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Development and Transformation of the Aortic Arches in the Equine Embryos with Special Attention to the Formation of the Definitive Arch of the Aorta and the Common Brachiocephalic Trunk* **

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Summary. The development and transformation of the aortic arches were studied in 84 equine embryos (5 to 35 mm CRL; approximately 21—49 days of gestation). The arch of the aorta and the vessels which originate from it were also examined in several fetuses (41—335 mm CRL) and in a full-term fetus.

There are six pairs of aortic arches that originate from the ventral aortic root. The first and second aortic arches regress very early, while the fifth pair appears in a vestigial form relatively late in the development, when the truncus arteriosus divides into the aortic and pulmonary channels. The development of the cervical intersegmental arteries is described and the formation of the subclavian arteries is discussed. The primitive arch of the aorta appears at the earliest in the 14—15.5 mm CRL equine embryos (approximately 35 days of gestation). The segments of the aortic arches system which are incorporated in the formation of the definitive arch of the aorta are discussed.

Three vessels, the innominate (brachiocephalic) artery, the left common carotid artery, and the left subclavian artery, originate from the primitive arch of the aorta. This arrangement of the vessels is regarded as the *primitive mammalian pattern.*

Two more stages precede the development of the definitive arch of the aorta and the common brachiocephalic trunk in the equine embryos, at approximately 42 days of gestation. The secondary changes, which occur in the process of formation of the arch of the aorta and the common brachiocephalic trunk, are described and discussed. Certain anomalies of the arrangement of the vessels from the arch of the aorta are also discussed.

Key-Words: Arch of the aorta — Equine — Development.

Introduction

In normal adult equines a unique vessel, the common brachiocephalic trunk (CBT), is given off directly from the arch of the aorta. This vessel, also called the anterior aorta in the old nomenclature, gives rise to the arteries that supply the cranial part of the thoracic wall, the thoracic appendages, and the neck and head.

According to comparative anatomy, the number of vessels that originate directly from the arch of the aorta in different mammalian species vary from three (four ?) to one. A comprehensive account on this subject is given by WIEDERSHEIM (1886), HOCHSTETTER (1891, 1906), KEITH (1895), GROSSER (1901), BRONNS (1902), PARSONS (1902), LASSILA (1927/28), HAFFERL (1933) and MEINERTZ (1966).

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* *In memoriam* of Professor Dr. L. KUNDZIŅŠ (1855—1940).

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The embryonic development of the aortic arches has been investigated in numerous mammalian species. For references see BAER (1827), BOAS (1888), ZIMMERMAN (1889, 1890), HOCHSTETTER (1890, 1891, 1906), TANDLER (1902, 1909), LEHMANN (1905), LEWIS (1906), LOCY (1906, 1909), SOULIÉ and BONNÉ (1908), COULTER (1909), REINKE (1910), REAGAN (1912), SICHER (1912), HOFMANN (1914), HAFFERL (1919), CONGDON (1922), HEUSER (1923), LLORCA (1933), MOFFAT (1959), and KREDIET (1962). Of particular importance are reports by RATHKE (1843), LEWIS (1923), GOLUB (1931), and HAMMOND (1937), in which the transformation of the aortic arches and formation of the definitive arch of the aorta and the common brachiocephalic trunk have been investigated in the ruminants.

The early development of the aortic arches in the equine embryos has been studied by VITUMS (1949, 1951); but, as far as can be determined, no investigation has been reported concerning the transformation of the aortic arches in this species. Therefore, the present investigation has been performed in order to examine the development and transformation of the aortic arches in the equine embryos, with special attention to the formation of the definitive arch of the aorta and the common brachiocephalic trunk.

Material and Methods[1]

Equine embryos used in the present investigation were collected from the Alsask Processors Ltd. in Swift Current, Saskatchewan, and Edmonton, Alberta, Canada, the Hansen Packing Co., Butte, Montana and the Central Nebraska Packing Co., North Platte, Nebraska. The author wishes to express his appreciation to all of these packing plants for their cooperation and permission to obtain these embryos. Furthermore, special credit is due to the colleagues, veterinary meat inspectors, of the above mentioned packing plants, Dr. S. P GIEBELHAUS, Edmonton, Alberta; Dr. R. D. ZAJAC, Swift Current, Saskatchewan; Dr. H. F. WINIECKI, Butte, Montana (at present Omaha, Nebraska); and Dr. A. NEIMANIS, North Platte, Nebraska, for their excellent work in removing embryos from the pregnant uteri, preserving and shipping them to Pullman, Washington. Altogether, over two hundred embryos ranging from 5 to 165 mm CRL were collected.

Most of the embryos were preserved in *Bouin* fixative; some of them were also fixed in 10% formalin. Smaller embryos were stained by Delafield hematoxylin or alum-carmine *in toto* and afterward dehydrated and embedded in paraffin. Larger embryos were embedded first in paraffin and then stained after they were serially sectioned. Eighty-four embryos from 5 to 35 mm CRL were prepared in frontal, transverse, and sagittal serial sections (10, 15 and 20 microns) and used for this investigation. Reconstructions of the aortic arches with pharyngeal pouches from the representative stages of the first period of the development and from the representative stages of the second period of the development were made from the serial sections. A modification of the method of BORN, using a Plaster of Paris technique was applied in the reconstruction of the vessels and related structures. Eighteen models of the aortic arches and of their transformation stages were prepared. The author is greatly indebted to Dr. A. BARRY, Professor of Anatomy, University of Michigan, Ann Arbor, Michigan, for his advice and assistance in perfecting this modified method of reconstruction. Numerous photomicrographs were prepared from the selected serial sections using a Zeiss photomicroscope. In addition to the serial sections, the blood vessels of twelve older embryos (41 to 88 mm CRL) were injected with vinyl acetate solution and subsequently were corroded

1. The author is greatly indebted to his former students Dr. S. WEISBROTH and Dr. M. HAMLET for preparation of the serial sections and Dr. KATHLEEN SEXTON and Mr. S. KRAKOWKA for preparation of the drawings. The author wishes to thank Mrs. SUMIKO SUMIDA for technical assistance.

in 10% KOH. The arch of the aorta, and the vessels which originate from it were also examined in several older fetuses (165 and 335 mm CRL, and a full-term fetus). The age of an embryo or fetus was mainly determined by crown-rump-length (CRL). However, it should be noted that CRL is not an entirely reliable indicator of the age of an embryo. Several embryos, the CRL's of which were smaller, were actually older in their general development than their CRL indicated, and vice versa. Therefore, the general development of the embryos has been used in addition to CRL in estimating the actual age (see Table 1 and 2). Only fragmentary information is available concerning the estimation of the age in equine embryos. For references see EWART (1915), VITUMS (1936, 1951), STOSS (1940), ZIETZSCHMANN and KRÖLLING (1955), and BARONE and LAPLACE (1965). The estimated age of gestation in the present investigation is only approximate, based on the general development of an embryo as compared with similar developmental stages reported elsewhere. Included with each illustration of a reconstruction of the vessels is a drawing from the photograph of the embryo from which the reconstruction was made.

Nomenclature used in this investigation is in part adapted from BARRY (1951). The term "primitive" is frequently used for a structure that has not as yet achieved its definitive state.

Observations

Two major periods, the development of the aortic arches and the transformation of the aortic arches, can be recognized in the evolution of the definitive arch of the aorta and in the formation of the common brachiocephalic trunk (CBT). The division of the truncus arteriosus into the pulmonary and aortic trunks and the regression of the right sixth aortic arch can be regarded arbitrarily as a landmark between the two periods.

First Period. Development of the Aortic Arches

Since the development of the aortic arches is well documented in numerous mammalian species, only a brief description of this period of the development will be presented.

Twenty embryos from 5 to 12 mm CRL were available for examination of this period (Table 1). The youngest embryo 5 mm CRL (about 21 days gestation), has four pharyngeal pouches. The ventricular region of the heart is located rostral to the sinoatrial region at the level of the first and second pharyngeal pouches. The truncus arteriosus courses toward the ventral aspect of the second pharyngeal pouch where it forms a dilated distal end which is designated as the ventral aortic root. The first and second aortic arches originate from it (Fig. 1). The third aortic arch is just appearing. The left and right dorsal aortic roots, after receiving the first and second aortic arches, are reduced rostrally to very small vessels which can be traced in serial sections to the Rathke's pouch. The left and right dorsal aortic roots extend caudad to the level of the primordium of the thoracic appendage to form a single dorsal aorta. Just caudal to this junction, a pair of very small intersegmental arteries originate from the dorsal aorta and course toward the primordium of the thoracic appendage. Other intersegmental arteries which originate from the dorsal aortic roots are very indistinct and their serial number cannot be determined with certainty.

The next group consists of thirteen embryos from 6 to 8.5 mm CRL (about 22 to 25 days of gestation). The ventricular region of the heart is still oriented rostral to the sinoatrial region. The latter extends caudad as far as the developing lungs.

Table 1. *First period*

Number of embryos used	CRL mm	Approx. gestation age in days	Aortic arches present	General development
1	5	21	1; 2; (3)[a]	Similar to 21-day-old embryo (EWART, 1915). Approximately 25 somites. Primitive auditory vesicles are still connected with superficial ectoderm. Primary optic vesicles just appearing. A typical loop formation of the ventricle of the heart. Rathke's pouch just appearing
6	6—6.5	22	(1); 2; 3; 4; 6	Primary optic vesicles are distinct. Lens placode formed. Rathke's pouch and infundibulum distinct
7	7—8.5	25	(2); 3; 4; 6	Similar to 7.5 mm CRL embryo (VITUMS, 1936, 1951). First appearance of the optic cup. Lens vesicle still connected with superficial ectoderm. Auditory vesicles separated from the superficial ectoderm. Distinct endolymphatic duct
4	9—9.5	27—28	(2); 3; 4; 6	Lens vesicle completely separated from the superficial ectoderm. Auditory vesicles begin to differentiate into cochlear and vestibular portions. Rathke's pouch has a cup-shape. First trace of division of the truncus arteriosus
1	11.5	30	(2); 3; 4; (5); 6	Similar to 10 mm CRL embryo (VITUMS, 1936, 1951). Distinct division of the truncus arteriosus. Appearance of a vestigial 5th aortic arch
1	12.0	32	(2); 3; 4; 6	Distinct assymetry between the left and right 4th and 6th aortic arches. Left fourth aortic arch predominates and indicates already the future primitive arch of the aorta

[a] Parentheses indicate incompleteness of an aortic arch.

