DEVELOPMENT OF THE VASCULAR SYSTEM
OF THE BOVINE EMBRYO TO 40 DAYS GESTATION

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INTRODUCTION

Most of the literature concerning the embryonic development of circulation in mammals consists of investigations on the human by Congdon (1922), Streeter (1951) and Patten (1968) and a lesser work on the dog by Martin (1958). There are several minor works on the development of the dorsal aorta and the aortic arches by Bremer (1912) in the rabbit, Schulte (1914) and Watson (1924) in the cat, Parker (1915) in marsupials, Wang (1917) in the ferret and Heuser (1923) in the pig.

The formation of the vascular system by vasofactive strands, or angio-blastic cords, has been well substantiated by several investigations. Following the formation of definitive vessels, it has been demonstrated by Clark and Clark (1932) that new vessels arise as outgrowths of pre-existing vessels.

The final derivatives of the aortic arches have been described by previous workers and a good summary of these findings can be found in Arey (1965) or Patten (1964). The formation of the dorsal aorta as a caudal progression of the vasofactive cells of the first aortic arch has been described by Watson (1924), Martin (1958) and Patten (1968).

The formation of the venous system has not been as completely investigated. The major descriptions are summarized by Arey (1965) and Patten (1968). These descriptions are general and seriously lacking in either observational or experimental evidence.

In order to clarify some of the observations and descriptions of previous workers concerning the development of the vascular system in mammals, a detailed study of bovine embryos from 21 to 40 days gestation was undertaken.

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 53 embryos 21 to 40 days development. Twenty 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, front and hind foot measurements, and in embryos under 32 days, somite number. Ovulation was considered as zero time for calculating the age of an embryo.

Photographs were routinely made of each embryo. The embryos were then de-hydrated in a graded series of isopropyl alcohol, embedded in paraffin, and sectioned at 10 or 15u. Sections were cut transversely, sagittaly, or frontally and stained with modified iron hematoxylin and periodic acid-Schiff reagent, or with Harris' Hematoxylin followed by acid fuchsin, Mallory's triple stain, or Masson's trichrome. Small embryos were stained by a single method, but most larger embryos were 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 micro-projection outline drawings of sagittal sections on acetate transparencies. Then a composite sketch was made with further details from cross-sections of equivalent age embryos.

TABLE 1: EMBRYOS USED IN THIS STUDY

Embryo number[a]	Age in days	Somite number	Crown-rump length(mm)	Contour (mm)	Type of section[b]
361	21	6	5.5	6.1	X
304x	21	9	5.4	6.4	X
743x	21	15	5.4	6.7	X
313x	22	19	5.3	7.0	X
146x	22	22	5.9	8.0	F
314x	23	27	6.5	10.3	L
419	23	28	6.0	12.4	X
233	24	28	5.8	6.2	X
206	24	30	6.0	9.0	L
254	24	30	7.0	11.1	X
143x	25	33	6.0	16.3	F
234x	25	34	7.0	16.0	X
415	25	33	7.0	18.0	X
391x	25	34	7.1	22.0	L
807	25	35	---	-----	X
12x	25	35	6.1	16.5	L
426	26	39	7.0	18.0	L
427	26	39	7.2	23.0	X
83x	26	40	8.0	22.0	X
265	27	41	---	-----	F
509	27	44	8.0	22.0	L
135x	28	41+	7.5	22.0	X
418	28	45	9.0	24.0	X
432	28	46	9.1	24.0	L
428	28	46	8.8	26.0	L
431	28	47	9.2	24.0	L
267	29	45+	9.0	23.7	L
574x	29	48	9.5	25.0	X
149x	29	49	10.5	-----	X
620-11	30	52	11.3	30.0	L

TABLE 1 (continued)

Embryo number[a]	Age in days	Somite number	Crown-rump length(mm)	Contour (mm)	Type of Section[b]
437-8	30	53	10.0	30.0	X
20-2x	31	52	8.2	22.4	X
385-26	31	50+	11.0	33.0	L
434	32	--	11.4	30.0	X
385-15	32	54	12.0	40.0	L
189	32	--	13.5	32.0	L
80	32	--	12.5	35	X
154x	32	55	13.5	34	X
327x	32	54	14.0	40.0	L
4x	32	54	14.0	40.7	L
385-8	33	55	14.0	----	X
96x	34	--	13.0	38.0	L
217	34	--	14.0	40.0	L
291	34	--	15.0	----	X
191	35	--	16.0	43.0	X
430	35	--	15.5	45.0	X
429	36	--	16.5	45.0	F
437-27	36	--	17.0	45.0	X
437-28	37	--	16.4	46.0	X
620-6	38	--	20.0	48.0	L
73x	38	--	22.0	53.0	X
163x	39	--	24.0	----	L
696x	40	--	----	----	X

[a] An "x" after the cow number indicates one of known age from the Kansas State University dairy herd.

[b] F = frontal, L = sagittal, X = transverse.

OBSERVATIONS

General Development of the Vascular System

The general features of the vascular development in bovine embryos are
depicted in figures 1, 2, 3, and 4; details of structure are illustrated by photo-
graphs in succeeding figures 5 through 31.

The vascular system of the bovine has its beginning early in the 21st day
of gestation. In the 6-somite embryo, the first aortic arches are simply two
rows of vasofactive cells (Noden, 1968, and Figs. 5 and 6). By late 21 days (15
somites) both the first and second aortic arches are formed and the dorsal aortae
are present as discontinuous tubes to the "tail bud" with paired vitelline
arteries (Fig. 7) throughout much of the body region. The venous system consists
mainly of two large umbilical veins in the lateral body wall (Figs. 8 and 9),
two small posterior cardinal veins dorso-lateral to the mesonephros, and two
anterior cardinal veins in the head region. By the end of day 26 (39 somites)
the basic fetal circulatory system is almost complete (Fig. 1). At this stage,
aortic arches 1 and 2 have degenerated leaving aortic arches 3 and 4 as the
functional arches. The radices aortae extend caudally from aortic arch 3 to the
region of somite 7; thus, the intersomitic arteries 1 to 6 are directly off the
radices aortae (Figs. 10, 11), whereas intersomitic arteries 7 to 35 are branches
of the dorsal aorta. There are at least 8 large vitelline arteries (Figs. 8 and
10) plus the paired umbilical arteries ventrally from the dorsal aorta. The
lateral aortic branches into the mesonephros are present, but were omitted in
Figure 1.

The venous system at 34 days (Fig. 2) consists mainly of the anterior and
posterior cardinal system, the vitelline veins and the umbilical veins. The
anterior cardinal veins drain the head region from the eye caudally to somite 7
where they empty into the common cardinal veins and thence into the sinus
venosus and the heart. The posterior cardinal veins drain the mesonephros and
caudal regions of the embryo and empty cranially into the common cardinal veins.
The umbilical veins carry nutrients from the placenta into the liver, through the
ductus venosus, into the sinus venosus. The vitelline veins drain the still
extensive yolk-sac complex also by way of the ductus venosus which originally
resulted from a fusion of the two vitelline veins caudal to the sinus venosus.

By 34 days (Figs. 2 and 4) aortic arch 6 is complete, with a large pulmonary
artery into the pulmonary mass. The radices aortae extend caudally to the region
of somite 14 (T-2) and are beginning to degenerate between aortic arches 3 and 4.

The right radix caudal to aortic arch 6 has a slightly smaller diameter than the left radix aorta in the same region. The intersomitic arteries cranial to somite 12 have essentially degenerated although their position along the radices aortae are still marked by remnants of the original intersomitic arteries. Circulation to this area is now provided by the vertebral artery which is supplied by the dorsal branch of intersomitic artery 12. The lateral branch of intersomitic artery 12 is the subclavian artery (Fig. 4).

The vitelline arteries have mostly degenerated by 34 days. Two vitelline arteries in the region of somites 21 and 23 (Fig. 8) remain as the anlagen of the superior mesenteric artery. The vitelline artery in the region of somite 27 is the anlage to the posterior mesenteric artery and the caudal-most pair remains as the umbilical arteries. One somite-length cranial to the superior mesenteric artery, the celiac artery has developed as a branch of the aorta.

The greatest changes, however, are in the venous system, which is now composed of the jugular veins, common cardinals, a posterior vena cava system comprised of thoracic, hepatic, and renal portions, and the large umbilical vein into the liver and hepatic portion of the post vena cava (Fig. 2).

The post cardinal veins are discontinuous in the 34 day embryo. They are present cranially from the anterior one-third of the mesonephroi to the common cardinal veins and caudally from the posterior one-third of the mesonephroi to the tail region. The middle one-third of the mesonephroi are drained by the sub- and supra- cardinal veins and their anastomoses.

The right common cardinal vein remains essentially unchanged, but the left common cardinal has become thinner and stretched around the heart in the atrio-ventricular groove.

Most of the essentials of adult circulation are established in the 39 day embryo (Figs. 3 and 4). Aortic arches 3 form the bases of the internal carotid arteries. The external carotid arteries are formed by the elongation and medial splitting of the sinus arteriosis between aortic arches 2 and 3. The right aortic arch 4 remains as the base of the right subclavian artery, whereas the left aortic arch 4 remains complete as the definitive aortic arch. The left sixth aortic arch remains as the pulmonary arch proximal to the connection to the pulmonary arteries and as the ductus arteriosis distal to the pulmonary arteries.

By 39 days, the radices aortae between aortic arches 3 and 4 (Fig. 4) are completely degenerated; a thin radix aorta remains caudal to the right subclavian

artery but it does not connect into the dorsal aorta. What was the radix aorta caudal to left aortic arch 4 is now the cranial part of the dorsal aorta. A summary of these changes in the aortic arches and radices aortae is illustrated by Fig. 4. The ventral branches of the dorsal aorta remain essentially the same as in the 34 day embryo with the superior mesenteric artery now a single trunk from the dorsal aorta.

The posterior vena cava is established by 39 days (Fig. 3). The thoracic vena cava has elongated between the right atrium and the diaphragm. The hepatic portion of the vena cava is continuous with the subcardinal sinus. The renal vena cavae consist of the subcardinal sinus and the sub-supracardinal anastomosis. The caudal segments of the double post cava is composed of supra-post cardinal anastomoses.

