VASCULARIZATION OF THE SPINAL CORD OF SUS SCROPHA

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Part I. Material and Methods.

Pig embryos in abundance may be obtained at any large packing house. For a study of this kind, where the smallest blood vessels are to be demonstrated, the embryos should be injected. This is best done while they are still living. For an injection mass, it is well to use warm India ink diluted one half with weak ammonia water. Instead of a complicated injecting apparatus, such as is usually recommended, good results may be obtained with an ordinary hypodermic syringe. For the very small embryos it is necessary to employ a small syringe with a very fine, sharp, needle, and the instrument must work smoothly, as any sudden pressure exerted upon the blood vessels is likely to rupture the smaller ones. If the placenta is gripped with a hemostatt near where the umbilical vessels join it, the pressure from within the embryo causes the arteries in it to become distended, and the needle can be introduced with greater ease. An artery should be used in preference to a vein, because the arteries are less readily ruptured, and because the route between them

and the vessels of the spinal cord is much more direct.

With small embryos a very slight, steady pressure will soon completely fill all the arteries and capillaries of the spinal cord, and partially fill the veins. As the embryonic skin is quite translucent, the operator can tell when sufficient ink has been injected. The veins containing much blood and a slight amount of ink will have a grayish brown appearance when cleared, while the arteries being full of carbon will become a shiny black.

With embryos larger than 25 or 30 mm. in length, less caution need be exercised. With these a larger syringe can be used, and the umbilical cord is large enough so that it can be tied, or clamped, and the needle inserted directly into the umbilical artery. Both arteries should be closed to prevent loss of ink from the back flow, and a slit should be made in the vein between the embryo and the hemostat to allow as much blood as possible to escape. It is advantageous with very large embryos to allow the blood to be pumped out through the arteries for a time before injecting. The umbilical cord should always

be tied close to the pig after the injection is complete and before the needle is withdrawn to prevent loss of ink from the vessels. With this very simple technique, embryos of all sizes above 9 mm. were easily injected.

Embryos for this work less than 9 mm. in length could not be obtained, so the youngest stages had to be worked out from uninjected material already in the embryological collection of this department.

Embryos for thin serial sections should be congested. This is accomplished as follows. The umbilical arteries are tied or clamped while the embryo is yet living, thus causing an increase in the blood pressure in the aorta. One of the most direct outlets for this extra pressure is the system of segmental arteries, and through these the blood vessels in and around the spinal cord soon become congested. When this condition has been reached, as evident from the increased redness of the dorsal region of the embryo, the living pig with the umbilical cord tied should be dropped into a rapidly penetrating fixing fluid, in order that the capillaries may become fixed

before they collapse. Embryos treated in this manner will show the smaller vessels much more plainly than those fixed in the usual way.

For fixing congested pigs and embryos in general, Bouin's fixative gives best results, but injected embryos intended for clearing with the Schultze KOH method, should be fixed in 95 per cent alcohol.

Injected embryos may be studied by several different methods. Small whole animals can be made nearly transparent with the above mentioned Schultze clearing method, and studied with a high power binocular microscope. The viscera of such embryos must be removed before the pigs are cleared, as they obstruct the light. Small embryos may be cleared in Origamun oil directly or embedded in celloidin and then cleared. These may be dissected under the binocular microscope and all the external vessels of the cord demonstrated, or they may be sectioned to show the internal vessels.

From pigs larger than 25 mm. or 30 mm. the cord with its membranes may be dissected, and embedded in celloidin

and cleared, or for temporary preparations may be cleared directly.

Following Bouin's fixative, the embryos are stained yellow from the picric acid, and the cord needs no additional stain, but following other fixing solutions it is well to stain it slightly with Orange G. before clearing.

Sectioning is best accomplished "free-hand" with a very sharp thin bladed knife, although where sections of uniform thickness are desired, the use of the microtome is preferable. The sections can be kept indefinitely between two pieces of tissue paper soaked in oil, or can be transferred to slides and mounted in damar gum. To make slide preparations, the sections are cut in oil and placed on a piece of thin paper in the same order they are to have on the slide. Another piece of paper soaked in oil is laid down upon them and the whole is reversed. The first paper is now peeled off and the other paper holding the sections is reversed onto a slide, and peeled off. This leaves the sections on the slide in their proper order, and they may be blotted to remove excess oil, or

carefully washed with xylol, and then mounted in damar under a cover glass.

There are several advantages in a study of this kind, in sectioning free hand in oil. Thick sections may be made nearly transparent and will show many more blood vessels than thin ones. The cord can be turned so that sections may be cut through any plane, and sectioning is more rapidly done than with a microtome, and much time is saved. It is easy to make transverse, sagittal and frontal sections from any region of the same cord. The block can be examined with a lens, during the sectioning, and any particular vessel or vessels included in a section. Also, sections may be of different shapes. For instance, the section used to demonstrate the anterior central arteries in figure 3 was quite thick in the middle and thin in the ventral and dorsal parts, giving the best possible exposure of these vessels.

Congested embryos used in this study were stained in toto and sectioned serially in paraffin in the usual manner. A few injected embryos were treated with this

method, but the carbon particles soon dull the microtome knife and perfect sections can not be obtained.

The size of the embryos in this work was taken as the longest diameter in 75 per cent alcohol.

With these methods all the blood vessels in and around the cord can easily be demonstrated.

Part II. Historical.

Until 1904 little work had been done upon the development of the blood vessels of the spinal cord, except that of His ('88) who undertook to follow the growth of these vessels in human embryos. The observations of this author have been largely disproven by Sterzi '04, and Evans '09, the two writers who have done most of the work in this field. His noticed in early stages two arteries on the anterior surface of the cord, and one in later stages. He concluded that the one is formed by a fusion of the two, a process which has been since shown not to be the case. Also, His states that the arteries which develop in the ventral part of the cord as separate

vessels (a.a. sulci) and later shifted together in the mid line, a statement which Sterzi and Evans show to be incorrect.

By far the most comprehensive publication upon the development of the vessels of the cord is that of Sterzi '04. In this he discusses the development of the vessels in Pisces, Amphibia, Reptilia, Aves, and Mammalia. As a type specimen of the latter class of vertebrates, he uses Ovis aries. Since it is the purpose of the present paper to show the growth of the vessels of the cord in another mammal, Sus scropha, it may be well to include here some of the observations of Sterzi, of conditions which he considers to be the normal mammalian plan.

According to this writer, the blood vessels first approach the cord at the ventro-lateral border and spread over the ventral surface, then over the lateral, and finally over the dorsal surface. The vertebro-medullary arteries as they approach the cord each divides into a ventral and a dorsal ramus, the ventral and dorsal radical arteries. The ventral radicals from either side halt at

the later edges of the "Basalplatte", and each divides into a cranial and a caudal ramus. These anastomose with those of adjacent segments and form two longitudinal arteries on the ventral surface of the cord, the "Tractus arteriosi primitive". These later send out medial rami and become connected to each other through these. Still later, parts of the two degenerate while other parts continue to develop, and in this way alternate parts of both become large. These enlarged parts are jointed together through their medial rami and form a single anterior artery which Sterzi calls the tractus arteriosus ventralis, and which is the anterior spinal artery of most writers.

From the primitive tractus, dorsal rami enter the cord. Each of these forms a loop and gives rise to a vein, which courses ventrally and opens out in the primitive sulcus. Later other vessels extend into the cord from the lateral, and still later from the dorsal surface.

The dorsal radical arteries form many small longi-

tudinal capillaries just ventral to the points of emergence of the posterior nerve roots, where they divide. From these capillaries there is formed later, a longitudinal artery on each side of the cord, in this plane. (Tractus arteriosi lateralis).

The vessels entering the cord are first solid and later become hollow.

The Tractus art. prim. do not remain long as two vessels, but begin to break down and form one vessel in sheep of 12.5 mm., and in sheep of 20.5 mm. only one vessel is to be seen.

Evans, '09, shows by a series of injected pigs the early development of anterior spinal artery. In his preparations the mid ventral surface of the cord is shown to be free from vessels until the embryos are 8.5 mm. in length, and the mid dorsal surface until after the pigs are between 8 mm. and 10.5 mm. in length. He does not take up the later stages of this species.

Part III. Blood vessels of a near full-term Foetus.

In writing a description of any developing structures, it is desirable to know when the permanent condition has been reached. Also, it is impractical in a study of this kind, to inject the blood vessels of an adult pig. Hence, in order to get as near as possible to the adult condition, several near full-term foetal pigs were injected and their spinal cords dissected out and studied. They showed some variation as to blood vessels, as is to be expected, since these develop from capillaries, but a general plan was to be observed. The following description is of a typical condition found in the blood vessels in and around the spinal cord of pigs of circa 240 mm.

On the surface of the cord in this stage are four main arterial systems which course longitudinally, and which are located as follows. One lies on the median anterior surface, two on the postero-lateral surfaces and one on the posterior surface.

The ventral radical arteries from the vertebro-medullary arteries are about 14 or 15 in number. They

approach the cord along the cranial surfaces of the spinal nerves and ganglia, and reaching the cord course cranially. They may be equally distributed to the two sides of the cord and to the different regions of it, but on the other hand, most of them may be on one side and some regions may have more than others. In places the ventral and dorsal radical arteries have lost their connection with the vertebro-medullary artery and extend between the artery on the anterior surface and one of those on the postero-lateral surfaces.

Soon after reaching the cord the anterior radical arteries branch, giving off a ramus which courses cranially, and one which courses caudally. These divisions anastomose with those of neighboring anterior radicals, on the same or opposite side of the cord, and form in this way the anterior spinal artery, which lies in or near the median ventral line. Occasionally a radical, instead of dividing, goes across the cord and joins the cranial or caudal ramus of the radical on the

other side. The anterior spinal artery has a winding course bending laterally to meet the vessels which form it, and making many smaller bends to one side or the other. In some places it may lie outside the mid-line for several segments and where this occurs there lies in the anterior sulcus one or more small arteries which are formed from numerous longitudinal rami of the anterior spinal artery, or the cranial and caudal divisions of the ventral radicals. These may be called secondary anterior spinal arteries, and are present in places even where the anterior spinal artery lies in the mid-line. Here they are located between this vessel and cord, at the mouth of the anterior median fissure. They are evidently the remnants of the "Tractus arteriosis primitivi" of Sterzi. See figure 1.