In an embryo 6.5 mm CRL four pairs of the aortic arches, the second, third, fourth and sixth can be observed (Fig. 2a). Only the paired third, fourth and sixth aortic arches are completely developed in the older embryos of this group (Fig. 2b). The first two pairs of the aortic arches are already regressed leaving only small ventral and dorsal remnants. The truncus arteriosus is located at the

Fig. 2a and b. A reconstruction (50×) of the aortic arches with related vessels of an embryo ca. 23 days (a) and 25 days (b) of gestation (6.5 mm CRL). Left lateral aspect. Reduced $^1/_2$ (a) and $^1/_5$ (b). *I* aortic arch already interrupted (in a); *II*, *III*, *IV* and *VI* aortic arches (in a); and *III*, *IV* and *VI* aortic arches (in b); *I* and *II* aortic arches interrupted (in b); *1—4* see Fig. 1; *5* primitive pulmonary artery

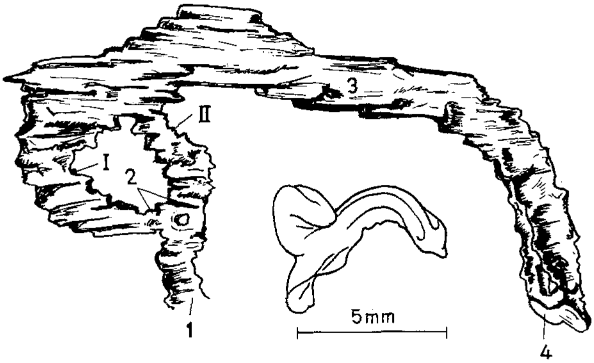


Fig. 1. A reconstruction (50 ×) of the aortic arches with related vessels of an embryo ca. 21 days of incubation (5 mm CRL). Left lateral aspect. Reduced $^1/_5$. *I* first aortic arch; *II* second aortic arch; *1* truncus arteriosus; *2* ventral aortic root; *3* dorsal aortic root; *4* dorsal aorta

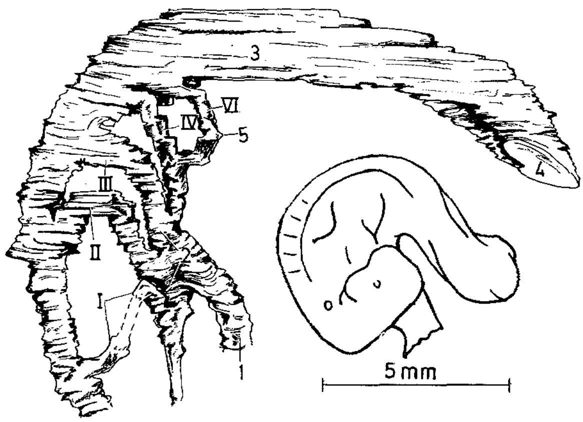


Fig. 2a

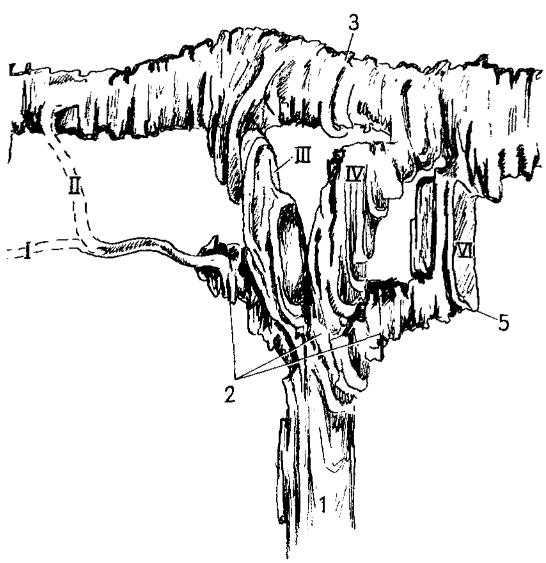


Fig. 2b

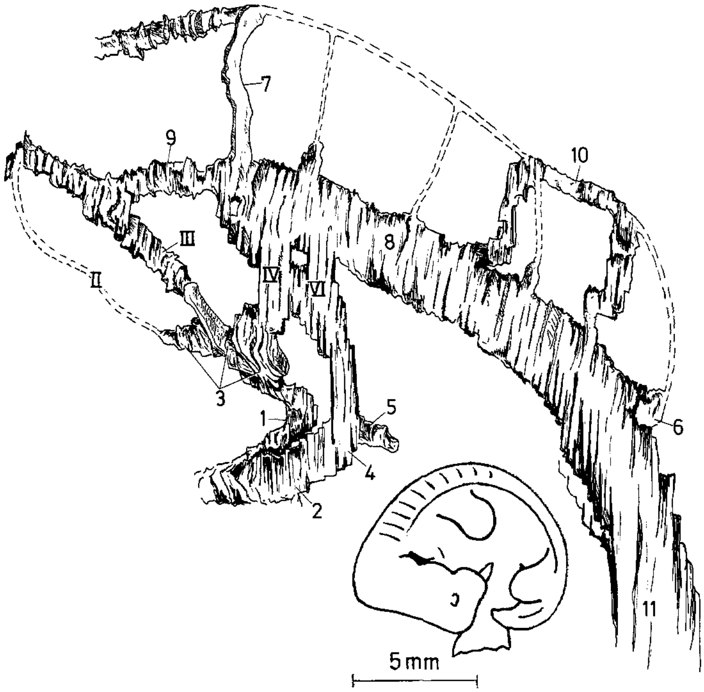


Fig. 3. A reconstruction (50×) of the aortic arches with related vessels of an embryo ca. 27 days of gestation (9.5 mm CRL). Left lateral aspect. Reduced $^1/_2$. *II* second aortic arch regressed; *III, IV, VI* see Fig. 2; *1* aortic trunk; *2* pulmonary trunk; *3* ventral aortic root; *4* ventral root of the sixth aortic arch; *5* primitive pulmonary artery; *6* sixth cervical intersegmental artery; *7* preatlantal artery; *8* dorsal aortic root; *9* carotid duct; *10* longitudinal anastomosis; *11* dorsal aorta

level of the third pharyngeal pouch. The middle, dorsoventrally flattened part, of the aortic root, from which the third and fourth aortic arches originate, appears to be unpaired. However, the left and right halves of the ventral aortic root are quite distinct. A paired outgrowth from the ventral aortic root extends rostrad from which the remnants of the first two aortic arches originate. In older embryos of this group, a paired outgrowth from the caudal part of the ventral aortic root can also be observed, with which the sixth aortic arches are connected. A pair of small primitive pulmonary arteries are observed at the junction of the sixth aortic arches with the ventral aortic roots. The left and right dorsal aortic roots unite at the level of the first thoracic segment.

The first trace of division of the truncus arteriosus into the aortic and pulmonary channels can be observed in four embryos from 9 to 9.5 mm CRL (about 27—28 days of gestation). This division first begins at the ventral aortic root area, between the fourth and sixth aortic arches, and progresses into the truncus arteriosus. The caudal part of the ventral aortic root together with the sixth aortic arches becomes related to the pulmonary trunk, while the cranial part of the ventral aortic root together with the other aortic arches remains associated with the aortic trunk (Fig. 3). The ventricles of the heart are faced mainly rostral. Only in one embryo, of 9.5 mm CRL, was the ventricular region already ventral to the atrial region.

The third aortic arch courses from the ventral aortic root dorso-rostrad and the segment of the dorsal aortic root between the third and fourth aortic arches, the carotid duct, is considerably attenuated. An extensive fusion can be observed between the fourth and sixth aortic arches at their junction with the dorsal aortic root. Mesodermal islands are developing in this area. The primitive pulmonary arteries originate at the junction of the sixth aortic arches with their ventral roots. The course of the primitive pulmonary arteries can be traced to the developing lungs. The union of the left and right dorsal aortic roots takes place at the level of the first rib. Just rostral to this junction, a pair of well developed sixth cervical intersegmental arteries is given off from the dorsal aortic roots. These arteries supply the thoracic appendage buds. Five more pairs of cervical intersegmental arteries originate from the dorsal aortic roots. A relatively well developed pair of intersegmental arteries originates from the dorsal aortic roots at the level of the fourth aortic arch. According to their position between the occipital segment and atlas and relation to the first cervical nerves, these arteries are regarded as the preatlantal arteries. A longitudinal anastomosis extends from the preatlantal artery caudad, receiving on its way the first to fifth cervical intersegmental arteries, and terminating on the sixth cervical intersegmental artery.

