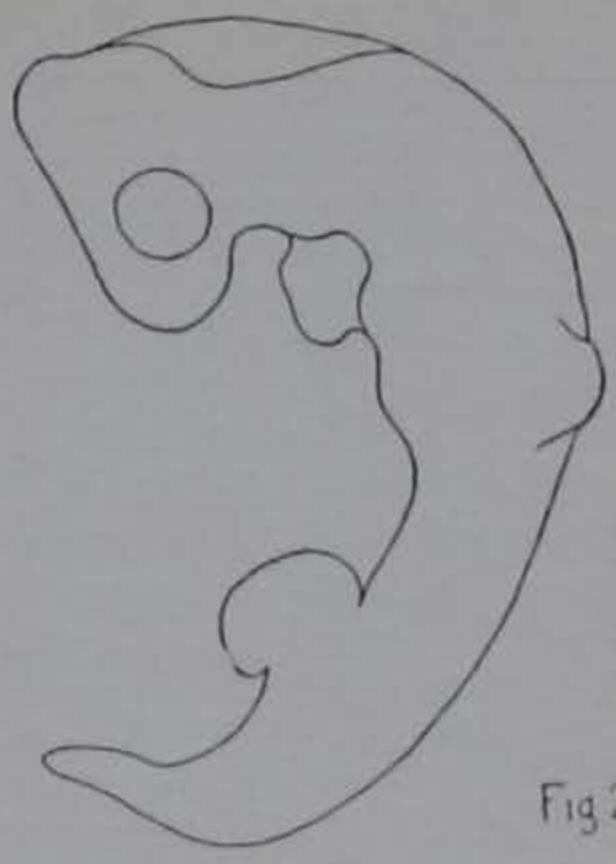


Fig 2

Fig 3