The right common cardinal vein now forms the base of the superior vena cava, whereas the left common cardinal is being further reduced to the coronary sinus.

The Aortic Arches and the Radix Aorta

The first aortic arch appears as a double row of vasofactive cells about 270μ long, continuous with and anterior to the endocardial plates in the 21 day, 6 somite embryo. By mid 21 days (7 somites), aortic arch 1 is complete and functioning. It extends from the aortic sinus cranio-dorsally through the mandibular arch to the region of the infundibulum and then caudally as the radix aorta. With the formation of the third aortic arch on day 24, the first arch degenerates leaving its ventral portion as the mandibular artery (Fig. 12) and its dorsal portion as a part of the internal carotid artery.

Aortic arch 2 is established late in day 21 (15 somites) as a row of vaso-factive cells within the second pharyngeal arch and subsequently lumenates. This is the dominant aortic arch during days 23 and 24. It regresses as the fourth arch forms (Figs. 3 and 12) and by 27 days its connection with the dorsal aorta has been severed. The ventral portion persists as the hyoid artery, thus supplying most of the second pharyngeal arch.

Aortic arch 3 is first seen as a row of vasofactive cells extending from the aortic sinus, through the third pharyngeal arch and contacting the radix aorta immediately ventral to the first somite in the 23 day, 28 somite embryo. Early in day 24, it is a small, but continuous vessel, but by late 24 days (33 somites) it is equal in size to aortic arch 2.

It is the dominant aortic arch through days 25 to 28 at which time aortic arch 4 equals it. Both of the third aortic arches persist as the bases of the internal carotid arteries.

As the mandibular arches enlarge, the first aortic arches are pulled apart, thus causing a splitting of the aortic sinus caudally (Fig. 4). This splitting and subsequent elongation of the aortic sinus between aortic arches 2 and 3 result in the formation of the external carotid arteries which are established by 26 days (Fig. 4). Further elongation and medial splitting of the aortic sinus between aortic arches 3 and 4 result in formation of distinct common carotid arteries by day 28 (Figs. 4 and 20). Still further elongation, but not splitting, of the aortic sinus between aortic arches 3 and 4 begin at day 38 and thus form the median carotid trunk (Figs. 3 and 4).

An incomplete fourth aortic arch is present in the 35 somite embryo consisting of a ventral root of vasofactive cells from the aortic sinus meeting a dorsal root off the radix aorta (Figs. 5 and 6). By early day 26 (37 somites), arch 4 is

complete (Fig. 12) and functions as the dominant arch by 29 days. The left arch becomes the definitive aortic arch and the right arch persists as the base of the right subclavian artery (Fig. 4) as described by Noden (1968). The radices aortae are essentially equal through day 32 and the subclavian arteries form as enlargements of intersomitic arteries 12 (Fig. 13).

The sixth aortic arch begins during day 27 (40 somites) and becomes functional on day 28 (45 somites). The pulmonary arteries are formed by direct posterior continuation of the line of vasofactive cells, part of which form aortic arch 6, and are distinct and open late in 28 day, 49 somite embryos (Figs. 21 and 22). The sixth arch is never as large as either aortic arches 3 or 4. By 34 days, the truncus arteriosus has completely split (Smith, 1970) into aortic and pulmonary trunks (Figs. 15 and 18). By 38 days, the right sixth arch degenerates, leaving the ventral portion of the left arch as part of the pulmonary arch (Fig. 14). The portion of the left aortic arch 6 dorsal to the connection of the pulmonary arteries persists as the ductus arteriosus.

The fifth aortic arch has its beginnings during the latter part of day 28; it is complete by day 29 (Figs. 16 and 17) and by day 32 it is completely degenerated. It is vestigial throughout its short existence. It usually consists of a loop off the posterior surface of aortic arch 4 (Fig. 14); occasionally it is a loop off the anterior surface of arch 6. In the eleven embryos exhibiting aortic arch 5, none showed it as a vessel from the posterior base of aortic arch 4 to the antero-ventral surface of 6 as previously described (Congdon, 1932). The fifth arch is not present in all embryos between days 28 and 32.

The radix aorta is nominally formed as the two dorsal aortae begin fusing during day 23 at which time it extends from just ventral to the infundibulum (the anterior tip or aortic arch 1) caudally to the region of somite 7 where fusion of the dorsal aorta begins. As the first and second aortic arches degenerate, the part of the radices anterior to the anterior-most functional aortic arches become directly the internal carotid arteries. Thus, by day 26 (Fig. 1), the radix aorta extends from the anterior edge of somite 1 (the anterior edge of aortic arch 3) caudally to somite 7. This remains the anterior limit of the radix aorta until day 35 when the radix between aortic arches 3 and 4 degenerates, thus leaving the radix aorta on either side connecting aortic arch 4 postero-medially to the dorsal aorta (Fig. 4). By day 30, the anterior end of the dorsal aorta has split so that the radices extend posteriorly to the region of the

seventh cervical vertebra (C-7, somite 12). By 32 days the split has progressed caudally to the region of T-1; by 34 days the radix aorta extends caudally to the region of T-2, and on day 38 they extend caudally to T-4 (Fig. 4, 19).

During day 35, right aortic arch 6 closes completely; the right radix aorta constricts as does right aortic arch 4 (Fig. 4) until they carry the blood for the right subclavian artery and a greatly reduced amount to the dorsal aorta (Figs. 4, 15, and 19). By day 39, the connection of the right radix aorta between the right subclavian artery and the dorsal aorta has degenerated, leaving a cranial portion between aortic arch 4 and the right subclavian artery as an integral part of the definitive subclavian artery (Figs. 4 and 15).

Splitting of the dorsal aorta has not been discussed previously, although such is illustrated by Congdon (1922) and Heuser (1923). Posterior extension of the radices must result from a secondary splitting of the previously fused dorsal aortae since the segmental arteries continue to extend straight out dorso-laterally throughout the occipital and cervical regions. Those segmental arteries degenerate during day 38 by which time the aorta has split from the first cervical posteriorly to the fourth thoracic vertebra.

The Dorsal Aorta and its Branches

The dorsal aorta is first seen as a double row of vasofactive cells resulting in double dorsal aortae from a dorso-cranial, then caudal progression of the vasofactive cells of the first aortic arch, as described by Noden (1968).

Late in day 21, the dorsal aortae extend caudally to the "tail" region of the embryo although the lumen is discontinuous with only strands of vasofactive cells connecting the tubular segments.

Fusion of the dorsal aortae begin during day 23 in the region of somite 7 forming a single dorsal aorta caudally to somite 19. In some embryos, the fusion progresses anteriorly to somite 6. Posterior fusion of the dorsal aorta continues until day 32 when the last somite is formed and a single dorsal aorta then extends from the region of the first thoracic to the 10th caudal vertebra.

The first branches to form off the dorsal aorta are the vitelline arteries. During the latter part of day 21, four pairs of vitelline arteries connect the dorsal aortae to the arterial plexus of the yolk sac (Fig. 10). By day 24, 13 pairs of vitelline arteries have been established from the paired dorsal aortae. As the aortae fuse into a single dorsal aorta, the right and left vitelline arteries of a pair are brought into close proximity resulting in fusion of each pair into single, ventro-medial branches off the dorsal aorta (Patten, 1968) (Fig. 8). In the 25 day, 33 somite embryo, the anterior vitelline arteries are fused, but caudally, where there is still a visible cleft in the recently fused dorsal aorta, the vitelline arteries are yet paired. Later in the 25 day embryo, all vitelline arteries within the future abdominal region have fused into a series of ventro-medial unpaired arteries.

Of the 13 or more pairs of vitelline arteries formed in the embryo, only 2 single and one paired arteries remain at 40 days (Fig. 3). The most anterior vitelline artery remaining at 33 days is the anlage of the anterior mesenteric artery. At 34 days, there are two or three vessels, but by 34 days the anterior and posterior (if present) branches have disappeared leaving a single artery. The separate, linearly arranged vitelline arteries do not fuse, as commonly assumed (Arey, 1968), rather one artery, ventral to somite 21 enlarges and assumes the total function of the original numerous vessels.

The second persisting vitelline artery is the anlage of the posterior mesenteric artery, which consists of a single vessel after the original pair has fused and the lesser vitelline arteries both anterior and posterior to it

disappear by day 32 (Figs. 2 and 8).

The caudal-most pair of vitelline arteries never fuses and with the formation of the allantois, is directly incorporated into the allantoic system and remains as the paired umbilical arteries. Branches off the umbilical arteries supply the developing hind limb buds. The iliac branches condense into a single vessel, the common iliac artery, by 34 days.

The celiac artery is also a ventral branch of the dorsal aorta and is described by Patten (1968) and Hamilton and Mossman (1972) as originally being a vitelline artery. However, in the bovine, all but one of the vitelline arteries degenerate in the region of the stomach during day 26. There is no evidence of an artery entering the stomach directly from the dorsal aorta until day 30 when there is a definite celiac artery approximately one somite length anterior to the superior mesenteric artery (Fig. 2).

The second set of branches to appear off the dorsal aorta are the inter-somitic arteries. These develop as paired dorso-lateral branches into the inter-somitic grooves. The first intersomitic artery forms in the first intersomitic groove during day 23 and progressively each intersomitic groove is supplied with an artery. Thus, there are 5 pairs of occipital arteries, all off the radices aortae, and 7 pairs of cervical arteries arising from the single dorsal aorta. As the dorsal aorta secondarily splits throughout the cervical region (days 29-36) the paired cervical arteries remain with their respective radices, and continue their dorsolateral course until their demise between day 34 and day 38.

With the formation of the anterior limb bud, the intersomitic arteries of that region send branches into it. The anterior-most intersomitic artery supplying the limb is in the tenth intersomitic groove and the posterior-most intersomitic artery contributing to the anterior limb bud circulation is in the fifteenth intersomitic groove (Fig. 4). Thus, there are 5 possible intersomitic arteries that contribute to the circulation of the fore leg. In the period from 27 to 32 days, the number of intersomitic arteries supplying the fore limb is either 4 or 5, with that between vertebrae C-7 and T-1 (intersomitic artery 12) becoming dominant by day 31 and persisting as the subclavian artery.

