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Arterial Anatomy of Chicken Embryo and Hatchling

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ABSTRACT The arterial pattern in chicken hatchlings was investigated by microangiography and microscopic analysis of cleared specimens. The hatchling arterial pattern was found to resemble strongly the pattern that has been described for the adult chicken. Several minor variations in this pattern were found which were probably due to species, strain, or age differences. We also investigated the arterial pattern in chicken embryos aged 4.5 to 21 days of incubation. The hatchling pattern was fully developed by approximately 8 days of incubation. Some similarities were found to exist between the embryonic pattern in the chicken embryo and that described for the human embryo.

The anatomy of the definitive arterial system in a variety of birds including the adult domestic chicken has been described (Fitzgerald, 1969; Grzimek, 1933; Kaupp, 1918; Kolda and Komarek, 1978; Lucas and Stettenheim, 1972; Malinovsky et al., 1973; Nishida, 1960, 1963; Orr and Riddell, 1977). Although the embryonic development of the avian vasculature has also been investigated (Bakst and Chafee, 1928; Evans, 1909a,b; Nilsen, 1981; Romanoff, 1960; Sabin, 1905; Seichert and Rychter, 1971, 1972a,b,c; White, 1974), little attention has been paid to the transition from the early embryonic vascular pattern to that of the adult.

Recently, we demonstrated an association between several different bony anomalies in human lower limbs and the presence of an unusual arterial pattern characterized by the deficiency of some arteries and the retention of embyronic arteries (Hootnick et al., 1980a,b, 1982, 1983a,b, 1984). In order to learn more about this association, we have investigated the relationship between arterial and bony anatomy in the developing limbs of birds. By means of microangiography, we studied the arterial anatomy of the limbs and bodies of chicken embryos between 4.5 days of incubation and hatching. The anatomical nomenclature used in this description was derived from Fitzgerald's description of the Coturnix quail (Fitzgerald, 1969).

MATERIALS AND METHODS

Fertile white Leghorn chicken eggs (Spafas, Inc., Norwich, CT) were incubated at 38°C in a forced-draft incubator. The contrast material used in the angiography was a 60% aqueous suspension of barium (Barosperse 95% barium sulfate; Malinckrodt). The injection technique was tailored to meet demands imposed by animal size and is described below. The embryos were staged according to Hamburger and Hamilton (1951).

After the injection of the barium, the embryos were placed onto a surface of bee's wax in the supine position with legs and wings spread away from the bodies. They were held in this position with dissecting needles and fixed overnight in a solution of one part glacial acetic acid to four parts of 95% ethanol. Radiographs of the fixed embryos were made, and the embryos were then stained for cartilage and bone, and cleared as described by Watson (1977).

In order to visualize very small vascular branches, a radiographic technique to optimize resolution and contrast was employed. The animals were placed directly onto Kodak

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X-Omat TL nonscreen film in such a way as to maximize animal-to-film contact. Exposures averaging 140 mAs at 37 kVP for hatchlings were made using a Picker Mammorex radiographic unit with a focal film distance of 36 in (91.44 cm); lower exposures were used for smaller animals. Radiographs were taken using a 1.2-mm focal spot.

To facilitate the visual separation of otherwise superimposed vascular structures, stereoscopic radiographs were obtained on all animals (Culligan, 1972). These were then magnified photographically to enable identification of very small arteries. A Lietz desktop magnifying stereoscope was used routinely for interpretation of stereoscopic radiographs. The radiographic findings were confirmed by comparing them to the stained and cleared specimens, which were analyzed with a stereoscopic operating microscope.

Since the animals were placed in the supine position with the wings fully abducted, the terms proximal and distal refer to the proximity of the area in question to the central axis of the animal. The terms cranial and caudal refer respectively to the pre- and postaxial aspects of the limb.

The labeling system used assigns a whole integer to the main arteries of the upper and lower extremities of the hatchling, while the smaller named branches are designated by a decimal added to the integer. Hatchling body arteries were labeled with capital letters, while those identified to be either transient or evolving into recognizable adult arteries were labeled with lower-case letters.

Injection technique

One-day-old hatchlings were anesthetized with 100% ether in a closed container. Ethanol was applied to the surface of the chest to dampen the feathers and thus allow better visualization of the hatchling's skin. A midline chest incision was made, and the heart and proximal great vessels were identified. A 5 "0" Ethicon silk suture was placed around the great vessels at their origins from the heart, and tied. This allowed traction to be put on the heart and great vessels and helped to prevent the retrograde flow of blood into the heart. The proximal aorta then was cannulated directly with a 30-gauge needle (Lymphangiography set, .038 I.D. × .065 O.D., Becton, Dickinson & Co., Rutherford, NJ) and an aortogram with full body runoff was obtained. Approximately 0.5 cc. of barium solution was injected over about a 30-sec interval until the barium appeared in the arteries of the eyes, wings, and legs. Twelve chicken hatchlings that had been injected with barium were selected for detailed study. A similar technique was used for embryos between 12 and 21 days of incubation. Since these embryos were removed from the shell and rinsed in saline, it was not necessary to moisten the chest wall any further. With embryos between 10 and 18 days of incubation, the vitelline arteries were ligated prior to barium injection; this prevented the extravasation of barium out through these arteries. Because of atrophy of the vitelline arteries, ligation of these arteries was not necessary in embryos older than approximately 18 days.

Angiograms of embryos between 10 and 12 days of incubation were made by injecting barium directly into the heart. Cardiac contraction forced the barium into the embryonic great vessels, and satisfactory total body arteriograms were obtained.

In embryos between 6 and 9 days of incubation, a hole was made in the shell and the vitelline arteries were identified with an operating microscope. A vitelline artery was isolated with silk sutures and an intraarterial retrograde injection was performed. Barium injected into the vitelline artery flowed against arterial pressure into the abdominal aorta. Here the embryonic blood pressure pushed it into those branches distal to the origin of the vitelline arteries. This required the injection of approximately 0.02 to 0.05 cc of barium suspension.

Vitelline vein injections were performed in embryos between 4.5 (the youngest studied) and 5 days of incubation. After removing a small section of the shell, the vitelline veins were identified with an operating microscope, and 0.05 to 0.07 cc of barium suspension was injected by hand into one of them. The injected barium returned to the embryonic heart and, after passing through the heart chambers, the embryonic great vessels were filled by the embryo's own cardiac activity.

RESULTS
Arterial anatomy of the hatchling

Arteries of the upper limb (Figs. 1–3)

The right and left brachiocephalic arteries (1) arose from the proximal part of the aorta. After giving off the common carotid arteries (2) which coursed cranially toward the neck and head, the brachiocephalic arteries continued craniolaterally as the subclavian arteries (3).