The dorsal radicular rami of the vertebro-medullary arteries are much more numerous than the ventral ones. These course dorsally along the cord and in a slightly cranial direction, to a plane just ventral to the emergence of the fibers of the posterior roots, where they

divide into two rami, one extending cranially and one caudally. These divisions anastomose as do the corresponding ones of the ventral radicals, and form on either side an irregular longitudinal vessel, the postero-lateral artery (tractus arteriosus postero-lateralis of Kadyi). See figure 2. From this artery recurrent rami help to supply the dorsal nerve roots and spinal ganglia, and the lateral surface of the cord. Other rami, two or three in each segment, and much larger than these, course dorsally and by longitudinal anastomoses with each other, and with similar rami from the opposite side form an artery in the mid dorsal line, the median dorsal artery.

Very small rami from the postero-lateral arteries course ventrally along the cord and unite with others from the anterior spinal, forming a plexus on the ventral and lateral sides. These ventral rami of the postero-laterals anastomose freely in a longitudinal direction and form in some parts of the cord, between the ventral and dorsal nerve roots, one or more small longitudinal arteries, (Tracti arteriosi laterales, and ventro-

laterales of Kadyi). Still other small rami from the postero-lateral and median dorsal arteries form on the dorsal and dorso-lateral surfaces of the cord an arterial capillary plexus. In a few places along the cord the postero-lateral arteries are double, one division perhaps lying dorsal to the posterior nerve roots, and corresponding to the "tractus arteriosus posterior" of Kadyi.

The median dorsal artery is a very irregular longitudinal vessel formed by the dorsal rami of the postero-lateral arteries, as mentioned above. In places it is double or may show a longitudinal capillary arrangement. Many of its lateral rami anastomose longitudinally forming small arteries parallel with the median dorsal artery. See figure 2. This is also true of the dorsal rami of the postero-laterals. By the anastomoses of the rami of the various arteries just described, the entire cord is surrounded by an arterial vascular system, and from all parts of this, smaller arteries enter the cord.

The veins of the spinal cord are in three principal longitudinal systems, and other smaller ones. Of the

three, two are dorsal and one ventral. All three show evidence of their capillary origin. The ventral vein, or anterior spinal vein, is the smallest of the three. See figure 1. It lies between the cord and the arteries in the median ventral line. It is larger than the secondary anterior spinal arteries, but never attains the size of the anterior spinal, proper, this being indicative of the fact that it has not the same relative importance. It is very irregular and in some regions is entirely replaced by a narrow network of capillaries.

On both sides of the median ventral sulcus, the cord is covered with large venous capillaries, some of which lie between the cord and the arteries, and some of which are to the outside of the latter. They are often two or three times as large as the arterial capillaries to which they correspond. They anastomose freely with the anterior spinal vein and laterally, empty into the ventral radical veins which are in close relation with the ventral nerve roots and ventral radical arteries, but which are much more numerous than the latter, one being present on

nearly every root. They drain blood also from the lateral surface. Their ventral and dorsal rami often form short, small, longitudinal veins by anastomoses, some of which in other animals have been given names (antero-lateral, etc.). The blood from the anterior spinal veins and venous capillaries of the general ventral surface form, in places, transverse channels which are nearly large enough to be called veins.

On the dorsal surface of the cord, one large irregular vein, the postero-lateral, courses longitudinally along either side of the cord, about half way between the arteries of the same name, and the median dorsal artery. Some parts of these vessels and their rami, like the ventral venous capillaries, lie external to the arteries and some internal to them. They are the largest vessels on the cord except the anterior spinal artery. Compare figures 1 and 2. Dorsally they are united through large capillaries, and blood leaving the cord in the median line may flow either to the right or left. Half way between two consecutive nerve roots the postero-lateral

veins usually break up into many rami, so that each may be seen to drain blood from adjacent halves of two segments. Laterally they empty into the large dorsal radical veins, one of which lies upon each dorsal nerve root, through one or more divisions. See figure 2.

A fourth longitudinal venous system, smaller than the three described, lies in the median posterior sulcus. It resembles the postero-lateral veins except that it is more irregular, and in places is entirely lacking. Its lateral rami empty in the dorsal venous capillary plexus or directly through larger vessels into the postero-lateral veins.

The veins in and around the ganglia and nerve roots drain into the radical veins. These last, unite to form the vertebro-medullary veins.

Some of the venous capillaries of the lateral surface drain into the dorsal radicals, some into the postero-laterals, and some into ventral radicals, and these with the anastomoses of the ventral and dorsal surfaces already mentioned above, completely surround

the cord with a venous system, corresponding to the system described for the arteries.

Of the arteries entering the cord, the largest are those in the ventral fissure, the anterior central arteries, which form two nearly parallel rows, but which are not paired. They arise from the anterior spinal arteries, or the secondary anterior spinals. They show evidence of their capillary origin in longitudinal anastomoses between those of the same sides, these anastomoses being numerous in the fissure, especially near the vessels from which they arise.

The anterior central arteries vary considerably in size, some being as large as the vessels they come from, and others quite small. See figure 3. The course of the smaller is usually more irregular than that of the larger. They pierce the substance of the cord at different levels, some entering near their origin and others extending some distance into the fissure. Their general course is dorso-lateral, but those entering near the mouth of the fissure may bend very sharply to the side and enter the anterior

horn of the gray matter. The others course more dorsally to near the level of the central canal where they make a decided lateral bend, and divide into two or more rami, although sometimes they give off rami more ventrally than this. See figures 3 and 4. The principal divisions of these arteries extend in a longitudinal plane, and anastomose with similar rami of adjacent vessels. They also give off smaller arteries and capillaries which ramify through the gray matter in all directions, helping to form a dense plexus in this region. The longitudinal arteries tend to form loops after they have coursed in one direction for a short distance, as they do in young embryos, as shown in figure 6. One artery may form several loops and produce several longitudinal vessels, each succeeding one above, or lateral to, and smaller than, the last. These smaller longitudinal vessels anastomose with each other dorso-ventrally and laterally by rami which leave them usually at or near right angles, and also anastomose with rami from vessels other than the anterior central arteries. These vessels will be described later.

Besides the main rami of these central arteries, others extend farther laterally into the gray matter before branching. Some of these, instead of forming longitudinal vessels, form small irregular ones which ramify through the gray matter in all directions, anastomosing with similar vessels from other arteries in this region and forming a dense capillary plexus in the anterior and posterior horns.

Other arteries, smaller than the anterior centrals, enter the cord from the posterior median sulcus and course ventrally and laterally to the posterior horns of the gray matter. Here they form still smaller vessels resembling to some extent those formed by the anterior central arteries, but most of their rami are short and do not extend in a longitudinal plane. These may be called the posterior central arteries, but they are more like the peripheral arteries from other surfaces of the cord, than like the anterior centrals, and perhaps should be called posterior peripheral arteries. They give off many small lateral rami in the white matter and in the outer part of the gray

matter.

In addition to these, other small arteries enter the cord from all sides, from the arteries and arterial capillaries that surround it. These are the peripheral arteries referred to above. They are very numerous, and in a single thick cross section as many as fifty or sixty of them may be counted. They give off short rami in the white layer of the cord and extend into the gray layer. These rami branch and anastomose and form a loose capillary network. The vessels entering the gray substance enter into the longitudinal plexus already described and give off lateral rami which branch freely and anastomose.

In a longitudinal section of the cord as many as eight longitudinal arteries may be seen. See figure 3. The first ones formed by the anterior central arteries are quite large, but the other ones formed from these vessels and those formed from the posterior central and peripheral arteries are much smaller. A very thick section presents a picture of an inner core of longitudinal vessels with others extending into them at right angles from all points on the periphery of the cord. See figures 3 and 4.

Like the arteries, the principal veins are to be found in the median plane, but unlike them, the largest and most numerous are in the dorsal half. They arise from short, branching and anastomosing capillaries in both the gray and white layers, and through these are continuous with the arteries. The central veins corresponding to the central arteries have mostly to do with the gray matter. The veins begin very suddenly from their capillaries and have the same course as the central and peripheral arteries. There are a very few small longitudinal veins in the gray matter, but most of them course at right angles to this. The central veins empty into the anterior spinal and the posterior median veins, and the peripherals empty into the venous capillaries on the various surfaces of the cord.

Part IV. Development of the Blood Vessels.

The early development of the anterior spinal artery in the pig resembles that described by Evans ('09) in most ways. Differences found are due probably to measurement of the pigs, although it is well known that not all embryos of

the same length show the same degree of development. Sterzi ('04) described the growth of this vessel in the sheep and several other mammals.

Capillaries grow out from the segmental arteries to the ventro-lateral border of the spinal cord and form a capillary plexus there. This plexus grows dorsally along the lateral side and medially along the ventral surface to near the mid line. For each segment one vessel develops larger than the others, and becomes the vertebro-medullary artery (Sterzi '04), and this in the same way obtains two large rami, a ventral and a dorsal, the ventral and dorsal radical arteries, which extend along the dorsal and ventral surfaces, respectively. The ventral capillaries rapidly increase in size and number on either side of the mid line just below the lateral angle of the "Basalplatte", and by longitudinal anastomoses establish two parallel arterial systems, (the tracti- arteriosi primitivi of Sterzi, ('04)). Evans shows that these two tracts first unite by median anastomoses in a pig 8.5 mm. in length, but I find many such anastomoses in pigs as small as 7.5 mm. from the hind

brain to the lumbar region of the cord, and one pig of 6.2 mm. shows them in the cervical region.