The third major group of branches off the dorsal aorta constitute the mesonephric arteries which are paired and supply the mesonephric corpuscles with blood. The mesonephric arteries are irregularly spaced and do not coincide cranial-ventrally with the intersomitic arteries. The fate of the mesonephric arteries is beyond the scope of this study.

The Venous System

The venous system has its beginnings concurrently with or very shortly
after the formation of the arteries during day 21 of gestation. In the 9 somite
embryo, the vitelline veins connect the yolk sac venous plexus to the sinu-
atrial anlagen. After the sinus anlage complete their fusion into a single sinus,
the paired vitelline veins fuse progressively posteriorly, forming the single
ductus venosus around which the liver forms in the 23 day embryo (Fig. 9).
Ingrowth of numerous hepatic cords into the ductus, and expansion of ductus en-
dothelium outward between the hepatic cords results in a complex anastomosis
of venous sinusoids throughout the liver. By 24 days (30 somites) the ductus
venosus extends from the posterior edge of the liver into the sinus venosus.
Also during this time, the numerous vetelline veins leading from the yolk sac
into the liver have been fusing until by 24 days there is a single vitelline
vein. This vitelline vein is the anlagen to the hepatic portal vein (Figs. 2
and 3).

The umbilical veins can first be seen in the lateral body wall at the angle
of the body fold in the late 21 day embryo. They communicate directly with the
sinu-atrial anlage and with the formation of the sinus venosus, they connect to
the heart through the common cardinal veins (Fig. 9). The umbilical veins expand
medially just posterior to the liver until they come in contact with the ductus
venosus. By 25 days (34 somites), the umbilical veins have fused with the
ductus venosus, forming a confluent channel between the two umbilical veins.
With the fusion of the umbilical veins to the ductus venosus, their lateral
connections to the common cardinal veins begin degenerating, and by 26 days (40
somites), these lateral umbilical vein channels are totally degenerated (Fig. 1).
The umbilical veins communicate with the posterior cardinal veins by several
branches in the lateral body wall (Fig. 8) until early in day 26.

The anterior cardinal veins are present in the early 22 day (19 somite)
embryo as blind tubes about 100μ long that run cranio-laterally into the head
region from a point about 70μ cranial to the margin of the anterior intestinal
portal. By 23 days they connect caudally into the common cardinal veins and
thence into the sinus venosus. By 40 days, essentially all of both anterior
cardinal veins have condensed into the internal jugular veins.

The common cardinal veins, or ducts of Cuvier, are originally the communal
receptors of the anterior and posterior cardinal veins and empty directly into
the dorso-lateral surface of each sinus anlagen in the 23 day (27 somite)

embryo. As the heart fuses and enlarges, the left common cardinal is stretched around the curvature of the heart. By 28 days (45 somites) the left common cardinal is much smaller than the right and lies within the atrio-ventricular groove. At 40 days, the right common cardinal has maintained its large size and remains as the trunk of the superior vena cava (Fig. 3). The left common cardinal, however, is much reduced and persists as the coronary sinus, opening into the sinus venosus caudo-medially to the orifice of the right common cardinal vein.

The posterior cardinal veins are first evident in the late 21 day embryo, dorso-lateral to the developing mesonephroi. At this stage they have no direct connections into the heart anlagen, but rather communicate indirectly via frequent connections to the umbilical veins through vessels in the lateral body wall (Fig. 8). By 23 days the posterior cardinal veins connect cranially into the common cardinal veins.

There are several types of branches into the posterior cardinal veins. The first are a complex system of sinusoids that drain the mesonephroi. The posterior cardinal veins also receive frequent branches from the umbilical veins that drain the lateral body wall. Finally, they receive intrasomitic veins that drain the somite region. This third function is later taken over in the region of the mesonephros by the supra-cardinal veins (Fig. 2). By 40 days, the posterior cardinals have degenerated in the mesonephric region, but portions remain cranially as the azygous and hemiazygous veins and caudal to the meso-nephros as the common and internal iliac veins.

The sub-cardinal veins first appear in the 26 day (38 somite) embryo along the ventro-medial border of the cardal one-half of the mesonephroi, connected to the posterior cardinal veins only by way of the numerous venous sinuses of the mesonephroi. The sub-cardinal system remains essentially unchanged until day 29 when a discontinuous subcardinal anastomosis forms. During day 32 connections are formed through the medial borders of the mesonephroi, immediately lateral to the dorsal aorta, with the newly formed supracardinal veins (Fig. 2). As the subcardinal and sub-supracardinal anastomoses enlarge, the function of the posterior cardinal veins is progressively pirated and by 35 days the posterior cardinals are evident in the mesonephroi only at the cranial and caudal ex-tremes. Thus, at 35 days the posterior cardinals extend caudally from the mesonephroi, connecting into the supracardinals over the caudal end of the

mesonephroi. The supracardinals are continuous, with occasional inter-
connections to the subcardinals, to the cranial end of the mesonephroi, at a-
bout somite 17, where they again become broadly interconnected with their res-
pective posterior cardinals which then carry the blood to the common cardinal
vein (Fig. 2). At 40 days, the supracardinal veins are essentially bilaterally
symmetrical posterior to the large sub-supracardinal *anastomosis* anterior to
the metanephroi. A plexus of veins from each metanephros joins its respective
supracardinal vein.

The posterior vena cava is a compound vessel resulting primarily from the
consecutive fusion of veins. The most anterior segment of the post 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 and accelerated
development of the lungs (Figs. 2, 6, and 27).

The hepatic segment of the vena cava is formed in the 28 day (45 somite)
embryo as a condensation of liver sinusoids inside the dorsal rim of the liver,
offset slightly to the right. During days 30 and 31, the right dorsal portion
of the liver presses dorso-medially between the mesonephroi, into direct con-
tact with the floor of the subcardinal anastomoses. Late in day
31, the wall of the liver fuses with the wall of the subcardinal sinus, the
fused walls break down, and the subcardinal sinus becomes continuous with the
hepatic segment of the post cava (Fig. 26). Immediately posterior to this
connection in the 32 day embryo, there is a large sub-supracardinal anastomosis
(Fig. 29), allowing the anlage of the post cava to attain a position dorsal to
the dorsal aorta, thus completing the "pre-renal" portion of the vena cava.
Posterior to the developing metanephroi in the 38 day embryo, the supra-
cardinal veins receive the segmental veins, and become the paired "post-renal"
portion of the vena cava (Fig. 30). The caudal end of the post cava is formed
from the post-supracardinal anastomosis and drains the hind limbs and tail
region. The internal iliac vein is a direct transformation of the post cardinal
vein caudal to the lumbar region.

The pulmonary vein is first seen entering the left atrium through the dor-
sal mesocardium during day 28. It consists of a single trunk draining two pul-
monary veins, one on either side of the pulmonary mass. By 37 days, the trunk
pulmonary vein has been so expanded that the 4 branches each become pulmonary
veins (Fig. 31) entering the posterior surface of the left atrium (Smith, 1970).

DISCUSSION

The origin of the vascular system by vasofactive, adventitial, or angioblastic cells is well substantiated in mammals. It has been described in the rabbit by Bremer (1912), in the cat by Schulte (1914) and Watson (1924), in the human by Bremer (1914), Congdon (1922) and Patten (1968), in marsupials by Watson (1915), in the ferret by Wang (1917), in the pig by Sabin (1917), Heuser (1923) and Patten (1948), in the dog by Martin (1958), and in the bovine by Noden (1966). The subsequent lumenation of the double-cell vasofactive strands is by a separation between the two cells of the strand (Figs. 5 and 6), not by a vacuolization of the cell body of single cell strand as described by Sabin (1922).

With the formation of the third aortic arch in the mammals previously studied, there are 3 functional aortic arches (Congdon, 1922; Heuser, 1923; Martin, 1958; Patten, 1968). The first arch often remains dominant for some time after the third aortic arch is formed (Heuser, 1923; Martin, 1958). However, in the bovine as aortic arch 3 is forming, the first arch degenerates, and as the fourth arch forms the second degenerates, such that there is no more than 2 fully functional aortic arches in the bovine until the formation of the sixth arch on day 28.

The existence of the fifth aortic arch was questioned by Congdon (1922), Heuser (1923) and several other investigators. The question arises mainly on the definition of an aortic arch. The fact remains, that in the bovine and other animals, there is often a "so-called" fifth aortic arch, and in the bovine, at least, it can attain a substantial diameter (Figs. 14 and 17).

The splitting of the dorsal aorta, thus elongating the radices aortae, has not been previously described. Although Congdon (1922) and Heuser (1923) illustrated aortic splitting with their discussion of the subclavian arteries, they described the shifting of the subclavian arteries in reference to the bifurcation of the dorsal aorta as movement of the branch cranially along the dorsal aorta (Congdon, 1922) or as climbing upward beyond the bifurcation (Heuser, 1923). In this study, the posterior extension of the radices aortae was deduced to be the result of secondary splitting of the dorsal aorta because the intersomitic arteries retain their position on the dorsal aorta both relative to the somites and to the developing subclavian artery. The external carotid arteries were described by Patten (1968) as consisting of portions of the

ventral roots of aortic arches 1 and 2 and were described by Hamilton and Mossman (1972) as new branches from the ventral aspects of the third aortic arches; and by Congdon (1922) and Heuser (1923) as irregular and inconsistent sprouts of the aortic sinus. Our material, however, shows the external carotid arteries forming from the aortic sinus by splitting of the aortic sinus from the base of aortic arch 2, posteriorly to aortic arch 3 and subsequent elongation of the resultant parts of the aortic sinus (Fig. 4).

Further, Patten (1968) and Hamilton and Mossman (1972) described the common carotid arteries as forming from the ventral aortic root of the third arch. However, I found that the common carotid arteries result from a further elongation and medial splitting of the aortic sinus posterior to aortic arch 3 with the carotid trunk established from the undivided aortic sinus anterior to the base of aortic arch 4 (Fig. 4).