The dorsal artery (4) arose from the common carotid artery. It ran dorsally and cranially and bifurcated into the vertebral (5) and caudal cervical arteries (6). The vertebral artery ran cranially for a short distance and terminated as the cranial vertebral artery (5.1) and the caudally directed caudal vertebral artery (5.2). The caudal cervical artery, which originated on the cranial aspect of the dorsal artery, coursed cranially, giving off a laterally directed branch, the omocervical artery (6.1). The bronchoesophageal artery (7) arose from the common carotid artery[1] and passed cranially and ventrally into the neck, terminating as a cranially directed ascending esophageal branch (7.1).

The first branch of the subclavian artery was the coracoid artery (8), which originated on the caudal side of the subclavian artery, looped dorsally, then ventrally, and coursed craniomedially as a small artery, and came to lie on the medial side of the coracoid bone. The clavicular artery (8.1) originated from the proximal part of the coracoid artery and was directed craniodorsally toward the shoulder joint. The subclavian artery then bifurcated into two major arteries, the pectoral trunk (9) and the axillary artery (10).

There was variability in the origin of the internal thoracic artery. In some specimens it originated from the subclavian artery (Fig. 1), while in others it originated from the proximal aspect of the pectoral trunk. The internal thoracic artery ran a short distance and bifurcated into its ventral (11.1) and dorsal (11.2) branches (Fig. 1). The ventral

[1]Fitzgerald (1969) describes the bronchoesophageal artery originating from the subclavian artery just lateral to the origin of the common carotid artery. We found the bronchoesophageal artery to branch directly off of the common carotid artery.

Abbreviations

Abbreviations for Figures 1–3.

A	aorta
H	humerus
R	radius
U	ulna
I–IV	digits
1	brachiocephalic artery
2	common carotid artery
3	subclavian artery
4	dorsal artery
5	vertebral artery
5.1	cranial vertebral artery
5.2	caudal vertebral artery
6	caudal cervical artery
6.1	omocervical artery
7	bronchoesophageal artery
7.1	ascending esophageal artery
8	coracoid artery
8.1	clavicular artery
9	pectoral trunk
10	axillary artery
11	internal thoracic artery
11.1	ventral branch of internal thoracic artery
11.2	dorsal branch of internal thoracic artery
12	external thoracic artery
12.1	cranial branch of external thoracic artery
12.2	caudal branch of external thoracic artery
13	dorsal thoracic artery
14	subscapular artery
15	deep brachial artery
16	anterior (cranial) humeral circumflex artery
17	posterior (caudal) humeral circumflex artery
18	radial collateral artery
18.1	proximal (cranial) branch of radial collateral artery
19	ulnar collateral artery
20	brachial artery
21	radial artery
21.1	proximal (caudal) branch of radial artery
21.2	nutrient artery to the ulna
21.3	cranial terminal branch of radial artery
21.4	branch to second digit
22	ulnar artery
23	cubital artery
24	metacarpal artery
24.1	radial metacarpal artery
24.2	third digital artery
25	patagial artery
25.1	anterior patagial branch

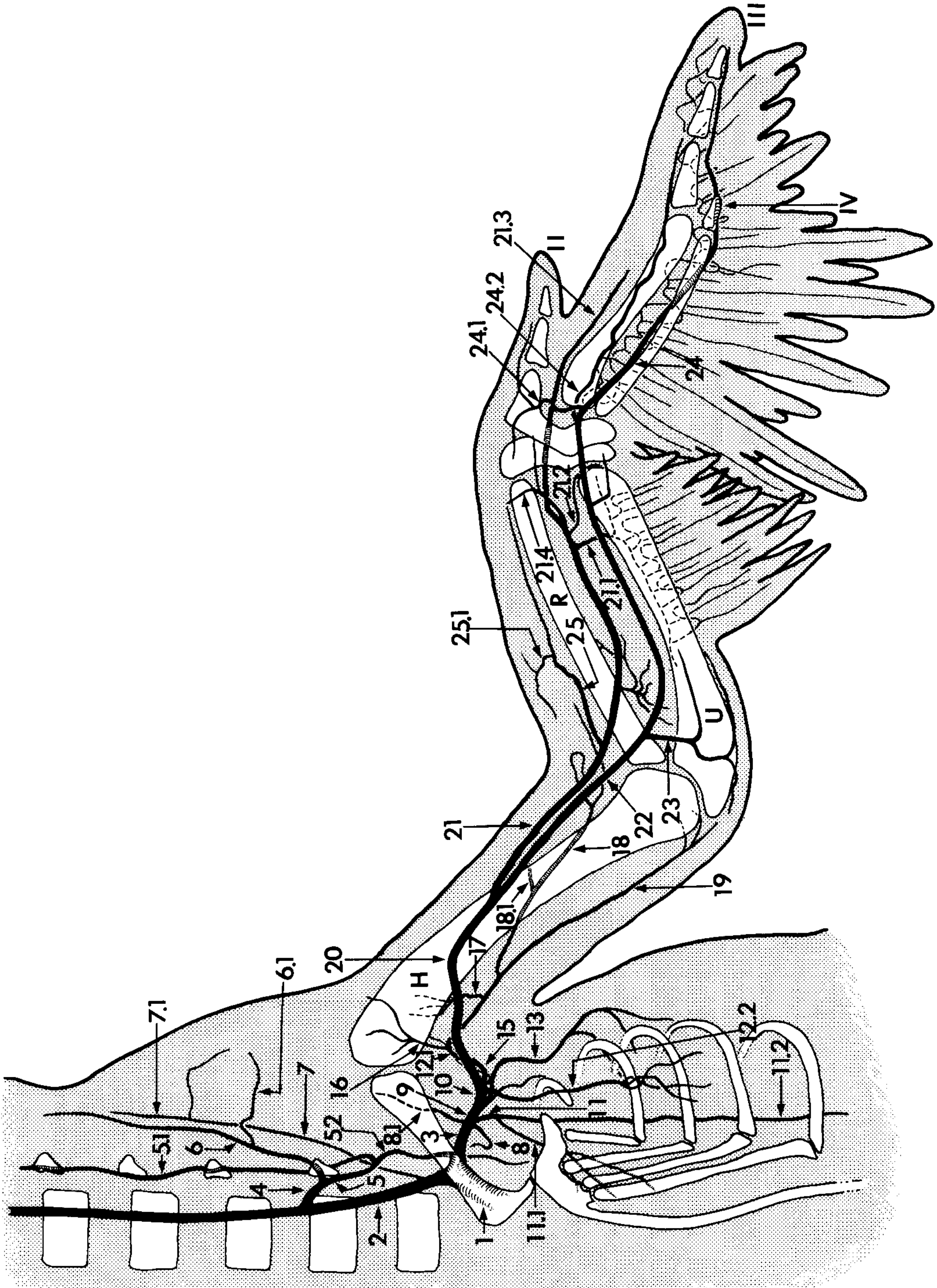

Fig. 1. Labeled diagram of the arteries of the hatchling upper extremity.