In two older embryos of 11.5 and 12 mm CRL (about 30—32 days of gestation) the ventricles of the heart are located mainly ventral to the atrial region but the apex of the heart is still directed rostrad and reaches the level of the second visceral arch. The division of the truncus arteriosus into the aortic and pulmonary trunks has progressed considerably but a total separation of both trunks has not been completed. The aortic trunk courses at the right aspect of the pulmonary channel and divides at the level of the third pharyngeal pouch into the left and right ventral aortic roots from each of which the fourth, third and remnants of the second aortic arches originate. The cranio-dorsal course of the third aortic arch is distinct. The pulmonary trunk divides into the left and right ventral roots from which the left and right sixth aortic arches, respectively, originate. Distinct primitive pulmonary arteries originate from the point of junction between the sixth aortic arches and their ventral roots. In the embryo of 11.5 mm CRL, a small vessel originates from the left ventral aortic root very close to the origin of the fourth aortic arch. This vessel courses dorsad between the fourth and sixth aortic arches and eventually joins the fused part of the fourth and sixth aortic arches (Fig. 4). On the right side, a similar small vessel originates from the ventral aortic root and after a short course dorsad joins the right fourth aortic arch. According to their position, these vessels are regarded as the vestigial fifth aortic arches. A small outpocketing from the pharynx which projects toward the rudimentary fifth aortic arch may be regarded as the fifth pharyngeal pouch. The left fourth and sixth aortic arches are larger than their respective arches of the right side. This assymetry is well marked in the embryo of 12 mm CRL in which the outlines of the primitive arch of the aorta can already be seen (Fig. 5). The fusion between the fourth and sixth aortic arches at their junction with the

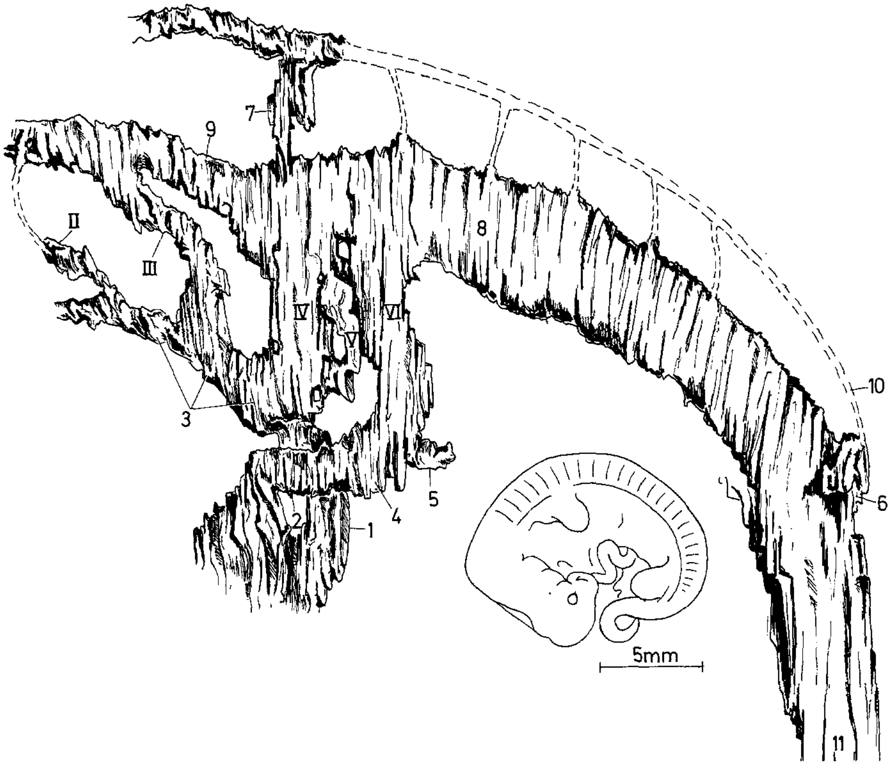


Fig. 4. A reconstruction (50×) of the aortic arches with related vessels of an embryo ca. 30 days of gestation (11.5 mm CRL). Left lateral aspect. Reduced $^1/_2$. *II* second aortic arch regressed; *III—VI* third through sixth aortic arches; *1—11* see Fig. 3

dorsal aortic roots with the formation of the mesodermal islands can be observed as in the previous group of embryos.

The left dorsal aortic root is considerably larger than the right one. The carotid duct is markedly attenuated. The preatlantal artery originates from the caudal end of the carotid duct. The longitudinal anastomosis extends from the preatlantal artery to the sixth cervical intersegmental artery. Other cervical intersegmental arteries are very small and partially regressed. The left and right dorsal aortic roots unite at the level between the first and second ribs. The left and right sixth cervical intersegmental arteries originate from the dorsal aortic roots at the level of the sixth cervical vertebra. They course to the developing thoracic appendages.

Second Period. Transformation of the Aortic Arches and Formation of the Definitive Arch of the Aorta and the Common Brachiocephalic Trunk

Three distinct stages of development precede the formation of the definitive arch of the aorta and the common brachiocephalic trunk.

Stage 1 (Figs. 6, 7a and b, 11a and b; Table 2). Observations are based on six embryos from 14 to 15.5 mm CRL (about 34—35 days of gestation). The base

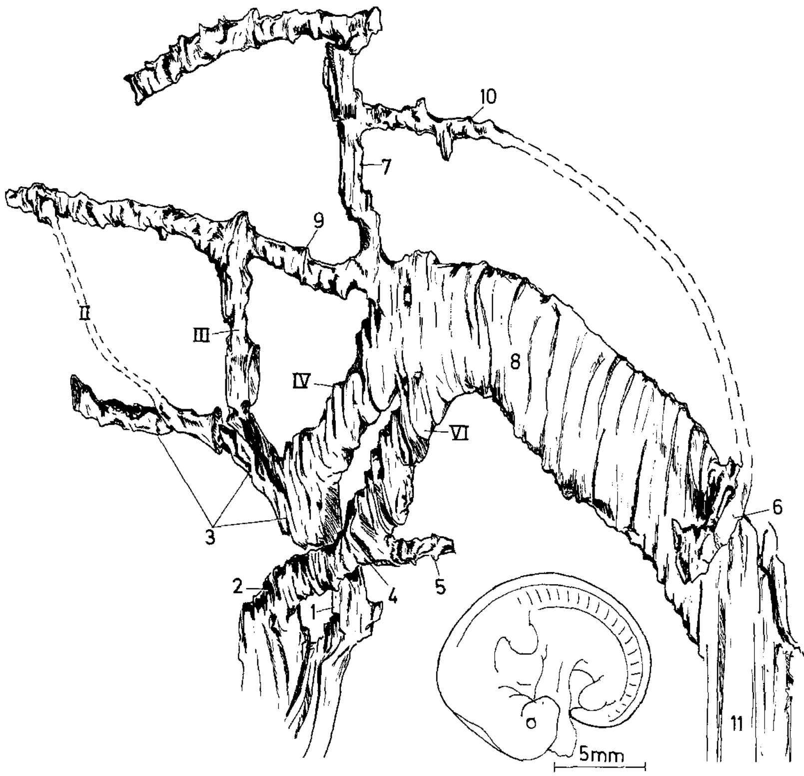


Fig. 5. A reconstruction (50×) of the aortic arches with related vessels of an embryo ca. 32 days of gestation (12 mm CRL). Left lateral aspect. Reduced $^1/_2$. *II* second aortic arch regressed; *III, IV, VI* see Fig. 2; *1—11* see Fig. 3

of the heart extends craniad as far as the level of the sixth cervical vertebra. The apex of the heart is oriented caudo-ventral and reaches the level of the fourth thoracic vertebra. The truncus arteriosus is completely subdivided into the pulmonary and the aortic channels. The right sixth aortic arch is regressed leaving only its ventral root from which the right primitive pulmonary artery originates. The origin of the left primitive pulmonary artery is very close to the right one. The left sixth aortic arch, the ductus arteriosus, is relatively short. It joins the ventral aspect of the primitive arch of the aorta at an angle of 90 to 100° at the level of the sixth or seventh cervical vertebra. The lumen of the ductus arteriosus at the junction with the primitive arch of the aorta is relatively smaller than the lumen of the latter. The longitudinal axis of the ductus arteriosus and the pulmonary trunk is directed ventrad. The left recurrent laryngeal nerve branches from the vagal nerve at the point where the ductus arteriosus joins the primitive arch of the aorta. The left recurrent laryngeal nerve courses around the caudal aspect of the ductus arteriosus craniad and is located between the trachea and the left fourth aortic arch.

The relatively long aortic trunk divides into a larger left ventral aortic root and a smaller right ventral aortic root. The larger left and much smaller right

Table 2. *Second period*

Number of embryos used	CRL mm	Approx. gestation age in days	Position of the heart base	Position of the heart apex	Position of the arch of the aorta[a]	Position of the ductus arteriosus	Position of the origin of the left subclavian artery
First stage: Primitive mammalian pattern — 3 vessels — innominate artery, left common carotid artery, left subclavian artery							
6	14—15.5	34—36	C6	T4 to T5	C5 to C6	C6 to C7	Caudal to the ductus arteriosus
Second stage: 2 vessels — brachiocephalic artery, left subclavian artery							
7	14.5—16.6	36—37	T1	T6 to T7	C7 to T1	T1 to T2	At the junction of the ductus arteriosus with the primitive arch of the aorta
Third stage: 2 vessels as in the second stage. First appearanc of the bicarotid trunk							
17	16—20.5	38—40	T2 to T3	T6 to T9	T1 to T3	T2 to T4	Cranial to the ductus arteriosus
Final stage: Common brachiocephalic trunk							
34	19—35	42—49	T3 to T4	T8 to T9	T3 to T6	T4 to T6	On the CBT. Level of T3

C = cervical vertebra; T = thoracic vertebra.
[a] Primitive in stage 1—3.

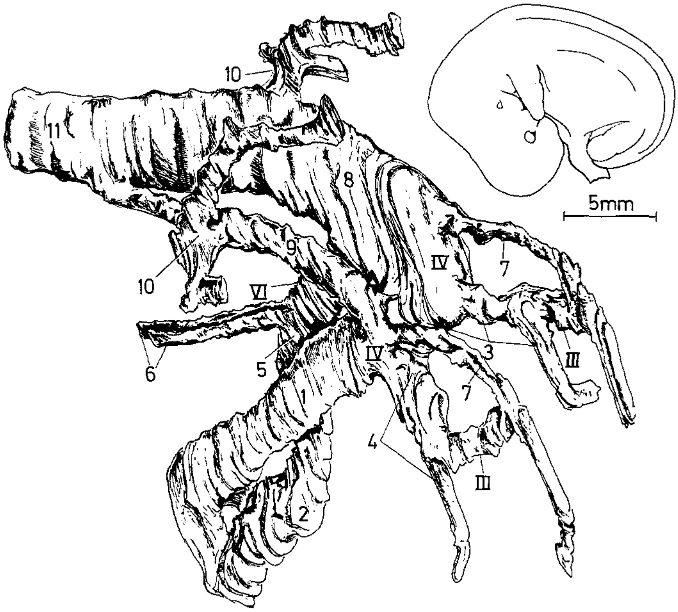
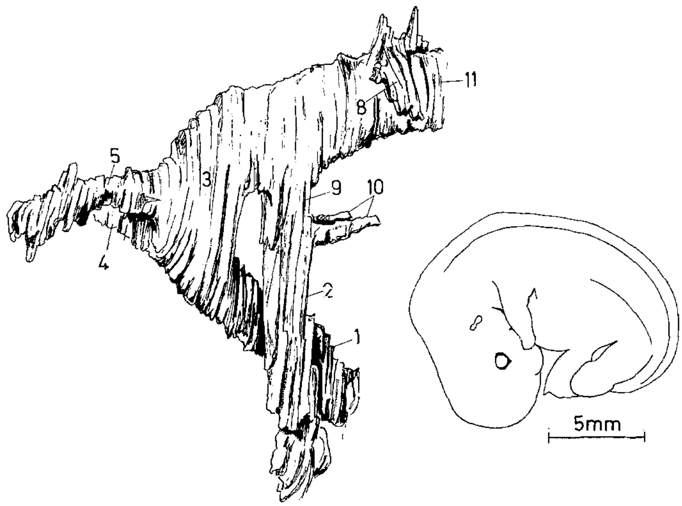
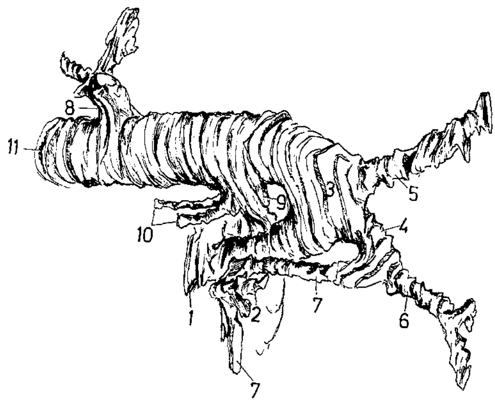