The arterial supply to anterior limb bud originates as a capillary net supplied by 4 or 5 intersomitic arteries. As the embryo develops, the artery in the C-7, T-1 junction dominates and remains as the subclavian artery. The subclavian artery has previously been described in the pig by Wollard (1922), Heuser (1923) and Patten (1948) as being the seventh segmental artery when in actuality it is the twelfth intersomitic artery. In an attempt to clarify the numbering of segmental arteries, Padget (1945) discounted those in the occipital region, thereby perpetuating the confusion. There are arteries to the somites through each intersomitic groove from the first intersomitic groove caudally to the fifty-second groove. Since the cranial 5 somites provide the material for the base of the skull, it is somite 12 that becomes the seventh cervical vertebra and therefore intersomitic artery 12 that becomes the subclavian artery (Fig. 4).

The vitelline arteries are essentially ignored by mammalian embryologists as unimportant due to the questionable function of the yolk sac and to the fleeting existence of the arteries, other than their contribution to the celiac and superior and inferior mesenteric arteries (Nelson, 1953; Arey, 1965; Patten, 1968). However, in the bovine, the vitelline artery system is complex, consisting of at least 13 pairs of vitelline arteries originally, and remaining connected to the yolk sac throughout the period studied. Also, the celiac artery is not a vitelline artery, rather it is a secondary branching of the dorsal aorta into the region of the stomach as several embryos taken during days

29 and 30 had good vitelline (superior mesenteric) arteries, but no artery to the stomach region (celiac artery) while 31 and 32 day embryos had both.

The caudal most pair of vitelline arteries become directly incorporated into the developing allantois as the umbilical arteries. The formation of the umbilical arteries has been previously described (Nelson, 1953; Patten, 1968). However the pirating of the caudal most pair of vitelline veins into the allantoic system has not been described previously except by Martin (1958).

The cranial-most section of the posterior vena cava, or "thoracic" vena cava (Figs. 26 and 27) was described by Patten (1968) as being derived from the right vitelline vein. The embryos used in this study, however, show a distinct stretching of the sinus venosus resulting from the shifting of the heart and consequent caudal migration of the liver, thus making the thoracic portion of the posterior vena cava a direct continuation of the sinus venosus.

Arey(1965) and Patten (1968) described the formation of a plica vena cava, mesenteric, or transabdominal vena cava as a condensation of blood vessels in the primary dorsal mesentery that theoretically connects the subcardinal anastomosis with the hepatic portion of the vena cava. However, in the bovine, the right dorsal portion of the liver comes in direct contact with the floor of the subcardinal anastomosis, fuses to it, the walls break down and the subcardinal sinus becomes confluent with the hepatic portion of the vena cava. Hence, there is no "plica vena cava".

ACKNOWLEDGEMENTS

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EXPLANATION OF FIGURE 1

This reconstruction of a 26 day, 39 somite embryo (#426) was made by microprojection outline drawings of sections, beginning with a median sagittal section and working out laterally to the right. Additional details were added by cross-sections of embryos #807, #427, and #83. The composite drawing shows the major circulation at the end of 26 days development.

Abbreviations for Figures 1, 2, and 3:

1, 2, 3, 4 = aortic arches of that number

A = atrium	Me = mesonephros
AC = anterior cardinal vein	O = otocyst
AS = aortic sinus	PC = posterior cardinal vein
CA = caudal artery	PP = pharyngeal pouch
CC = common cardinal vein	RA = radix aorta
CN = cranial nerve	SV = sinus venosus
DA = dorsal aorta	TA = truncus arteriosus
DV = ductus venosus	UA = umbilical artery
E = eye	UV = umbilical vein
ECA = external carotid artery	VA = vitelline artery
ISA = intersomitic artery	VV = vitelline vein
Li = liver	

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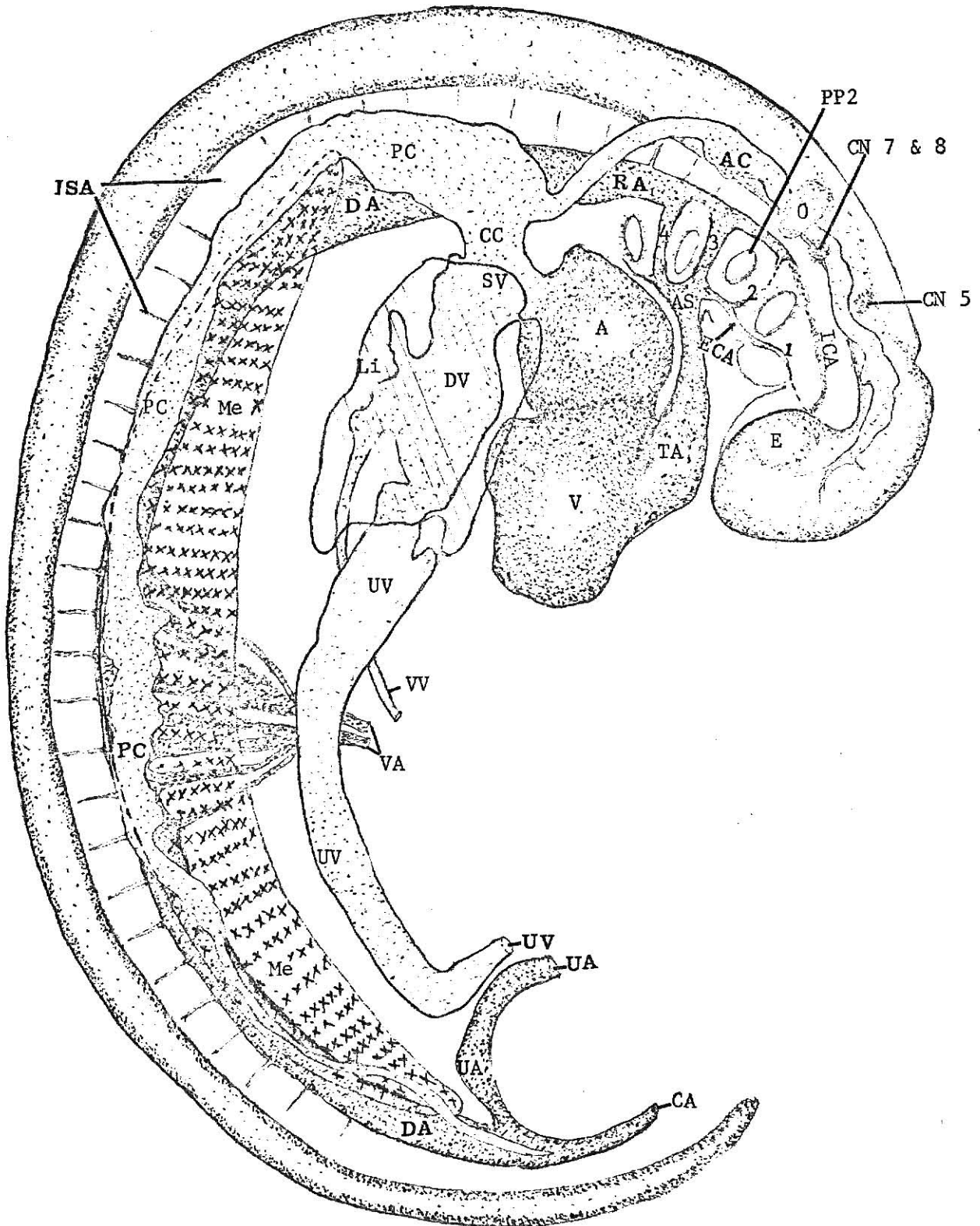
EXPLANATION OF FIGURE 2

This reconstruction of a 34 day embryo (#96) was made in the same manner as Figure 1. Additional details were added by embryos #217 and #291.

Additional abbreviations:

Ce = cerebrum

CeA = celiac artery

CS = coronary sinus

IMA = inferior mesenteric artery

HPV = hepatic portal vein

HVC = hepatic vena cava

PA = pulmonary artery

PT = pulmonary trunk

RtA = right atrium

RV = right ventricle

SC = supracardinal vein

ScA = subclavian artery

SMA = superior mesenteric artery

S-SA = sub-supracardinal anastomosis

SU = subcardinal vein

TV = thoracic portion of posterior vena cava

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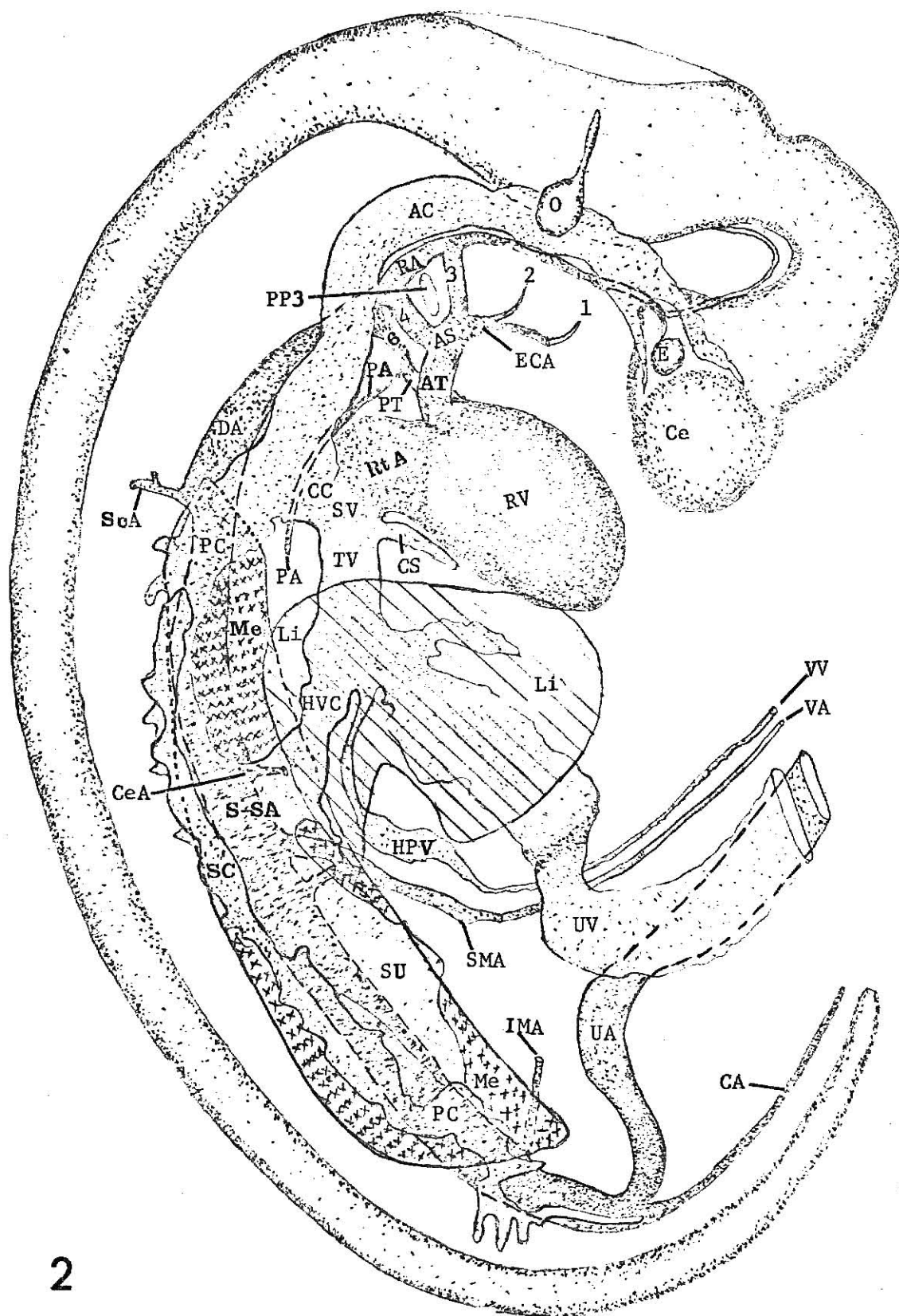
EXPLANATION OF FIGURE 3