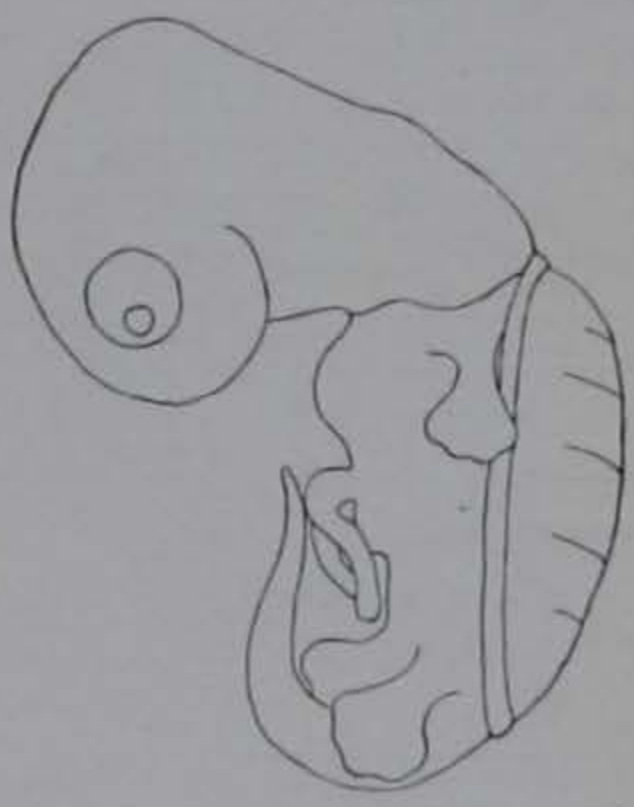


Fig 4

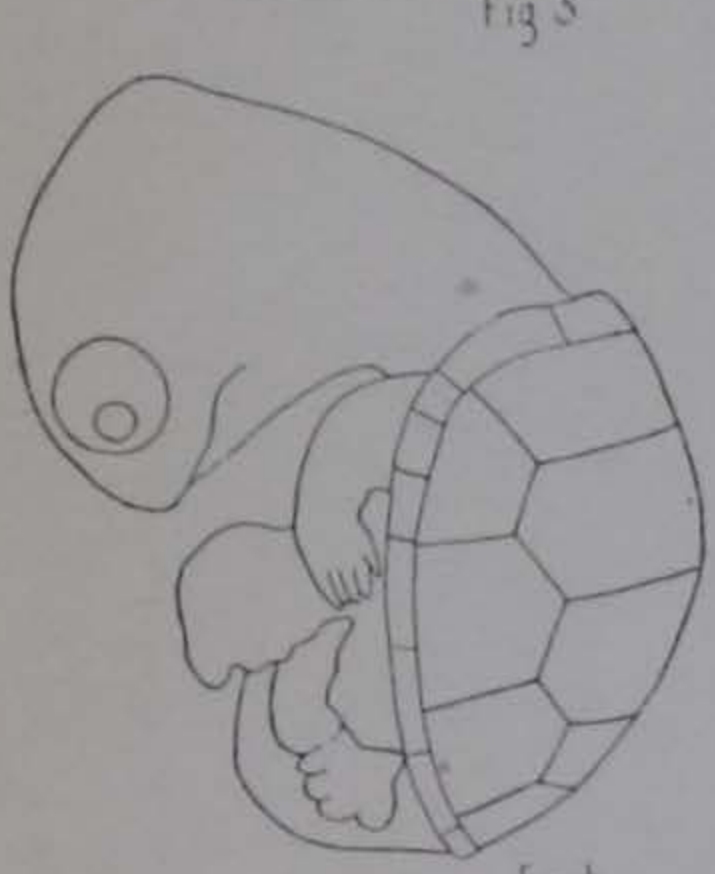