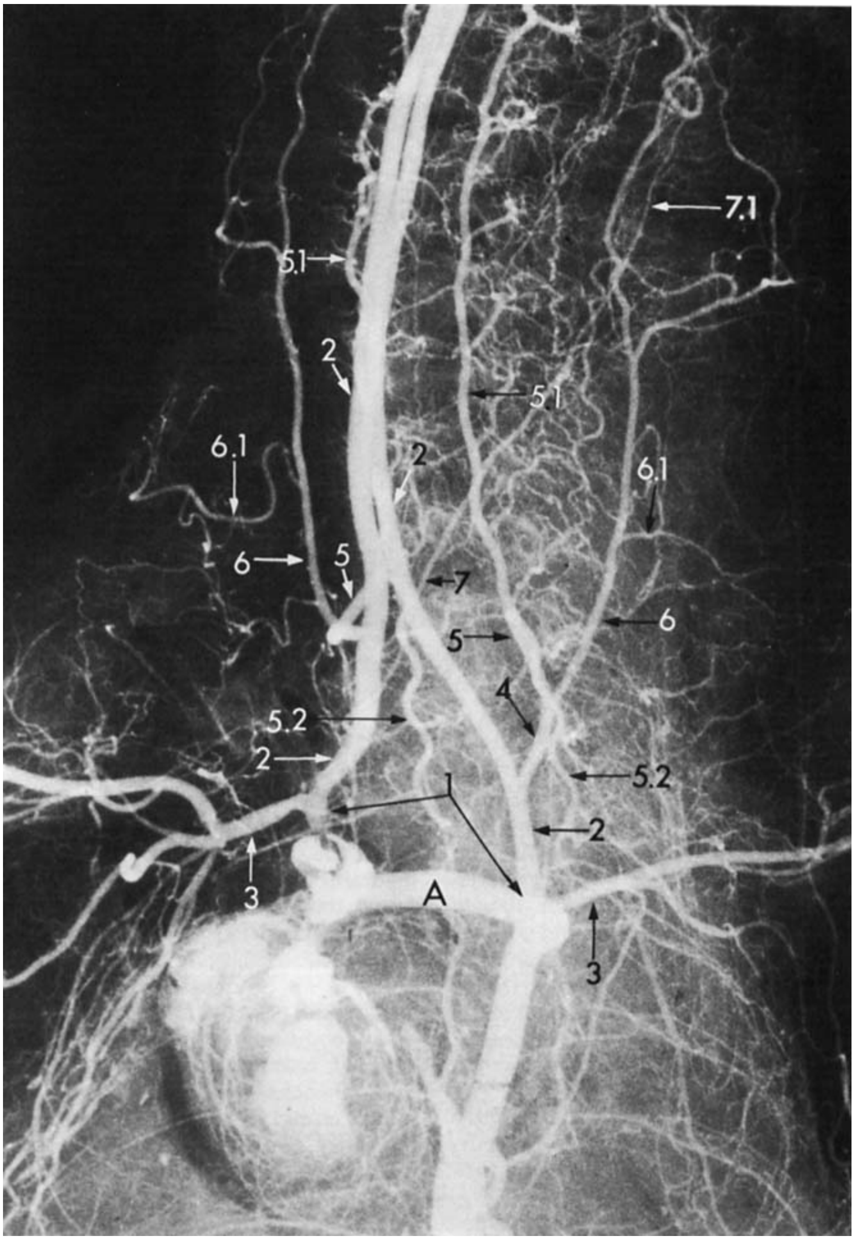

Fig. 2. Anteroposterior radiograph of upper thorax and neck of the hatchling.

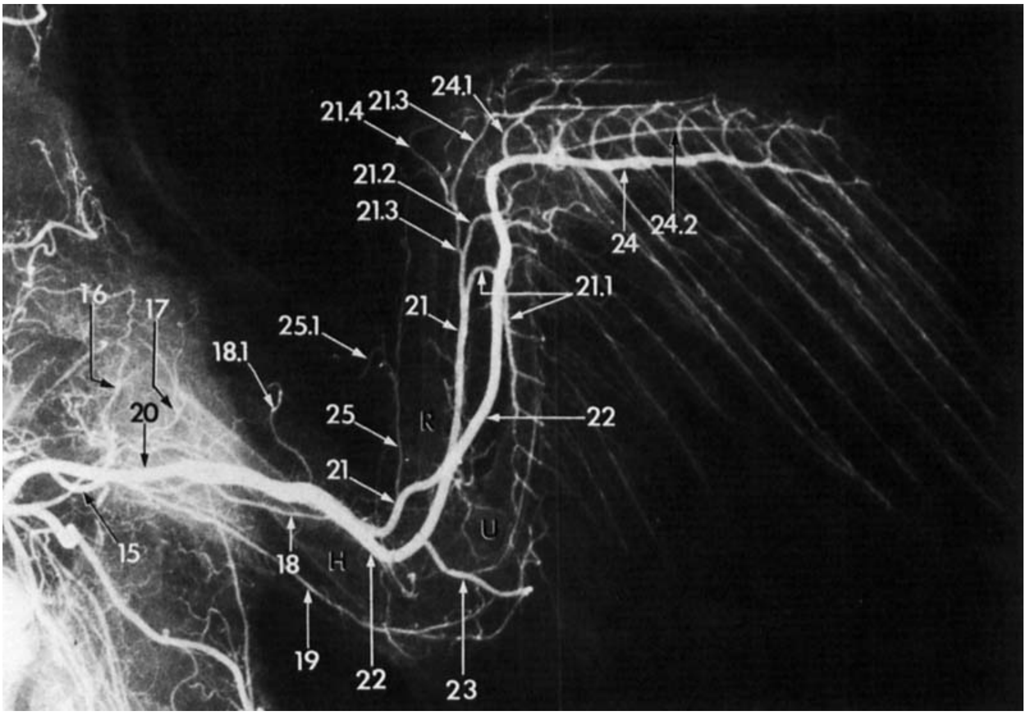

Fig. 3. Anteroposterior radiograph of the hatchling left wing.

branch descended caudally and appeared to anastomose with ascending branches from the femoral circumflex artery (Fig. 4A). The dorsal branch coursed caudally with a distribution similar to the ventral branch. It also gave rise to numerous small branches along its course, which seemed to anastomose with branches of the cranial gluteal artery. Distal to the origin of the internal thoracic artery, the pectoral trunk gave rise to the external thoracic artery which bifurcated to form a caudal (12.2) and a cranial (12.1) branch. The caudal branch passed laterally and slightly caudally on the external surface of the ribs where it descended to anastomose with branches of the femoral circumflex artery (Fig. 4A); the cranial branch ran into the muscles of the proximal part of the humerus and lateral chest wall. Beyond the origin of the external thoracic artery, the pectoral trunk continued a short distance caudolaterally before terminating as the dorsal thoracic arteries (13), which supplied branches to the adjacent musculature.