This reconstruction of a 39 day embryo (#163) was made in the same manner as Figure 1. Additional details were added by embryos #73 and #696.

Additional abbreviations:

AT = aortic trunk

CCA = common carotid artery

CeA = celiac artery

DAr = ductus arteriosus

HAV = hemi-azygous vein

ICA = internal carotid artery

IIV = internal carotid artery

JV = jugular vein

M = midbrain

MT = metanephros

PA = pulmonary artery

PVC = post renal vena cava

PT = pulmonary trunk

RtA = right atrium

RV = right ventricle

RVC = renal vena cava

ScA = subclavian artery

ScV = subclavian vein

TV = thoracic vena cava

VeA = vertebral artery

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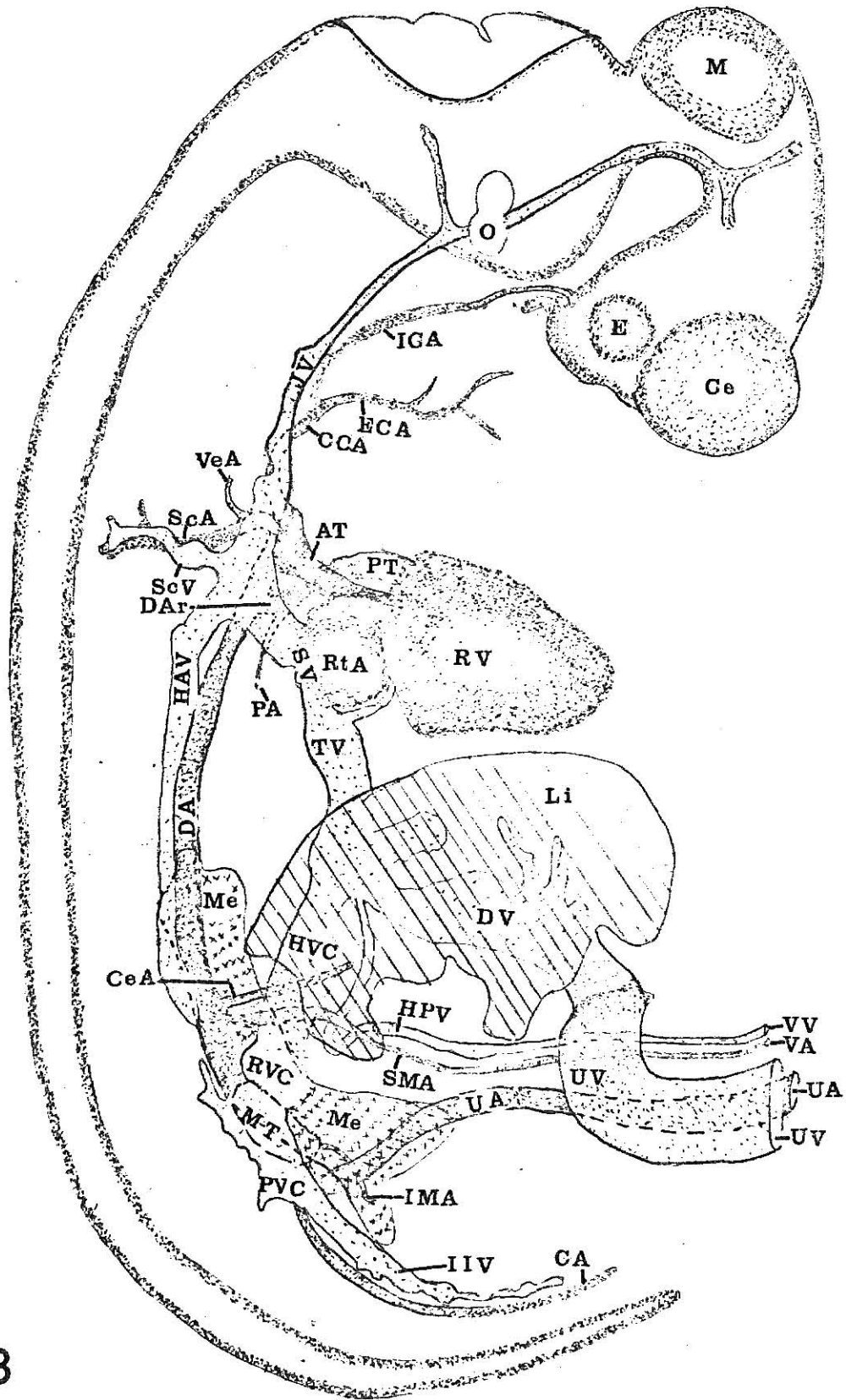
EXPLANATION OF FIGURE 4

This series of sketches illustrates the posterior progression of the radices aortae by a re-splitting of the dorsal aorta, the changes and shifting of the aortic arch system, and the "progression" of the subclavian arteries as the heart and radices progress caudally.

The details of the reconstructions were taken as: 30-day embryos #620-11, #437-8 and #20-2, 34-day embryos #217 and #291 were used; 35-day embryos #191 and #430, and 40-day embryos #163 and #696.

Abbreviations:

1, 2, 3, 4 = aortic arches of that number

AS = aortic sinus	ISA = intersomitic artery
AT = aortic trunk	LSA = left subclavian artery
CCA = common carotid artery	PA = pulmonary artery
CT = carotid trunk	PT = pulmonary trunk
DA = dorsal aorta	RA = radix aorta
ECA = external carotid artery	RSA = right subclavian artery
IC-1 = first intercortal artery	VA = vertebral artery
ICA = internal carotid artery	

EXPLANATION OF FIGURES

Figure 5: Transverse section of 21 day, 9 somite embryo (#304) showing the beginning of a segmented artery consisting of 2 vasofactive cells (V-ISA) just medial to the dorsal aorta (DA). 640x, Hx-Mallory.

Figure 6: Transverse section of the same embryo (#304), 4 sections cranial from Fig. 1 with a 2-cell stage intersomitic artery (ISA) showing a lumen formed between the vasofactive cells. 640x, Hx-Mallory.

Figure 7: Transverse section of a 21 day, 15 somite embryo (#743) showing the connection of the dorsal aortae (DA) with vitelline arteries (VA). This embryo had 4 such paired connections of the dorsal aortae and arterial complex of the yolk sac. 160x, Hx-PAS.

Figure 8: Transverse section of a 24 day, 28 somite embryo (#233) showing the now fused dorsal aorta (DA) connecting with unpaired vitelline artery (VA). Also shown are the posterior cardinal veins (PC) and sub-cardinal veins (SC) of the mesonephros and the large umbilical veins (UV) with feeder veins from the lateral body wall (VBW) that communicate directly with the posterior cardinal veins. 64x, Hx-PAS.

Figure 9: Frontal section through a 25 day, 33 somite embryo (#143) showing interconnection of the right common cardinal vein (CC), ductus venosus (DV) and right umbilical vein (UV). The left umbilical vein is broadly connected into the ductus venosus. 64x, Hx-PAS.

Figure 10: Sagittal section through a 26 day, 39 somite embryo (#426) showing 5 vitelline arteries (VA) and 6 intersomitic arteries (ISA) off the dorsal aorta (DA). This embryo (Fig. 1) had a total of 8 vitelline arteries. 64x, Hx-PAS.

