MAJOR CHANGES WITHIN THE VASCULARIZATION OF THE BOVINE EMBRYO 39 TO 60 DAYS GESTATION

by

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INTRODUCTION

The development of vascularization in the mammalian embryo and changes from embryonic to definitive circulation has been severely neglected during the general progress of science and the rush of new and exciting areas for investigation. Many scientists, including some morphologists, consider that all the developmental anatomy that we need has been completed.

On the contrary, all scientists involved directly with developmental anatomy, whether they are anatomists, teratologists, pathologists, or geneticists, repeatedly find gaps in our knowledge that prevent proper interpretations of normal versus abnormal, induced versus spontaneous, or genetic versus accidental variations.

Increasing complexities are encountered in trying to interpolate embryonic structures to fetal and definitive states. Great numbers of detailed developmental studies have been consumated on early embryonic development and reasonable studies have been made on fetal structures, but extremely few and fragmentary studies, mostly philosophical, have been done on that awkward stage that is too late to be embryonic and too early to be considered fetal. The individuals are too small to be dissected, too large to be serially sectioned, and too complex to be imagined. Unfortunately, many of the transformations from embryonic, phylogenetically archaiac structures to definitive, functional structures occur during this inadequately studied period.

In view of known deficiencies in the knowledge of embryonic-fetal changes, the Kansas State University Embryology Laboratory, under the auspices and with the support of the Kansas Agriculture Experiment Station, has amassed a large number of bovine embryos and early fetuses for use in such studies. That collection was available and used for this study.

The present study was initiated in an effort to establish a more realistic, documented story of the changes in the blood vessels of the trunk of bovine embryos from 39 to 60 days gestation. Vascular development up to 39 days development was done by Byrnes (1973), and the details of heart development for this period was the object of studies by Smith (1970).

LITERATURE REVIEW

The development of the major blood vessels was first described and interpreted on a phylogenetic comparative basis by such pioneers as Kingsley, 1917 and Nelsen, 1953 and a fair understanding of the total process was derived from these generalizations.

The dorsal aorta is derived by fusion of the two originally separate, paired aortae and is modified such that the five original definitive pairs of aortic arches in the pharyngeal region are reduced to the systemic arch (left fourth aortic arch) in the thoracic region, while the remnants of aortic arch 1, 2, and 3 remain within the head. According to Patten (1943), the trunk of the common carotid arteries are the remnants of the third aortic arch. The major portion of the common carotids are formed by the ventral aortic root.

The subclavian arteries orginally consisted of branches from intersegmental arteries C-5 through T-3 but are progressively reduced to C-7 by the time the cartilagenous bone models begin to form -- about day 30 in the bovine embryo (Warwick & Williams, 1973; Byrnes, 1973). The base of each subclavian artery gradually "walks up" the dorsal aorta so that by

40 days development, it emerges from the dorsal aorta on the left side immediately opposite the junction of aortic arch 6 and on the right it is continuous with the base of old aortic arch 4 (Byrnes, 1973).

The segmental (intersomitic) arteries have been variously numbered, and inconsistently described. Byrnes (1973) described the segmental arteries as consisting of 5 pairs of occipital arteries, all from the radices aortae, 7 pairs of cervical arteries, 13 pairs of thoracic arteries, and 6 pairs of lumbar arteries, all from the dorsal aorta. Patten (1968), Arey (1968), and Warwick & Williams (1973) ignored the transient occipital arteries, and considered the subclavian arteries to be the seventh pair.

The iliac arteries, like the subclavians, begin as branches from a series of segmental arteries (L-5 to S-2) that coalesced and reduced to a single S-1. Since the original body stalk was in the sacral region, the same set of arterioles expanded to the allantios, so it appears that the allantoic arteries arise from the iliacs (Byrnes, 1973). The umbilicals, however, have been described as the fourth of four vessels which remain after the degeneration of the vitelline arteries. (See Medial Arteries to Gut, below)

Mesonephric arteries, according to Nelsen (1953) are merely branches of the segmental arteries, and to other workers (Patten, 1968) are derivatives of the segmental arteries. Byrnes (1973) described them as an entirely separate entity. That is, they arise independent of the segmentals as outgrowths off the dorsal aorta. Arey (1968) further described the subsequent loss of the majority of these vessels as the mesonephros degenerates leaving only paired vessels to the suprarenal, kidney, and gonad remaining in the adult configurations.

Medial arteries to the gut were described by Patten (1968) as consisting of the celiac, superior mesenteric, and inferior mesenteric which are formed from paired ventral segmental arteries by these paired vessels being pulled into approximation of each other by the developing mesenteries. These vessels were described as being derived vrom the ventral branches primitively constituting the paired vitelline arteries to the yolk sac and allantois. As the paired dorsal aortae combine, single ventral vessels were formed apparently by fusion. Further degeneration of these vessels results in four vessels remaining, three of these passing by way of the mesenteries to the gut and becoming, craniad to caudad, celiac, superior mesenteric, and inferior mesenteric arteries (Arey, 1968). The remaining, fourth pair continues as the umbilicals (Nelsen, 1953; Patten, 1968).

Studies on development of the veins have been even less consistent than have those of the arteries. The early mammalian embryo with 25 to 50 somites has a system of cardinal veins comparable to those of a dogfish shark (Arey, 1968). The capillaries from the forelimb empty into the anterior cardinal veins, and gradually condense into subclavian veins (Patten, 1943). The anterior cardinal veins remain directly as the internal jugular veins; the right common cardinal remains as the anterior vena cava, and a transverse connection develops between the left anterior cardinal-subclavian junction to the right common cardinal as the "innominate vein". The left common cardinal then deteriorates except for the segment remaining as the coronary sinus (Patten, 1968; Arey, 1968).

The iliac veins are the remains of the old post cardinal veins and exit the body cavity around position L-5 to S-1 (Arey, 1968).

The mesonephric veins are formed by the anastamosis of the embryonic veins of the abdomen. These consist of the subcardinal anastamosis, and supra-subcardinal anastamosis. These anastamosies remain functional in the adult as the renal portion of the posterior vena cava (Arey, 1968).

The posterior vena cava is a composite vessel which gradually takes shape by the enlargement and straightening of originally small, local channels which are pressed into service as the degeneration of the posterior cardinal veins occurs which begins first in the area of the subcardinal sinus (Patten, 1968). The subcardinal sinus is formed by the mesonephros forcing the subcardinal veins into close association resulting in the fusion of these vessels (Arey, 1968). The formation of the posterior vena cava begins in the pre-renal area by a coalescence of small branches which reach between the head of the right mesonephros and the lower part of the liver, the renal portion from the subcardinal anastamosis, the area between the renal portion and the iliacs forming from the right supracardinal vein, and finally the common iliacs forming from the post cardinal veins (Patten, 1968). The posterior vena cava has also been described as consisting of four portions by Arey (1968): (1) an hepatic segment which is derived from the hepatic vein (proximal right vitelline) and hepatic sinusoids, (2) a pre-renal segment from the subcardinal anastamosis, (3) a renal segment from the supra-subcardinal anastamosis and (4) a post renal segment from the right supracardinal. The renal veins appear as the kidney becomes functional and reaches its final position, and drain into the supra-subcardinal anastamosis (Warwick & Williams, 1973). The gonadal veins are the remnants of the paired subcardinals below the kidney (Patten, 1968; Arey, 1968).

MATERIALS AND METHODS

The embryos used in this study were obtained from the collection made by Dr. H. T. Gier, Division of Biology, Kansas State University. Those used constituted a continuous series of 41 embryos 39 to 63 days development. Twenty-three of the embryos were of known age and were obtained from the Kansas State University dairy herd (TABLE 1). The other embryos were collected from area abattoirs and aged by the method described by Gier and Marion (1960) on the basis of weight, crown-rump, contour, head and foot measurements. Ovulation was considered as zero time for calculating the age of an embryo.

The embryos obtained during the course of this study were fixed by perfusion with ten per cent formalin, then immersed in Bouin's fluid, washed, dehydrated in a graded series of isopropyl alcohol, embedded in paraffin, and sectioned at 15 or 20 mu. Sections were cut either transversely or sagitally (TABLE 1) and stained with periodic acid-Schiff reagent (PAS) followed by Harris hematoxylin or with Harris hematoxylin followed by acid fuchsin, or Mallory's triple stain. Each embryo was stained by two or more methods using alternate slides within a series for each stain.

Critical sections were routinely photographed. Selected embryos were graphically reconstructed by making microprojection outline drawings of sagittal sections on acetate transparencies. Composite sketches were then made from the transparencies with further details added from cross-sections of equivalent-age embryos.

Four dissections were made on fetuses that had arteries injected with liquid latex (TABLE 1) to establish an overall picture of definitive structures. Photographs were made of these dissections.

TABLE 1: BOVINE EMBRYOS USED IN THIS STUDY

Embryo number	Age in days	Crown-rump length (mm)	Contour (mm)	Type of section[b]
620-6	38	20	48	L
163	39	24	---	L
696	40	----	---	X
169	41	23	53	L
583-6	41	----	---	X
1	41	----	---	L
600-3	42	21	56	L
600-58	43	32	55	L
75	43	24	56	X
195	44	24	58	L
551	44	----	---	X
583-17-4	44	----	---	L
600-54	44	34	---	X
600-27	45	25	---	X
724	45	26	---	X
583-8-6	45	----	---	X
583-1	45	----	---	L
583-11	46	----	---	X
437	48	39	83	L
600-56	48	46	82	L
209	49	42	92	X
385-12	49	35	78	L
274	49	35	76	X
583-17-3	49	----	---	X
583-17-2	49	----	---	X
709	50	44	82	X
577-3	50	40	88	X
607	50	41.5	89	X
620	50	49	103	X
577-2	51	52	110	X
600-57	51	52	100	L
300	52	42	80	X
144	52	49	100	X
579	55	52	100	L
342	58	61	111	L
810	60	78	120	X
349	62	81	145	X
812	63	87	140	L
900-7	56	60	112	D
900-8	56	----	---	D
1042	150	----	---	D

[b] X=transverse L=saggital D=injected and dissected

OBSERVATIONS

This report is a continuation of the work completed by Byrnes, 1973, which covered the vascular development of the bovine embryo from day 21 through day 39 of gestation.

Although embryos of every day stage from 39 through 60 days were processed and examined, essential changes can be well illustrated and described by embryos differing in age by approximately four days. Consequently, stages 39, 44, 51, 56, and 60 days will first be considered, then changes between these stages will be evaluated in a continuous manner in discussion of each vessel or complex of vessels.

VASCULARIZATION OF THE 39 - 40 DAY BOVINE EMBRYO

Three embryos constituted the basis for this stage, and the illustrations are essentially those prepared in the previous study by Byrnes.

ARTERIES. The essentials of the adult arterial circulation are established in the 39 day embryo. The dorsal aorta has established itself medially along the dorsal body wall ventral to the developing vertabrae from vertebra C-7 through S-1 and has well-defined intersomitic arteries occuring as branches which course between the somitic derivatives from T-4 through S-1.