Fig 5

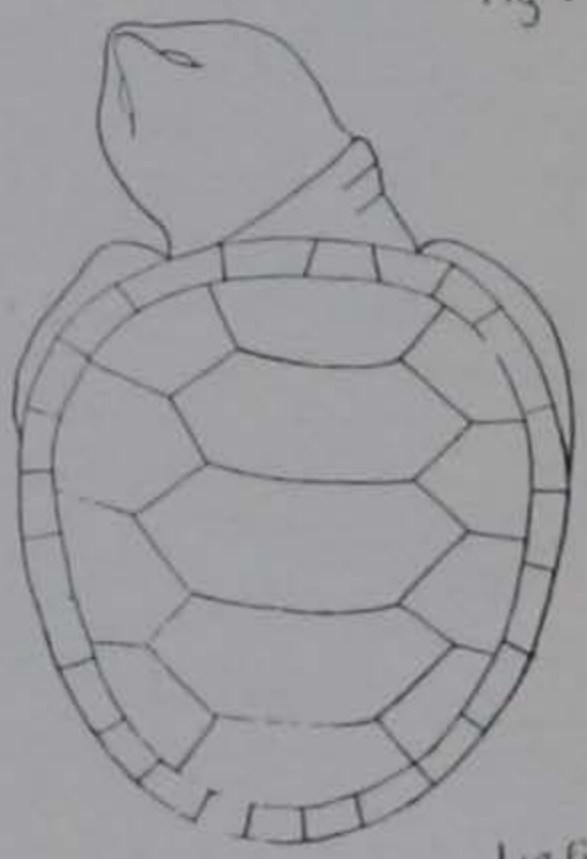


Fig 6

PLATE II