Figure 11: The same embryo (#426), the 7th sagittal section lateral to Fig. 10 showing intersomitic arteries (ISA) 4, 5, and 6 off the radix aorta (RA) and the anterior limit of the dorsal aorta (DA) in the region of somite 8. Aortic arches 3 and 4 are the two functional arches during day 26. 64x, Hx-PAS.
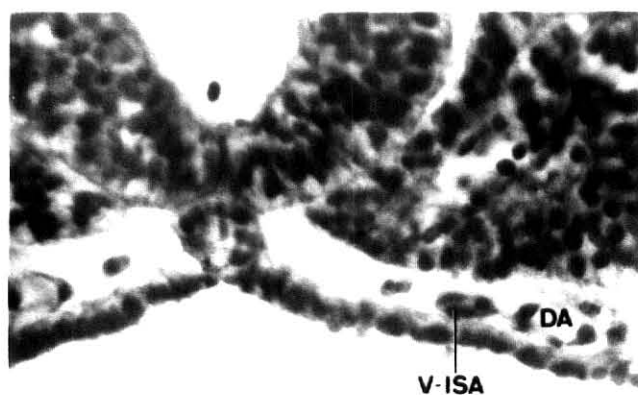
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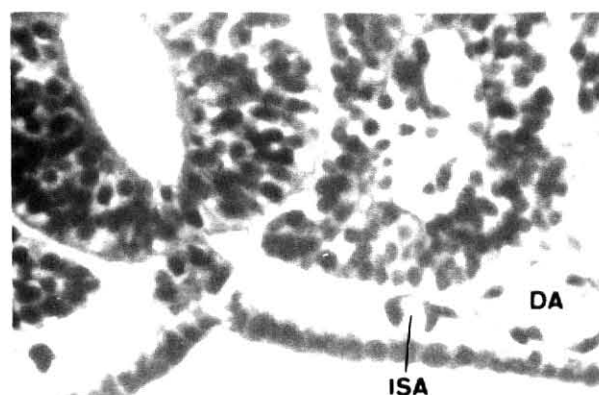
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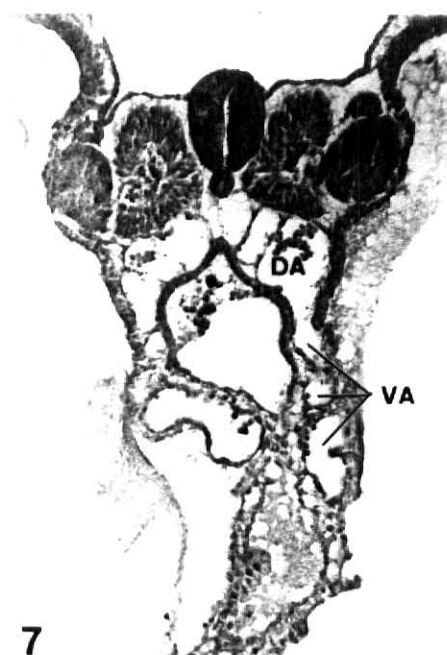
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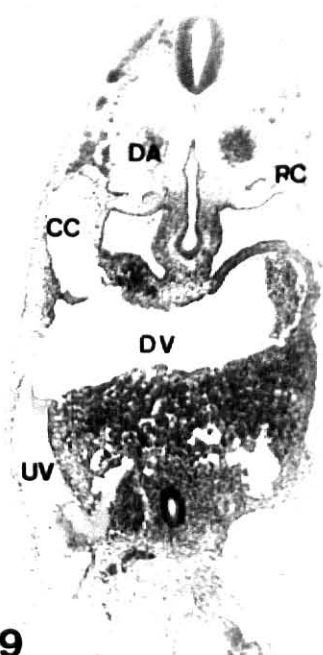
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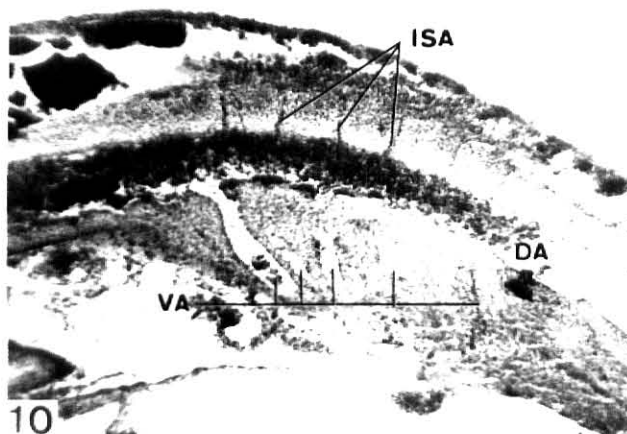
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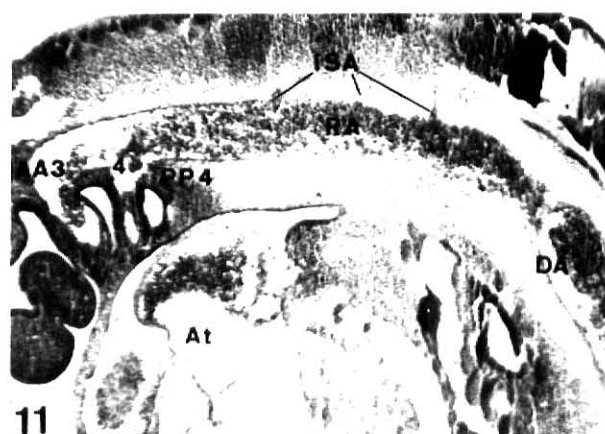
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EXPLANATION OF FIGURES

Figure 12: Sagittal section through a 25 day, 35 somite embryo (#12) showing the rudiment of aortic arch 4 (AA4), and AA3 connecting with the radix aorta (RA), AA2, and the mandibular artery (MA). 160, Hx-Mallory.

Figure 13: Transverse section through a 32 day, 55 somite embryo (#434) showing the future subclavian arteries (ScA). There are two branches off each radix aorta into the anterior limb bud cranial to the artery shown and one posterior to it. The future subclavian artery is intersomitic artery 12, between vertebra C-7 and T-1. The posterior cardinal vein (PC) joins broadly with the common cardinal vein (CC). 64x, Hx-PAS.

Figure 14: Sagittal section of a 30 day, 52 somite embryo (#620-11) showing the ventral root of aortic arch 5 (AA5) off the base of AA4. Aortic arches 3 and 6, along with AA4 are the functional aortic arches at this time. Intersomitic artery 5 (ISA-5) originates from the radix aorta (RA) almost opposite the connection of AA6. 64x, Hx-PAS.

Figure 15: Transverse section through a 38 day embryo (#73) immediately posterior to cervical vertebra 7, showing the right subclavian (RScA) and vertebral arteries (VtA) coming off the right radix aorta (RRA). The left AA4, or definitive arch, is continuous with the aortic trunk (AT). 64x, Hx-Mallory.

Figure 16: Frontal section through the pharyngeal region of a 30 day, 53 somite embryo (#437-8) showing the maximal size of AA5. 64x, Hx-Mallory.

Figure 17: Enlarged segment of the section in Fig. 16 to show relationships of AA4. 150x, Hx-Mallory.

Figure 18: Transverse section through a 38 day embryo (#73) showing the left subclavian artery (LScA). This section was 5 sections (50μ) caudal to Fig. 15. 64x, Hx-Mallory.
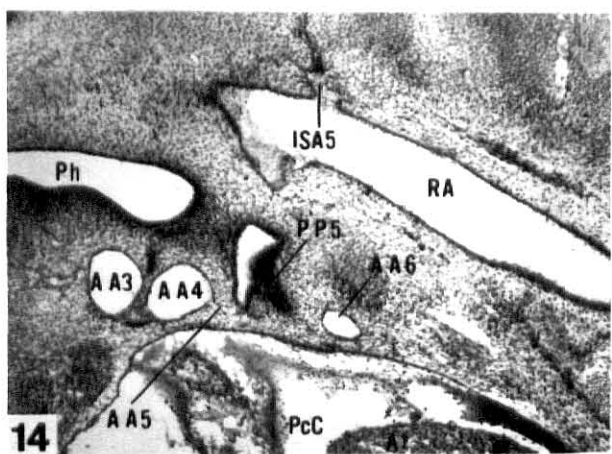
Additional abbreviations:
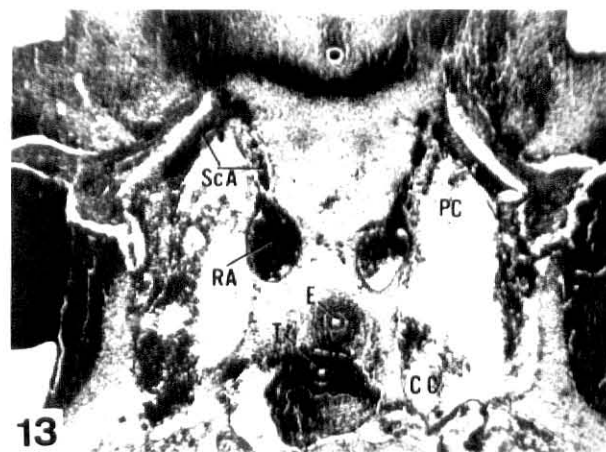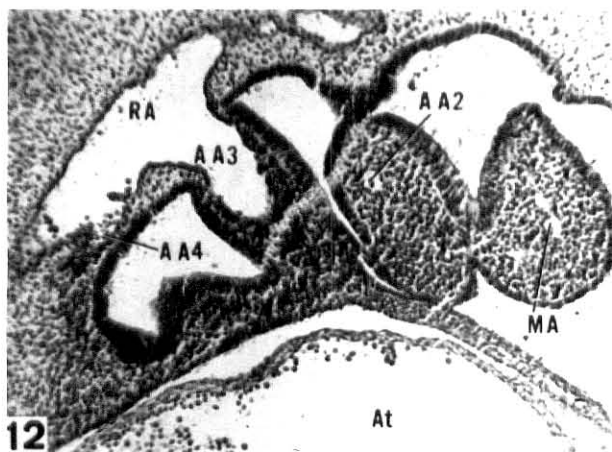 At = atrium

  E = esophagus

  T = trachea

  Ph = pharynx

  VN = vagus nerve

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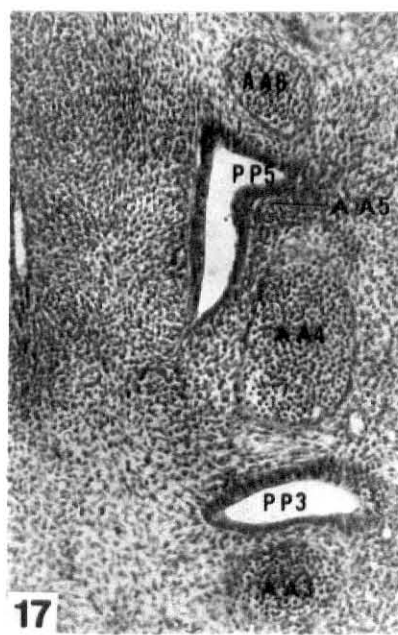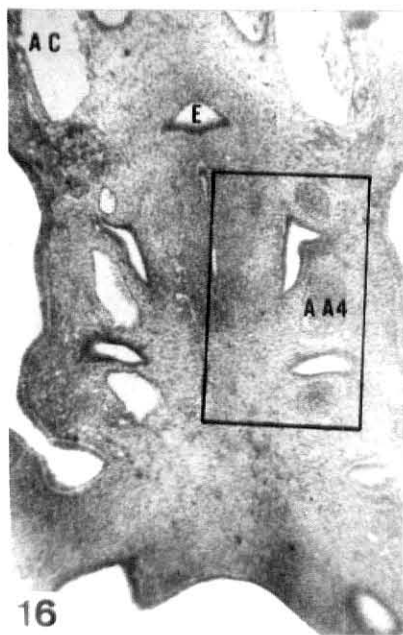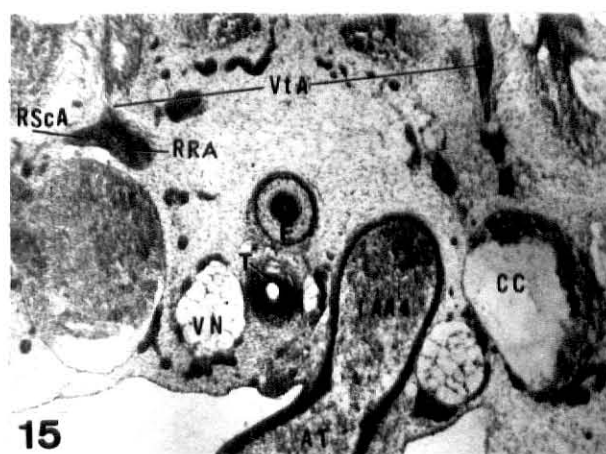
EXPLANATION OF FIGURES

Figure 19: Transverse section through a 35 day embryo (#191) showing the posterior limit of the radix aorta (RA) in the region of the third thoracic vertebra (T-3). Also shown is the posterior cardinal vein (PC) and an intra-somitic vein (ISV). 64x, Hx-PAS.