The axillary artery (10) was the continuation of the subclavian artery beyond the origin of the pectoral trunk. Its first branch was a small cranially directed artery, the subscapular artery (14), which ran a short distance before it gave rise to small medial and lateral branches.

The deep brachial artery (15) arose from the caudal side of the axillary artery and, after looping caudally for a short distance, coursed craniolaterally and terminated as four branches[2]: the anterior (cranial) humeral circumflex artery (16), which coursed cranially and divided into numerous small branches that supplied the adjacent soft tissues; the posterior (caudal) humeral circumflex artery (17), which coursed distally and terminated at the middle third of the proximal part of the humerus; and two other distally directed branches, the radial collateral

[2]We found the anterior and posterior humeral circumflex arteries to originate off the deep brachial artery. Nishida (1960) describes them as originating from the brachial artery.

(18) and the ulnar collateral arteries (19). Of the last two, the more cranial was the radial collateral artery, which descended into the cranial soft tissues of the distal part of the humerus to the level of the elbow where it gave off a small cranial branch (18.1) supplying the cranial superficial tissues. The ulnar collateral artery was directly caudally and terminated at the level of the elbow.[3]

The axillary artery beyond the point of the origin of the deep brachial artery continued as the brachial artery (20). This vessel bifurcated into two distally directed branches at the level of the proximal third of the humerus[4]; the more cranial branch was the radial artery (21), and the more caudal branch was the ulnar artery (22). At the level of the elbow a caudally directed artery, the cubital artery (23), took origin from the ventral surface of the ulnar artery and passed caudal to the olecranon where it terminated as three branches to the adjacent soft tissues; one branch ascended along the caudal aspect of the zygopod (forearm) and the other two descended caudally.

The ulnar artery continued ventrally as the dominant artery into the metacarpus where it became the metacarpal artery (24). Initially, the metacarpal artery gave off an artery, the third digital artery (24.2), which followed the volar surface of the third metacarpal and supplied arteries to the feathers. A cranially directed branch, the radial metacarpal artery (24.1), originated from the metacarpal artery on the volar side and, at the proximal articulation of the metacarpus, perforated the interosseus space to follow a cranial course sending recurrent branches proximally and descending branches cranially into the muscles. A few feather arteries were supplied by the radial metacarpal artery. The metacarpal artery passed between the metacarpals and, at the distal metacarpus, perforated the interosseus space to become dorsal and then caudal, giving origin to many feather arteries and their tributaries, all of which were dorsal.

The radial artery (21) coursed distally from its origin. At the level of the elbow, the radial artery gave rise anteriorly to the patagial artery (25), which ran distally and gave origin to a craniolateral branch, the anterior patagial branch (25.1). It then continued beyond the distal part of the radius where it terminated in radial soft tissues. The radial artery ran along the radial aspect of the zygopod and terminated as three major branches. The proximal (caudal) branch (21.1) originated from the ventral surface of the radial artery. It then perforated the interosseus space between the radius and ulna to become dorsal where it sent ascending and descending branches, which gave origin to many feather arteries and their tributaries. The next caudal branch of the radial artery was the nutrient artery (21.2), which coursed to the ulna and appeared to supply some feather arteries. The cranial terminal branch (21.3) of the radial artery descended on the radial aspect of the autopod where it gave origin to additional feather arteries, a branch to the second digit (21.4), and distal branches to the dorsal surface of the third digit.

Major branches of the abdominal aorta (Fig. 4 A,B)

The first major branch of the abdominal aorta (A), the celiac artery (C), arose distal to the 5th rib and coursed caudoventrad into the abdomen where it branched extensively to the abdominal viscera. The cranial mes-

Abbreviations

Abbreviations for Figure 4

A	aorta
A′	continuation of aorta beyond ischiatic artery
C	celiac artery
CC	common carotid artery
CM	caudal mesenteric artery
CrM	cranial mesenteric artery
CrV	cranial vertebral artery
CV	caudal vertebral artery
EI	external iliac artery
I	ischiatic artery
IC	6th intercostal artery
II	internal iliac artery
IP	internal pudendal artery
MS	middle sacral artery
P	perineal artery

[3]Fitzgerald (1969) describes the deep brachial artery as continuing distal to the elbow; this distal continuation is termed the ulnar collateral artery by Nishida. (1960) We found the ulnar collateral artery to be a branch of the deep brachial artery. These did not continue distal to the elbow.

[4]Fitzgerald (1969) shows this bifurcation at the elbow.