Fig. 6. A reconstruction (50×) of the aortic arches and their derivatives of an embryo ca. 34 days of gestation (14 mm CRL). Right lateral aspect. Reduced $^{1}/_{2}$. *III*, *IV*, *VI* see Fig. 2; *1* aortic trunk; *2* pulmonary trunk; *3* left ventral aortic root; *4* right ventral aortic root; *5* remnant of the right ventral root of the sixth aortic arch; *6* primitive pulmonary arteries; *7* carotid duct; *8* left dorsal aortic root; *9* right dorsal aortic root; *10* sixth cervical intersegmental artery; *11* dorsal aorta



a



b

Fig. 7a and b. A reconstruction (50×) of the primitive arch of the aorta and the vessels of the primitive mammalian pattern of an embryo ca. 35 days of gestation (15 mm CRL). 7a Left lateral aspect; 7b Right dorsal aspect. Reduced $^1/_2$. *1* ascending aorta; *2* pulmonary trunk; *3* primitive arch of the aorta; *4* innominate artery; *5* left common carotid artery; *6* right common carotid artery; *7* right subclavian artery; *8* left subclavian artery; *9* ductus arteriosus; *10* primitive pulmonary arteries; *11* dorsal aorta

dorsal aortic roots can still be observed in younger embryos of this stage. Both dorsal aortic roots unite caudal to the origins of the sixth cervical intersegmental arteries. The segments of the left and right dorsal aortic roots between the fourth and third aortic arches, the carotid ducts, are still present, as very attenuated vessels in younger embryos of this stage. The preatlantal artery is already regressed. Cranial to the third aortic arches, the dorsal aortic roots can be traced in serial sections to the infundibulum.

The left and right fourth aortic arches are easily recognizable in an embryo of 14 mm CRL. The dorsal limit of the left fourth aortic arch is marked by the caudal end of the carotid duct. The proximal limit of the left fourth aortic arch is marked by the caudal end of the ventral aortic root between the third and fourth aortic arches. Also the same landmarks form the dorsal and ventral limits of the very short right fourth aortic arch. The right recurrent laryngeal nerve is given off from the vagal nerve caudal to the right fourth aortic arch and curves around its caudal and medial aspect.

As soon as the carotid ducts disappear in older embryos of this stage, the dorsal limits of the left and right fourth aortic arches no longer can be determined with certainty. The left fourth aortic arch, including the proximal part of the ventral aortic root and the dorsal aortic root, as far caudal as the sixth cervical intersegmental artery, becomes the *primitive arch of the aorta* (Fig. 7a, b). Its curvature has a U-shape in embryos of this stage but changes its form to a V-shape in older embryos. The curvature of the primitive arch of the aorta is located at the level of the fifth or sixth cervical vertebra. The aortic trunk from the semilunar valves to its bifurcation into the ventral aortic roots constitutes the ascending aorta.

After the right dorsal aortic root looses its caudal connection with the left dorsal aortic root, the proximal part of the right ventral aortic root to the origin of the fourth aortic arch becomes the so-called innominate artery, which appears as a branch of the primitive arch of the aorta. The right sixth cervical intersegmental artery, which originates from the right dorsal aortic root, together with this root and the right fourth aortic arch forms the right subclavian artery, which appears as a branch of the innominate artery. The left sixth cervical intersegmental artery originates from the left dorsal aortic root just caudal to its junction with the ductus arteriosus, and becomes the left subclavian artery. The other cervical intersegmental arteries cranial to the sixth cervical intersegmental artery are regressed.

The left and right third aortic arches, although much shorter than in the embryos of 12 mm CRL, can still be recognized in younger embryos of this stage. However, after the regression of the carotid ducts, the distal ends of the third aortic arches cannot be determined with certainty. The segment of the ventral aortic root between the left third and fourth aortic arches becomes the left common carotid artery, which in this stage appears as a direct branch of the primitive arch of the aorta. The segment of the right ventral aortic root between the right third and fourth aortic arches becomes the right common carotid artery which appears as a branch of the innominate artery. Cranial to the origins of the third aortic arches, the left and right ventral aortic roots can be traced in serial sections toward the mandibular region as relatively small vessels, the external carotid arteries.

Summary. This stage of transformation of the aortic arches is characterized by complete division of the truncus arteriosus into the aortic and pulmonary trunks, by regression of the right sixth aortic arch, and by formation of the *primitive arch of the aorta* from which three vessels, the innominate, the left common carotid, and the left subclavian arteries are given off. This arrangement of vessels can be regarded as the *primitive mammalian pattern.*

Stage 2 (Fig. 8; Table 2). Included in the specimens examined are seven embryos from 14.5 to 16.5 mm CRL (about 36—37 days of gestation). The general development of the embryos of this stage is only slightly advanced beyond that of the embryos of the preceding stage.

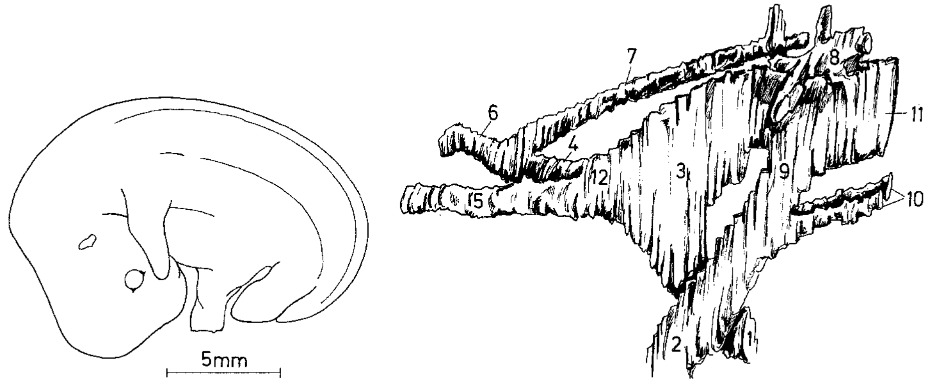


Fig. 8. A reconstruction (50×) of the primitive arch of the aorta with related vessels of the second stage of development of an embryo ca. 36 days of gestation (16 mm CRL). Left lateral aspect. Reduced $^1/_2$. *1—11* see Fig. 7; *12* brachiocephalic artery

The base of the heart lies just cranial to the first thoracic vertebra at which level is also located the curvature of the primitive arch of the aorta. Its curvature has assumed the form of a letter V and with an angle of about 80°. The apex of the heart is directed slightly caudo-ventrad reaching the level of the sixth intercostal space. The short ductus arteriosus joins the ventral aspect of the primitive arch of the aorta in an angle of about 140° at the level of the first to second thoracic vertebra. The lumen of the primitive arch of the aorta at this junction is larger than that of the ductus arteriosus. The longitudinal axis of the ductus arteriosus and the pulmonary trunk is directed slightly dorso-craniad. The proximal ends of the left and right primitive pulmonary arteries are approaching each other. However, they still originate separately.

The proximal end of the left common carotid artery (the old left ventral aortic root between the third and fourth aortic arches) and the innominate artery (the caudal part of the old right ventral aortic root) are joined as a short common vessel, the brachiocephalic artery, which appears as a cone-like extension of the primitive arch of the aorta. The innominate artery, which still can be identified, at least as a part of the old right ventral aortic root, divides at the level of the fifth cervical vertebra into two vessels which course in opposite directions to each other. One of these, the right subclavian artery, courses caudad along the trachea and esophagus, the other vessel, the right common carotid artery, runs craniad along the trachea. The proximal part of the right subclavian artery, the old right fourth aortic arch, can still be identified by its relation to the right recurrent laryngeal nerve. The left subclavian artery originates from the primitive arch of the aorta at the level of the junction of the ductus arteriosus with the primitive arch of the aorta.

Summary. Characteristic features of this stage are the further caudal location of the heart, primitive arch of the aorta, and ductus arteriosus, and the formation of the brachiocephalic artery by the fusion of the left common carotid and innominate arteries. The left subclavian artery originates now from the primitive arch of the aorta at the level where the latter joins with the ductus arteriosus. Two vessels, the brachiocephalic and left subclavian arteries, originate from the primitive arch of the aorta in this stage.