The external carotid arteries, from the common carotid artery to the lingual-mandible bifurcations (Fig. 1), are formed by the elongation and medial splitting of the aortic sinus between the second and third aortic arches. The common carotid arteries are formed by the splitting and elongation of the aortic sinus between the bases of aortic arches 3 and 4 (Fig. 1). The fourth aortic arch on the right side remains as the base of the right subclavian, while the left fourth aortic arch remains as the adult aortic arch. The left sixth aortic arch remains as the pulmonary

trunk from the right ventricle to the bifurcation of the pulmonary arteries and continues to the dorsal aorta as the ductus arteriosis (Fig. 2). The right sixth aortic arch was completely closed by day 35 and so is no longer present. The subclavians at 39 days result from the expansion of the original segmental artery, C-7, between the last cervical and first thoracic vertebrae.

Of the 13 or more pairs of original vitelline arteries formed in the embryo, by 40 days there are only two single arteries to the gut as a result of the pairs either joining (Arey, 1968) or one of the pairs degenerating. The most anterior of those remaining is the superior mesenteric, ventral to L-1 and the other is the inferior mesenteric, ventral to L-5. The celiac artery, here ventral to T-13, L-1, was described by Patten (1968) and Arey (1968) as being originally a vitelline artery. However, in the bovine embryos the original vitelline arteries in this region degenerate to a single vessel, the superior mesenteric artery. There is no artery entering the stomach until day 30 when a definitive celiac artery is formed approximately one-half somite length anterior to the superior mesenteric artery (Byrnes, 1973).

Of the original 20± pairs of mesonephric arteries from C-6 through L-5, the anterior mesonephric arteries have degenerated leaving 11 pairs in the posterior thoracic and lumbar region.

The umbilical arteries appear as the posterior branches of the dorsal aorta, running posterolaterally, then ventrally through the body wall into the umbilical cord. The external iliac arteries appear as direct lateral branches from the umbilical arteries, while the internal iliac arteries are continuations of the dorsal aorta at the base of the umbilical arteries. The caudal artery originates on the median dorsal surface of the dorsal aorta between the bases of the umbilical arteries and extends caudally

down the median dorsal body wall along the ventral surface of the sacral and caudal vertebrae.

VEINS. The original cardinal system has been only slightly modified by this time. The anterior cardinal veins can now be called jugular veins. The right common cardinal has maintained its size and remains as the trunk of the superior vena cava. The left common cardinal, however, is somewhat reduced and persists around the atrio-ventricular sulcus as the coronary sinus, opening into the sinus venosus caudomedially to the opening of the right common cardinal vein. The left common cardinal vein continues to carry blood from both the left anterior and posterior cardinal veins.

Supracardinal veins are continuous throughout the length of the mesonephroi, connecting at irregular intervals laterally with the post cardinals and ventrally with the subcardinal veins which are confined to the lumbar portion of the mesonephroi.

The posterior vena cava is a compound vessel which can be considered in sections, relating to the origins of each. The thoracic vena cava is continuous anteriorly with the sinus venosus and superior vena cava and caudally at the diaphragm with the hepatic segment which is primarily ductus venosus. The hepatic segment is continuous posterodorsally with the renal segment, at the point where liver and mesonephros are fused (Byrnes, 1973). The renal segment of the posterior vena cava is the anastamosis of the supracardinal and subcardinals. The paired supracardinal veins are continuous posteriorly from the supra-subcardinal anastomosis of the renal segment proper, and in turn are continuous posteriorly with the old post-cardinal veins which are now the internal iliac veins. The external iliac veins enter the post-supracardinal junction at L-6, S-1.

VASCULARIZATION IN THE 44 - 45 DAY BOVINE EMBRYO

The major changes in the vascular system between days 39 and 45 consist of 1) further posterior migration of the heart, with beginning of the carotid trunk; 2) disintegration of the anterior mesonephric arteries; 3) establishment of a metanephric artery; and, 4) formation of the innominate vein.

ARTERIES. The dorsal aorta is a large, single vessel originating at the left ventricle, progressing anteriorly to T-2, and then posteriorly along the dorsomedial line of the body wall immediately ventral to the vertebral column. The dorsal aorta technically ends near L-5 where it splits into the paired common iliac arteries. The caudal artery leaves the dorsal medial surface of the aorta at L-6 and extends along the ventral surface of the sacral vertebrae.

The carotid trunk originates from the anterior surface of the aortic arch and runs anteriorly to where it splits at T-1 into the common carotid arteries which run anteriorly on either side of the trachea (Fig. 4). The right subclavian emerges from the carotid trunk about the middle of T-1 and runs slightly anteriorly. The left subclavian artery comes off the anterolateral surface of the arch (at T-2) and runs anteriorly to the C-7, T-1 junction.

The segmental arteries are paired branches off the dorsolateral surface of the dorsal aorta and run laterally between the somites and, in the thoracic region, between the ribs. The three intersomitic arteries to T-1 through T-3 are branches off the costo-cervical artery which is a branch of the vertebral artery. The connections between the origin of the segmentals off the dorsal aorta and this longitudinal vessel then break down leaving the vertebral artery coursing anteriorly from the subclavian and the anterior intercostal running posteriorly and supplying a "trunk" for the

segmental arteries T-1 to T-3. The segmentals between T-4 and T-5 to the final branches between S-1 and S-2 all originate directly from the dorsal aorta and run laterally between the somites (and ribs in the thoracic region) and terminate in the ventral body wall.

The nephric arteries now consist of six pairs of mesonephric arteries and a single pair of metanephric arteries. The first pair of mesonephric arteries not only serve the anterior-most aspect of the mesonephros but have now sent a branch to the developing suprarenal gland which is becoming a well-developed organ. The second pair of mesonephric arteries serves only the anterior part of the mesonephros. The next three pairs of mesonephric arteries supply only the mesonephros. The posterior-most mesonephric artery sends a branch into the posterior end of the gonad.

The iliac-umbilical arteries constitute a series of branches off the aortic trunk. The external iliac arteries branch off the base of the umbilical arteries approximately one-half a somite length posterior to the origin of the umbilicals. The circumflex iliac (ileolumbar) arteries are branches off the external iliac and continue laterally while the external iliac arteries run posterolaterally toward the hind limbs. The internal iliac arteries are a bilaterally symmetrical pair continuous posteriorly from the base of the umbilical arteries along the ventrolateral margin of the sacral vertebrae.

VEINS. A single pair of jugular veins run ventrolateral to the trachea from the head to the common cardinal veins. A new vessel, which consists of a single capillary, connects the left subclavian-jugular junction across the ventral surface of the trachea to the right anterior cardinal posterior to the subclavian-jugular junction. This vessel will soon expand to form the definitive innominate vein.

The anterior vena cava is the old right common cardinal vein and a relatively short section of the old right anterior cardinal. The anterior vena cava extends from the right atrium to the innominate-jugular-subclavian connection and is not noticeably changed from the condition noted at 39 days. The left anterior cardinal vein from the jugular-subclavian junction to the common cardinal is not noticeably smaller than the comparable vessel on the right as the innominate vein is not fully functional at this time.

The segmental veins of the thorax empty into the posterior cardinal veins. Segmentals of the lumbar region empty into a large complex -- the supra-subcardinal anastomosis. The mesonephric veins empty into the supracardinal vein and supra-subcardinal anastomosis. The metanephric (renal) veins are lateral extensions of the supra-subcardinal anastomosis at L-3.

The old posterior cardinal veins remain as the internal iliac veins which extend from the common iliac vein at L-6 into the pelvic cavity. The left common iliac vein forms a bridge between the two old post-cardinal veins at L-6 so connects left and right iliac complexes. The external iliacs join the common iliac near the posterior margin of the last lumbar vertebra. The caudal vein is a median posterior branch of the iliac complex.

The posterior vena cava is a continuous channel from the right atrium through the diaphragm, the liver, then caudally immediately ventral to the dorsal aorta into the right supra-subcardinal anastomosis. The supracardinal portion of the posterior vena cava receives the segmental veins of the lumbar region. The left supra-subcardinal vein is broadly connected to the posterior vena cava on the right, ventral to L-3 and L-4 by a broad subcardinal anastomosis, continues laterally with the metanephric venous sinuses.

VASCULARIZATION OF THE 50 - 51 DAY BOVINE EMBRYO

By 50 days, the heart is nearing its terminal position with the aortic outlet ventral to vertebra T-4, and the anterior tip of the aortic arch at the posterior margin of T-3 with subsequent elongation of the brachiocephalic trunk. The innominate vein is fully functional and both arteries and veins of the segmental thoracics are nearing the definitive state.

ARTERIES. The brachiocephalic trunk extends from the anterior tip of the ascending aorta, ventral to the posterior edge of centrum T-3, anteriorly to the middle of T-1 where it splits off the right subclavian artery (Fig. 7). At the anterior edge of T-1, the carotid trunk separates into left and right common carotid arteries which extend anteriorly along the ventrolateral aspect of the trachea to the angle of the jaw where each common carotid artery splits into internal and external carotid arteries. The left subclavian artery has moved up on the aortic arch until it appears to emerge from the left margin of the base of the brachiocephalic trunk at T-2 (Fig. 7).

Each subclavian artery sends a branch, the vertebral artery, anterodorsally with the main artery passing between vertebrae C-7 and T-1 into the transverse foramina of the cervical vertebrae. A lesser branch leaves the vertebral artery ventral to T-1 and runs posteriorly along the medial margin of the vertebrae T-1 through T-3 and supplies intercostal arteries T-1, T-2, and T-3 (Fig. 7). On the right side of one specimen, the tip of the anterior intercostal artery connected posteriorly into the segmental artery T-4.

Segmental arteries T-5 through S-1 arise directly from the dorsal aorta, with T-5 originating at the level of T-5, T-6 intervertebral disc, then running diagonally anteriorly to the T-4, T-5 intercostal space. Arteries T-6 and T-7 are less diagonal, T-9 through L-3 extend almost directly dorsolaterally, while L-5 through S-1 extend progressively more posteriorly (Fig. 7).

Mesonephric arteries have been reduced to five pairs, off the ventrolateral margin of the dorsal aorta ventral to vertebrae L-3, L-4, and L-5 (Figs. 6 & 7). On specimen 600-57, the anterior two arteries on the left side came off the dorsal aorta as a common trunk which separated almost immediately into two. The anterior artery supplies all the anterior lobe of the mesonephros; the second pair supplies the median narrow portion of the mesonephroi; the third and fourth pairs supply the posterior lobes of mesonephros; the last pair runs along the ventromedial margin of the mesonephros into the gonad. One gonadal artery in this group retained branches into the mesonephros while others supplied only the gonad.

Metanephric arteries, first seen in the 44 day embryos, are at this stage straight, single arteries on each side, arising from the lateral surface of the dorsal aorta near the middle of L-3 vertebra, and extending slightly anteriorly to the metanephric hilus where they branch throughout the metanephros. No branches to the adrenal glands were found at this stage. In one specimen, the left metanephric artery separated into two immediately outside the dorsal aorta.

Ventral aortic branches consisted of (1) phrenic, (2) celiac, (3) superior mesenteric, (4) accessory mesenteric, and (5) inferior mesenteric arteries. The phrenic artery arises from the ventromedial surface of the dorsal aorta at the diaphragm between T-13 and L-1 and runs ventrally into the developing diaphragm. The celiac artery is a single, relatively large vessel off the ventromedial surface of the dorsal aorta at L-1 and continues ventrally to the stomach, spleen and pancreatico-duodenal area. The superior mesenteric artery is one-half somite length posterior of the celiac, off the ventromedial surface of the aorta from where it continues ventrally along the developing gut, into the body stalk. The accessory mesenteric(s) consist of one or more small arteries off the ventral surface of the aorta which either join the superior mesenteric

or inferior mesenteric arteries or continue into the mesenteries. The inferior mesenteric artery arises off the aorta at L-5 and courses posteroventrally to the colon where it divides into anterior and posterior branches.