As growth continues, the median rami of the tract. art. prim. becomes large and anastomose with each other, as shown by an embryo of 9.6 mm. See figure 5. From this system the anterior spinal artery of the adult forms in the following manner. Parts of both tract. art. prim. and their median rami grow more than others and parts degenerate. Those parts that increase in size lie on opposite sides of the cord in alternate areas. These are connected by the enlarged median rami. This has been recorded by both Sterzi ('04) and Evans ('09).

This degeneration of parts of the tract. art. prim. may be due to the fact that some of the ventral radical arteries do not continue to develop, and thus parts of the tract. art. prim. receive a more direct blood stream than others. Those having the more direct blood stream have a greater blood pressure, and according to Thoma's Laws, would tend to increase in size more rapidly than the other parts.

Some pigs of 12 mm. show a fairly well developed anterior spinal artery, while in others of 14 or 15 mm. it is just beginning to form. After this vessel is onee formed it does not undergo very many changes. However, there is some change. For instance, the anterior radicals meet it at right angles or nearly so, until the embryo is about 40 or 45 mm. in length. After that, the growth of the cord seems to cause the artery to be pulled laterally by the radicals, and a gradually decreasing angle is formed at the places where the radicals meet it. See figure 1.

As the length of the pig increases, the number of the radicals continues to decrease even after the anterior spinal artery is well formed. This seems to be true until the pig reaches the size of about 100 mm.

The arterial capillaries on the ventral surface of the cord are formed as has been described above. Some of these are continuous with the anterior spinal directly, or indirectly through remains of the tract. art. prim., and others are continuous with the capillaries of the lateral

surfaces.

A postero-lateral artery is formed in the capillary plexus on each of the lateral surfaces of the cord, just ventral to the point of emergence of the dorsal nerve roots. The dorsal radical arteries branch in this region and give off dorsal and lateral rami, which are continuous with the lateral capillaries just mentioned. A very irregular longitudinal vessel develops where certain of these capillaries increase in size owing to the increased pressure from the dorsal radical arteries. This longitudinal vessel is indicated in embryos of 12 mm. and is quite strongly developed in embryos of 15-18 mm. In these stages it seems to dip ventrally to meet the approaching radicals, as pointed out by previous writers. As the embryo grows, this postero-lateral artery becomes more and more regular. It is still somewhat irregular in embryos of 60 mm. but quite regular in those of 75 mm. A postero-lateral artery never attains the size of the anterior spinal nor is it ever so regular in its course. In places it may develop as two or more vessels, but these

are always smaller than where the artery is single. The postero-lateral arteries are each continuous with the capillaries of half the cord in the early stages, but as the cord increases in size they supply directly only the dorso-lateral and latero-dorsal surfaces.

The capillary network on the lateral surface of the cord is at first continuous with that extending through the mesenchyma of this region as far, laterally and dorsally, as the myotomes and body wall respectively, as shown in figure 5. In later stages when membranes have begun to develop around the cord, the connections between the vessels of the cord and those in the mesenchyma around it are lost, and the blood vessels on the cord are to be found in the pia mater.

Evans ('09), in the Anat. Record, pictures a part of the spinal cord of an 8 mm. pig embryo, showing the dorsal surface to be quite bare of blood vessels, but my preparations show capillaries extending nearly to the median line in an embryo 6.2 mm. in length and in embryos of 7.5 mm., the dorsal surface is bridged across with many small

vessels in all but the lower part of the cord. These capillaries are continuous latero-ventrally with the plexus on the ventral side of the cord, and with that on the ganglia, and laterally with that in the mesenchyma. They form a plexus which is both venous and arterial in the early stages, but in which definite veins and arteries are to be distinguished by the time the embryo has reached the length of 12 or 14 mm.

The median dorsal artery develops last of all the vessels on the cord. In pigs of 30 mm. it is still very irregular and indefinite, and is entirely lacking in places, although the vessels which go to form it, the dorsal rami of the postero-lateral arteries, may be seen in embryos of 20 mm. In pigs of 45 mm. it is quite definite, lying in or near the mid line of the dorsal surface, as described above for the 240 mm. embryo. It never becomes very regular, but in pigs of 100 mm. it resembles the condition it shows in the 240 mm. pig. It has not been described in the papers of other writers who have worked only on the smaller embryos. It is continu-

ous with the arterial capillaries of the dorsal surface of the cord and with the postero-lateral arteries, as stated before.

In addition to these main arterial trunks there develop on various parts of the cord, especially on the lateral surfaces, short longitudinal arteries. These are never large or regular. They have been described for the adult human under the names of "Tractus arteriosus; ventro-lateral, posterior, and lateralis" (Kadyi). Of these, the "tractus arteriosus posterior" is the most prominent and corresponds to the description in this paper of parts of the postero-lateral artery, where it sometimes has two divisions, one of which runs dorsal to the posterior nerve roots and the other ventral to them. These dorsal divisions are evidently the same as this "Tractus".

The veins on the cord develop in much the same way that the arteries do. As stated above, the ventro-lateral surface of the cord in very young embryos is covered with capillaries, and these are continuous laterally with the capillaries in the mesenchyma round the neural tube.

Medially they become continuous with the lateral rami of the primitive arterial tract. When this tract becomes separated from the cord by mesenchyma, these capillaries send medial rami between the tract and the cord, as seen in embryos of 12 to 15 mm. Dorsally they grow along the cord and spread over the dorso-lateral surface (pig 6.2 mm) and later over the dorsal surface (pigs 7.5 mm). Laterally they spread over the ganglia.

From the ventral surface, the blood draining away through the capillaries soon establishes segmental vessels the ventral radical veins, which course laterally along the nerve roots (see figure 6). Each radical vein on one side drains adjacent halves of two segments. These receive blood from the capillaries of the ventral, lateral, and ventro-lateral surfaces. Lying in the ventral median sulcus in young embryos, small longitudinal veins may be seen in different regions of the cord, and in embryos of 25 to 30 mm. a fairly definite longitudinal vessel may be seen here. This in still older embryos becomes more definite, and may be called the anterior spinal vein.

It never attains the size of the anterior spinal artery. Laterally it drains into the ventral radical veins.

Some of the dorsal and lateral capillaries of the younger embryos, early become differentiated into veins. This is especially true of the dorsal vessels. From these, some of the blood drains laterally out through the mesenchyma to the myotomes. A pig of 6.2 mm. shows three planes in which this occurs, one on a level with the dorsal surface, one just above the level of the ventral surface, and one about half way between the other two. At the myotomes the blood drains ventrally into the inter-segmental veins. Some of the capillaries of the lower of these three planes, draining the blood from the lateral surface of the cord and from the ganglia, soon become large and are called the vertebro-medullary veins, one pair of which is formed for each segment. In older embryos they course along the spinal nerves with the vertebro-medullary arteries. They receive the blood from the ventral and dorsal, radical veins. The former have been described. The latter develop along the sides of the

ganglia in the capillaries already described. At first they carry only a part of the blood from the dorsal surface, but later (pigs 25 mm.) they carry practically all of it. They are more numerous than the corresponding ventral radicals, and are found in every segment.

The venous capillaries of the dorso-lateral surface on either side draining toward the nerve roots early establish longitudinal veins. These are only about half as long as a segment of the cord. Figure 6, of an mm. pig shows an indifferent plexus on this surface, but in 15 to 17 mm. embryos, fairly definite vessels may be seen. These become more and more regular as the animal develops, and as embryos of 50 to 60 mm. show, they form on either side a venous system just dorsal to the dorsal nerve roots, much like that described for the 240 mm. stage. These systems constitute the postero-lateral veins. See figure 2.

In addition to these, small segmental longitudinal veins develop on the lateral surfaces of the cord, but these are not sufficiently large or regular to deserve a

name.

The blood leaving the cord in the median line establishes irregular longitudinal venous capillaries in the median posterior sulcus, and in older embryos these form one or more longitudinal veins in some areas. This may be called the median dorsal venous system. It drains laterally at irregular intervals, into the postero-lateral veins. Some of these lateral communications may become quite large as shown in figure 2.

The first blood vessels entering the cord grow in as capillaries from the ventral surface. Sterzi ('04) reports vessels in the cord of a sheep of 5.5 mm., but they are not apparent in the cord of pig embryos of less than 7.5 mm. These vessels are the dorsal rami of the primitive arterial tracts, of their lateral rami, and of the other capillaries near the median line. They are the first indications of the central arteries and veins. They form two nearly parallel rows, one on either side of the ependymal layer, or some of them may lie in this layer. They grow dorsally about half way to the dorsal surface. They exhibit numerous longitudinal anastomoses and form a plexus

along the lateral side of the ependyma in each half of the cord. These are true capillaries at first, but soon become differentiated into arteries and veins. Those coming directly from the primitive arterial tracts all become arteries, while those coming from the vessels lateral to the tract may become either veins or arteries.

In embryos of 9.6 mm. another group of capillaries may be seen to have entered the cord. These come from the lateral surface, extending medially nearly to the central canal. Later they anastomose dorso-ventrally and longitudinally, among themselves and with those from the ventral surface.

The vessels in the cord of a pig of 11 mm. present the following characteristics, as shown in figure 6. Rami from the primitive arterial tract may anastomose with those from the ventral capillaries. Neighboring vessels of the same kind anastomose freely and give aff lateral rami into the anlagen of the ventral horns of the gray matter. These rami branch and anastomose with each other and form loops which anastomose with the central vessels they arise from,

or with neighboring ones. In a plane just above the anlagen of the ventral horns each of the central vessels ends blindly, or divides into a caudal and a cranial ramus, which anastomose with adjacent similar rami and form irregular longitudinal vessels. By ather anastomoses among the central vessels, a longitudinal plexus is formed, which covers the lower half of the lateral side of the ependyma very completely.