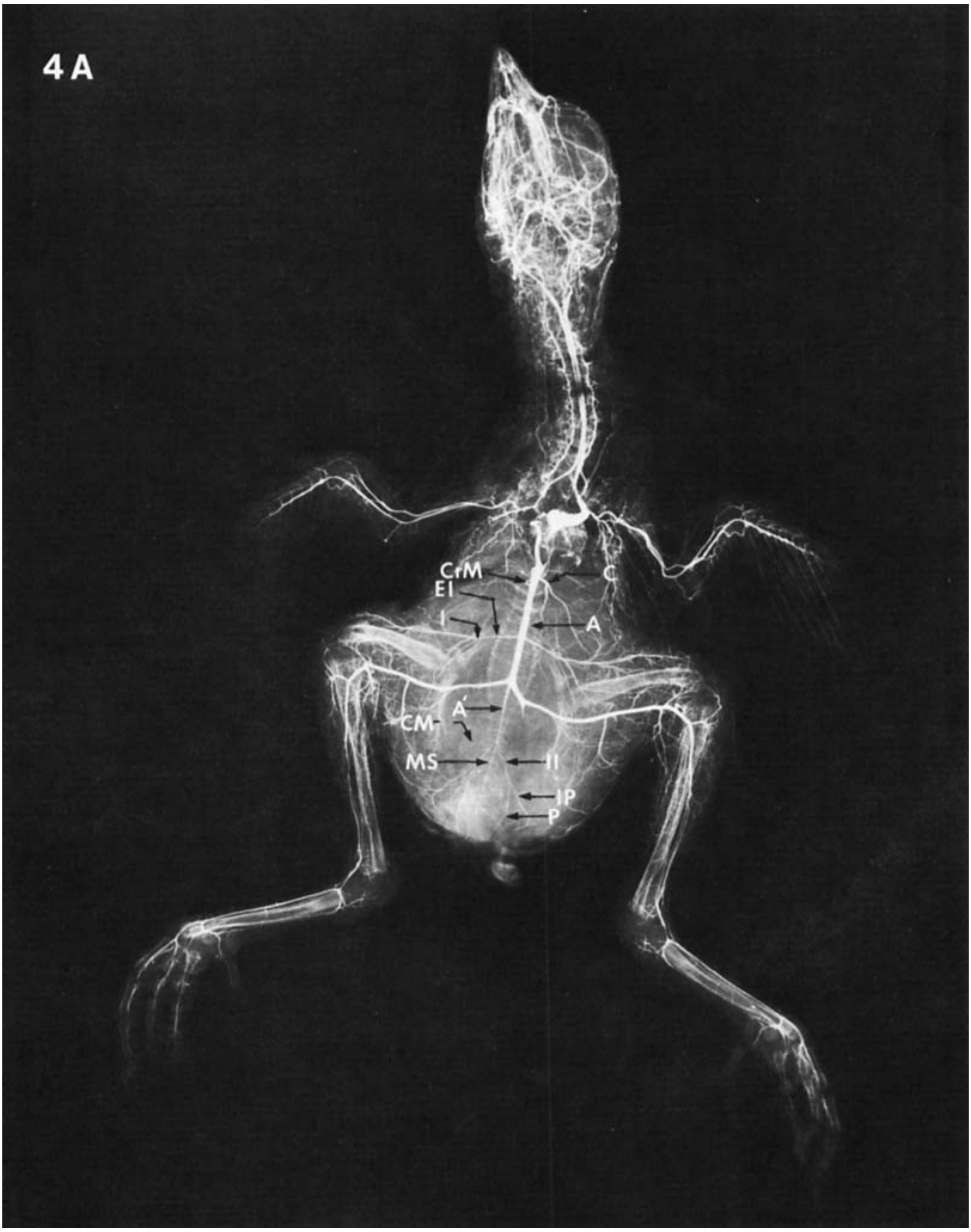

Fig. 4A. Anteroposterior radiograph of the hatchling body.

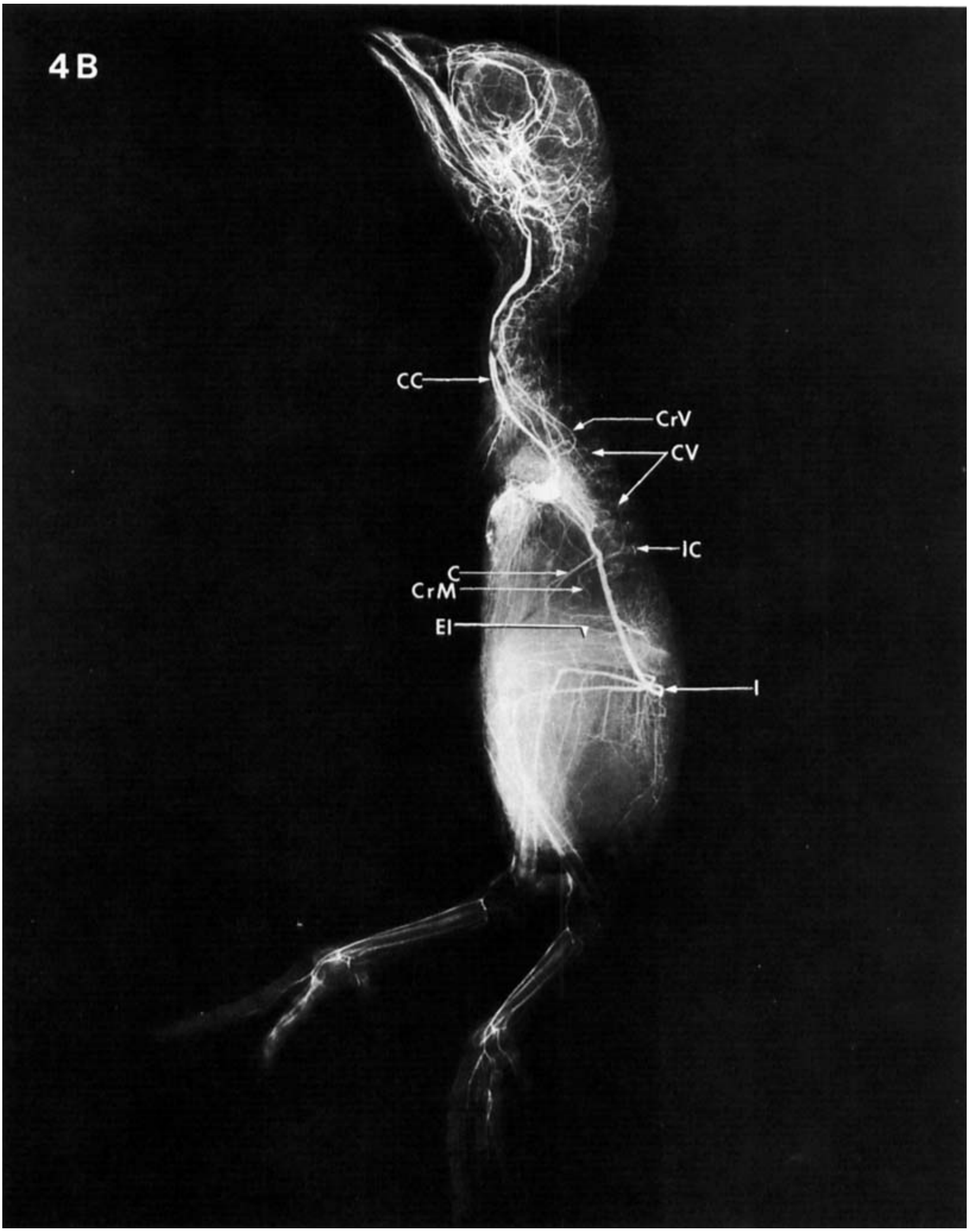

Fig. 4B. Lateral radiograph of the hatchling body.

enteric artery (CrM) originated next and coursed ventrolaterad, sending numerous arteries to the abdominal viscera. A dorsally directed artery arose at the same level. This vessel bifurcated into the 6th intercostal artery (IC) and an ascending cranial branch, the caudal vertebral artery (CV). The latter ascended into the dorsal soft tissues of the upper thorax where it anastomosed with the cranial vertebral artery (CrV). The next major branches of the aorta are the cranial renal arteries and gonadal arteries, which were not seen in our specimens. Small lumbar branches originated from the aorta at each vertebral level and coursed circumferentially around each vertebral body.