Figure 20: Transverse section through a 38 day embryo (#73) showing the right AA4 and the left common carotid artery (LCCA) joining the carotid trunk. This section was 220µ cranial to Fig. 15. 64x, Hx-PAS.

Figure 21: Transverse section through a 30 day, 53 somite embryo (#437-8) showing the pulmonary arteries (PA) exiting the right and left AA6. The right AA6 is continuous with the pulmonary trunk. Also shown are aortic trunk (AT), the common cardinal veins (CC), the radices aortae, and relationships to the pleural cavity. 64x, Hx-Mallory.

Figure 22: Sagittal section through a 32 day embryo showing the pulmonary artery (PA) exiting the left AA6, or pulmonary arch (PAr). Also shown is the aortic sinus (AS) and the aortic trunk (AT). 64x, Hx-Mallory.

Figure 23: Transverse section through a 38 day embryo (#73) showing the right pulmonary artery (PA) exiting the left AA6, or pulmonary arch (PAr). The loop, or ductus arteriosus (DAR), connects into the left radix aorta (LRA).

Figure 24: Sagittal section of a 38 day embryo (#620-6) showing the pulmonary artery (PA) leaving the pulmonary arch (PAr) and the definitive aortic arch (AA4) leading from the aortic trunk (AT). 64x, Hx-Mallory.
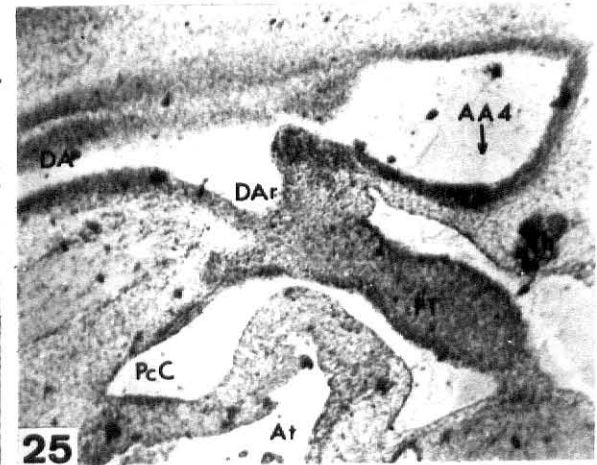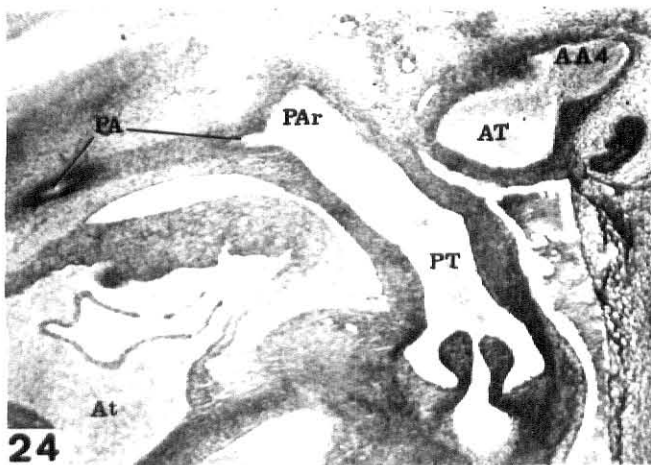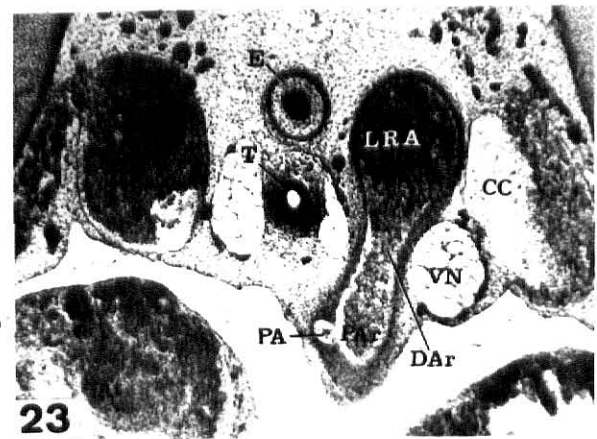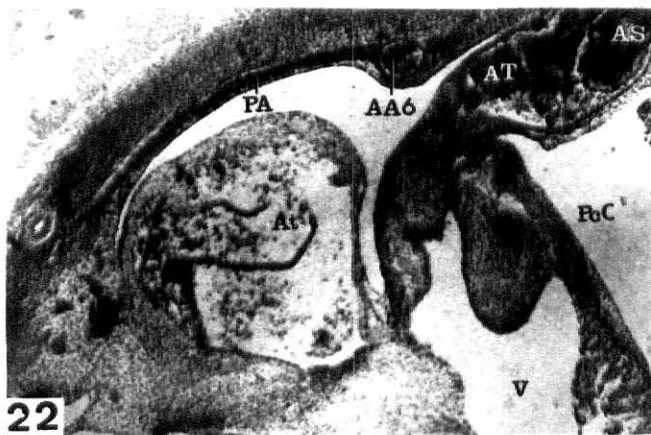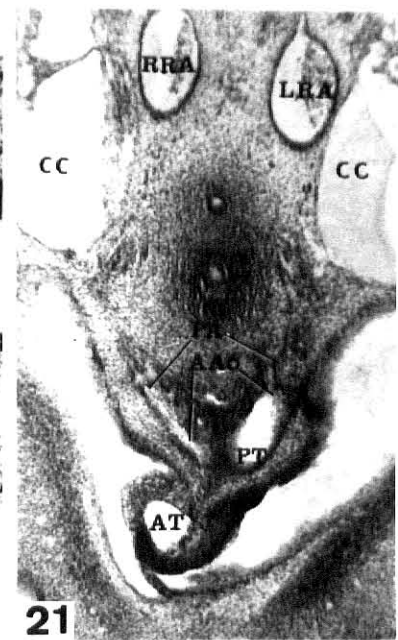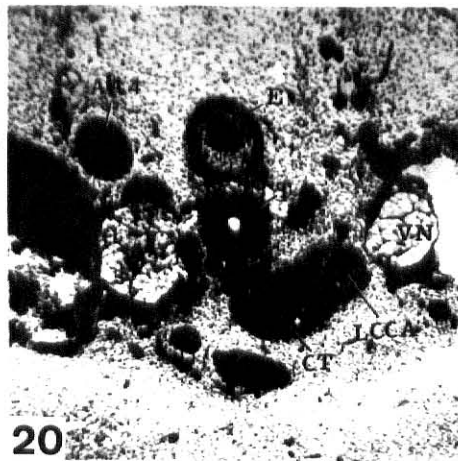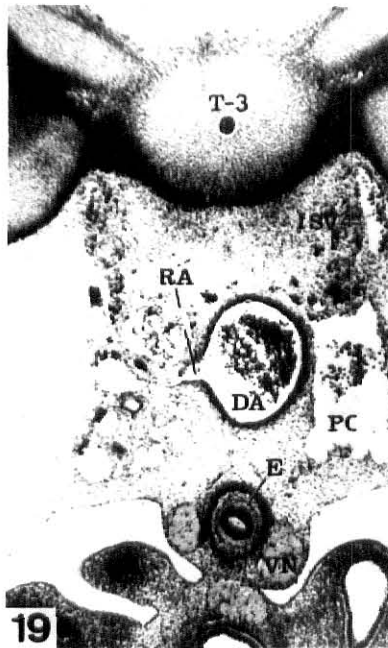
Figure 25: Sagittal section of the 38 day embryo (#620-6) 200u to the right of the section in Fig. 24, showing the ductus arteriosus (DAr) joining the dorsal aorta (DA). 64x, Hx-Mallory.

Additional abbreviations:

At = atrium

PeC = pericardial cavity

V = ventricle

Fig. 19
Fig. 20
Fig. 21
Fig. 22
Fig. 23
Fig. 24
Fig. 25

EXPLANATION OF FIGURES

Figure 26: Sagittal section through a 38 day embryo (#620-6) showing the post cava from the heart into the mesonephros (Me). The "thoracic" vena cava (TVC) is a posterior elongation of the sinus venosus (SV); the hepatic portion of the vena cava (HVC) extends through the liver to the "pre-renal" vena cava (RVC) which connects into the subcardinal sinus. 64x, Hx-PAS.

Figure 27: Sagittal section of the 38 day embryo, 260µ mesially from that shown in Fig. 26 showing the stretching of the sinus venosus to form the "thoracic" vena cava (TVC) connecting into the hepatic portion of the vena cava (HVC). The coronary sinus (CS) is within the atrio-ventricular groove. 64x, Hx-PAS.