A comparison of figures 3 and 6 shows how strongly the form and arrangement of these capillaries indicate what form and arrangement of the future central arteries and veins are to have. Besides these main capillaries two lateral groups, smaller than these, are present in this stage. These may be called the ventro- and dorso-lateral groups, and later form the peripheral arteries and veins. Both groups enter the cord from the capillaries on the lateral surface between the dorsal and ventral nerve roots. The ventro-lateral group entering on a level with the dorsal extremities of the central vessels, course medially and anastomose with these, occasionally

giving off rami which extend into the anlagen of the ventral horns. The capillaries of the other group are confined to the dorsal two-fifths of the cord, and in this stage do not anastomose with the central, or ventro-lateral capillaries, although they anastomose with each other. They course medially and dorsally along the ependyma, ending blindly or forming loops. They do not reach the dorsal surface.

The capillaries within the ganglia are more numerous in this stage than in earlier embryos. They enter from all sides and form a plexus within each ganglion. Later as the ganglia are removed more and more from the cord, and as the capillaries lying upon the ganglia are differentiated into veins and arteries, the blood supply of the ganglia comes through recurrent rami of the radical arteries and the blood is drained from them into the venous capillaries surrounding the spinal nerves, or directly into the radical veins.

As development proceeds, the lateral groups of capillaries shown in figure 6, spread dorso-ventrally and

peripheral capillaries enter the cord from other parts. With the exception of the above mentioned dorso-lateral group of capillaries, all the vessels entering the side of the cord grow toward a common center, namely, the place on the lateral border of the ependyma about half way between the dorsal and ventral surfaces, shown in figure 6. The dorso-lateral group of capillaries shown in the same figure send rami toward this center in pigs of 14 mm. and more. After the capillaries of this group unite with vessels entering from the dorsal surface (embryos 20 mm.), the dorsally coursing rami become inconspicuous and only the medial rami may be seen (embryos 45 mm.). These dorsal rami seem to be replaced by lateral rami of the vessels entering from the dorsal surface.

The vessels from the dorsal surface grow ventrally along the ependyma and unite with the dorsal rami of the primitive arterial tract, and by longitudinal anastomoses continue dorsally the plexus on the lower part of the ependyma, so that the ependymal layer, except below the "Basalplatte" and above the "Deckeplatte", is entirely

surrounded by a capillary plexus. A thick transverse section of the cord of a 25 mm. pig shows this plexus with numerous vessels extending from it laterally at right angles or nearly so. These lateral vessels are joined together by dorso-ventral rami. This picture is characteristic of the cord until the pig attains the size of 30 or 35 mm. when it is changed by other peripheral vessels meeting the ependymal plexus obliquely and by the branching of the vessels in the anlagen of the gray substance.

By this time the central arteries from both the ventral surface (anterior central arteries) and from the dorsal surface (posterior central or posterior peripheral afteries) have become quite large, although those from the dorsal surface are not nearly as large as the ventral ones. The anterior central arteries have formed more longitudinal loops like those shown in figure 6. They are separated more and more from each other, owing to the growth of the cord, and as this separation continues the longitudinal vessels grow in length.

In pigs of 35 to 40 mm. the peripheral arteries from all sides, and the lateral rami of the central arteries have formed a dense plexus in the gray matter, although the white matter contains only the peripheral arteries running through it, and the short branching rami given off at right angles from them. By the time the pig is 50 mm. long the capillaries of the white layer have much the same appearance as those of the near full term foetus, except that in the latter they branch and anastomose more, and the growth of the cord tends to separate the peripheral vessels somewhat, as it does the central vessels. Pigs of 75 to 100 mm. show the arteries in the cord to be developed quite as much as they are in the 240 mm. pig.

The number of dorsal rami of the primitive arterial tract in the ventral part of the cord of embryos of 12 to 15 mm. is larger than the number of central arteries in the 240 mm. pig that are formed from them.

The veins within the cord develop in the same planes as the arteries, and in the same plexus of capillaries that form the arteries. They may be called the central

and peripheral veins corresponding to the same named arteries. They are shown in figures 5 and 6 in a fully developed condition.

SUMMARY.

According to Sterzi's account of the vascularization of the spinal cord in the sheep, each dorsal ramus of the primitive arterial tract grows into the cord, and forms a loop, giving rise to a vein which grows back along the artery to the ventral surface. As shown in this paper, these dorsal rami and others from the capillaries in the immediate vicinity of the primitive arterial tractus enter the cord, forming an undifferentiated capillary plexus (see figure 6) and this plexus later becomes differentiated into arteries and veins.

Sterzi reports solid blood vessels in the cord of sheep of 5.5 mm. and hollow ones in those of 6.6 mm. The first pig shows the blood vessels within the cord as hollow vessels, and they first appear in embryos of 7.5 mm.

The "Tractus arteriosi laterales" of Sterzi, are the

postero-lateral arteries of this and other papers, and are the posterior spinal arteries of descriptive anatomy.

The pigs described in this paper show the mid ventral and mid dorsal surfaces of the cord to be covered with blood vessels in earlier stages than in those described by Evans ('09).

As reported by Sterzi ('04),and Evans ('09), blood vessels first appear on the ventro-lateral surface of the cord, then on the ventral, and then on the dorso-lateral, and finally on the dorsal.

The blood vessels on the cord are continuous with those in the mesenchyma surrounding it until the membranes of the cord are formed.

Texts of anatomy state that the spinal artery arises from the vertebral arteries, and is reinforced by segmental spinal arteries, (Piersol '07). It is rather to be considered that this artery arises from the segmental spinal arteries, and anastomoses with or is reinforced by the vertebrals.

For a study of this kind injected embryos are indis-

pensable. These are best examined by the thick section method described in part I.

The plates and figures in this paper, except numbers 3 and 4, were drawn with a camera lucida from thick sections of injected embryos.

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EXPLANATION OF FIGURES.

Figure 1. Ventral surface of the middle dorsal region of the spinal cord of a foetal pig, 240 mm. in length. A.S.A.= anterior spinal artery; A.R.V.= ventral radical artery; T.A.P.= secondary anterior spinal artery (remains of primitive arterial tract). V.R.V.= ventral radical vein. V.S.A.= anterior spinal vein; C.P.= capillary plexus. -X 9.

Figure 2. Dorsal surface of the same part of the cord shown in Fig.1. A.M.D.= median dorsal artery; A.P.L.= postero-lateral artery; A.R.D.= dorsal radical artery; V.M.D.= median dorsal vein; V.P.L.= postero-lateral vein and plexus; V.R.D.= dorsal radical vein; V.L.= postero-lateral venous plexus. X 14.

Figure 3. Sagittal section from the lower dorsal region of the spinal cord of a 240 mm. foetal pig. A.S.A.= anterior spinal artery; A.C.A.= anterior central artery; A.P.= peripheral artery; A.C.P.= posterior

central artery; V.S.A.= anterior spinal vein; V.C.A.= anterior central vein; V.C.P.= posterior central vein; V.P.= peripheral vein. - X 50.

Figure 4. Transverse section through the lower dorsal region of the spinal cord of a 240 mm. foetal pig. A.S.A.= anterior spinal artery; A.C.A.= anterior central artery; S.A.S.A.= secondary anterior spinal artery; A.P.= peripheral artery; A.= artery; A.P.L.= postero-lateral artery; A.M.D.= median dorsal artery; A.S.V.= anterior spinal vein; V.= vein; V.P.= peripheral vein; V.P.L.= postero-lateral vein; V.M.D.= median dorsal vein. - X 50.

Figure 5. The primitive arterial tracts of a 9.6 mm. pig, viewed from the dorsal side. T.A.P.= primitive arterial tract; R.M.T.A.P., R.D.T.A.P.,R.L.T.A.P.= medial, dorsal and lateral rami of the primitive arterial tract; R.D.T.A.P.L.R.= dorsal ramus of a lateral ramus of the primitive arterial tract; A.R.D.= dorsal radical artery; A.R.V.= ventral radical artery; A.C.= anterior central artery; A.P.= peripheral artery; L.B.R.A.V.M.= lateral

ramus of the vertebro-medullary artery; R.H.L.B., L.H.L.B. = right and left hind limb buds; A.V.M.= vertebro-medullary artery.- X 120.

Figure 5. Transverse section of the mid dorsal region of an 11 mm. pig embryo. T.A.P.= primitive arterial tract; R.D.T.A.P., R.L.T.A.P.,R.M.,= dorsal, lateral, and medial rami of the primitive arterial tract; A.V.M.= vertebro-medullary artery; A.R.V.,A.R.D.,= ventral and dorsal radical arteries; C.R.,Cr.R., D.R.,V.R.,= caudal, cranial, dorsal and ventral rami of the dorsal radical artery; D.P.,D.L.P.,= dorsal and dorso-lateral capillary plexuses; D.L.C.G.,V.L.C.G.,= dorso-lateral and ventro-lateral groups of peripheral capillaries; V.L.V.P.,= ventro-lateral venous plexus; V.R.V.,V.R.D.,= ventral and dorsal radical veins; S.P.G.= spinal ganglion; V.N.R., D.N.R.,= ventral and dorsal nerve roots; S.N.= spinal nerve.- X 390.

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ON THE VASCULARIZATION OF THE SPINAL CORD OF THE PIG

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FIVE FIGURES

HISTORICAL

Until 1904 little work had been done upon the development of the blood-vessels of the spinal cord, except that of His ('86) who undertook to follow the growth of these vessels in human embryos. The observations of this author have been largely disputed by Sterzi ('04) and Evans ('09), the two writers who have done most of the work in this field.

By far the most comprehensive publication upon the development of the vessels of the spinal cord is that of Sterzi ('04). In this he discusses the development of the vessels in the five higher classes of vertebrates. As a type of the Mammalia he uses the sheep. He brings out the following points:

The blood-vessels first approach the cord at the ventro-lateral border and spread over the ventral surface, then over the lateral, and finally over the dorsal surface. Each vertebro-medullary artery as it approaches the cord divides into a ventral and a dorsal ramus, the ventral and dorsal radical arteries. The ventral radicals from either side halt at the lateral edges of the floor-plate, and each divides into a cranial and a caudal branch. These anastomose with those of adjacent segments and form two longitudinal arteries on the ventral surface of the cord, the "tractus arteriosus primitivus." Later they send out medial rami and through these become connected. Still later, alternate parts of the two tracts degenerate while other parts continue to develop. These enlarged segments are joined together through their medial rami and form a single ventral artery which Sterzi terms the tractus arteriosus ventralis, and which is the anterior spinal artery

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of most authors. From the primitive tract, dorsal rami enter the substance of the cord. Each dorsal ramus forms a loop and gives rise to a vein, which courses ventrally and enters the primitive sulcus. Later other vessels extend into the cord from the lateral, and still later from the dorsal surface.