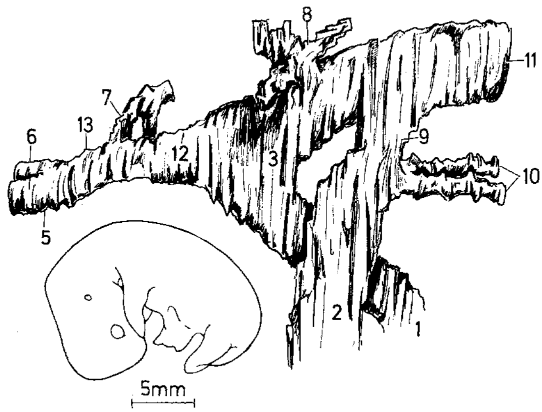


Fig. 9. A reconstruction (50×) of the primitive arch of the aorta with related vessels of the third stage of development of an embryo ca. 38 days of gestation (17 mm CRL). Left lateral aspect. Reduced $^1/_2$. *1—12* see Fig. 8; *13* bicarotid trunk

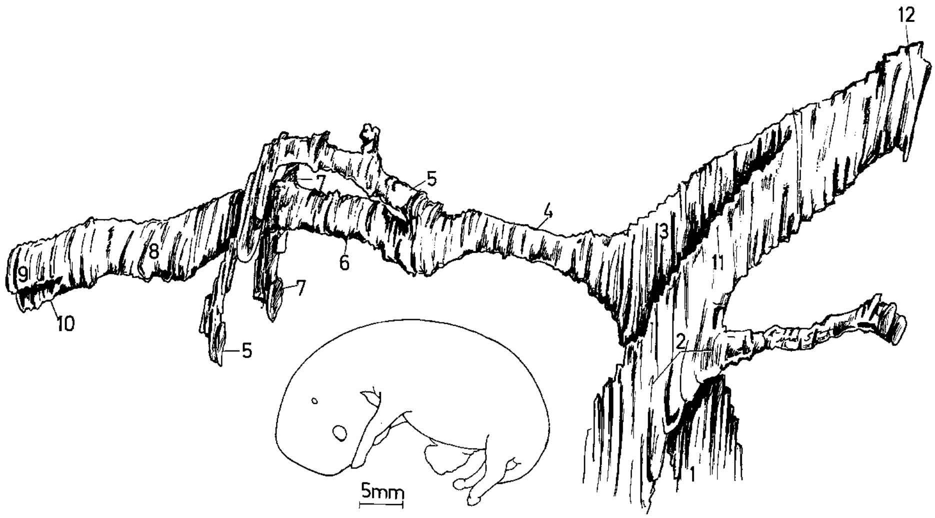


Fig. 10. A reconstruction (50×) of the definitive arch of the aorta with related vessels of the final stage of development of an embryo ca. 42 days of gestation (34.5 mm CRL). Left lateral aspect. Reduced $^1/_2$. *1* ascending aorta; *2* pulmonary artery; *3* arch of the aorta; *4* common brachiocephalic trunk; *5* left subclavian artery; *6* brachiocephalic artery; *7* right subclavian artery; *8* bicarotid trunk; *9* left common carotid artery; *10* right common carotid artery; *11* ductus arteriosus; *12* dorsal aorta

Fig. 11a—d. Cross section (25×) of embryos: 14 mm CRL (a); 15 mm CRL (b); 17 mm CRL (c) and 34.5 mm CRL (d). Delafield hematoxylin. (a) and (d) 20 microns; (b) and (c) 15 microns. Notice position of the ductus arteriosus with relation to the axial skeleton in different developmental stages. *1* aortic trunk; *2* ductus arteriosus; *3* primitive arch of the aorta (definitive arch of the aorta in d); *4* right dorsal aortic root; *5* pulmonary artery (primitive pulmonary artery in b); *C6, C7* sixth and seventh cervical vertebrae; *T2, T5* second and fifth thoracic vertebrae; *a* trachea; *b* esophagus; *c* vagus nerve; *d* left recurrent laryngeal nerve

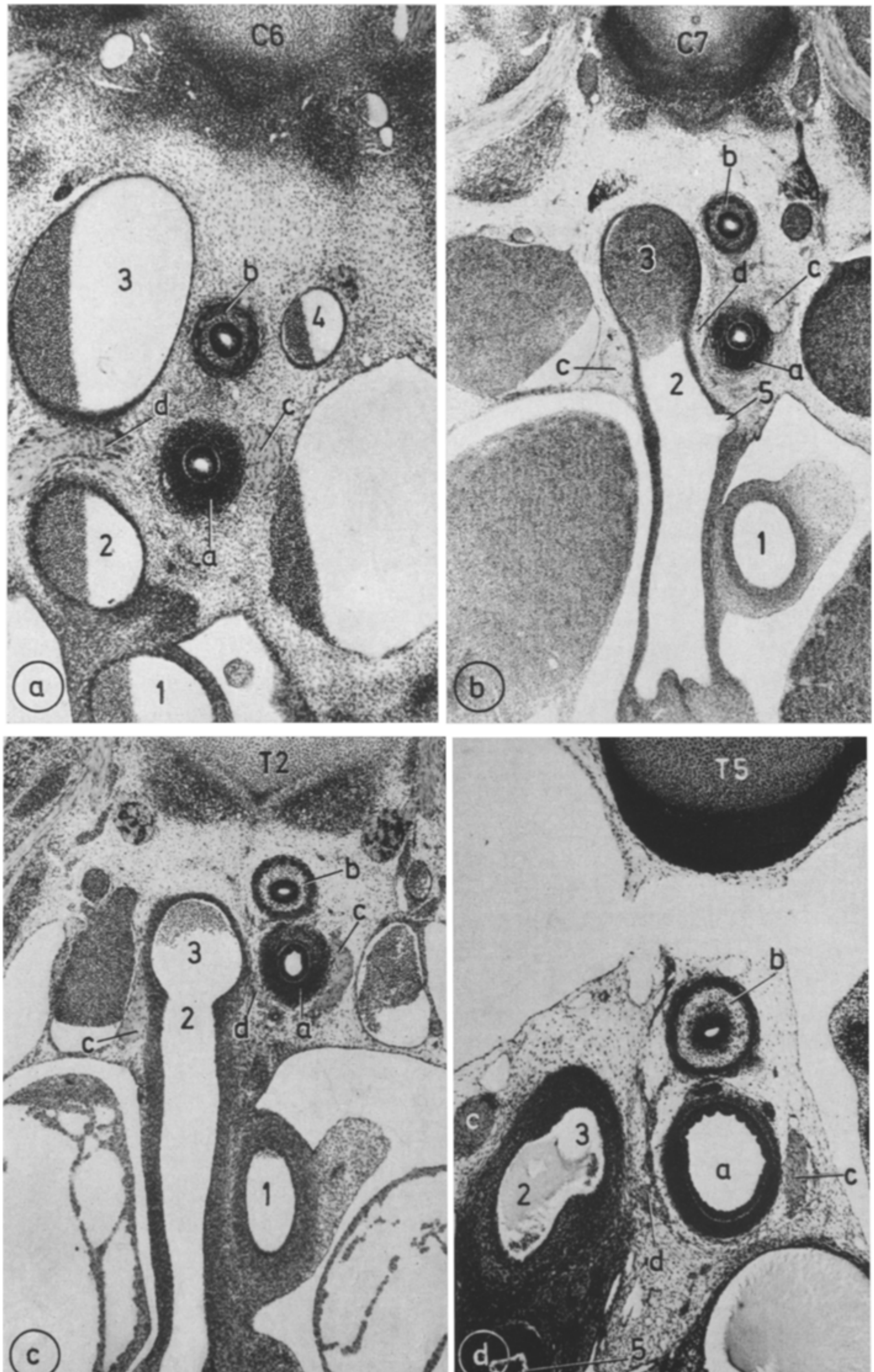


Fig. 11 a—d

Stage 3 (Figs. 9, 11c; Table 2). Observations are based on seventeen embryos from 16.0 to 20.5 mm CRL (about 38—40 days of gestation). The heart has moved into the thoracic cavity. The base of the heart lies at the level of the first or second rib in the younger embryos, and at the level of the third or fourth rib in older embryos of this stage. The apex of the heart extends to the level of the sixth or seventh rib in younger embryos, and to the level of the eighth or ninth rib in older embryos of this stage. The primitive arch of the aorta has a typical V-shape with an angle of 70 to 80°. The cranial border of the primitive arch of the aorta is located at the level of the first rib in younger embryos and at the level of the second or third rib in older embryos of this stage. The ductus arteriosus is relatively short. Its lumen, at the junction with the primitive arch of the aorta in younger embryos of this stage, is still smaller than that of the primitive arch of the aorta. However, in older embryos of this stage, the lumina of both channels have almost the same diameter. It joins the primitive arch of the aorta at the ventral aspect at an angle of 120° at the level of the second to fourth thoracic vertebra. The longitudinal axis of the ductus arteriosus and the pulmonary trunk is directed as in stage 2. The right and left primitive pulmonary arteries are united at their origins to form a short common trunk.

The brachiocephalic artery is considerably longer than in the preceding stage. It originates with a cone-like enlargement from the primitive arch of the aorta. Both the left and right common carotid arteries are already fused at their proximal ends to form a short bicarotid trunk. The right subclavian artery, which is shorter than in the preceding stage, originates at the level of the sixth cervical vertebra. The left subclavian artery originates from the primitive arch of the aorta cranial to the distal end of the ductus arteriosus, between the latter and the brachiocephalic artery.

Summary. Typical for this stage is the elongation of the brachiocephalic artery and first appearance of the bicarotid trunk. The location of the origin of the left subclavian artery is cranial to the ductus arteriosus.

Final Stage (Figs. 10, 11d; Table 2). Included are 34 embryos from 19 to 35 mm CRL (about 42—49 days of gestation), seven older embryos (41—88 mm CRL, about 50—65 days of gestation), and several fetuses (165 mm to 335 mm CRL, about 100—150 days of gestation), and a full-term fetus. The first trace of fusion of the sternal primordia can be observed in the embryos of 24 mm CRL and older.