The umbilical arteries arise ventral to the last lumbar vertebra (L-5 or L-6 as the case may be) as a bifurcation of the dorsal aorta and proceed caudally to S-1 where they then curve ventrally along the body wall to exit via the umbilical cord. The internal iliac arteries are posterior continuations of the umbilical arteries and continue from S-1 posteriorly ventrolateral to the sacral vertebrae. The external iliac artery comes off the lateral margin of the dorsal aorta at L-5 and continue diagonally ventrolaterally into the leg. The circumflex iliacs arise off the anterior surface of the external iliac arteries a short distance from their origins and course laterally to the body wall.

VEINS. The anterior vena cava consists of a short segment of vein from the junction of the innominate and right brachiocephalic veins at T-2 posteriorly to its opening into the sinus venosus at T-4. Anterior to the innominate junction is a short segment of brachiocephalic vein, between the junction of right subclavian and right jugular vein which continues anteriorly to the head. The right subclavian vein joins the jugular vein at T-1 so the right brachiocephalic vein is about the equivalent of one vertebra in length.

The azygous vein empties into the lower portion of the anterior vena cava between T-3 and T-4 and extends posteriorly receiving segmental veins from T-4 through T-12 on the right side. The hemiazygous vein maintains this connection with the left jugular-innominate connection at C-7, T-1 but empties primarily through the old left common cardinal vein into the coronary sinus. It extends posteriorly receiving segmental veins to T-4 through T-12 on the left side. Segmental veins to T-1 through T-3 are drained by the anterior intercostal vein which originates from the vertebral vein at C-7, T-1 on both sides. The

vertebral veins arise from the subclavian veins and run cranially to the head within the transverse foramina of the cervical vertebra which have formed.

The five mesonephric veins present all enter into the renal portion of the post cava between L-3 and L-4. The metanephric veins coalesce within the hilus of the kidney and run medially into the condensing post cava at L-3. In embryo 600-57, the adrenal veins of the two sides have different attachments. The left adrenal vein originates within the anterior lobe of the mesonephros, expands into a large central sinus within the adrenal gland, then opens into the anterior aspect of the left renal complex at L-3. The right adrenal vein extends from the mesonephros between T-13 and L-1 and extends through the adrenal gland directly into the post cava at L-1, L-2 (Fig. 10).

The right external iliac vein opens into the right and left remnants of the supra-subcardinal anastomosis at L-5; the left one opens into the posterior remnant of the left supra-subcardinal veins, joins the internal iliac vein and crosses the midline into the posterior end of the right supra-subcardinal anastomosis at the posterior end of the dorsal aorta, between the caudal artery and umbilical arteries. The circumflex iliac vein branches off the external iliac vein immediately lateral to the last lumbar and extends craniolaterally within the body wall. The internal iliac veins are remnants of the old post cardinal veins and extend from the common iliacs at L-6 posteriorly lateral to the center line.

The posterior vena cava extends from the opening of the right atrium at T-4 posteriorly as the "thoracic" vena cava, through the liver, running on the the ventromedial surface of the dorsal aorta to the iliac vein complex at L-6. The entire length of the post cava is well established and requires only a firming up and smoothing of the walls to attain the definitive configuration.

VASCULARIZATION OF THE 58 - 60 DAY BOVINE EMBRYO

The principle changes between 50 and 60 days involve the degeneration of mesonephros and dominance of metanephros. Other changes are relative and not basic.

ARTERIES. The dorsal aorta extends from its origin at the exit of the left ventricle, continues as the aortic arch at T-3 and then posteriorly to L-5 or L-6 where the umbilicals exit. Branches are essentially those found in the adult (Fig. 15).

The brachio-carotid complex consists of the carotids and subclavians with the right and left common carotid arteries and the right subclavian artery branching off the brachiocephalic artery at T-1, the carotids extending from the apex of the brachiocephalic at T-1 along the throat on either side of the trachea to the head. The left subclavian artery has moved well up the brachiocephalic trunk and now emerges at the level of T-2, about half way between the anterior tip of the arch and the carotid bifurcation. Each subclavian extends laterally to the forelimb and sends off two branches: 1) the vertebral trunk which separates in the C-7, T-1 groove into the vertebral artery anteriorly and the anterior intercostal posteriorly; and 2) the cervical artery which supplies most of the muscles of the neck.

The anterior intercostal artery extends caudad providing intersomitic arteries T-1 through T-3. Segmental arteries branch off the dorsal aorta at regular intervals to each intersomitic region from T-4 through S-2. The first lumbar segmental artery has a branch to the anterior aspect of the adrenal gland.

The mesonephros is present only as a small degenerating structure. Although there are still three pairs of arteries supplying the mesonephros, they follow the mesonephros in degeneration and disappear between 60 and 65 days. The last mesonephric artery off the dorsal aorta (L-4) passes along the ventromedial

border of the mesonephros and runs directly to the gonad which it serves, now as the ovarian or spermatic artery. The renal artery leaves the dorsal aorta at L-3 and is much larger than the mesonephric arteries. A branch to the adrenal gland is present off the anterior surface of the renal artery.

The celiac artery is a large, single vessel off the dorsal aorta at L-1 and extends to the stomach and associated structures. The superior mesenteric is one-half somite length posterior to the celiac artery. This vessel supplies the intestines. The inferior mesenteric artery branches off the ventromedial surface of the dorsal aorta ventral to L-5 and supplies the descending colon and lower colon. No accessory mesenteric arteries were found in four fetuses 56 to 61 days gestation.

The iliac-umbilical complex consists of the paired umbilical arteries, internal iliac arteries, external iliac arteries and circumflex iliac (ileo-lumbar) arteries. The internal iliac arteries continue posteriorly from the umbilical arteries at the point at which they begin their turn to the umbilical cord which is at S-1. The external iliac arteries branch off the lateral aspect of the dorsal aorta one somite anterior to the origin of the umbilical arteries. The circumflex iliac arteries branch off the external iliacs and run laterally in the body wall at L-4 to L-5.

VEINS. The anterior vena cava extends from the connection of the innominate artery at T-1 to the right atrium. The right brachiocephalic vein extends anteriorly from the connection of the innominate vein to the region of C-7 where it splits into right subclavian and jugular veins. The innominate vein extends from the left jugular-subclavian vein junction at C-7 diagonally to the base of the right brachiocephalic vein of the jugular vein and the left subclavian at T-1. The left jugular vein extends from the innominate vein anteriorly

on the mediolateral surface of the throat. Subclavian veins have vertebral, anterior intercostal, and cervical branches that exactly parallel the comparable arteries.

The nephric veins anastomose into the condensing supra- and subcardinal sinuses. The metanephric (renal) vein is a relatively larger vessel from the renal portion of the post cava at L-3 to the hilus of the kidney. The mesonephric, adrenal and gonadal veins all empty into this anatomosis on the left, but the right adrenal vein opens separately into the post cava slightly anterior to the adrenal vein.

The segmental veins of T-4 through T-12 empty into the hemiazygous and azygous veins on the left and right sides, respectively. The azygous vein connects into the posterior portion of the anterior vena cava at T-3, while the hemiazygous vein in all four specimens at my disposal continued to empty into the coronary sinus. The segmental veins to the lower body, T-13 to S-1 or S-2, connect into the supra-subcardinal anastomosis.

The iliac complex of veins parallels that of the arteries except there are no umbilical veins in the complex. The iliac vein complex is the remnant of the old sub-supra-post cardinal anastomosis into which the external iliac veins open laterally at the level of L-6, the internal iliac veins open into the posterior surface immediately lateral to the L-6, S-1 joint, and a small caudal vein empties into the medial posterior terminal.

DISCUSSION

At 40 days gestation, the dorsal aorta is a single, comparatively large artery originating at the anterior point of the curve of the aortic arch at C-7 or T-1. It continues posteriorly along the dorsal body wall to the bifurcation of the umbilical-iliac complex at L-5 or L-6. The caudal artery is a single vessel extending from the dorsal surface of the aorta at L-5. It is not clear if the caudal artery is a direct continuation of the dorsal aorta or if it is a new, medial artery as it appears to be. As the embryo develops, the only change in position which occurs in the dorsal aorta is a caudal movement of the anterior end due to the caudal migration of the heart. Such posterior movement was described for the human by Barry (1951) and explained as resulting from differential growth. From the uppermost position at C-7 at 40 days, the anterior end of the dorsal aorta migrates to T-2 at 60 days and increases in diameter from 285 mu at 40 days to 365 mu at 60 days. No other significant changes of the dorsal aorta occur after 40 days.

The brachio-carotid complex in the 40 day embryo consists of paired common carotid arteries and subclavian arteries. All these vessels exit directly from aortic arch. The base of the right subclavian is formed from the right fourth aortic arch which extends anteriorly to C-7. The radix aorta degenerates below the junction of the right subclavian and fourth aortic arch leaving the subclavian artery as the sole recipient of blood from this arch. The carotid arteries bifurcate from the carotid trunk at the level of C-6. The left subclavian artery leaves the left upper curve of the aortic arch at C-7. The carotid arteries elongate with the downward migration of the heart and the left subclavian artery migrates anteriorly around the aortic arch and along the carotid trunk, resulting in a common channel, the brachiocephalic trunk, from the anterior curve of the aortic to the left subclavian artery about half way

up the trunk, then the right subclavian is given off at T-1 and a common carotid trunk about one vertebra length long bifurcates into the two common carotid arteries ventral to C-7. The elongation of the carotids and shift of the left subclavian artery anteriorly has been previously noted but no attempt has been made to analyze the process or even to develop age relationships.

The segmental (intersomitic) arteries at 40 days are paired branches off the dorsal aorta from T-4 through S-1. The anterior intercostal arteries serve T-1 through T-3 as the segmental arteries from the dorsal aorta in that region degenerate between 35 and 40 days. The segmental arteries from T-4 through the lumbar region are direct branches off the dorsal aorta. The segmentals to S-1 and S-2 are branches of either the dorsal aorta or the umbilical arteries. Between 51 and 55 days, a branch develops off segmental arteries L-1 which supply the adrenal glands. The dorsal aorta elongates a little slower than does the body so the bases of the anterior thoracic arteries are pulled posteriorly while the posterior lumbar and sacrals are pulled anteriorly (Fig. 6).

The umbilical arteries formed with the external iliac arteries from the dorsal aorta at L-4 or L-5. The internal iliac artery branches off the posterior dorsal curve of the umbilical artery and continues to the pelvic region. The external iliac artery by day 45 appears as a branch off the dorsal aorta at the anterior lateral margin of the junction of the umbilical artery and the dorsal aorta, and progressively separates from the umbilical artery until by 60 days the two are separate by about one vertebra length.

There are no major changes between day 40 and day 60 in the celiac artery which originated as a new outgrowth from the dorsal aorta ventral to the thoraco-lumbar intervertebral arteries (Byrnes, 1973). The superior mesenteric artery, the remnant of the original vitelline arteries, supply blood to the intestine and leaves the dorsal aorta about one-half somite length posterior to the celiac artery. The inferior mesenteric is a new median branch off the dorsal aorta

immediately anterior to the umbilical arteries (Byrnes, 1973), supplies the hindgut, and undergoes no change in position throughout life except with the slight anterior movement of the end of the dorsal aorta. Accessory mesenteric arteries between the superior and inferior mesenteric arteries were irregular in number, appearance and disappearance. They varied from none to four in the embryos 40 to 50 days old. None were found before 40 days nor after 55 days. These accessory arteries must be considered as new derivatives from the dorsal aorta and not remnants of vitelline arteries as has been assumed (Patten, 1943).