The paired external iliac arteries (EI) arose from the aorta just cranial to the femur, to course distally on the cranial aspect of the thigh. The paired ischiatic arteries (I) arose at the level of the caudal aspect of the femur; these arteries are the major terminal branches of the abdominal aorta. The continuation of both the external iliac arteries and the ischiatic arteries will be described below along with the arteries of the lower extremity. Beyond the origin of the ischiatic arteries, the aorta continued as a small median artery running ventral to the sacral vertebrae. This distal continuation of the aorta gave origin to the unpaired caudal mesenteric artery (CM), which coursed caudolaterad to the caudal viscera, the paired internal iliac arteries (II) which bifurcated into the internal pudendal arteries (IP) laterally, the perineal arteries (P) medially, and the middle sacral artery (MS) centrally. The middle sacral artery sent branches to the muscles of the tail.

Arteries of the lower extremity (Figs. 5–9)

The external iliac arteries (1) originated bilaterally from the aorta (A) approximately three vertebral segments below the most caudal rib pair and coursed within the thigh to run craniolaterally to the femur. Each artery continued laterally and slightly caudally just dorsal to the kidney. Immediately lateral to the innominate bone,[5] a branch, the pelvina interna artery (2), was given off, which coursed caudolaterally. This artery continued caudally, lateral to the bony pelvis, where it contributed branches to the ventral abdominal wall and it terminated by anastomosing with branches of the ischiatic and internal iliac arteries. Farther laterally, the external iliac artery gave rise to a cranial branch, the cranial gluteal artery (3), which passed cranially, medially, and dorsally dividing into numerous muscular branches. At the same level, a caudally directed artery, the femoralis artery (4), arose from the external iliac artery and passed laterally, caudally, and ventrally crossing the proximal femur medially traversing the caudomedial aspect of the thigh deeply. This artery terminated medially within the proximal part of the leg. The external iliac artery continued distally as the femoral circumflex artery (5), which terminated as three major muscular branches in the cranial aspect of the thigh. The most proximal of these branches (5.1) originated at a level near the proximal third of the femur. It passed craniomedially and terminated as numerous muscular branches, some of which ascended to anastomose with descending branches of the internal thoracic artery. The femoral circumflex artery continued as a major vessel to the midthigh where it divided into large middle branches (5.2) to the cranial aspect of the distal part of the thigh and a caudal branch (5.3) to the muscles on the medial aspect of the distal part of the thigh.

The ischiatic arteries (6) originated as the largest branches of the distal aorta, approximately four vertebral segments caudal to the origin of the external iliac artery, and passed caudolaterally to supply the lower limbs. Neither the renal nor the gonadal branches were identified in our specimens. The vitelline arteries (7) took origin from each ischiatic artery just lateral to the sacral vertebrae, continued caudally for a short distance with rapidly diminishing diameters, and terminated abruptly. The left vitelline artery had a larger diameter than the right. The ischiatic artery left the pelvis through the ischiatic foramen. The caudal gluteal artery (8) originated from the ischiatic artery just inside the pelvis[6] and ascended laterally, cranially, and ventrally around the pelvis giving a branch, the trochanteric artery (9), which ascended to the region of the acetabulum and a second branch to the muscles external to the obturator foramen. Shortly after giving off the trochanteric artery, the caudal

[5]This differs from Nishida's (1963) depiction ot the umbilical artery originating from the external iliac artery just before it exits the pelvis.

[6]Nishida (1963) and Fitzgerald (1969) describe the caudal gluteal artery as originating from the ischiatic artery just outside (lateral to) the pelvis; some of our specimens show it originating within the bony pelvis.

gluteal artery bifurcated outside the pelvis into two terminal branches. The distal branch (8.1) was directed laterally into the caudal muscles of the proximal thigh, and the caudal branch (8.2) passed caudally supplying the external pelvic muscles. The obturator artery was not seen in any of our specimens.

The next major branch of the ischiatic artery was the profunda femoris artery (11), which emerged as a caudally directed artery at the junction of the proximal and middle thirds of the thigh. This artery continued caudally without significant branching to the muscles and soft tissues of the caudal part of the thigh. In its course it gave off superficial branches that anastomosed with the pelvina interna artery. The superior femoral nutrient artery (10), a small cranially directed artery that arose from the ischiatic artery at

Abbreviations

Abbreviations for Figures 5–9

A′	continuation of aorta beyond ischiatic artery
M	metatarsus
F	femur
T	tibia
R	rete tibialis arteriosus
A	aorta
L	lumbar arteries
I–IV	digits
1	external iliac artery
2	pelvina interna (umbilical-allontois) artery
3	cranial gluteal artery
4	femoralis artery
5	femoral circumflex artery
5.1	cranial branch
5.2	middle branch
5.3	caudal branch
6	ischiatic artery
7	vitelline artery
8	caudal gluteal artery
8.1	distal branch (lateral branch)
8.2	caudal branch (medial branch)
9	trochanteric artery
10	superior femoral nutrient artery
11	profunda femoris artery
12	caudal femoral artery
13	popliteal artery
14	comitans nervi ischiatica artery
15	middle femoral nutrient artery
16	caudal tibial (posterior tibial) artery
17	cranial tibial artery
18	inferior femoral nutrient artery
18.1	genicular branch
19	medial tibial artery
20	genu suprema artery
21	peroneal artery
21.1	articular branch
21.2	transverse branch
21.3	descending branch
22	ramus tibialis artery
23	ramus fibularis artery
24	lateral tibial artery
25	cranial recurrent tibial artery
26	lateral tarsal artery
26.1	descending branch
27	lateral recurrent tibial artery
28	medial tarsal artery
29	accessory (descending) branch of dorsalis pedis artery
30	caudolateral metatarsal artery
31	caudomedial metatarsal artery
31.1	proximal (ascending) branch of caudomedial metatarsal artery
31.2	distal branch of caudomedial metatarsal artery
32	dorsalis pedis artery
33	craniolateral metatarsal artery
34	craniomedial metatarsal artery
35	perforating metatarsal artery
36	lateral digital artery
37	medial digital artery
38	lateral plantar metatarsal artery
39	middle plantar metatarsal artery
40	second digital artery
41	medial plantar metatarsal artery
42	first digital artery