The base of the heart lies in younger embryos of this stage at the level of the second rib, while in the older embryos and in the fetuses, the base is at the level of the third intercostal space. The apex of the heart in younger embryos of this stage reaches the level of the eighth intercostal space, while in the older embryos and fetuses, the apex is at the level of the ninth rib. Individual variations have also been observed. The longitudinal axis of the heart is directed dorso-ventrad with a slight caudal deviation. The arch of the aorta has achieved its definitive position and shape. It lies at the level of the third intercostal space. Variations in the position of the arch of the aorta range from fourth to fifth intercostal space. The angle of the flat V-shaped arch of the aorta has increased to 110°. The lumen of the arch of the aorta at the junction with the ductus arteriosus is markedly smaller than that of the ductus arteriosus. The ductus arteriosus joins now

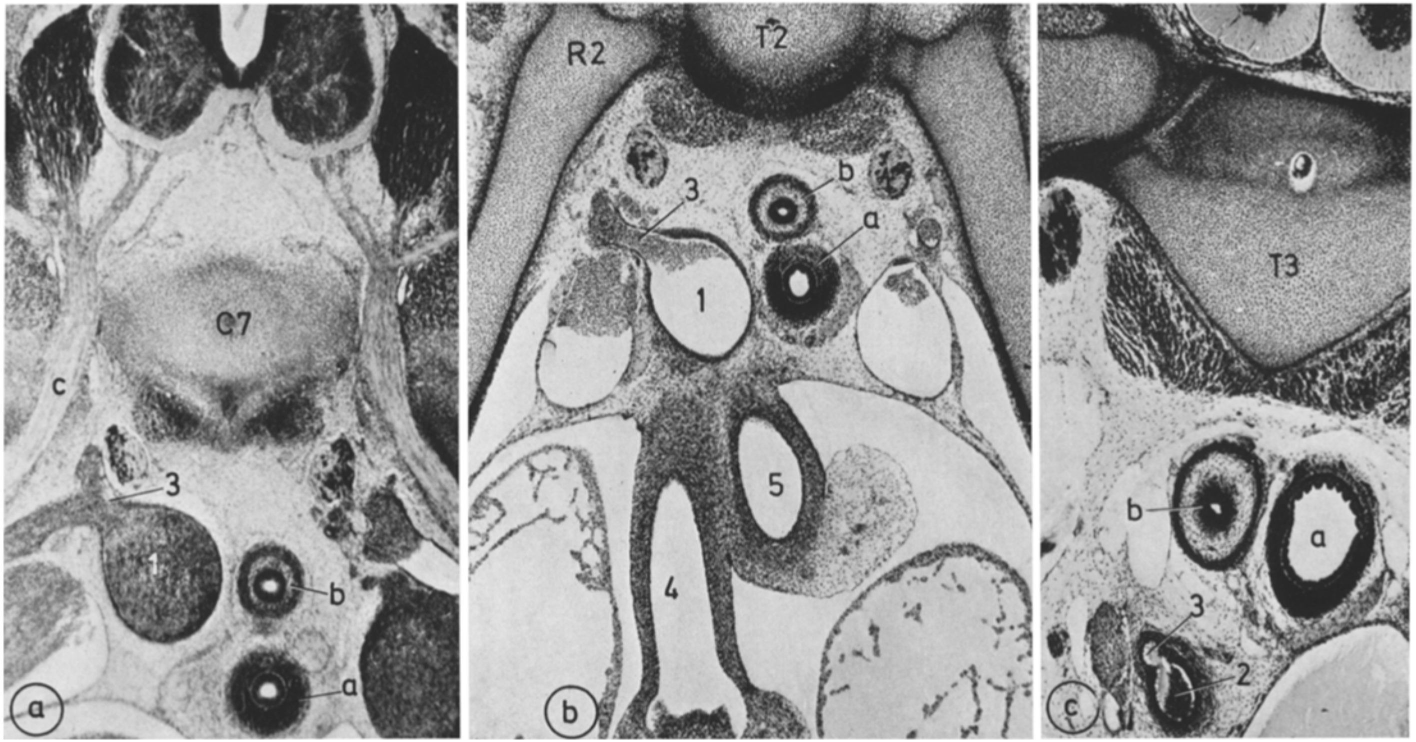


Fig. 12a—c. Cross section (25×) of embryos: 15 mm CRL (a); 17 mm CRL (b); and 34.5 mm CRL (c). Delafield hematoxylin. (a) 15 microns; (b) and (c) 20 microns. Notice position of the origin of the left subclavian artery with relation to the axial skeleton in different developmental stages. *1* primitive arch of the aorta; *2* common brachiocephalic trunk; *3* left subclavian artery; *4* pulmonary trunk; *5* aortic trunk; *a* trachea; *b* esophagus; *c* seventh cervical nerve; *C7* seventh cervical vertebra; *T2*, *T3* second and third thoracic vertebrae; *R2* second rib

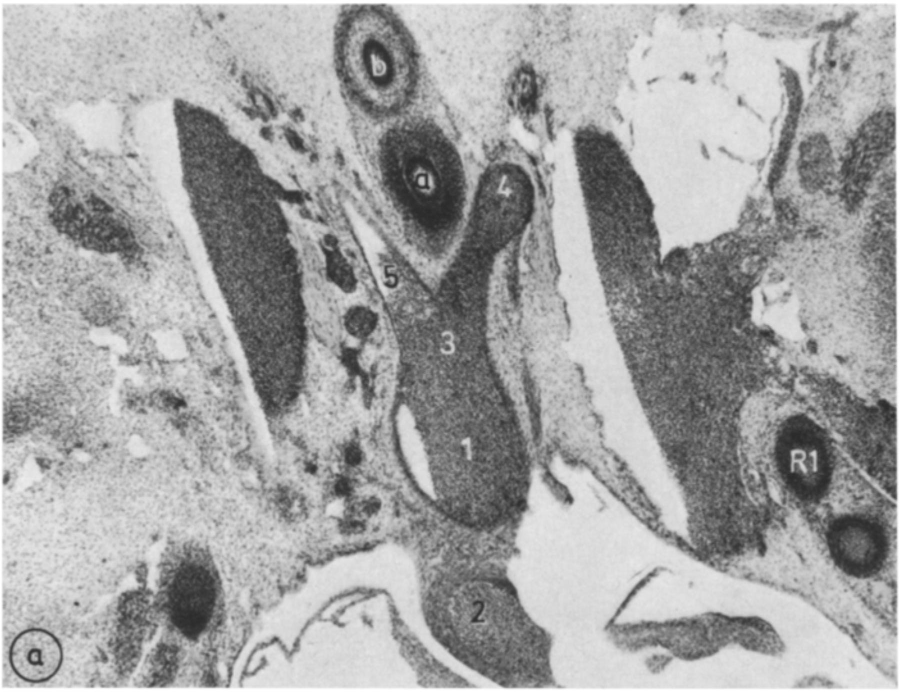


Fig. 13a—c. Frontal section (25×) of embryos: 16.5 mm CRL (a); 17 mm CRL (b) and 20 mm CRL (c). Alum-carmine (a and b); Delafield hematoxylin (c). 20 microns. Notice position of the origin of the right subclavian artery with relation to the axial skeleton in different developmental stages. *1* primitive arch of the aorta; *2* ductus arteriosus; *3* brachiocephalic artery; *4* right subclavian artery; *5* left common carotid artery; *R1* first rib; *a* trachea; *b* esophagus; *c* left recurrent laryngeal nerve; *d* vagus nerve

at the lateral aspect of the arch of the aorta at the level of the fifth thoracic vertebra. In the earlier stages, this junction was at the ventral aspect of the primitive arch of the aorta and its lumen at this point was larger than that of the ductus arteriosus (compare Figs. 7—10 and 11a—d). Also the angle of junction has increased to 150°, and the longitudinal axis of the ductus arteriosus and the pulmonary trunk is directed distinctly craniad. Both the left and right branches of the pulmonary artery originate by a relatively long common trunk.

The origin of the left subclavian artery has joined at the level of the third thoracic vertebra the brachiocephalic artery, which now is regarded as the common brachiocephalic trunk (Figs. 10 and 12c). It originates with a typical cone-like enlargement at the summit of the arch of the aorta. The segment of the vessel from the origin of the left subclavian artery to the origin of the right subclavian artery is of variable length and can be recognized as the brachiocephalic artery. The right subclavian artery is considerably shorter than in the earlier stages; it originates at the level of the first rib (compare Fig. 13a—c). The lengths of the bicarotid trunk and the CBT also show individual variations.

The formation of the arch of the aorta and the CBT in the older embryos (41—88 mm CRL) and in the fetuses is basically similar to that of the embryos of the final stage.