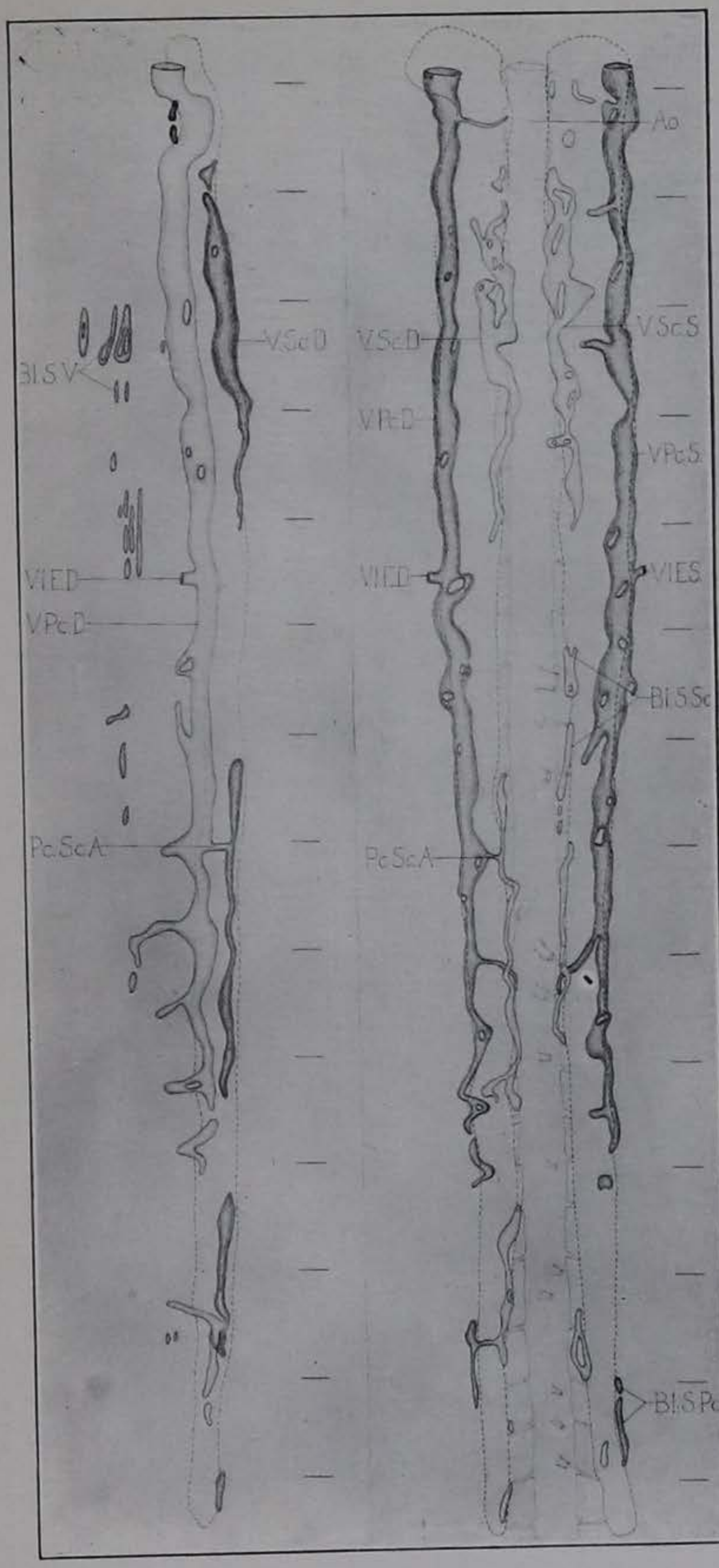
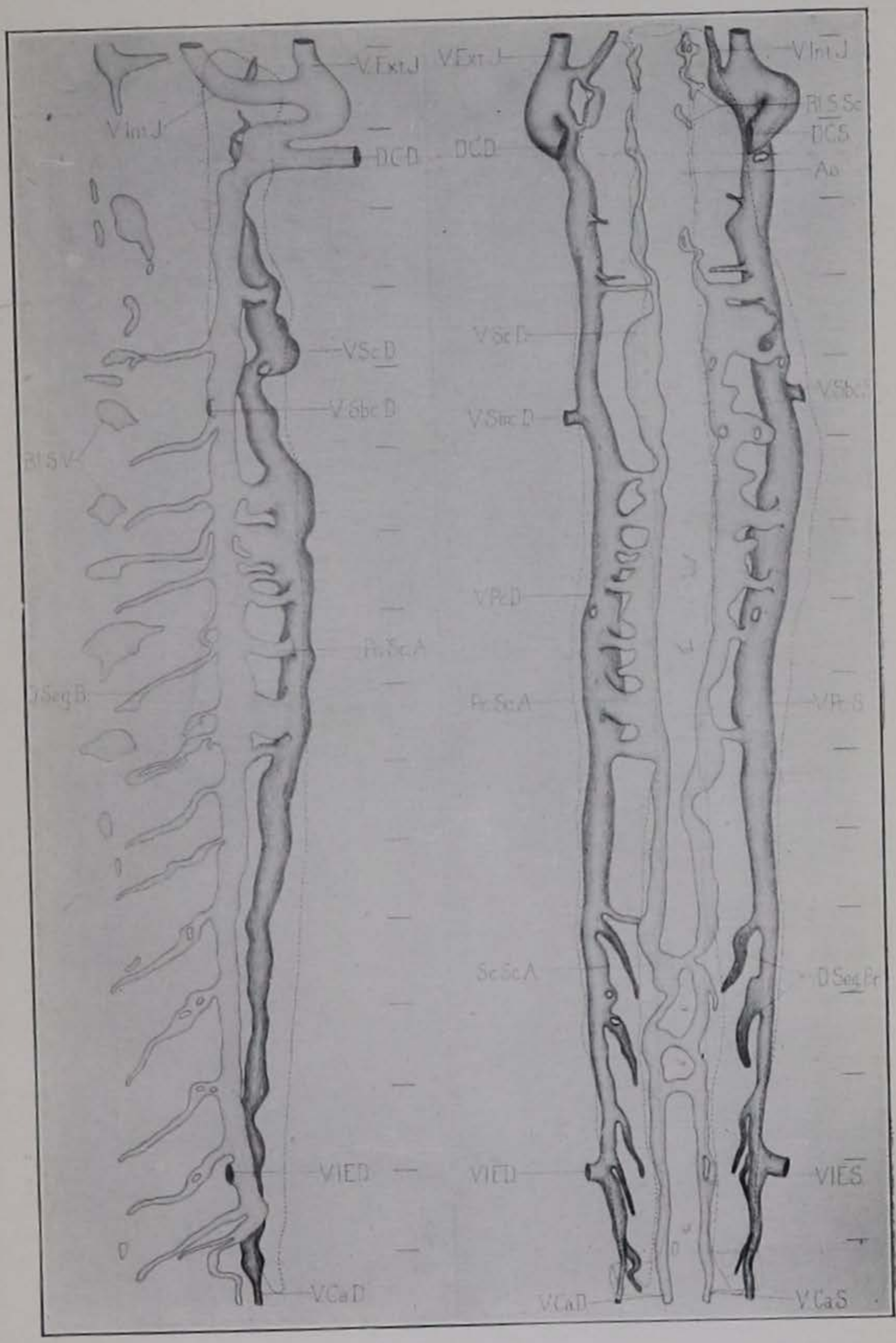