The 11 mesonephric arteries present at 40 days are the remnants of the 20± present at the peak of mesonephric function about day 35. Between 40 and 50 days, all mesonephric arteries anterior to the metanephric arteries disappear so that by 50 days the anterior-most of the mesonephric arteries leaves the dorsal aorta immediately posterior to the metanephric artery, runs anterolaterally past the base of the metanephros and supplies that part of the mesonephros anterior to the hilus of the metanephros. The next three arise irregularly from the ventrolateral margin of the dorsal aorta and supply the large posterior lobe of the mesonephros. The posterior "mesonephric artery" follows the margin of the mesonephros laterally and anteriorly and terminates in the gonadal ridge. By 51 days all branches of the gonadal artery to the mesonephros have degenerated; henceforth it is the ovarian or the spermatic artery. All these vessels except the gonadal artery degenerate by 60 days with the demise of the mesonephros. These observations conflict rather drastically with the general concept that the mesonephric arteries remain as the arteries of other organs of the region (Arey, 1968). The metanephric arteries which up until now were believed to be derived from the mesonephric arteries (Patten, 1968) are entirely separate from the mesonephric arteries and originate as outgrowing vessels from the dorsal aorta at L-3 about 43 days. At 55 days there is a branch off the renal artery which supplies the adrenal gland and persists thereafter as the main adrenal artery.

VEINS. At 40 days, the veins of the anterior thorax consist of the paired jugular veins, the old anterior cardinal veins, paired common cardinal vein, and subclavian veins (Byrnes, 1973). The left common cardinal vein is reduced by 55 days to form the coronary sinus opening into the sinus venosus caudomedially to the orifice of the right common cardinal vein but maintains connection with the postcardinal (hemiazygous) vein, in contrast to total separation in most other mammals (Patten, 1968). The right and left subclavian veins form at C-7. The innominate vein makes its appearance at 45 days as a single capillary connecting between the left subclavian-jugular connection across the ventral surface of the trachea to the anterior cardinal vein slightly posterior to the right subclavian-jugular connection. The innominate vein expands and by 50 days has shunted most of the blood flow of the left jugular-subclavian veins to the anterior vena cava with subsequent degeneration of the anterior cardinal connection to the left common cardinal vein. The hemiazygous and azygous veins are each formed from two remnants: the basal segments are the old post cardinal veins; from T-8 posteriorly they are supracardinal veins only, with the postcardinal disappearing by 45 days and the subcardinal postion gone by 50 days (Fig. 9). At 40 days, both of these vessels join the common cardinal veins in the standard embryonic pattern (Fig. 3). At 51 days, the left anterior cardinal vein between the left common cardinal vein and the innominate vein is drastically reduced and closes completely by 55 days, but the hemiazygous vein continues to utilize the common cardinal so opens into the coronary sinus and thence into the right atrium (Fig. 9). There is no cross-connection between the azygous vein and hemiazygous vein in any series of sections or dissections studied. No reference was found describing the continuity of the azygous vein with the left common cardinal vein. The implication has been that the left common cardinal breaks between the coronary sinus and the postcardinal, leaving the hemiazygous to drain into the azygous as

it does in the human. The azygous vein joins the anterior vena cava near the connection of the post cava and right atrium. The hemiazygous and azygous veins drain the segmental veins on their respective sides from T-4 through T-12. The anterior intercostal vein is a branch of the vertebral vein and drains the intercostal segmental veins T-1 through T-3. The lumbar segmental veins connect into the supracardinal veins on each side. As the supracardinals degenerate the segmentals join the post cava where they remain in their final form. At 50 days the azygous enters the anterior vena cava T-3 while the hemiazygous enters the coronary sinus at T-5. These veins remain in this definitive configuration.

At 40 days, the mesonephric arteries join the supracardinal veins at intervals from T-8 to L-5. As the posterior vena cava reaches its definitive configuration and with the degeneration of the mesonephros by day 60, the mesonephric veins degenerate. The metanephric veins at 40 days consist of a plexus of sub-subcardinal anastomoses which join the supracardinal veins on each side. By 50 days this plexus has condensed, leaving a large sinus, the future renal vein, to each kidney. The sub-subcardinal anastomosis remains between the left renal and the right sub-supra-subcardinal anastomosis directly to the left of the area where the right renal connects with the right supracardinal (L-3, L-4). The left renal vein complex becomes disconnected from the left supra-post cardinal complex before 40 days (Fig. 3) and is maintained independently as the mesonephros and mesonephric veins degenerate. The changes in the metanephric venous complex in the bovine are comparable to those described for the human (Patten, 1968). The posterior cardinal veins are still functional at 40 days as the internal iliac veins, and receive the external iliac veins and segmental veins from the lumbar and sacral regions. As the complex of veins on the right side coalesces to form the post cava, the sub-subcardinal anastomosis remains at the lower end (L-5 to L-6) and provides a cross-connection between the two iliac complexes as

it does in the renal portion. Definitive iliac veins are formed by condensation of the iliac sinus and smoothing of the walls.

The posterior vena cava is a compound vessel resulting primarily from the consecutive fusion of embryonic sinuses. The anterior-most segment of the posterior vena cava, the thoracic vena cava, evident at 35 days, results from a stretching of the sinus venosus as the liver is pressed caudally by the shifting heart (Byrnes, 1973). The hepatic portion is formed partly from the old ductus venosus and partly by a coalescence of sinusoids, in the right dorsal lobe, and as the liver is pressed caudally the portion of liver containing this sinus is brought into contact with the median surface of the supra-subcardinal sinus, fuses with it, and the intervening walls break down, forming a continuous channel throughout the post-supracardinal anastomosis.

The renal segment of the post cava is the right supra-subcardinal sinus from T-13 through L-3 with the definitive segment primarily subcardinal after the supracardinal portion degenerates with the demise of the mesonephros. The posterior end of the post cava (L-4, L-5) is formed by cross connections between the posterior portions of the right and left subcardinal veins, which in turn are anastomosed through the supracardinal veins to the post cardinal veins, thence with the iliac veins.

These observations on postcardinal development compare fairly well with the descriptions given by Warwick and Williams (1973) on the human, except that (1) in the bovine, a large hepatic sinus breaks through a thinned intervening membrane into the subcardinal sinus rather than by a "new formation which connects the right subcardinal and the common hepatic veins"; (2) in the bovine there are originally several interconnections between the posterior ends of the subcardinal veins which coalesce rather than the "oblique transverse anastomosis between the iliac veins" (Warwick and Williams, p. 165, 1973); and (3) supracardinal veins are totally independent of the post cava, receive segmental veins and become azygous and hemiazygous veins.

At about 60 days the mesonephros totally disappears, and with it, the mesonephric arteries and veins also disappear, leaving only the gonadal arteries and veins, not "vessels that supply the organs of the lumbar region" (Patten, 1968). All other vessels reached their definitive condition by 55 days, and henceforth to birth, the major blood vessels can be well illustrated by any fetus over 65 days gestation. A 157 day fetus, which appeared to be typical in all respects (Fig. 16) was used repeatedly for comparisons, relationships, and general anatomy.

ACKNOWLEDGEMENTS

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ILLUSTRATIONS

ABBREVIATIONS FOR FIGURES 1, 2, and 3.

AA = aortic arch
AdV = adrenal vein
AIA = anterior intercostal artery
AMA = anterior mesenteric artery
AT = aortic trunk
AzV = azygous vein
CA = caudal artery
CCA = common carotid artery
CeA = celiac artery
CJV = common jugular vein
DA = dorsal aorta
DAr = ductus arteriosus
DV = ductus venosus
ECA = external carotid artery
EIA = external iliac artery
EIV = external iliac vein
EJV = external jugular vein
HAV = hemiazygous vein
HPV = hepatic portal vein
HV = hepatic vein
HVC = hepatic vena cava
IcA = intercostal artery
ICA = internal carotid artery
IcV = intercostal vein
IIA = internal iliac artery
IIV = internal iliac vein
IJV = internal jugular vein
LCC = left common carotid artery
Li = liver
LRV = left renal vein
LScV = left subclavian vein
LSCV = left supracardinal vein
MA = mesonephric artery
Me = mesonephros
MT = metanephros
PA = pulmonary artery
PMA = posterior mesenteric artery
PT = pulmonary trunk
PVC = posterior vena cava
RA = renal artery
RCC = right common carotid artery
REIV = right external iliac artery
RRV = right renal vein
RtA = right atrium
RVe = right ventricle
RVC = renal vena cava
ScA = subclavian artery
ScV = subclavian vein
SU = subcardinal vein
SV = sinus venosus
TV = truncus venosus
UA = umbilical artery
UV = umbilical vein
VeA = vertebral artery
VeV = vertebral vein

EXPLANATION OF FIGURES

1. Reconstruction of a 39 day embryo (#163), was made by microprojection outline drawings of sections, beginning with a median sagittal section and working out laterally to the right. The composite drawing shows the major circulation at the end of 39 days development. 15x.

2. The arterial system of a 39 day embryo (#163) in a ventral view reconstruction from the parasagittal microprojections used in figure 1. Subclavian and carotid arteries leave the aortic arch independently. The anterior-most intercostal artery arising directly from the dorsal aorta is T-5 near the anterior edge of vertebra T-7. There are yet 11 pair of mesonephrics arteries (MeA - 1-11) with 5 pairs in the thoracic region. Renal arteries (RA) are established as lateral branches from the dorsal aorta slightly ventral to the exit of segmental artery L-3. 15x.

3. The venous system of a 39 day embryo (#163) in a ventral view reconstruction from the parasagittal microprojections used in figure 1. There is no indication of an innominate vein although the anterior cardinal on the right is much more expanded than that on the left. The azygous and hemiazygous veins (AzV and HAV) are well established as combination of the original posterior cardinal with the supracardinal in the thoracic region, while a remnant of the subcardinal vein (SV) continue to drain the anterior part of the mesonephros. Renal veins (RRV and LRV) are well established from the old subcardinal veins while the left supracardinal (LSCV) as a separate entity, draining posteriorly, receives the left lumbar segmental veins. The iliac vein complex is condensing from the original posterior cardinal-supracardinal-subcardinal anastomosis.