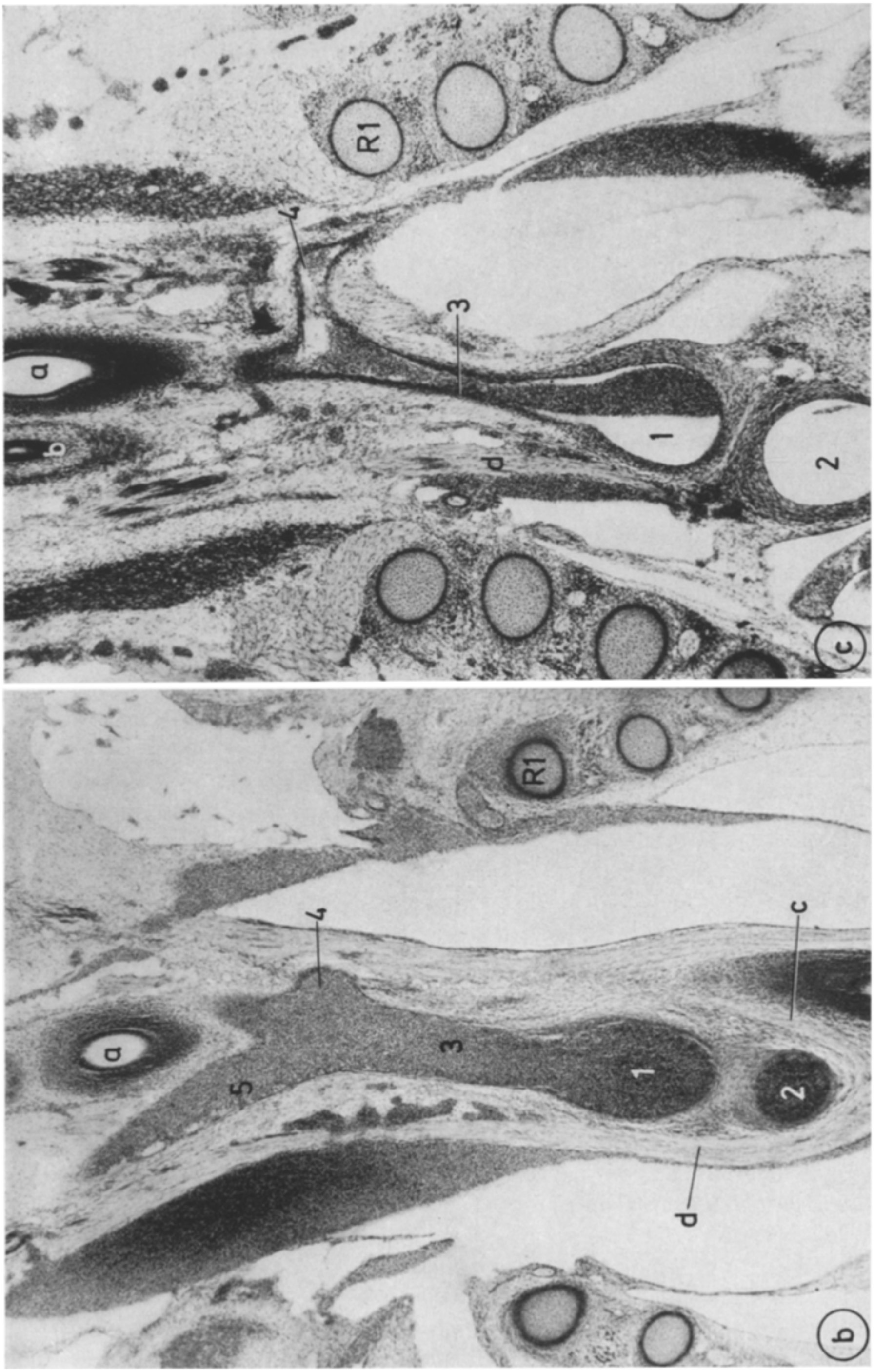


Fig. 13 b and c

Summary. The final stage of the transformation of the components of the aortic arches is characterized by the formation of the definitive arch of the aorta and by the development of a single arterial trunk, the common brachiocephalic trunk, which originates with a cone-like enlargement from the arch of the aorta.

Discussion

The aortic arches observed in the present study originate from a distinct root area at the distal end of the truncus arteriosus. CONGDON (1922) called the dilated distal end of the truncus arteriosus the aortic sac. In agreement with BARRY (1951), this root area of the truncus arteriosus is designated as the ventral aortic root, which is identical with the "ventral aorta" of the older nomenclature. When the truncus arteriosus divides into the aortic and pulmonary channels, the left and right ventral roots of the left and right sixth aortic arches, respectively, become related to the pulmonary channel, while the left and right ventral aortic roots of the other aortic arches remain associated with the aortic channel. The results of the present investigation do not support LLORCA's (1934) conclusion that the ventral aorta is absent in those animals in which both carotids and subclavian arteries originate from a common trunk. The paired dorsal aortae, representing the efferent channels of the aortic arches, are called in the present study the dorsal aortic roots, and the fused part of the originally paired dorsal aortae is designated as the dorsal aorta.

Six pairs of the aortic arches are observed in the first period of the development. The first two pairs of the aortic arches regress very early while the fifth aortic arch appears in a vestigial form relatively late in the first period of the development, when the truncus arteriosus divides into the aortic and pulmonary channels. This agrees with the author's earlier reports on the development of the aortic arches in the equine embryos (VITUMS, 1949, 1951). Extensive fusions with formation of the mesodermal islands and wide communications are observed between the distal ends of the fourth and sixth aortic arches especially in the later developmental stages of the first period. However, these communications, in agreement with TANDLER (1902, 1909), are not interpreted as the vestigial fifth aortic arch.

Seven pairs of the cervical intersegmental arteries are observed in the first period of the development. The sixth cervical intersegmental artery supplies the thoracic appendage-bud and is considered as the primitive subclavian artery. The origin of both the left and right primitive subclavian arteries changes from the dorsal aorta to the dorsal aortic roots in the older embryos of the first period of development. In agreement with BROMAN (1908), this is regarded as an apparent migration that is caused by the movement of the aortic arches complex caudad.

Rostral to the first cervical intersegmental artery, a distinct intersegmental artery is observed. According to its location between the occipital segment and the atlas, and its relation to the first cervical nerve, this artery is identified as the preatlantal artery. This vessel was already observed and correctly interpreted by FRORIEP (1886) in bovine embryos, and by HOCHSTETTER (1890) in rabbit embryos. SCHMEIDEL (1932), in his extensive report on the development of the vertebral artery in human embryos, called this artery the postoccipital artery.

The term proatlantal artery was proposed by PADGET (1955). A comprehensive study on this subject was made by MOFFAT (1957, 1959) in rat embryos. GISEL (1959) proposed the term arteria suboccipitosegmentalis, and named the sixth cervical intersegmental artery the arteria brachiosegmentalis. The present investigation has adapted with minor grammatical changes the term preatlantal artery (= proatlantal artery of PADGET, 1955).

Apparent discrepencies in the literature concerning the origin of the subclavian artery from the sixth or seventh cervical intersegmental artery result from different interpretations of the serial number of the cervical intersegmental arteries. If the preatlantal artery is counted as the first cervical intersegmental artery, then the serial number of the cervical intersegmental artery from which the subclavian artery originates is seven. However, if the preatlantal artery is not included, then the origin of the subclavian artery is the sixth cervical intersegmental artery. The present investigation concerning the serial numbering of the subclavian artery is in agreement with observations by HOCHSTETTER (1890), SICHER (1912), SCHMEIDEL (1932), PADGET (1955), MOFFAT (1957, 1959), and GISEL (1959).

The shifting of the position of origin of the preatlantal artery from the level of the sixth aortic arch to the level of the caudal end of the carotid duct in equine embryos is similar to that observed by MOFFAT (1957, 1959) in rat embryos. However, this "migration craniad" along the dorsal aortic root is only an apparent migration resulting from the relative movement of the aortic arches caudad. The present observations also indicate that the proximal part of the preatlantal artery in equine embryos disappears before a complete regression of the carotid duct. A relatively late persistence of the preatlantal artery was reported by MOFFAT (1959) in rat embryos.

Three distinct stages of development precede the formation of the definitive arch of the aorta and the common brachiocephalic trunk. The primitive arch of the aorta appears in the equine embryos at about 35 days of gestation. Three vessels, the innominate (brachiocephalic) artery, the left common carotid artery, and the left subclavian artery, originate from the primitive arch of the aorta in the first stage of development. This arrangement of the vessels can be regarded as the *primitive mammalian pattern*, as implicitly recognized by RATHKE (1843) and by HOCHSTETTER (1891, 1906). The primitive mammalian pattern can also be identified in the canine embryos (VITUMS, unpublished). It is suggested that the primitive mammalian pattern may also appear in the embryonic development of other mammalian species (see Figs. 1—3, HOFMANN, 1914; Fig. 27, HEUSER, 1923). Apparently, the stage of the primitive mammalian pattern in human embryos leads directly into the adult state, after the arch of the aorta and its three vessels have attained their definitive position and shape (see Figs. 15 and 40, CONGDON, 1922).

A congenital anomaly has been reported by HUTYRA (1890) in a donkey in which three vessels, the right brachiocephalic (innominate) artery, the left common carotid artery and the left subclavian artery, originated from the arch of the aorta. This case apparently represents an arrest of the primitive mammalian pattern in the early embryonic development of this animal.

The primitive arch of the aorta incorporates, in addition to the left fourth aortic arch, the proximal part of the ventral aortic root and left dorsal aortic root from the fourth aortic arch to the origin of the left subclavian artery. This is in agreement with the observation by ZIMMERMANN (1890) in the human embryo and with the interpretation by BARRY (1951).

The present investigation indicates that the innominate (brachiocephalic) artery is derived from the proximal part of the right ventral aortic root. A similar origin of the innominate artery has been described by ZIMMERMANN (1890) in the human embryo. There is no evidence in the present study that the right fourth aortic arch is incorporated in the formation of the innominate artery, as it was suggest by MOFFAT (1959) for rat embryos. However, the present observations support the evidence that the right fourth aortic arch is incorporated in the formation of the definitive right subclavian artery. This is in agreement with observations by ZIMMERMANN (1890), CONGDON (1922), LEWIS (1923), HEUSER (1923), and BARRY (1951), but disagrees with the observations by HOFMANN (1914), LLORCA (1934), and MOFFAT (1959). Various congenital anomalies of the right subclavian artery also support the view that the right fourth aortic arch has been incorporated in the formation of a normal right subclavian artery. For references see BANCHI (1907), HOLZAPFEL (1899), BARRY (1951), and VITUMS (1962).

The common carotid arteries are derived in equine embryos from the ventral aortic roots between the third and fourth aortic arches. The third aortic arch proper, however, becomes the proximal part of the internal carotid artery, while its distal part is formed by the dorsal aortic root cranial to the third aortic arch. This is in agreement with the observations by TANDLER (1902), GOLUB (1931), and BARRY (1951), but disagrees with the observations by CONGDON (1922), and HAMMOND (1937). The opinion of MOFFAT (1959) that the common carotid arteries are developed from the elongation of the cranial portion of the aortic sac is in agreement with the present observations, assuming that the aortic sac and the ventral aortic root are homologous structures. It is suggested that the extensions of the left and right ventral aortic roots cranial to the third aortic arches give rise to the left and right external carotid arteries, respectively, in equine embryos.

A rare congenital anomaly of the left and right common carotid arteries has been reported in a Shetland pony by VITUMS (in press). The bicarotid trunk, which originated as usual from the brachiocephalic artery, was very short and divided at the thoracic inlet into the left and right common carotid arteries. Both common carotid arteries were very short, and each divided into a larger external and smaller internal carotid artery which coursed within the carotid sheath toward the head. The elongation of the left and right ventral aortic roots between the third and fourth aortic arches apparently did not occur in this case during the embryonic development. The observations by MOFFAT (1959) suggested that the extremely short common carotid arteries may result from the persistent carotid duct. Certain rare congenital anomalies of the carotid arteries have been described in humans. These anomalies may be of significance in the interpretation of the embryonic primordium of the carotid arteries. For discussion and references see ADAMS (1957).

The left subclavian artery, as the third vessel of the primitive mammalian pattern, originates from the primitive arch of the aorta caudal to the distal end of the ductus arteriosus. Both primitive subclavian arteries are homologous structures derived from the sixth cervical intersegmental arteries. However, the right primitive subclavian artery in its further development incorporates, in addition to the sixth cervical intersegmental artery, the right fourth aortic arch and the caudal segment of the right dorsal aortic root, while the left primitive subclavian artery retains its primitive feature. Thus, morphologically, the left and right subclavian arteries in the adult are not homologous structures.