Ao
V.Sc.D
V.Sc.S
V.Pc.D
V.Pc.S
Bl.S.V
V.I.E.D
V.I.E.S
V.P.c.D
Bl.S.Sc
Pc.Sc.A
Pc.Sc.A
Bl.S.Pc

PLATE III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D.C.D
V.Sc.D
V.Sbc.D
V.P.D
Pr.Sc.A
Sc.Sc.A
V.I.E.D
V.Ca.D
V.Ext.J
V.Int.J
R.I.S.Sc
D.C.S.
Ao
V.Sc.D
V.Sbc.D
V.P.D
Pr.Sc.A
Sc.Sc.A
V.I.E.D
V.Ca.D
V.Int.J
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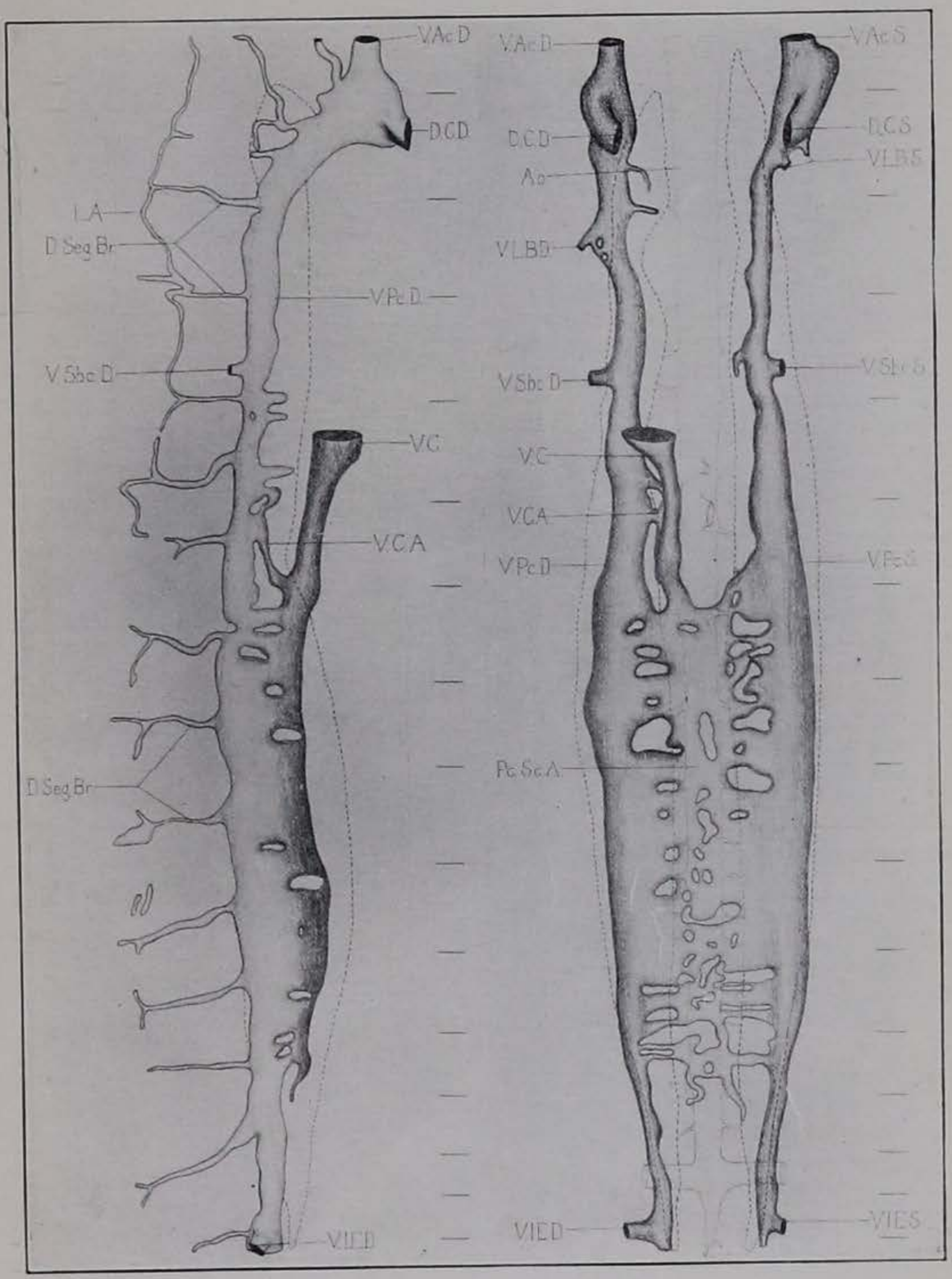
V.P.S
D.Seg.Pr
V.I.E.S
V.Ca.S