The dorsal radical arteries, where they divide, form many small longitudinal capillaries just ventral to the points of emergence of the dorsal nerve roots. From these capillaries there is formed later a longitudinal artery on either side of the cord, in this plane (tractus arteriosus lateralis). The vessels entering the cord are first solid and later become hollow.

Evans ('09) shows by a series of injected pigs the early development of anterior spinal artery In his figures the mid-ventral surface of the cord is shown to be free from vessels until the embryos are 8.5 mm. in length, and the mid-posterior surface until after the pigs are between 8 and 10.5 mm. in length. He does not take up the later stages.

MATERIAL AND METHODS

For a study of this nature, injected embryos are indispensable, and they are best injected while living, with warm india ink diluted one-half with weak ammonia water. It is preferable to inject through the umbilical artery rather than through the umbilical vein, because the arteries are less readily ruptured and because the route between them and the vessels of the spinal cord is much more direct.

Embryos used for thin serial sections are better if they are congested instead of being injected. This congestion is accomplished as follows: The umbilical cord is tied while the embryo is yet living, thus causing an increase in the blood pressure in the aorta. One of the most direct outlets for this increased pressure is the system of segmental arteries, and through these the bloodvessels in and around the spinal cord soon become engorged. When this condition is reached, as evidenced by the increased redness of the dorsal region of the embryo, the live embryo is dropped into a fixing fluid which penetrates rapidly so that the capillaries are fixed before they collapse. Bouin's picro-formo-acetic mix-

ture serves this purpose very well. Embryos treated in this manner show the smaller vessels much more plainly than those fixed in the usual way.

Small injected embryos which have been cleared in oil may be dissected under the binocular microscope and all the external vessels of the cord demonstrated, or they may be sectioned in celloidin to show the internal vessels.

From pigs larger than 25 or 30 mm. the cord with its membranes may be dissected out and embedded in celloidin and cleared, or for temporary preparations may be cleared directly.

Serial sections of the cleared embryo or spinal cord can be kept permanently between two pieces of paper soaked in oil, or can be transferred to slides and mounted in damar gum. To make slide preparations, the sections are cut in oil and placed on a piece of thin paper in the same order they are to have on the slide. Another piece of oiled paper is laid down upon them and the whole inverted. The first paper is now peeled off and the other paper holding the sections is inverted upon the slide. This paper is then peeled off, leaving the sections on the slide in their proper order. They may then be washed carefully with xylol, and covered.

There are several advantages in a study of this kind, in section ing celloidin-embedded embryos free-hand in oil. The cord can be turned so that sections may be cut through any plane. Sectioning is done more rapidly than with a microtome, and much time is saved. It is easy to make transverse, sagittal and frontal sections from any region of the same cord. The block can be examined with a lens, during the sectioning, and any particular vessel or vessels included in a section. Also, sections may be made of different shapes.

BLOOD-VESSELS OF THE NEAR FULL-TERM FETUS

In order to determine as near as possible the arrangement of the blood-vessels of the spinal cord in the adult condition, a number of fetal pigs, near full-term, were injected and their spinal cords dissected out for study. Although these showed some variation in the blood-vessels, as is to be expected, a general

plan was to be observed. The following description is of the typical condition found in the blood-vessels in and around the spinal cord of pigs of about 240 mm. in length:

The terminology used by Kadyi ('89) for the blood-vessels of the adult human cord will be referred to frequently.

On the surface of the cord at this stage are four main longitudinal arterial systems which are located: one, median on the ventral surface; one, on each dorso-lateral surface; and one median on the dorsal surface.

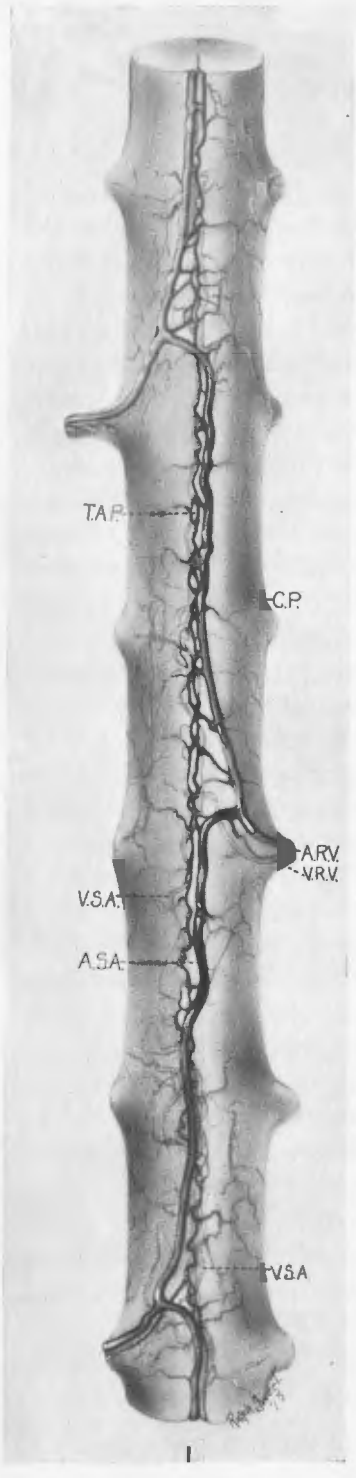
The vertebro-medullary branches of the dorsal segmental arteries approach the cord laterally and each divides into a dorsal and a ventral branch termed the posterior and ventral radical arteries respectively (figs. 1 and 2). The latter reach the cord along the cranial surface of the spinal nerves and ganglia, and, on the cord, run cranially. They may be equally distributed to the two sides of the cord and to the different regions of it, or some regions may have more than others. They average eighteen in number. The ventral and dorsal radical arteries have lost their connection with the vertebro-medullary artery in places and extend between the artery on the ventral surface of the cord and one of those on the dorso-lateral surfaces.

Soon after reaching the cord each ventral radical artery branches, giving off one ramus which courses cranially, and another which extends caudally. These divisions anastomose with those of neighboring ventral radicals, on the same or opposite side

Fig. 1[1] Ventral surface of the middle thoracic region of the spinal cord of a fetal pig, 240 mm. in length. *A.S.A.*, anterior spinal artery; *A.R.V.*, ventral radical artery; *T.A.P.*, accessory anterior spinal artery (remains of primitive arterial tract); *V.R.V.*, ventral radical vein; *V.S.A.*, anterior spinal vein; *C.P.*, capillary plexus. × 6.

Fig. 2 Dorsal surface of the same part of the cord shown in figure 1. *A.M.D.*, median dorsal artery; *A.P.L.*, dorso-lateral artery; *A.R.D.*, dorsal radical artery; *V.M.D.*, median dorsal vein; *V.P.L.*, dorso-lateral vein and plexus; *V.R.D.*, dorsal radical vein; *V.L.*, dorso-lateral venous plexus. × 10.

[1] The figures in this paper, except numbers 3 and 4, were drawn with a camera lucida. The size of the embryos is the greatest length, as measured in 75 per cent alcohol.



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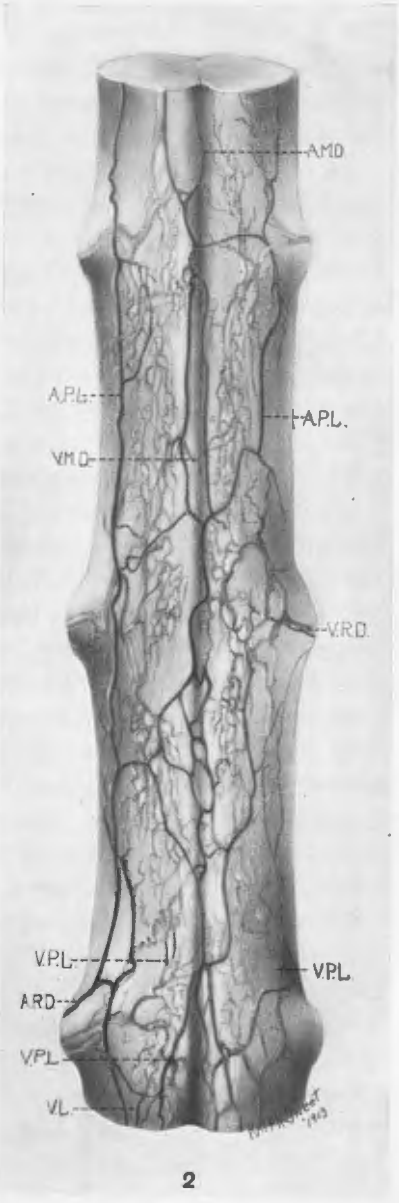

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of the cord, and form in this way the anterior spinal artery, which lies in or near the median ventral line. Occasionally a radical artery, instead of dividing, goes across the cord and joins the cranial or caudal ramus of the one on the opposite side. The anterior spinal artery has a winding course, bending laterally to meet the vessels which form it, and making many smaller irregular bends to one side or the other. In some places it may lie to one side of the mid-line for several segments and where this occurs there are found numerous longitudinal rami of the anterior spinal artery, or the cranial and caudal divisions of the ventral radicals. These may be called accessory anterior spinal arteries, and are sometimes present even where the anterior spinal artery lies in the mid-line. Here they are located between this vessel and cord, at the lip of the ventral median fissure. They are the remnants of the "tractus arteriosus primitivus" of Sterzi.