Owing to the descent of the heart, secondary changes occur that affect the shape of the primitive arch of the aorta and the arrangement of the vessels of the primitive mammalian pattern in equine embryos (Fig. 14). It seems that the curvature of the primitive arch of the aorta, as it follows the descent of the heart, is subject to a continuous tension by the vessels that originate from the arch of the aorta. As a result of this tension the curvature of the primitive arch changes its form from a U-shape, at the level of the fifth cervical vertebra, to a V-shape, at the level of the thoracic inlet. A cone-like extension appears at the summit of the primitive arch of the aorta, into which the origins of the innominate artery and the left common carotid artery are incorporated thus forming the brachiocephalic artery in the second stage of development. This agrees with the observation by Hofmann (1914) and Heuser (1923) on the formation of the brachiocephalic artery in pig embryos. The formation of the brachiocephalic artery by a cranial expansion of the aortic sac has also been described by Krediet (1962) in pig embryos, which basically agrees with the present observations, assuming that the aortic sac and the ventral aortic root are homologous structures. Following these changes, the origin of the left subclavian artery in the second stage of development is at the level of the ductus arteriosus.

An arrangement of vessels similar to that found in the second stage in the present investigations has been reported in an adult bovine with a congenital cervical ectopic heart (Vitums, 1964). Apparently this condition was a result of an arrest of the descensus cordis before the definitive position of the arch of the aorta was achieved and the formation of the common brachiocephalic trunk was initiated.

By further caudal movement of the primitive arch of the aorta, as it was demonstrated in the third stage of development, elongation of the brachiocephalic artery and fusion of the origins of the right and left common carotid arteries takes place, resulting in the formation of a bicarotid trunk. The origin of the left subclavian artery in the third stage of development is very close to the brachiocephalic artery.

The present investigation indicates that the bicarotid trunk appears early in the development of equine embryos, before the common brachiocephalic trunk is formed. A relatively late formation of the bicarotid trunk has been reported by Hammond (1937) in bovine embryos. An absence of the bicarotid trunk has been reported by Skoda (1912) in an adult horse, which may be explained by a failure to form a common trunk for the origins of both carotid arteries in the third stage of development.

Finally, when the primitive arch of the aorta reaches its definitive position at the level of the third thoracic vertebra in equine embryos of about 42—49 days of gestation the angle of the arch of the aorta is more than 100° and resembles the shape of the arch of the aorta of an adult equine.

The origin of the left subclavian artery is already incorporated in the common brachiocephalic trunk. There is no evidence in equine embryos that the definitive shape of the arch of the aorta is already achieved before the CBT is formed. This disagrees with the conclusions by GOLUB (1931) for bovine embryos.

The present investigation suggests that a part of the primitive arch of the aorta contributes to the formation of the CBT. However, there is no evidence about the components of the primitive arch of the aorta that may be involved in the formation of the CBT in equine embryos.

The opinion by RATHKE (1843), PITZORNO (1903), and LASSILA (1927/28) that the origin of the left subclavian artery first is fused with the origin of the left common carotid artery to form the left innominate artery (which then unites with the right innominate artery to form the CBT) cannot be supported by the present investigation. It is suggested that in other mammalian species in which the CBT is present the development of this trunk might be similar to that of the equine species (see Figs. 5—7, LEWIS, 1923; Figs. 6—8, GOLUB, 1931; Figs 3—5, HAMMOND, 1937).

The origin of the left subclavian artery in equine embryos, following the descent of the heart and the primitive arch of the aorta, is also shifted caudad from its original level at the sixth cervical vertebra to the level of the third thoracic vertebra (Figs. 12a—c, 14). Since the distal end of the left subclavian artery is relatively fixed in its position, the proximal part of this artery must elongate in order to follow the descent of the primitive arch of the aorta. On the other hand, the right subclavian artery, following the descent of the heart, becomes considerably shorter (Fig. 13a—c). This shortening affects mainly that part of the right subclavian artery that is derived from the right dorsal aortic root. It can no longer be identified with certainty after the right subclavian artery has assumed its definitive position at the level of the first rib. However, the proximal part of the right subclavian artery, which is derived from the right fourth aortic arch, can be recognized in all stages of the development by the presence of the right recurrent laryngeal nerve, which curves around the caudal aspect of this part.

Simultaneously with the caudal movement of the left subclavian artery, its origin gradually changes position along the primitive arch of the aorta. These changes are in relation to the distal end of the ductus arteriosus (Fig. 14). While the latter is shifted caudad, the origin of the left subclavian artery appears to be "shifted" along the wall of the primitive arch of the aorta in the opposite direction. However, this "migration" of the left subclavian artery is only apparent and is only relative to the distal end of the ductus arteriosus and the cranial border of the primitive arch of the aorta, but it is not relative to the axial skeleton. This is in agreement with the interpretation of the so-called "migration" of the vessels by BROMAN (1908). There is no histological evidence in equine embryos that rearrangement of cells around the origin of the left subclavian artery takes place during this shifting along the arch of the aorta "by spreading apart above and closing in below" as it was stated by LEWIS (1923).

The present investigation indicates that the change of the position of the distal end of the ductus arteriosus is in correlation with the changes of the position of the heart and the primitive arch of the aorta. The ductus arteriosus lies in the

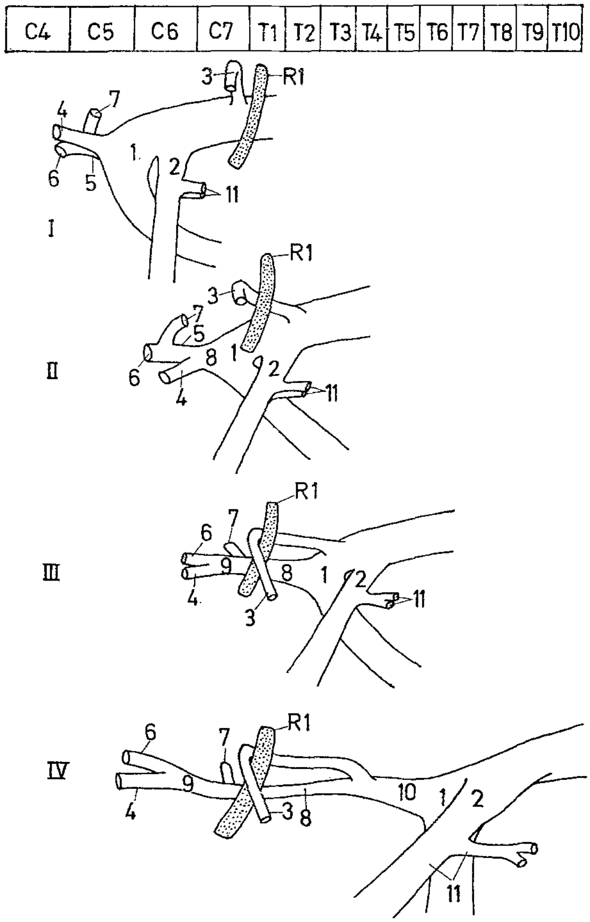


Fig. 14. Diagram of four developmental stages illustrating the positions of the arch of the aorta, the ductus arteriosus, and the left subclavian artery in relation to the axial skeleton. *I. First stage. Primitive mammalian pattern,* in which three vessels originate from the primitive arch of the aorta. *II. Second stage.* Formation of the brachiocephalic artery. Two vessels originate from the primitive arch of the aorta. *III. Third stage.* First appearance of the bicarotid trunk. *IV. Final stage.* Formation of the common brachiocephalic trunk. *1* primitive arch of the aorta (definitive arch of the aorta in *IV*); *2* ductus arteriosus; *3* left subclavian artery; *4* left common carotid artery; *5* innominate artery; *6* right common carotid artery; *7* right subclavian artery; *8* brachiocephalic artery; *9* bicarotid trunk; *10* common brachiocephalic trunk; *11* primitive pulmonary arteries (definitive pulmonary artery in *IV*); *R1* first rib; *C4* to *C7* fourth through seventh cervical vertebrae; *T1* to *T10* first through tenth thoracic vertebrae

stage of the primitive mammalian pattern at the level of the 6—7 cervical vertebra, while it has assumed its definitive position at the level of the 4—6 thoracic vertebra in the final stage of development (Fig. 14). Simultaneously with the translocation of the ductus arteriosus its caudal angle of the junction with the arch of the aorta increases. This angle is 90 to 105° in the stage of the primitive mammalian pattern, while it increases to 150° at the definitive position. Concurrently with increase of this angle the longitudinal axis of the ductus arteriosus and the pulmonary trunk also changes its direction from dorso-ventral to dorso-cranial. A similar translocation of the ductus arteriosus has been observed by Congdon (1922) in human embryos, and by Golub (1931) and Hammond (1937) in bovine embryos. Significant also are changes of the relative size of the lumen of the ductus arteriosus. The lumen of the ductus arteriosus at its junction with the primitive arch of the aorta is relatively smaller than that of the primitive arch of the aorta in the early stage of the development. However, the lumen of the ductus arteriosus at its junction with the arch of the aorta becomes considerably larger than that of the aorta in the final stage of the development. The narrow part of the arch of the aorta which appears at the junction with the ductus arteriosus may be regarded as the so-called isthmus aortae. A similar narrowing of the arch of the aorta at its junction with the ductus arteriosus has also been reported by Krediet (1962) in the bovine embryo.

The observations by Rathke (1843) and Hochstetter (1891, 1906) that the level of the arch of the aorta and the position of the heart are the main factors that may determine the number of vessels that originate from the arch of the aorta are in agreement with the present investigation. However, the shape of the thorax has no direct influence on the determination of the definitive form of the arch of the aorta and number of vessels that originate from it, because the form of the definitive arch of the aorta and development of the CBT in the equine embryos is already completed before the bilateral primordia of the sternum are united. This is in agreement with Rathke (1843) but disagrees with Parsons (1902).

A correlation between the shape of the arch of the aorta and the arrangement of the vessels which are given off from it has been pointed out by Lassila (1927/28) and Golub (1931). However, the present investigation indicates that this correlation is a result of the secondary changes that affect during embryonic development the position and shape of the arch of the aorta as well as the arrangement of the vessels that originate from it.

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