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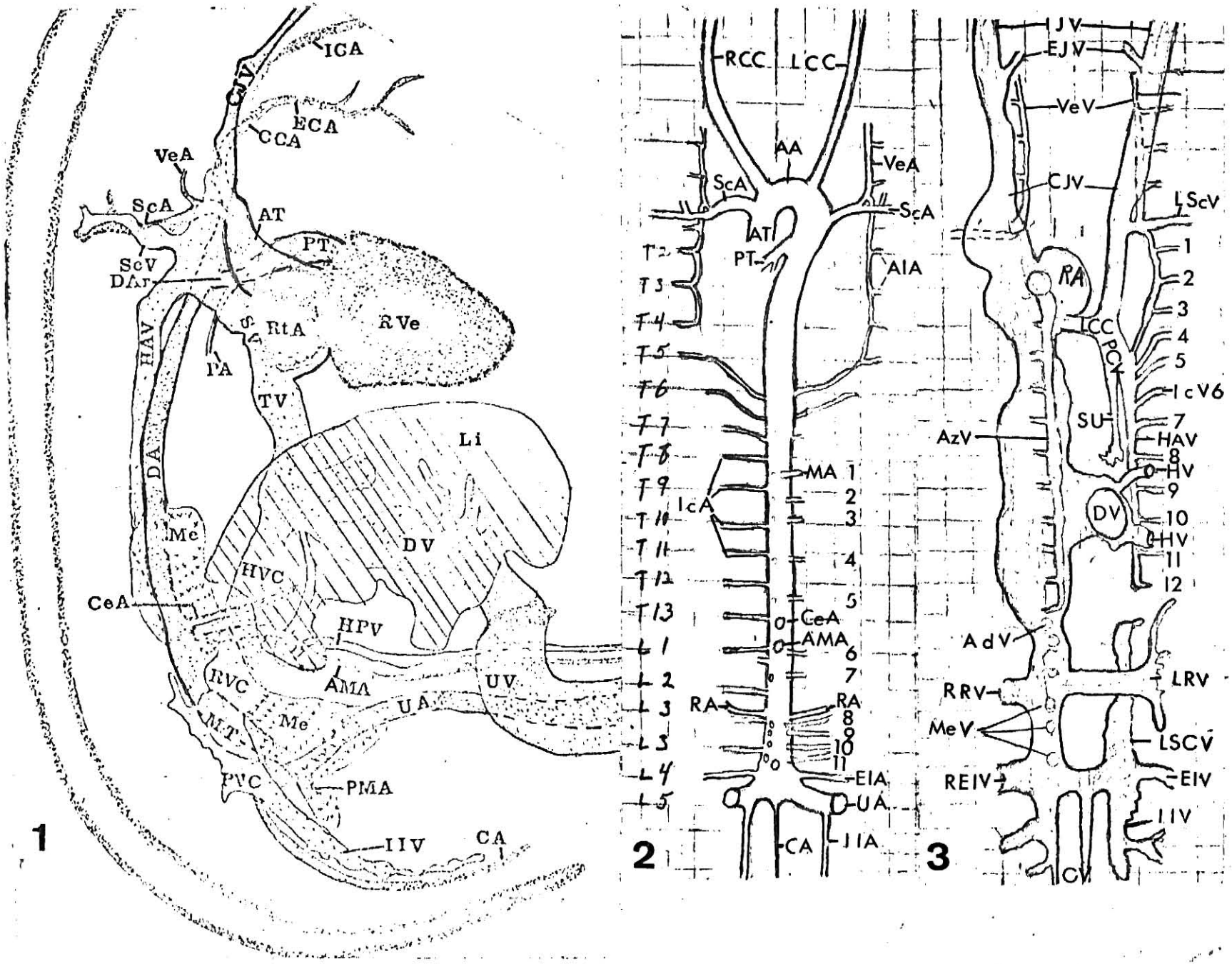
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EXPLANATION OF FIGURE 4

Reconstruction of a 45 day embryo (#583-1) in lateral view of the arterial system made in the same manner as Figure 1. The phrenic artery has formed and the mesonephric arteries have been reduced to five pair. 15 X.

Additional abbreviations.

BCT = brachiocephalic trunk

MeA = mesonephric arteries

PhA = phrenic artery

EXPLANATION OF FIGURE 5

Reconstruction of the venous system of a 45 day embryo (#583-1) in lateral view made in the same manner as Figure 1. The azygous vein has become distinct as receptor of the intercostal veins. The posterior vena cava in the lumbar region is a big, irregular sinus, receiving the complex of mesonephric veins, segmental veins, and iliac veins. 15 X.

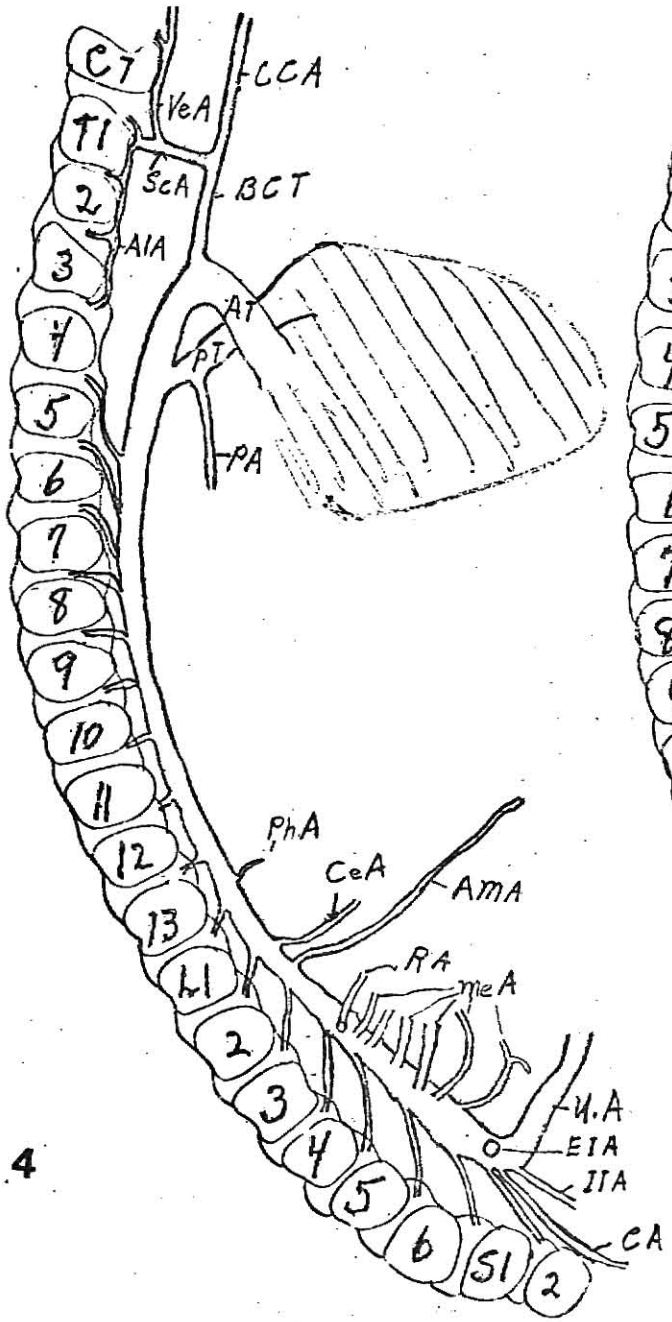
Additional abbreviations.

JV = jugular vein

AVC = anterior vena cava

TVC = thoracic vena cava

MeC = mesonephric veins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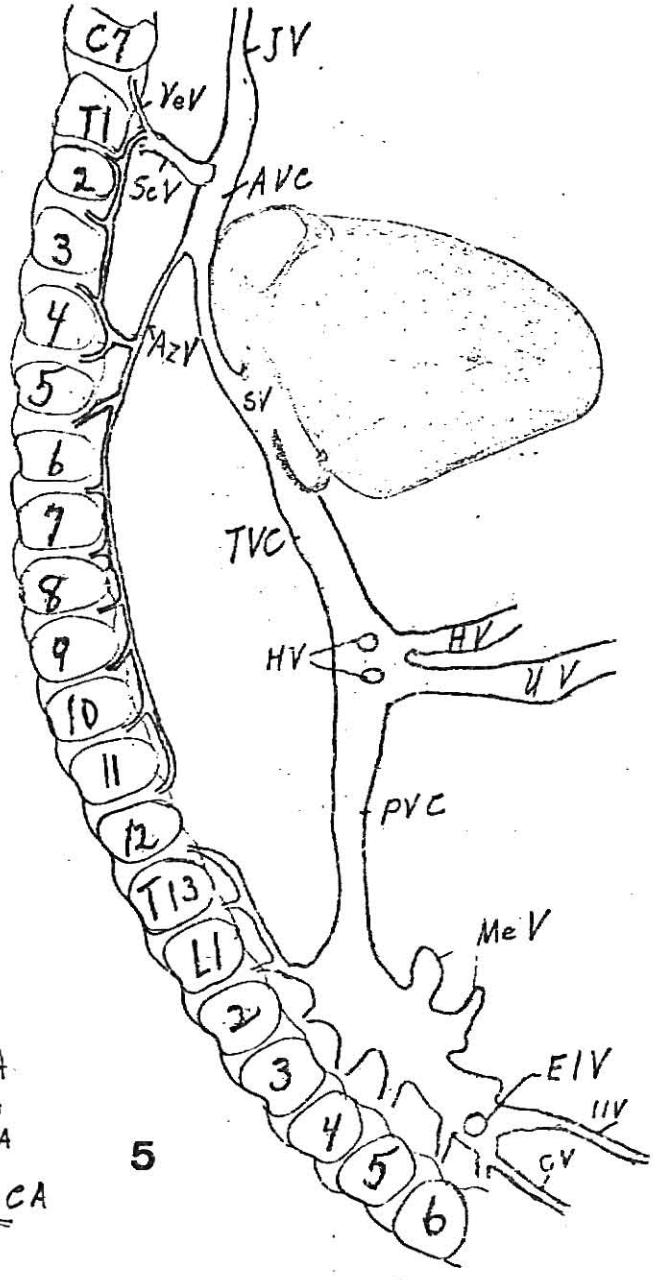
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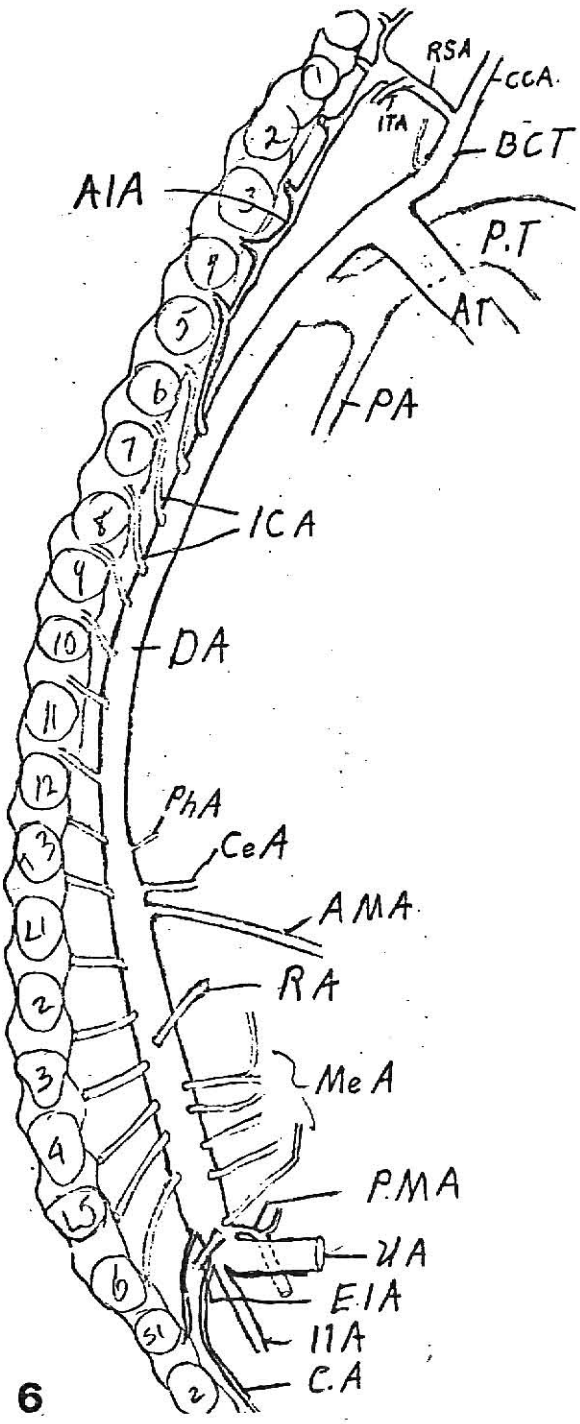
EXPLANATION OF FIGURES

6. Reconstruction of the arterial system of a 51 day embryo (600-57) in lateral view made in the same manner as Figure 1. The brachiocephalic trunk (BCT) has undergone distinct elongations; and a middorsal esophageal artery (EA) has formed from the BCT about half a somite length anterior to the aortic trunk. Otherwise there is little change since 45 days. 15x.