The dorsal radicular rami of the vertebro-medullary arteries are much more numerous than the ventral ones. They course dorsally along the cord and in a slightly cranial direction, to a plane just ventral to the emergence of the dorsal roots of the spinal nerves, where they divide into two rami, one extending cranially and one caudally. Each of these rami anastomoses with the one of the adjacent segment, and thus there is formed on either side an irregular longitudinal vessel, the dorso-lateral artery (fig. 2; tractus arteriosus postero-lateralis of Kadyi). From this artery recurrent rami supply the dorsal nerve roots and spinal ganglia, and the lateral surface of the cord. Other rami, two or three in each segment, and much larger than the above, run dorsally and by longitudinal anastomoses with each other, and with similar rami from the opposite side, form an artery in the mid-dorsal line which may be termed the median dorsal artery.

Very small rami from the dorso-lateral arteries run ventrally along the cord and unite with others from the anterior spinal artery, forming a plexus on the ventral and lateral sides. These ventral rami of the dorso-laterals anastomose freely in a longitudinal direction and form one or more small longitudinal arteries between the ventral and dorsal nerve roots in some parts of the cord. These are the tracti arteriosi laterales, and ventro-later-

ales, of Kadyi. Still other small rami from the dorso-lateral and median dorsal arteries form a capillary plexus on the dorsal and dorso-lateral surfaces of the cord. In a few places along the cord the dorso-lateral arteries are double, one division lying dorsal to the dorsal nerve roots, and corresponding perhaps to the "tractus arteriosus posterior" of Kadyi.

The median dorsal artery is a very irregular longitudinal vessel formed by the dorsal rami of the dorso-lateral arteries, as described above. In places it is double or may show a longitudinal capillary arrangement. Many of its lateral rami anastomose longitudinally forming small arteries parallel with the median dorsal artery (fig. 2). This is also true of the dorsal rami of the dorso-laterals. By the anastomoses of the rami of the various arteries just described, the entire cord is surrounded by an arterial vascular system, and from all parts of this network smaller arteries penetrate its substance.

The veins of the spinal cord are in three principal longitudinal systems, and other smaller ones. Of the three, two are dorsal and one ventral. All three show evidence of their capillary origin. The anterior spinal vein is the smallest of the three (fig. 1). It lies between the cord and the arteries, in the median ventral line. It is larger than the accessory anterior spinal arteries, but never attains the size of the anterior spinal artery proper. It is very irregular and in some regions is entirely replaced by a narrow network of capillaries.

On either side of the median ventral sulcus, the cord is covered with large venules, some of which lie between the cord and the arteries, and some of which are external to the latter. They are often two or three times as large as the arterioles to which they correspond. They anastomose freely with the anterior spinal vein and empty laterally into the ventral radical veins which are in close relation with the ventral nerve roots and ventral radical arteries, but which are much more numerous than the latter, one being present on nearly every nerve root. They drain blood also from the lateral surface of the cord. Their ventral and dorsal rami often form short, small, longitudinal veins by anastomoses, some of which in other animals have been named, antero-lateral.

etc. The blood from the anterior spinal veins and venous capillaries of the general ventral surface form, in places, transverse channels which are perhaps large enough to be called veins.

On either side of the dorsal surface of the cord there extends longitudinally a large irregular vein, the dorso-lateral, about half way between the artery of the same name, and the median dorsal artery. Some parts of these vessels and their rami, like the ventral venous capillaries, lie external to the arteries and some internal to them. They are the largest vessels on the cord with the exception of the anterior spinal artery (compare figs. 1 and 2). Dorsally these veins are united through large capillaries, and blood leaving the cord in the median line may flow either to the right or left. Half way between two consecutive nerve roots the dorso-lateral veins usually break up into many divisions so that each may be seen to drain blood from adjacent halves of two segments. Laterally they empty through one or more divisions into the large dorsal radical veins, one of which lies upon each dorsal nerve root (fig. 2).

A fourth longitudinal venous system, smaller than the three described, lies in the median dorsal sulcus. It resembles the dorso-lateral veins except that it is more irregular, and in places it may be entirely lacking. Its lateral rami empty in the dorsal venous capillary plexus or directly through larger vessels into the dorso-lateral veins. It may be termed median dorsal venous system.

Some of the venous capillaries of the lateral surface drain into the dorso radical veins, some into the dorso-lateral veins, and some into ventro radical veins, and all these vessels together with the anastomoses of the veins on the ventral and dorsal surfaces already mentioned above, completely surround the cord with a venous system, corresponding to the system described for the arteries.

Of the arteries entering the cord, the largest are those in the ventral fissure, the ventral central arteries, which form two nearly parallel rows, but which are not paired. They arise from the anterior spinal arteries, or the accessory anterior spinal arteries. They show evidence of the capillary origin in longitudinal anas-

tomoses found between vessels of the same side. These anastomoses are numerous in the fissure, particularly near the vessels from which the ventral central arteries arise.

The ventral central arteries vary considerably in size, some being as large as the vessels they arise from and others much smaller (fig. 3). The course of the smaller vessels is usually more irregular than that of the larger. They pierce the substance of the cord at different levels, some entering near their origin and others extending some distance into the fissure. Their general course is dorso-lateral, but those entering near the mouth of the fissure may bend very sharply to the side and enter the ventral horn of the gray substance. The others course more dorsally nearly to the level of the central canal where they make a decided lateral bend, and divide into two or more rami, although sometimes they give off rami more ventrally than this (figs. 3 and 4). The principal divisions of these arteries extend in a longitudinal plane, and anastomose with similar rami of adjacent vessels. They also give off smaller arteries and capillaries which ramify through the gray matter in all directions, helping to form a dense plexus. The longitudinal arteries tend to form loops after they have coursed in one direction for a short distance, as they do in young embryos (fig. 5). One artery may form several such loops, producing as many longitudinal vessels, each succeeding vessel lying dorsal or lateral to the last, and of a lesser caliber. These smaller longitudinal vessels anastomose with each other ventro-dorsally and laterally by rami which usually leave them at right angles, and also anastomose with rami from vessels other than the ventral central arteries, as will be described later.

Besides the rami of the central arteries just described, other rami extend farther laterally into the gray substance before branching. Some of these, instead of forming longitudinal vessels, form small irregular ones which ramify through the gray matter in all directions, anastomosing with similar vessels from other arteries in this region and forming a dense capillary plexus in the ventral and dorsal horns.

Other arteries, smaller than the ventral central arteries, enter the cord from the dorsal median sulcus and course ventrally and

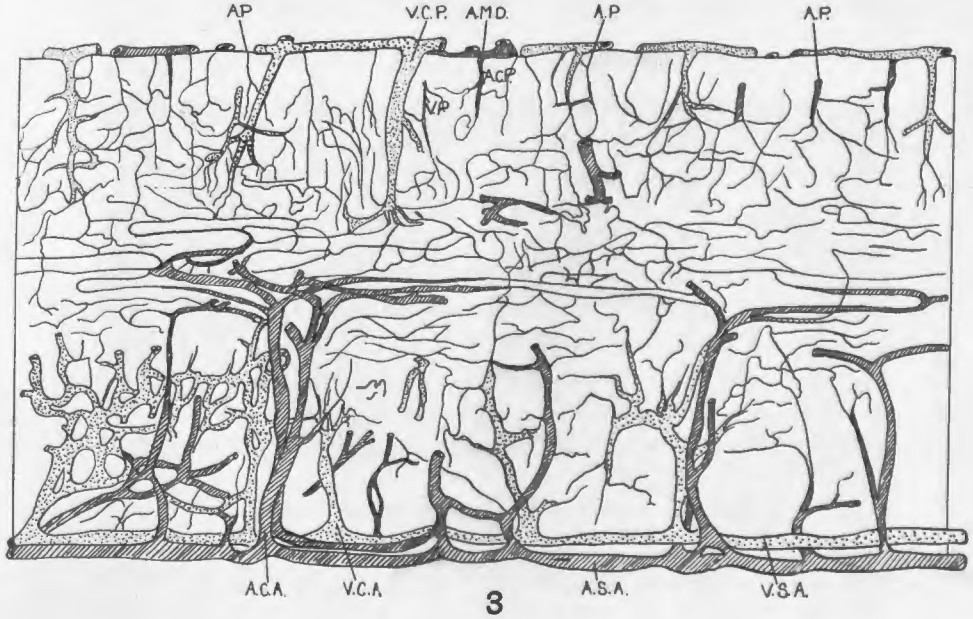
laterally to the dorsal horns of the gray substance. Here they form still smaller vessels resembling to some extent those formed by the ventral central arteries, but most of their rami are short and do not extend longitudinally. These may be called the dorsal central arteries, but they are more similar to the peripheral arteries from other surfaces of the cord, than to the ventral centrals, and perhaps should be called dorsal peripheral arteries. They give off many small lateral rami in the white substance and in the outer part of the gray substance.

In addition to these vessels, other small arteries enter the cord from all sides, from the arteries and arterioles which surround it. These are the peripheral arteries referred to above. They are very numerous and in a single thick cross section as many as fifty or sixty of them may be counted. They give off short rami in the white layer of the cord and extend into the gray layer. These rami branch and anastomose and form a loose capillary network. The vessels entering the gray substance enter into the longitudinal plexus already described and give off lateral rami which branch freely and anastomose.

The longitudinal vessels which arise from the ventral central arteries are quite large, but the other vessels formed from these trunks, and those formed from the dorsal central and peripheral arteries, are much smaller. A very thick section presents a picture of an inner core of longitudinal vessels with other vessels extending into it at right angles from all points on the periphery of the cord (figs. 3 and 4).

Fig. 3 Sagittal section from the lower thoracic region of the spinal cord of a 240 mm. fetal pig. *A.S.A.*, anterior spinal artery; *A.C.A.*, ventral central artery; *A.P.*, peripheral artery; *A.C.P.*, dorsal central artery; *V.S.A.*, anterior spinal vein; *V.C.A.*, ventral central vein; *V.C.P.*, dorsal central vein; *V.P.*, peripheral vein. × 35.