PLATE IV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D.C.D
I.A
D.Seg.Br
V.Pc.D
V.Sbc.D
V.C
V.C.A
D.Seg.Br
V.I.E.D
V.Ac.D
D.C.D
Ao
V.L.B.D
V.Sbc.D
V.C
V.C.A
V.Pc.D
Pc.Sc.A
V.I.E.D
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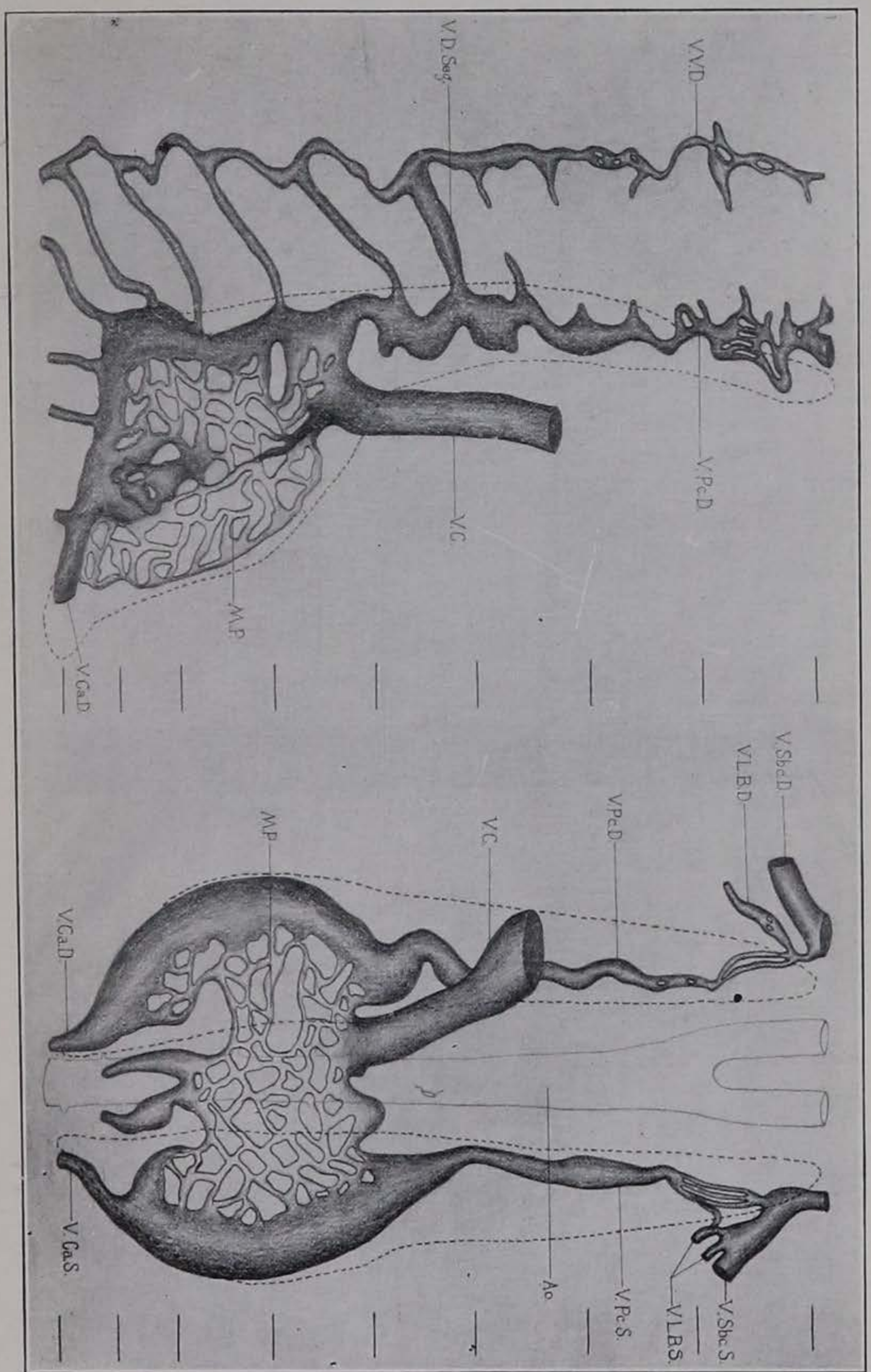
V.L.B.S
V.Sbc.S
V.Pc.S
V.I.E.S

PLATE V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V.V.D.
V.Pc.D.
V.C.
M.P.
V.Ca.D.
V.Sbc.D.
V.L.B.D.
V.Pc.D.
V.C.
M.P.
V.Ca.D.
V.Ca.S.
Ao.
V.Pc.S.
V.L.B.S.
V.Sbc.S.