7. Ventral veiw reconstruction of the arterial system of a 51 day embryo (#600-57) prepared in the same manner as Figures 2 and 3. 15x. Medial ventral arteries are phrenic (PhA) at T-12, Celiac (CeA) at T-12, 13 anterior and posterior mesenteric (PMA) at L-5. Segmental arteries arise dorso-laterally from the dorsal aorta from T-6 to L-6, while mesonephric arteries (M-1 to 5) arise ventrolaterally only from L-2 to L-4.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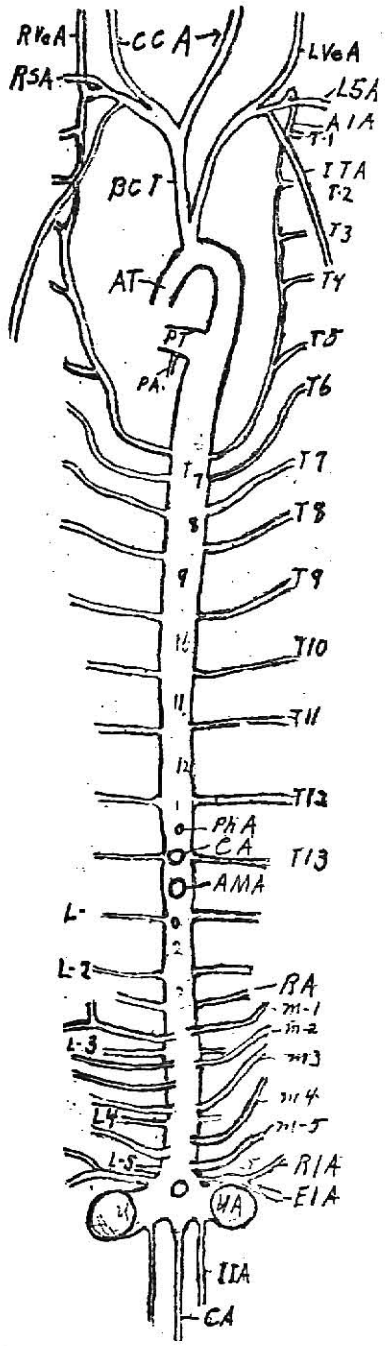
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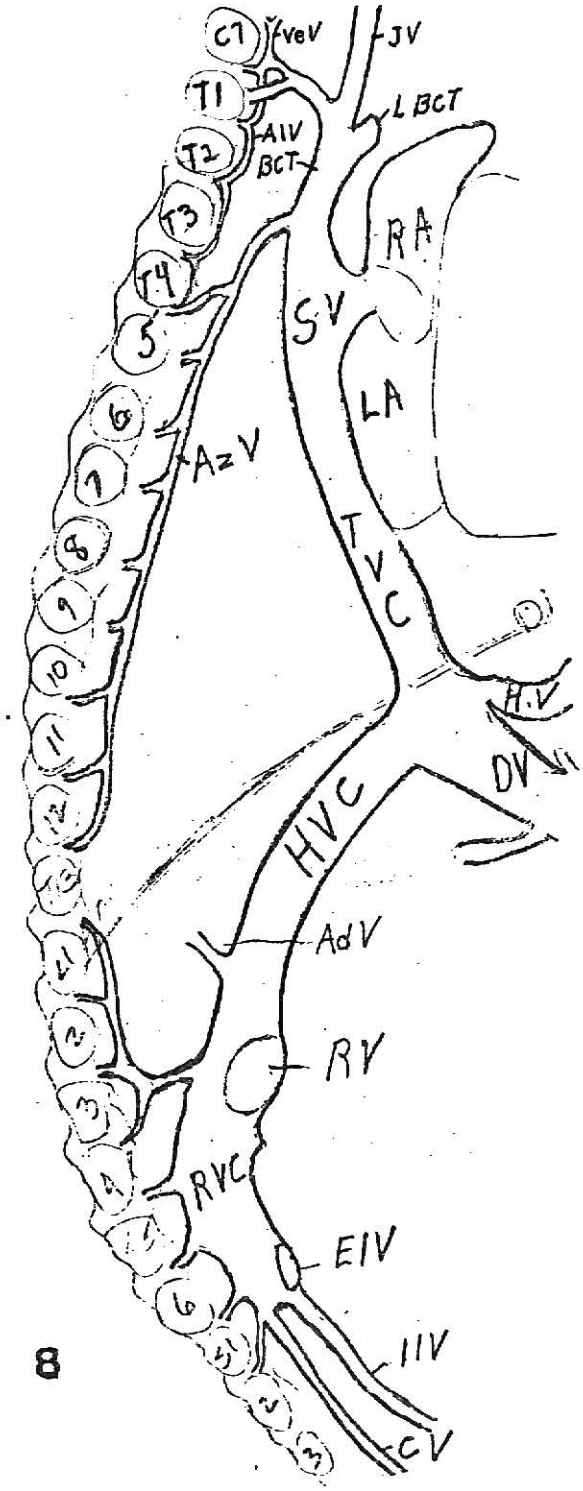
EXPLANATION OF FIGURES

8. Reconstruction of the venous system of a 51 day embryo (#600-57) in lateral view made in the same manner as Figure 1. There is no real change since the 45 day stage. 15x.

9. Ventral view reconstruction of the venous system of a 51 day embryo (#600-5 (#600-57), prepared in the same manner as Figures 2 and 3. The innominate vein (InV) and anterior vena cava (AVC) are well established, azygous (AzV) and hemiazygous (HAV) veins have reached definitive relations from T-4 to T-12 and the left anterior cardinal vein (LACV) between subclavian vein (LScV) and left common cardinal vein (LCCV) has begun decrease. The anterior intercostal veins (AIV) are established on both sides. The metanephric, now renal veins (RRV & LRV) dominate the lumbar drainage, although remnants of the old supra-cardinal veins (ASCV and LSCV) remain on both sides, receiving the lumbar segmental veins and remnants of the mesonephric veins. The right adrenal vein (PAdV) and remnants of the anterior mesonephric drainage empty directly into the posterior vena cava (PVC) while the left adrenal vein (LAdV) and associated mesonephric veins (AMeV) empty into the left renal vein (LRV). 15x.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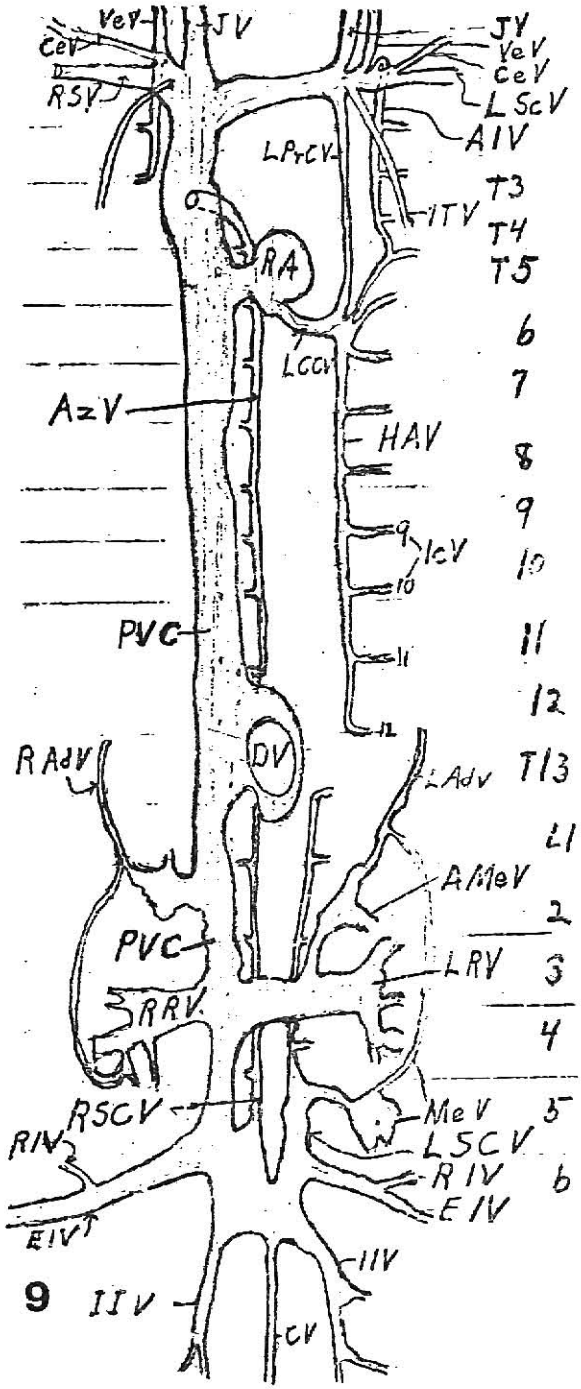
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EXPLANATION OF FIGURE 10

Sagittal section through a 38 day embryo (#620-6) showing the post cava from the area of the heart to the adrenal (Ad). The thoracic vena cava (TVC) is interpreted to be formed by elongation of the sinus venosus (SV) between the heart and the diaphragm (Di). The hepatic vena cava (HVC) is directly continuous with the renal vena cava (RVC) as the liver (Li) is directly continuous with the adrenal gland (Ad) medially and the mesonephros laterally, thus alleviating the necessity of hypothesizing a trans-abdominal growth between hepatic and renal segments of the post cava. 30x.