Fig. 4 Transverse section through the lower thoracic region of the spinal cord of a 240 mm. fetal pig. *A.S.A.*, anterior spinal artery; *A.P.*, peripheral artery; *A.*, artery; *A.C.A.*, ventral central artery; *S.A.S.A.*, accessory anterior spinal artery; *A.P.L.*, dorso-lateral artery; *A.M.D.*, median dorsal artery; *A.S.V.*, anterior spinal vein; *V.*, vein; *V.P.*, peripheral vein; *V.P.L.*, dorso-lateral vein; *V.M.D.*, median dorsal vein. × 35.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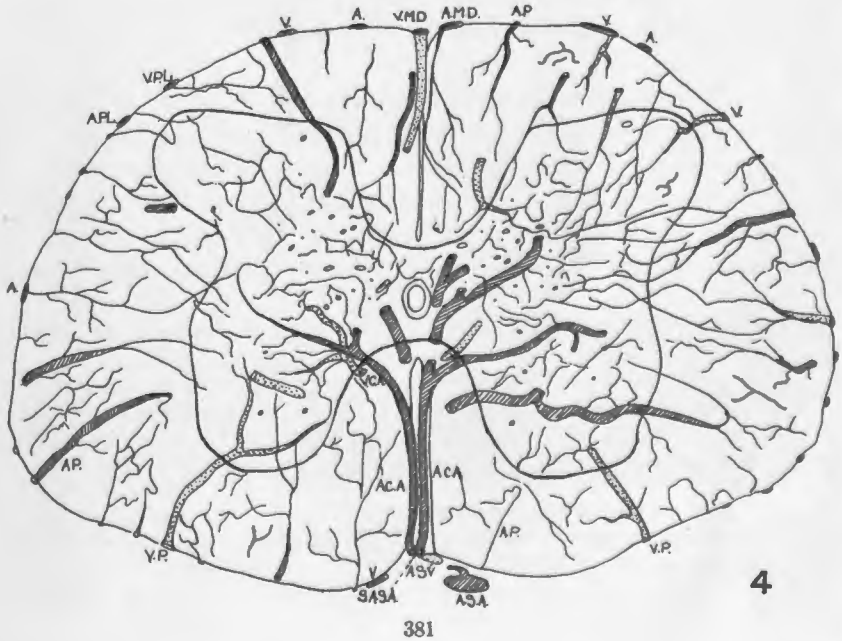
3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A.S.A.

4

DEVELOPMENT OF THE BLOOD-VESSELS

The early development of the anterior spinal artery has been described by Evans ('09) and Sterzi ('04).

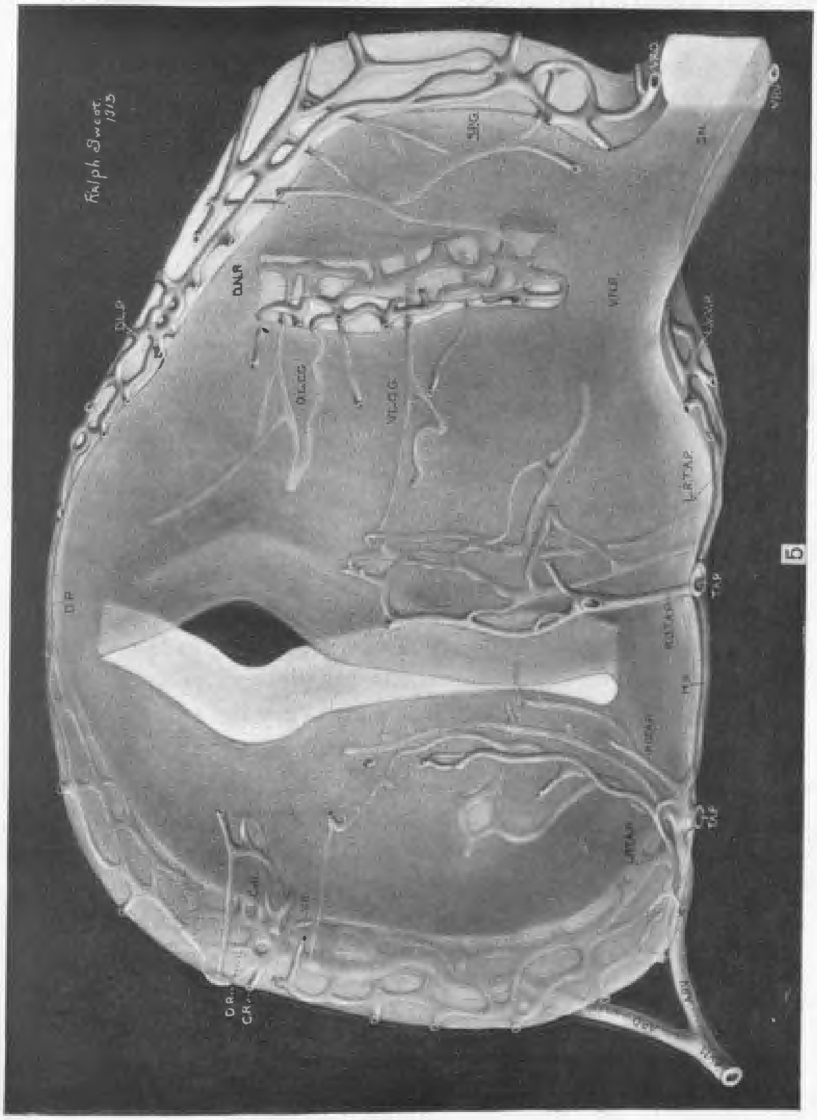
Some pig embryos of 12 mm. show a fairly well developed anterior spinal artery, while in others of 14 or 15 mm. it is just beginning to form. Although, after this vessel is once formed, it does not undergo marked changes, there is some modification. For example, the ventral radical arteries meet it at right angles or nearly so, until the embryo is 40 or 45 mm. in length. Thereafter, the growth of the cord and the fixed position of the radicals seem to cause the artery to be pulled laterally by the radicals, and a gradually decreasing angle is formed at the points where the radicals meet it (fig. 1).

As the embryo grows, the number of radical arteries continues to decrease even after the anterior spinal artery is well formed. This seems to be true until the embryo reaches the length of about 100 mm.

Some of the arterial capillaries on the ventral surface of the spinal cord are continuous with the anterior spinal artery directly, or indirectly through remains of the tractus arteriosus primitivus, and others are continuous with the capillaries of the lateral surfaces of the cord.

A dorso-lateral artery is formed in the capillary plexus on each of the lateral surfaces of the cord, just ventral to the point of emergence of the dorsal nerve roots. The dorsal radical arteries branch in this region and give off dorsal and lateral rami, which are continuous with the lateral capillaries just mentioned. A very irregular longitudinal vessel develops where certain of these

Fig. 5 Transverse section through the mid thoracic region of the spinal cord of an 11 mm. pig embryo. *T.A.P.*, primitive arterial tract; *R.D.T.A.P.*, *R.L. T.A.P.*, *R.M.*, dorsal, lateral, and medial rami of the primitive arterial tract; *A.V.M.*, vertebro-medullary artery; *A.R.V.*, *A.R.D.*, ventral and dorsal radical arteries; *C.R.*, *Cr.R.*, *D.R.*, *V.R.*, caudal, cranial, dorsal and ventral rami of the dorsal radical artery; *D.P.*, *D.L.P.*, dorsal and dorso-lateral capillary plexuses; *D.L.C.G.*, *V.L.C.G.*, dorso-lateral and ventro-lateral groups of peripheral capillaries; *V.L.V.P.*, ventro-lateral venous plexus; *V.R.V.*, *V.R.D.*, ventral and dorsal radical veins; *S.P.G.*, spinal ganglion; *V.N.R.*, *D.N.R.*, ventral and dorsal nerve roots; *S.N.*, spinal nerve. × 200



5

capillaries increase in size, perhaps on account of the increased pressure from the dorsal radical arteries. This longitudinal vessel is indicated in embryos of 12 mm. and is quite strongly developed in embryos of 15 to 18 mm. In these stages it seems to dip ventrally to meet the approaching radicals, as pointed out by Sterzi for the sheep ('04). As the embryo grows, this dorso-lateral artery becomes more and more regular. It is still somewhat irregular in embryos of 60 mm. but quite regular in those of 75 mm. The dorso-lateral artery never attains the size of the anterior spinal nor is it ever so regular in its course. In places it may develop as two or more vessels, but these are always smaller than the single artery. The dorso-lateral arteries are each continuous with the capillaries of half the cord in the early stages, but as the cord increases in size they supply directly only the dorso-lateral surface.

The capillary network on the lateral surface of the cord is at first continuous with that extending through the mesenchyma of this region as far, laterally and dorsally, as the myotomes and body wall respectively. In later stages when the membranes of the cord begin to develop, the connections between the vessels of the cord and those in the mesenchyma around it are lost.

The median dorsal artery is the last of all the vessels on the cord to develop. In pigs of 30 mm. it is still very irregular and indefinite, and is entirely lacking in places, although the vessels which go to form it, the dorsal rami of the dorso-lateral arteries, may be seen in embryos of 20 mm. In pigs of 45 mm. it is quite definite, lying in or near the mid line of the dorsal surface, as described above for the 240 mm. embryo It never becomes very regular, and in pigs of 100 mm. it resembles the condition seen in the pig of 240 mm. It is continuous with the arterial capillaries of the dorsal surface of the cord and with the dorso-lateral arteries.

In addition to these main arterial trunks there develop on various parts of the cord, especially on the lateral surfaces, short longitudinal arteries. These are never large or regular. They have been described in connection with adult human cord under the terms "tractus arteriosus; ventro-lateralis, posterioris, and

lateralis" (Kadyi). Of these, the "tractus arteriosus posterior" is the most prominent and corresponds to the description in this paper of parts of the dorso-lateral artery, where it sometimes has two divisions, one of which runs dorsal to the dorsal nerve roots and the other ventral to them. The dorsal divisions are evidently the same as this 'tractus.'