PLATE VI

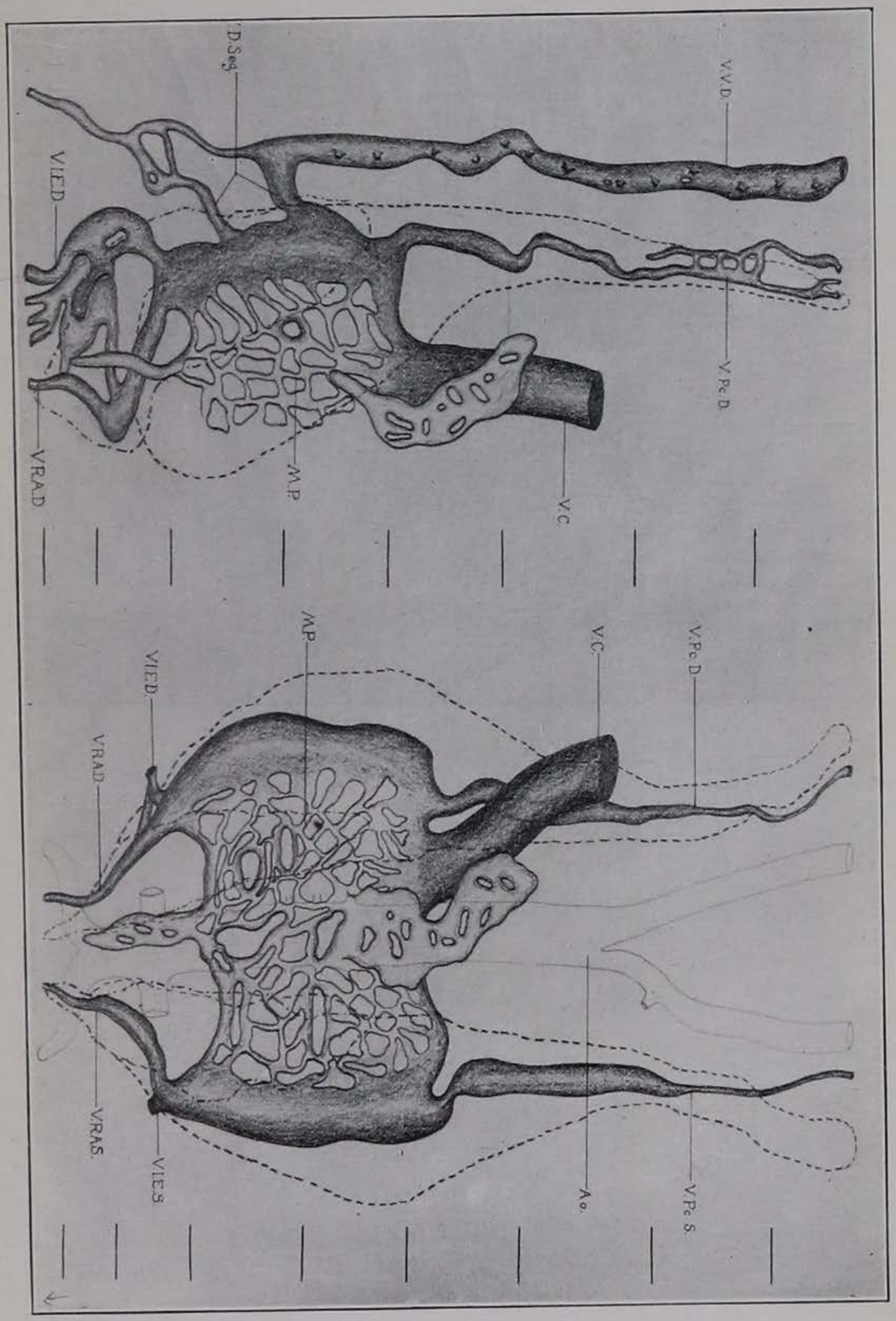
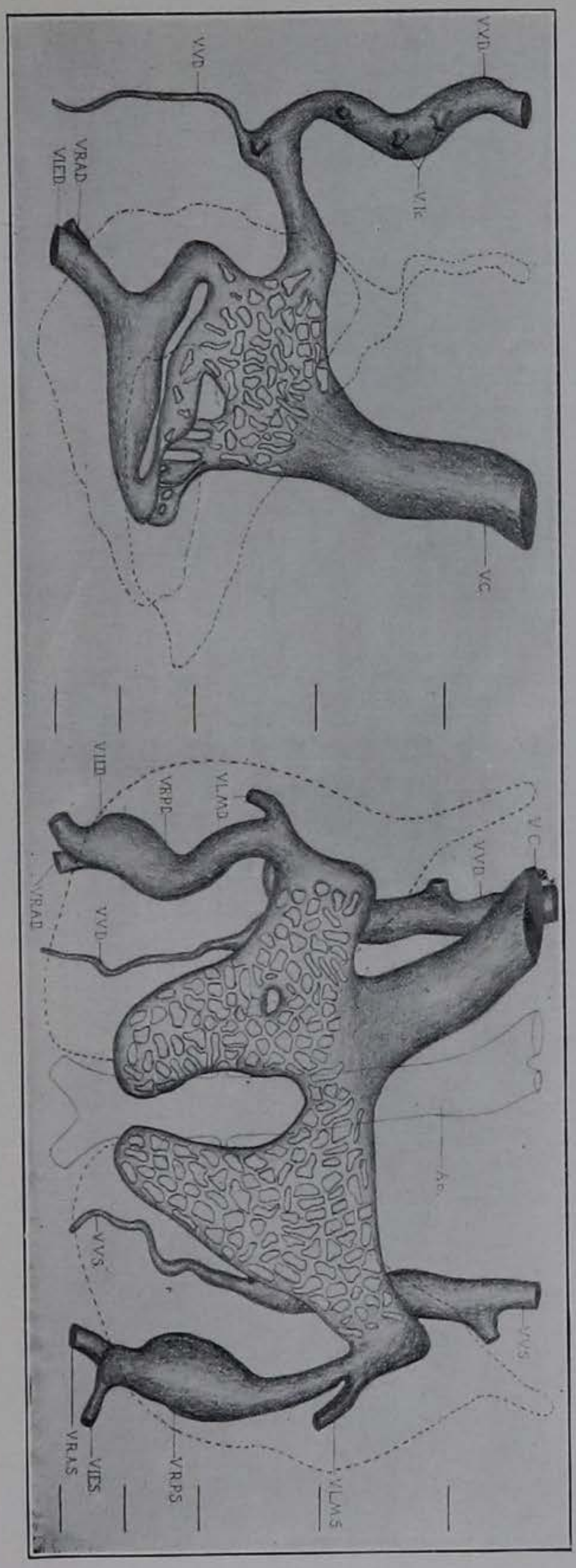

V.D.Seg.
V.I.E.D.
V.R.A.D.
V.M.P.
V.V.D.
V.C.
V.Pc.D.
V.M.P.
V.I.E.D.
V.R.A.D.
V.C.
V.Pc.D.
V.R.A.S.
V.I.E.S.
Ao.
V.Pc.S.

PLATE VII


VVD
VVD
VRAD
VIED
VIE
VIG
VIED
VLPD
VLMD
VVD
VRAD
VVD
VIS
VRPS
VLMS
VVS
VRAS