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RVC
HVC
LS
Li
PeC
Li
TVC
SV
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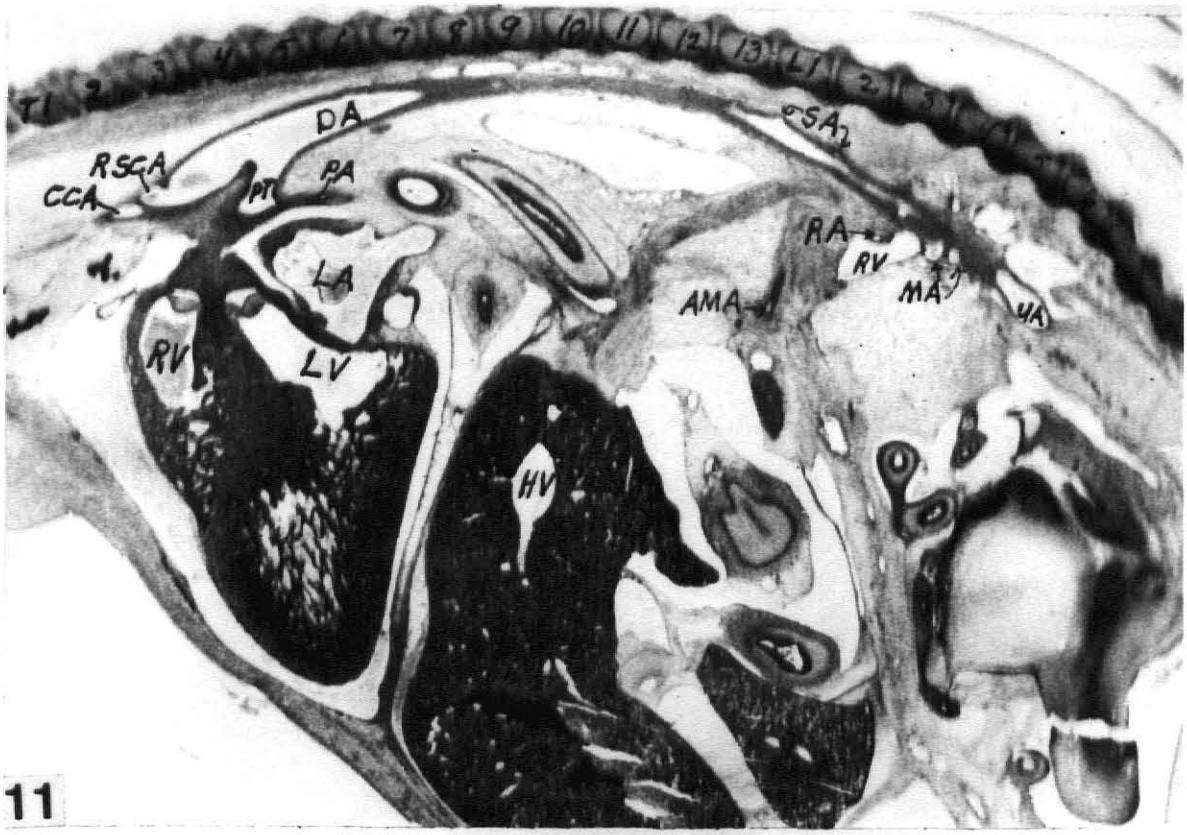
EXPLANATION OF FIGURES

11. Parasagittal section of the 51 day embryo (#600-57) showing the connection of the common carotid artery (CCA) and right subclavian artery (RScA) with the aortic arch. The pulmonary trunk (PT) is continuous with the dorsal aorta (DA) and the pulmonary artery (PA) is seen as a continuation of the pulmonary trunk. The dorsal aorta (DA) continues posteriorly to the umbilical artery (UA) between L-5 and L-6 and sends off branches dorsolaterally as segmental arteries (SA).

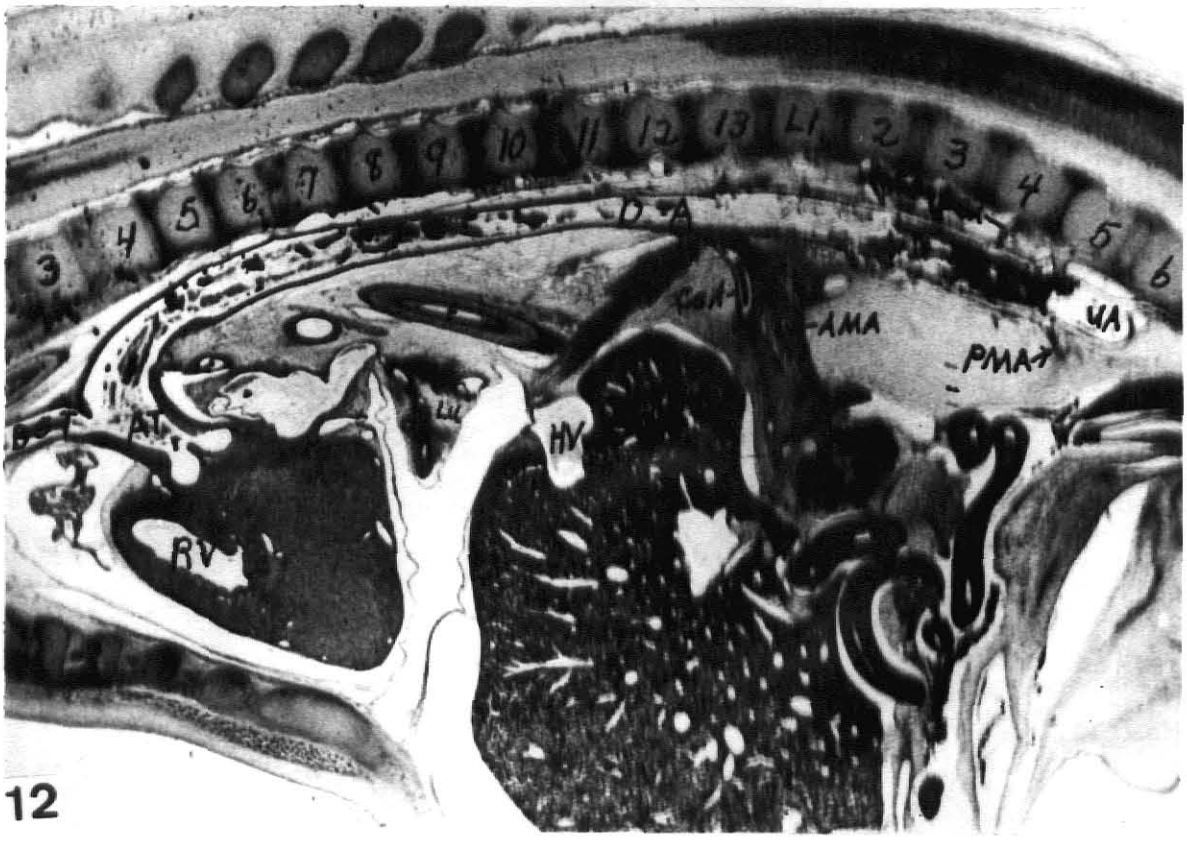
12. Sagittal section of the 48 day embryo (#600-56) showing the brachiocephalic trunk (BCT) and dorsal aorta (DA) from the aortic trunk (AT). The dorsal aorta continues posteriorly to the umbilical artery between L-5 and L-6 and sends branches dorsolaterally as the segmental arteries (SA). The celiac artery (CeA) and anterior mesenteric artery (AMA) are seen about to enter into the dorsal aorta at T-12 and T-13 respectively. The posterior mesenteric artery (PMA) opens into the dorsal aorta at L-5.

THIS BOOK CONTAINS NUMEROUS PAGES WITH PICTURES THAT ARE CROOKED COMPARED TO THE REST OF THE INFORMATION ON THE PAGE.

THIS IS AS RECEIVED FROM CUSTOMER.


T1 2 3 4 5 6 7 8 9 10 11 12 13 L1 2 3
DA
RSCA
CCA
PT
PA
LA
RV
LV
HV
SA
RA
RV
MA
AMA
UA

11

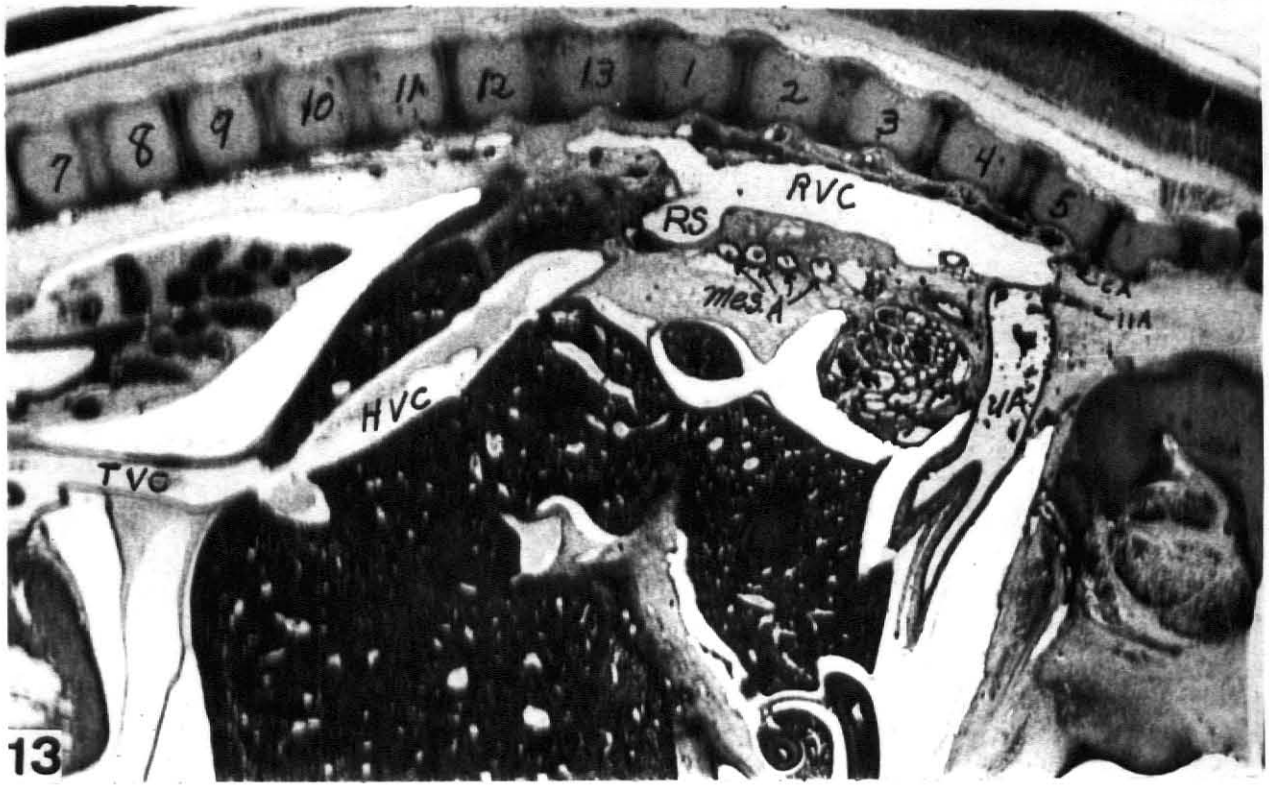

3 4 5 6 7 8 9 10 11 12 13 L1 2 3 4 5 6
DA
CoA
AMA
UA
PMA
AT
LV
HV
RV

12

EXPLANATION OF FIGURES

13. Parasagittal section of a 48 day embryo (#600-56) showing almost the entire posterior vena cava. The thoracic vena cava (TVC) continues posteriorly to the liver and then as the hepatic vena cava (HVC) posteriorly to the renal vena cava (RVC) and finally terminates at the iliac complex at L-5.

14. Parasagittal section of the 51 day embryo (#600-57) showing the vertebral vein (VV) and the common jugular vein (CJV) entering the anterior vena cava (AVC) at T-1. The section is so far lateral that none of the post caval system is involved. Posteriorly, only the external iliac vein (EIV), renal vein (RV), and part of the mesonephric arteries (MeA) were cut.