Figure 28: Transverse section of a 38 day embryo (#73) showing the supra-cardinal veins (SuCV) receiving the segmental veins (SV) in the region of the mesonephroi. 64x, Hx-PAS.

Figure 29: Transverse section through a 35 day embryo (#191) showing the sub-cardinal anastomosis (SbA) and the sub-supracardinal anastomosis (S-SA). A mesonephric artery (MA) supplies the mesonephros from the dorsal aorta (DA). 64x, Hx-PAS.

Figure 30: Transverse section through a 38 day embryo (#73) posterior to the mesonephroi showing the caudal artery (CA), the common iliac arteries (CIA), the common iliac veins (CIV), and the post renal vena cava (PRVC). 160, Hx-PAS.

Figure 31: Cross section of a 38 day embryo (#73) showing the pulmonary veins (PV) emptying into the left atrium (LA). 64x, Hx-PAS.

Additional abbreviations:
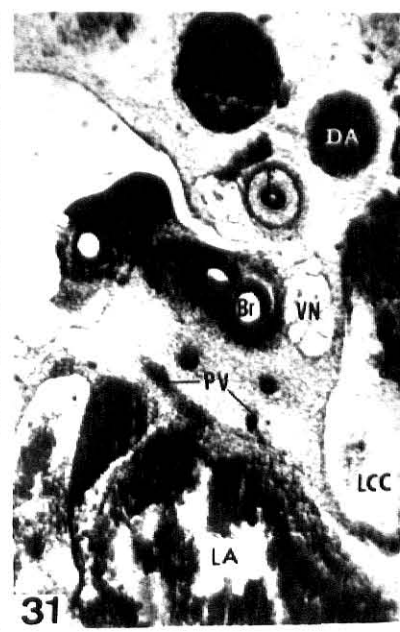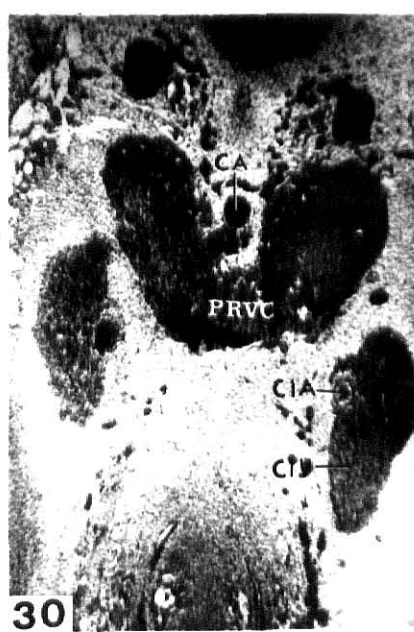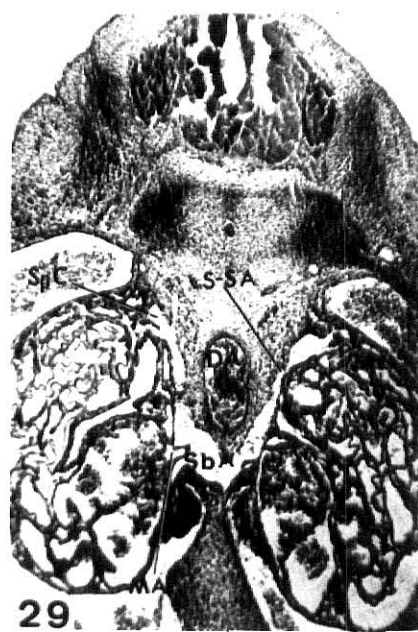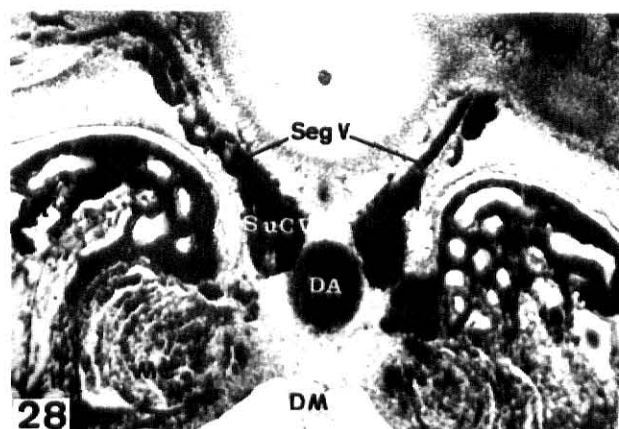
At = atrium

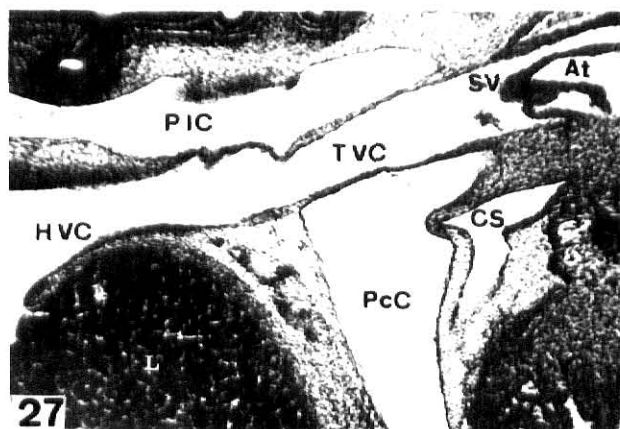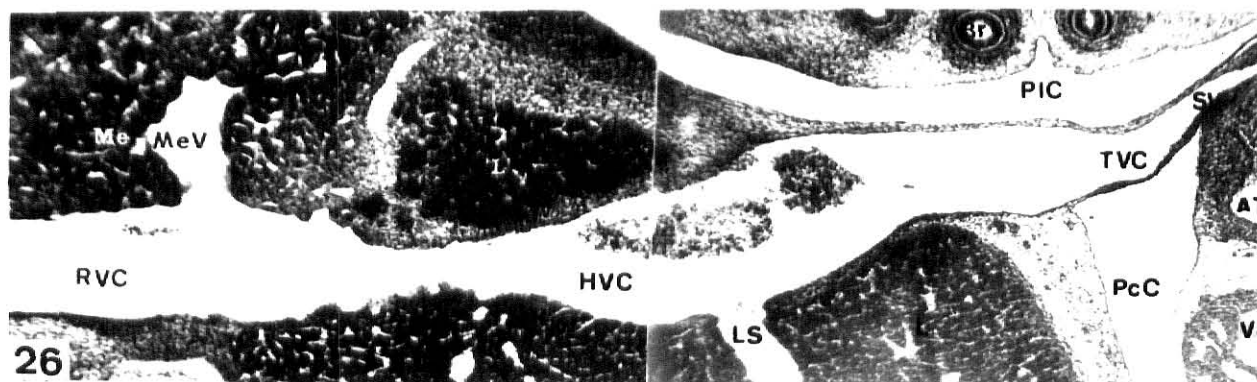Br = bronchus

L = liver

PeC = pericardial cavity

PlC = pleural cavity

SpC = supracardinal vein

V = ventricle

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DEVELOPMENT OF THE VASCULAR SYSTEM
OF THE BOVINE EMBRYO TO 40 DAYS GESTATION

by

WAYNE J. BYRNES

B. A., Culver-Stockton College, 1972

————————————

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Division of Biology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1973

A study of the development of the vascular system in the bovine was made from 53 embryos 21 to 40 days post-ovulation developmental age. This provided a closely-staged series from which all changes could be followed in short steps. Critical sections were photographed for illustrations. Composite drawings were made of 26, 34, and 39 day sagitally sectioned embryos.

Blood vessels form as strands of vasofactive cells which subsequently luminate by separation of the cells which make up the strand. The two dorsal aortae are formed as posterior continuations of the first aortic arches. The dorsal aortae begin fusing into a single vessel on day 23; fusion is complete from somite 16 through somite 27 by day 25, and progresses posteriorly until a single dorsal aorta is formed. By day 29, however, the radices aortae extend caudally to the region of somite 12 and, by day 38, to somite 16 (T-4). This indicates a re-splitting of the dorsal aorta since the intersomitic arteries associated with the radices and dorsal aorta are not distorted during this process. Intersomitic arteries in the occipital region disappear by day 33 and those to C-1 through C-6 disappear by 38 days.

The external carotid arteries begin forming during day 25 by stretching and splitting of the aortic sinus cranial to aortic arch 3. Further elongation and medial splitting of the aortic sinus between aortic arches 3 and 4 during day 34 result in formation of the common carotid arteries. The carotid trunk is formed by day 37 by stretching of the aortic sinus without further splitting.

The fifth aortic arch forms and is functional from day 29 through day 32. It may reach a fairly large diameter in the bovine although it is not always formed. Concurrent with the formation of the fifth aortic arch is the formation of a pharyngeal pouch 5 as a ventro-caudal evagination of pharyngeal pouch 4. Neither the arch not the pouch persist as a recognizable structure.

The arterial supply to the anterior limb bud originates as a capillary net supplied by lateral branches from 4 or 5 intersomitic arteries in the region between somites 10 and 14. Of these, intersomitic artery #12 (between C-7 and T-1) becomes dominant and persists as the subclavian artery.

The vitelline arteries, originally formed as 13 or more paired connections of the dorsal aorta to the yolk sac, remain only as 1) the superior mesenteric artery in the region of somite 21, 2) the inferior mesenteric artery ventral to somite 28, and 3) the umbilical arteries from the most posterior pair of vitelline arteries. The celiac artery is formed as a secondary branching of the

dorsal aorta into the stomach region.

The posterior vena cava forms in four basic segments. The most cranial, or thoracic vena cava, results from a stretching of the sinus venosus after day 34. The next section, the hepatic portion, forms as a condensation of liver sinusoids, between day 28 and 35. The dorsal surface of the liver over the hepatic portion of the vena cava fuses to the floor of the subcardinal sinus about day 35, the walls degenerate, and the "hepatic vena cava" becomes continuous with the sub-cardinal sinus. This renal portion of the vena cava receives the sub-supracardinal anastomosis in the posterior half of the mesonephrose. The most caudal section of the post cava, the post-renal vena cava, forms from a post-supracardinal anastomosis caudal to the developing metanephros.

The basic differences between the progress of vascular development in this report and that given in previous descriptions result from the large number of specimens from which critical stages could be studied.