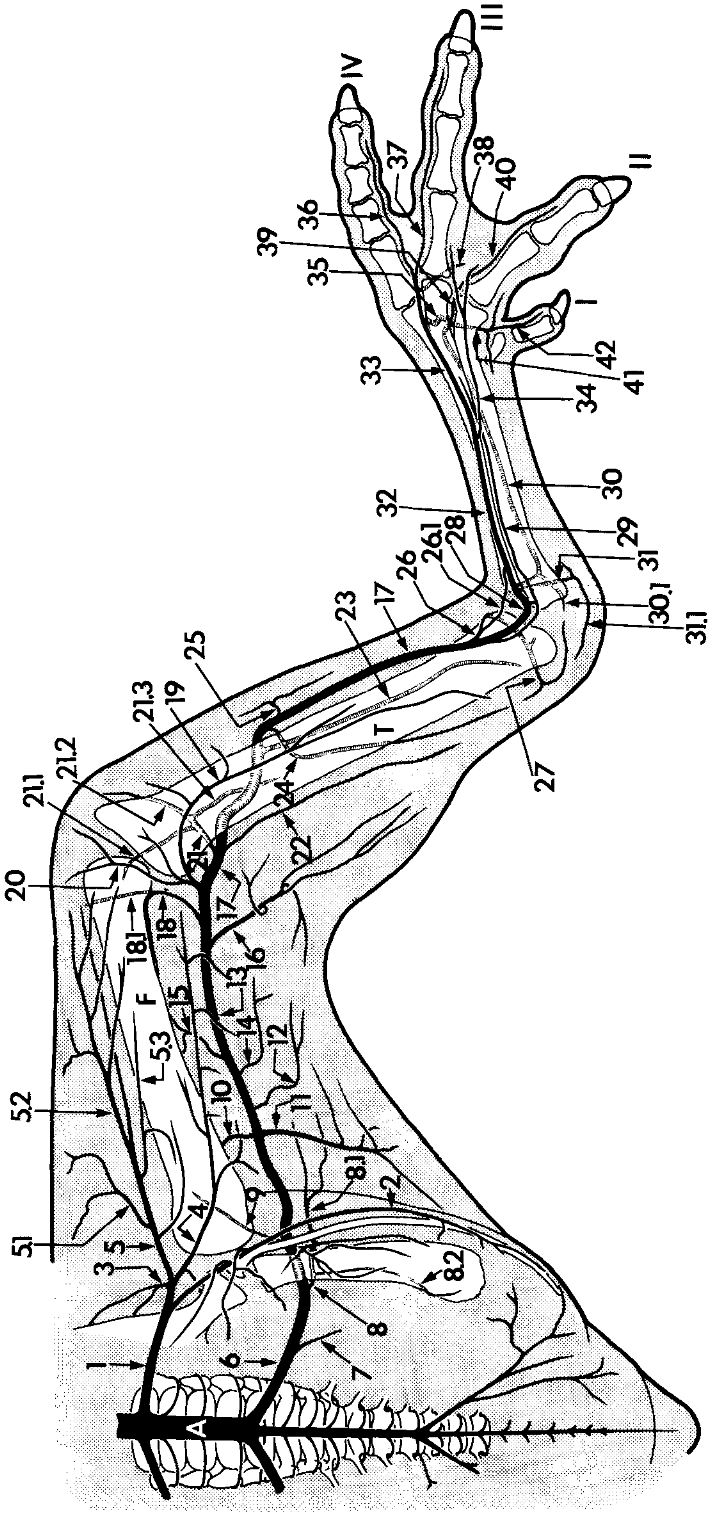

Fig. 5. Labeled diagram of the hatchling lower extremity.

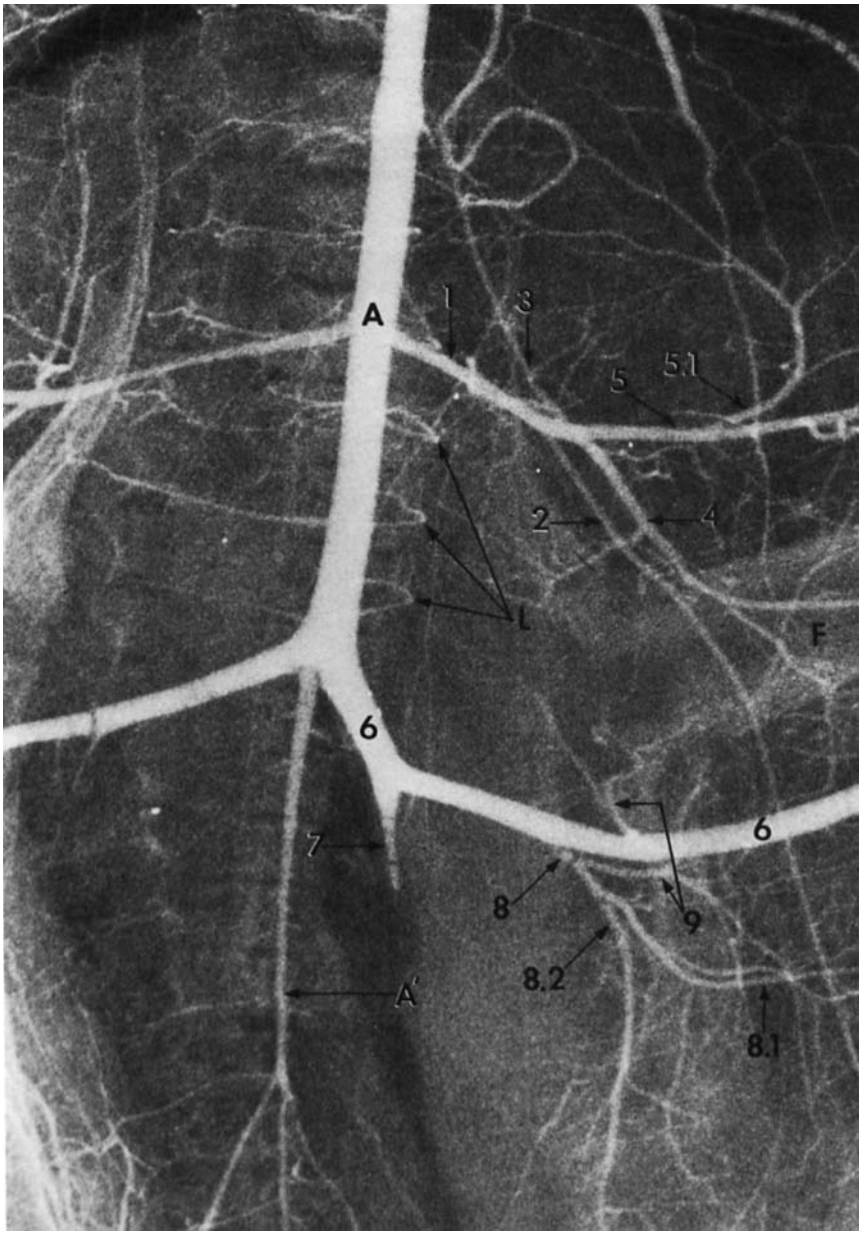

Fig. 6. Anteroposterior radiograph of the hatchling lower abdomen showing the aortic bifurcation and origin of the arteries to the lower extremity.