The veins on the cord develop in much the same way as do the arteries. The ventro-lateral surface of the cord in very young embryos is covered with capillaries, and these are continuous laterally with the capillaries in the mesenchyma round the neural tube. Medially they become continuous with the lateral rami of the primitive arterial tract. When this tract becomes separated from the cord by the ingrowth of mesenchyma, these capillaries send medial outgrowths between the tract and the cord, as seen in embryos of 12 to 15 mm. Dorsally they grow along the cord and spread over the dorso-lateral surface (pigs of 6.2 mm.) and later over the dorsal surface (pigs of 7.5 mm.). Laterally they spread over the ganglia.

From the ventral surface, the blood draining away through the capillaries soon establishes segmental vessels, the ventral radical veins, which course laterally along the nerve roots. Each radical vein on one side drains adjacent halves of two segments. These receive blood from the capillaries of the ventral, lateral, and ventro-lateral surfaces. Lying in the ventral median fissure in young embryos, small longitudinal veins may be seen in different regions of the cord, and in embryos of 25 to 30 mm. a fairly definite longitudinal vessel may be found here. This vessel in still older embryos becomes a more definite trunk and may be called the anterior spinal vein. It never attains the size of the anterior spinal artery. Laterally it drains into the ventral radical veins.

Some of the ventral and lateral capillaries of the younger embryos, early become differentiated into veins. This is especially true of the dorsal vessels. From these, some of the blood drains laterally out through vessels in the mesenchyma to the myotomes. A pig of 6.2 mm. shows three planes in which this occurs, one on a level with the dorsal surface, one just above the level of the ven-

tral surface, and one about half way between the other two. At the myotomes the blood drains ventrally into the intersegmental veins. Some of the capillaries of the lowest of these three planes, which drain the blood from the lateral surface of the cord and from the ganglia, soon become large and are called the vertebro-medullary veins, one pair of which is formed for each segment. In older embryos they course along the spinal nerves with the vertebro-medullary arteries. They receive the blood from the ventral and dorsal radical veins. The former have been described. The latter develop along the sides of the ganglia in the capillaries already mentioned. At first they carry only a part of the blood from the dorsal surface of the cord, but later (pigs of 25 mm.) they carry practically all of it. They are more numerous than the corresponding ventral radicals, and are found in every segment.

The venous capillaries of the dorsal-lateral surface on either side draining toward the nerve roots early establish longitudinal veins. These are only about half as long as a segment of the cord. Figure 5 of an 11 mm. pig, shows an indifferent plexus on this surface, but in 15 to 17 mm. embryos, fairly definite vessels may be seen. These become more and more regular as the animal develops, and as embryos of 50 to 60 mm. show, they form a venous system on either side of the cord just dorsal to the dorsal nerve roots, much like that described for the 240 mm. stage. These systems constitute the dorso-lateral veins (fig. 2).

The first blood vessels entering the cord grow in as capillaries from the ventral surface. Sterzi ('04) reports vessels in the cord of a sheep of 5.5 mm., but they were not apparent in the cord of pig embryos of less than 7.5 mm. These vessels are the dorsal rami of the primitive arterial tracts, of the lateral rami of these tracts, and of the other capillaries near the median line. They are the first indications of the central arteries and veins. They form two nearly parallel rows, one on either side of the ependymal layer, or some of them may lie in this layer. They grow dorsally about half way to the dorsal surface of the cord. They exhibit numerous longitudinal anastomoses and form a plexus along the ateral side of the ependymal layer in each half of the cord. These are true capillaries at first, but soon differentiate into arteries and veins.

Those coming directly from the primitive arterial tracts all become arteries, while those coming from the vessels lateral to the tract may become either veins or arteries.

In embryos of 9.5 mm. another group of capillaries may be seen to have entered the cord. These come from the lateral surface, extending medially nearly to the central canal. Later they anastomose ventro-dorsally and longitudinally, among themselves and with the vascular sprouts from the ventral surface.

The vessels in the cord of a pig of 11 mm. present the following characteristics, as shown in figure 5. Rami from the primitive arterial tract may anastomose with those from the ventral capillaries. Neighboring vessels of the same kind anastomose freely and give off lateral rami into the anlagen of the ventral horns of gray substance. These rami branch and anastomose with each other and form loops which anastomose with the central vessels from which they arise, or with neighboring vessels. In a plane just above the anlagen of the ventral horns each of the central vessels ends blindly, or divides into a caudal and a cranial ramus, which anastomose with adjacent similar rami and form irregular longitudinal vessels. By other anastomoses among the central vessels, a longitudinal plexus is formed, which covers very completely the lower half of the lateral side of the ependymal layer.

A comparison of figures 3 and 5 shows how closely the form and arrangement of these capillaries corresponds to that of the future central arteries and veins. Besides these main capillaries two smaller lateral groups are present at this stage. These may be called the ventro- and dorso-lateral groups, and later form peripheral arteries and veins. Both groups enter the cord from the capillaries on the lateral surface between the dorsal and ventral nerve roots. The ventro-lateral group enters at the level of the dorsal extremities of the central vessels, and courses medially and anastomoses with them. Occasionally the ventro-lateral group gives off rami which extend into the anlagen of the ventral horns. The capillaries of the dorso-lateral group are confined to the dorsal two-fifths of the cord, and although they anastomose with each other at this stage, they do not anastomose with the central or ventro-lateral capillaries. They course medially and

dorsally along the ependyma, ending blindly or forming loops, but do not reach the dorsal surface.

As development proceeds, the lateral groups of capillaries shown in figure 5 spread dorsally and ventrally and capillaries enter the cord from the periphery. With the exception of the above-mentioned dorso-lateral group of capillaries, all the vessels entering the sides of the cord grow toward a common center, namely, an area on the lateral border of the ependyma about half way between the dorsal and ventral surfaces. The dorso-lateral group of capillaries which are shown in the same figure send rami toward this center after the embryo attains the length of 14 mm.

The vessels from the dorsal surface grow ventrally along the ependyma and unite with the dorsal rami of the primitive arterial tract. This union continues the plexus on the lower part of the ependyma dorsally so that the ependyma except below the floor-plate and above the roof-plate, is entirely surrounded by a capillary plexus. A thick transverse section of the cord of an embryo of 25 mm. shows this plexus with numerous vessels extending from it laterally at right angles. These lateral vessels are joined together by dorso-ventral rami. This picture is characteristic of the cord until the embryo reaches the length of 30 or 35 mm. when it is changed by other peripheral vessels meeting the ependymal plexus obliquely and by the branching of the vessels in the anlage of the gray substance.

By this time the central arteries from both the ventral surface (ventral central arteries) and from the dorsal surface (dorsal central or dorsal peripheral arteries) have become quite large, although the latter do not nearly equal the size of the former. The ventral central arteries have formed more longitudinal loops similar to those shown in figure 5. They are separated more and more from each other, owing to the growth of the cord, and as this separation continues the longitudinal vessels grow in length.

In embryos of 35 to 40 mm. in length the peripheral arteries from all sides together with the lateral rami of the central arteries have formed a dense plexus in the gray substance, although the white substance contains only the peripheral arteries running through it, and the short branching rami given off at right angles

from them. By the time the embryo reaches a length of 50 mm. the capillaries in the white layer have much the same appearance as those of the full term fetus, except that in the latter they branch and anastomose more freely and the growth of the cord tends to separate both the peripheral vessels and the central vessels. Embryos of 75 to 100 mm. in length show the arteries in the cord quite as completely developed as in the 240 mm. embryo.

The posterior rami of the primitive arterial tract in the ventral part of the cord of embryos of 12 to 15 mm. are more numerous than the central arteries in the 240 mm. embryo which are formed from them.

The veins within the cord develop in the same planes as the arteries, and from the same plexus of capillaries that form the latter. They may be called the central and peripheral veins corresponding to the similarly named arteries. They are shown in figures 3 and 4 in a fully developed condition.

SUMMARY

The dorsal rami of the primitive arterial tract, and other rami from the capillaries in its immediate vicinity enter the cord, forming an undifferentiated capillary plexus (fig. 5) and this plexus later becomes differentiated into arteries and veins. It was not found, as stated by Sterzi for the sheep, that each dorsal ramus of the primitive arterial tract grows into the cord, and forms a loop, giving rise to a vein which grows back along the artery to the ventral surface.

The dorsal rami of the primitive arterial tract are more numerous than the ventral central arteries which develop from them.

Sterzi reports solid blood-vessels in the cord of sheep of 5.5 mm. and hollow ones in those of 6.6 mm. In pig embryos the blood-vessels within the cord seemed to appear first as hollow vessels. These are seen first in embryos of 7.5 mm. in length.

The "tracti arteriosi laterales" of Sterzi, are the dorso-lateral arteries of this and postero-lateral of other papers, and are the posterior spinal arteries of human descriptive anatomy. Evans shows these two tracts first united by medial anastomoses in a

pig of 8.5 mm. in length, but many such anastomoses are to be found in embryos as small as 7.5 mm. in the cervical and thoracic regions, and one specimen of 6.2 mm. showed them in the cervical region.

The embryos described in this paper show the mid-ventral and mid-dorsal surfaces of the cord to be covered with blood-vessels at a somewhat earlier stage than has been described.

As reported by Sterzi ('04) and Evans ('09), blood-vessels first appear on the ventro-lateral surface of the cord, then on the ventral, then on the dorso-lateral, and finally on the dorsal surface.

The blood-vessels on the cord are continuous with those in the mesenchyma surrounding it until the membranes of the cord are formed.

It is generally stated in textbooks of human anatomy that the spinal artery arises from the vertebral arteries, and is reinforced by segmental spinal arteries. It is rather to be considered that this artery arises from the segmental spinal arteries, and anastomoses with, or is reinforced by, the vertebrals.

The term median dorsal is suggested for the artery present in places in the median dorsal line of the spinal cord.

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