7
8
9
10
11
12
13
1
2
3
4
5
RS
RVC
Mes.A
HVC
TVC
UA

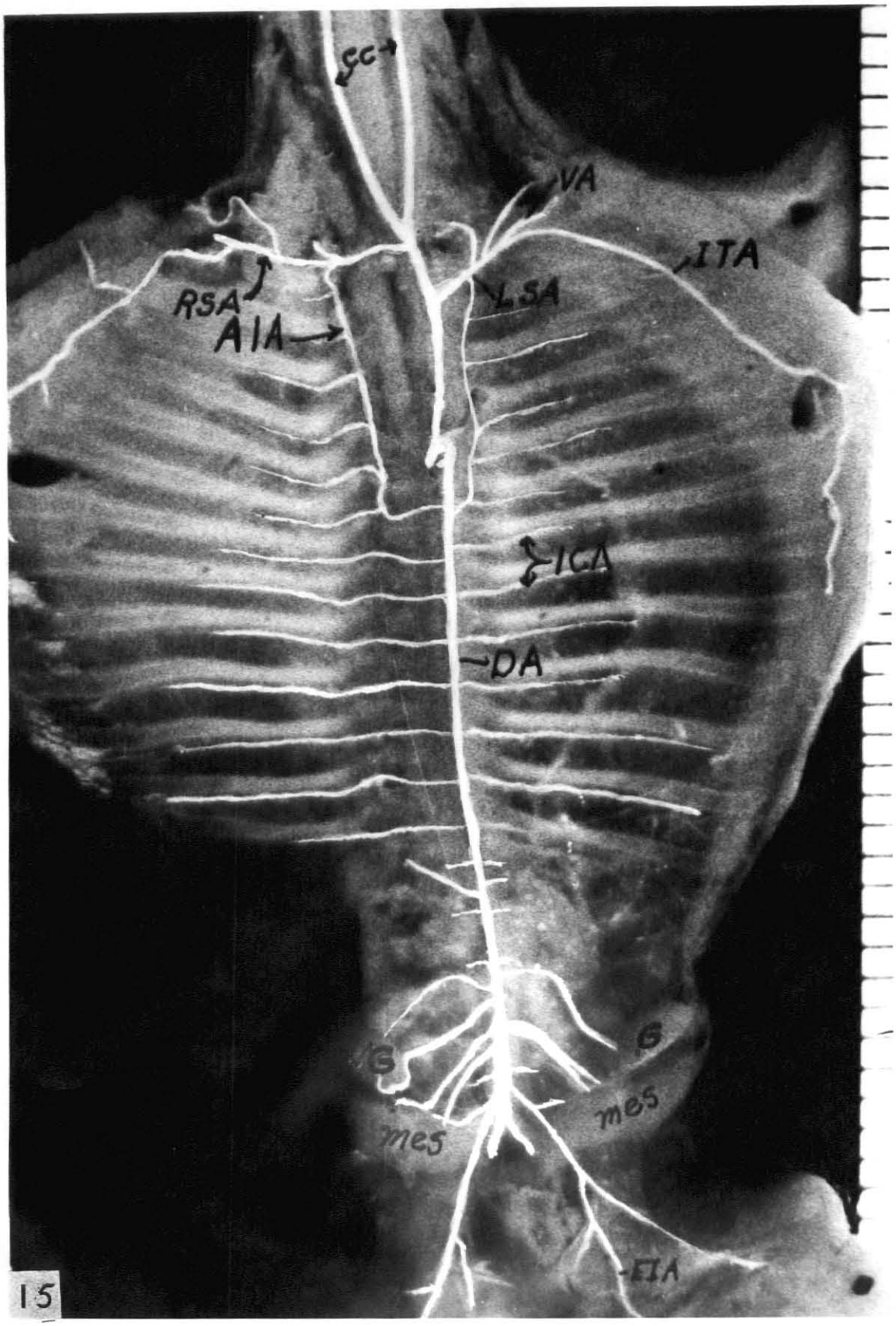
13


Mes
Lung
AVC
RA
RV
LV
HV
EIV

14

EXPLANATION OF FIGURE 15

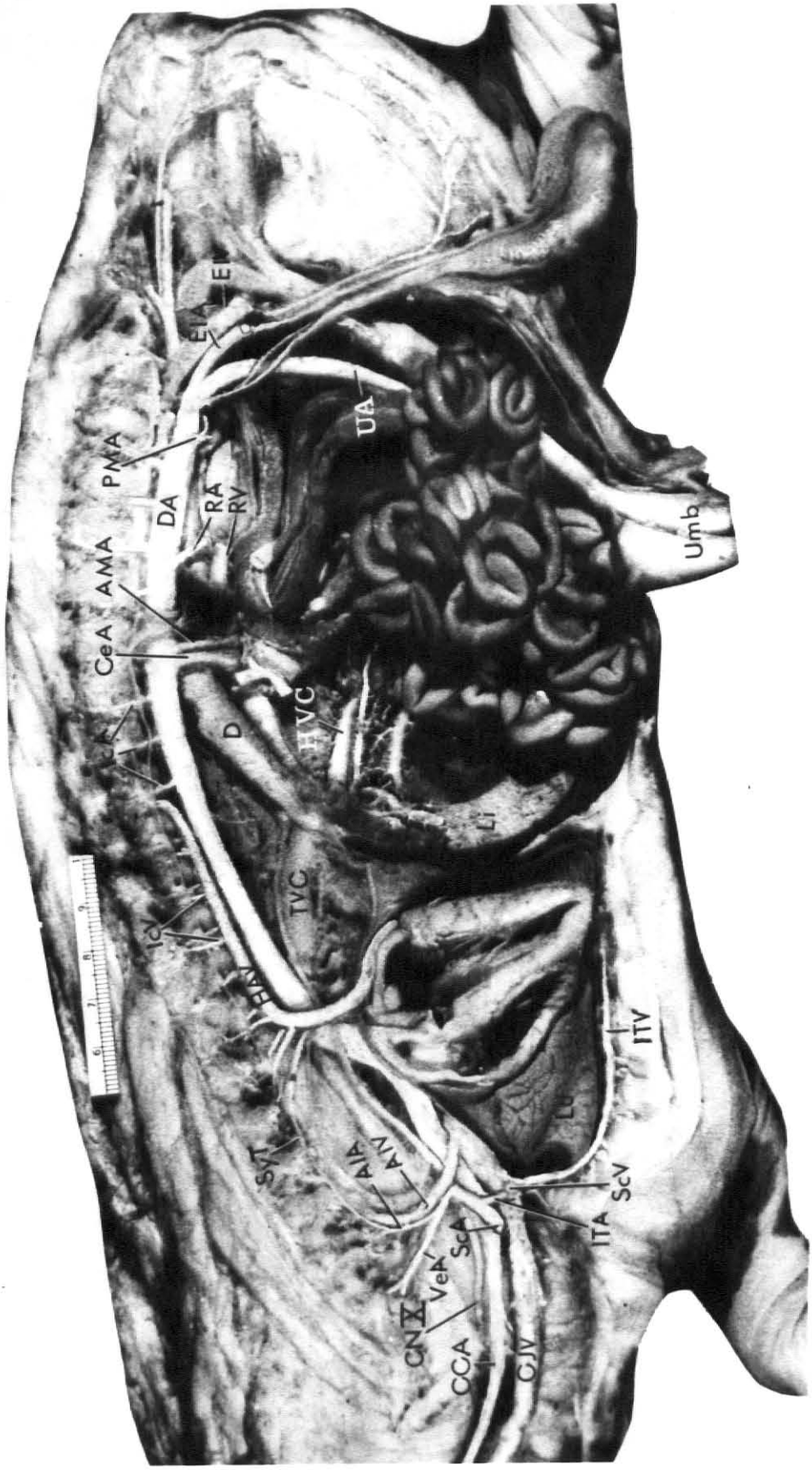
Ventral view of a dissection of a 56 day embryo (#900-7) with the arteries injected with red latex and the viscera removed. The red latex in the arteries appear as white liner in the photograph. The subclavian complex, carotid, internal thoracic (ITA), and anterior intercostal arteries (AIA) have attained definitive condition. Three pairs of mesonephric arteries persist, the posterior-most of which will remain as the gonadal arteries.



15

EXPLANATION OF FIGURE 16

Lateral dissection of a 157 day fetus, veins injected with yellow latex and arteries with red latex, which, unfortunately does not show in the photograph. All blood vessels have attained definitive condition. Of particular interest is the maintenance of the left common cardinal vein as the definitive connection of the hemiazygous vein (HAV) into the coronary sinus and thence into the right atrium.


EIA
EI
UA
PMA
DA
RA
RV
AMA
CeA
Umb
D
HVC
Li
ICV
TVC
HAV
SVT
AIA
AIV
Lu
ITV
ScV
ITA
ScA
VeA
CN XI
CCA
CJV

16

MAJOR CHANGES WITHIN THE VASCULARIZATION OF THE BOVINE EMBRYO 39 TO 60 DAYS GESTATION

by

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B. S. Kansas State University, 1973

ABSTRACT

OF A THESIS

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ABSTRACT

This study was undertaken to clarify the developmental sequence that results in definitive blood vessels. The basic difference between this study and others previously reported is the large number of specimens available which could be studied in detail allowing for direct observation rather than interpolation.

A study was made from 41 embryos from 38 to 63 days gestation, providing a closely-staged series from which all changes could be followed. Critical sections and dissections were photographed for illustrations. Composite drawings from acetate overlays were made of 39, 45, 48 and 51 day sagitally sectioned embryos.

The common carotid arteries are formed by stretching of the aortic sinus before day 37. By day 60 the brachiocephalic trunk has been formed by the pulling of the anterior tip of the aortic arch into an extended cone from which now branch the paired subclavian and carotid arteries at T-1.

The subclavian arteries are formed from the twelfth pair of intersomitic arteries (C-7). As the embryo develops, the subclavian arteries "migrate" anteriorly along the aortic arch until they reach their definitive positions off the brachiocephalic trunk by 55 days gestation. The celiac artery forms before 39 days as a ventral outgrowth from the dorsal aorta at T-13. The anterior mesenteric artery is the only remaining vitelline artery and is located, by 39 days, at its definitive position at L-1. The posterior mesenteric artery has formed before 39 days as a ventral outgrowth from dorsal aorta, immediately anterior to the umbilical arteries, and at 45 days it is in its final position at L-4.

At 60 days the iliac complex consists of the external iliac arteries emerging from the dorsal aorta at L-5, the circumflex iliac as a branch of the external iliac, and the internal iliac artery as a continuation of the base of the umbilical arteries at L-6.

The renal arteries are not derivatives of the mesonephric arteries as previously reported but are entirely separate entities emerging from the dorsal aorta at L-4. The only persisting mesonephric arteries are the gonadals which emerge from the dorsal aorta at L-1 and L-4, respectively.

The old anterior cardinal veins in the cervical region remain as the jugular veins. At 45 days the innominate vein (left brachiocephalic vein) joins the left jugular-subclavian. On the right, posteriorly from the connection of the jugular-subclavian-innominate vein complex, the anterior cardinal remains as the anterior vena cava. On the left, the anterior cardinal vein, posterior to the innominate vein, is reduced by 51 days and disappears completely by 58 days. The left common cardinal vein remains as the coronary sinus and the base of the hemiazygous vein.

The posterior vena cava develops as a vessel of many components. From the right atrium to the diaphragm, it is the result of stretching of the sinus venosus. The hepatic portion of the vena cava, from the diaphragm through the liver, is the result of coalescence and expansion of liver sinusoids. The lumbar portion of the post cava is the subcardinal anastamosis anteriorly continuing posteriorly with the right subcardinal vein. The intersomitic veins empty into the supracardinal vein while the renal veins form from the subcardinal.

The iliac junction with the posterior vena cava is totally subcardinal. The internal iliac veins are persistent post cardinal veins while the external iliac veins are derived from the segmental veins at L-4, L-5.