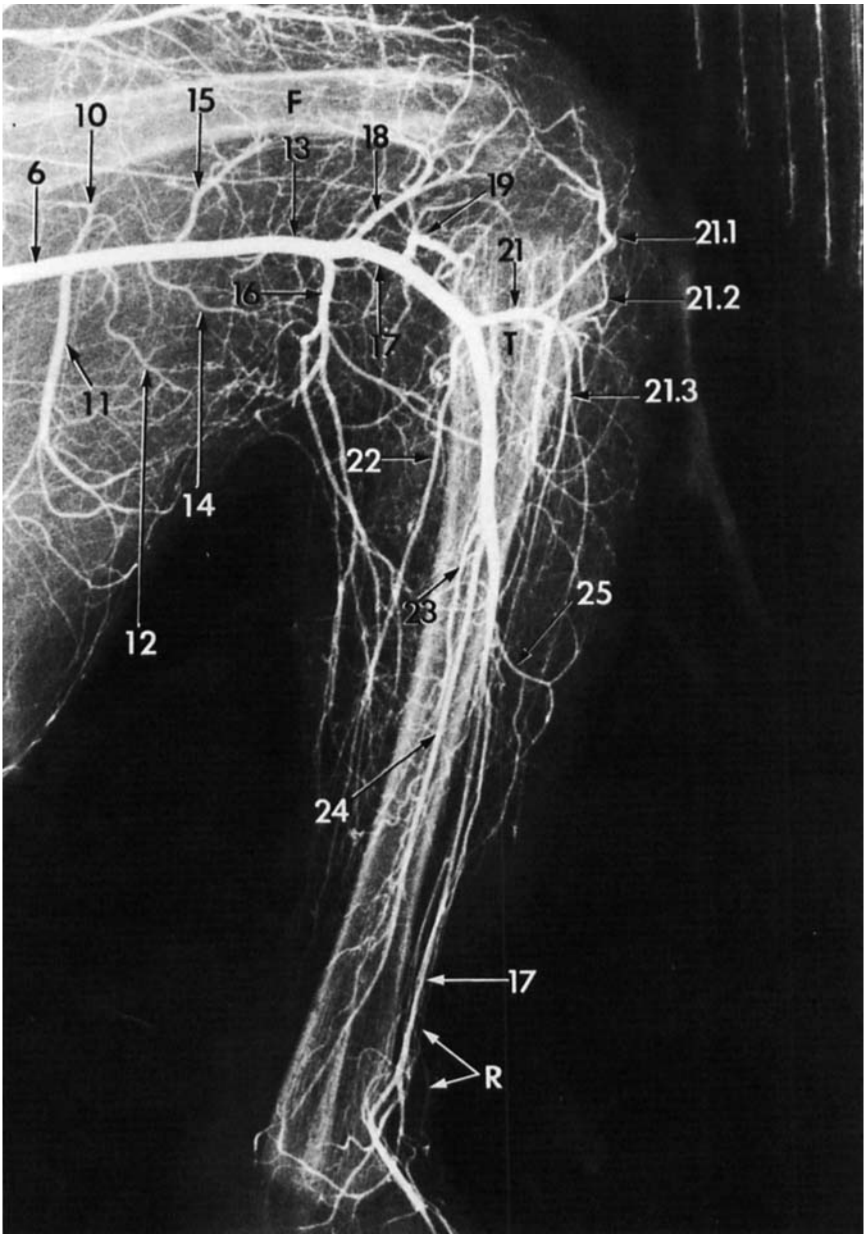

Fig. 7. Lateral radiograph of the hatchling left knee.

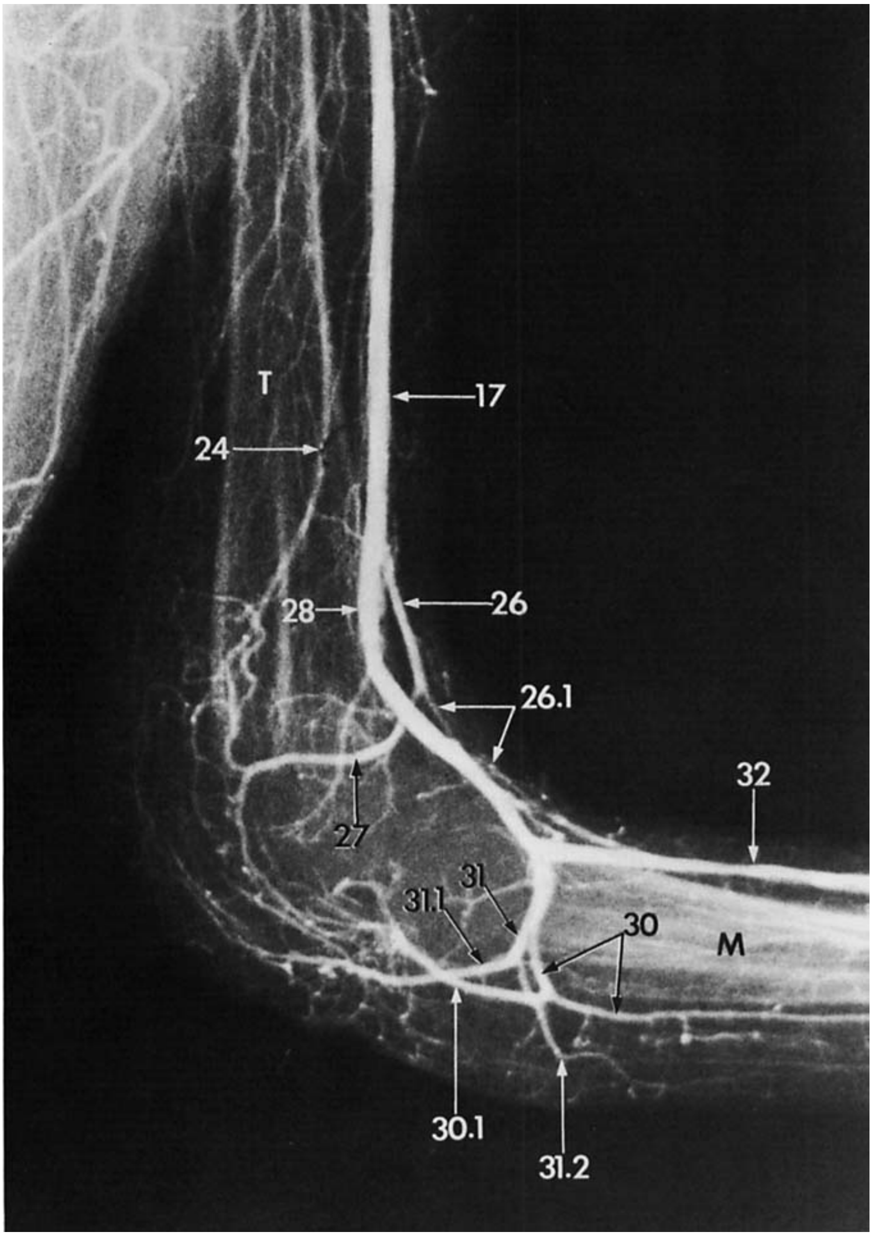

Fig. 8. Lateral radiograph of the hatchling left hock.

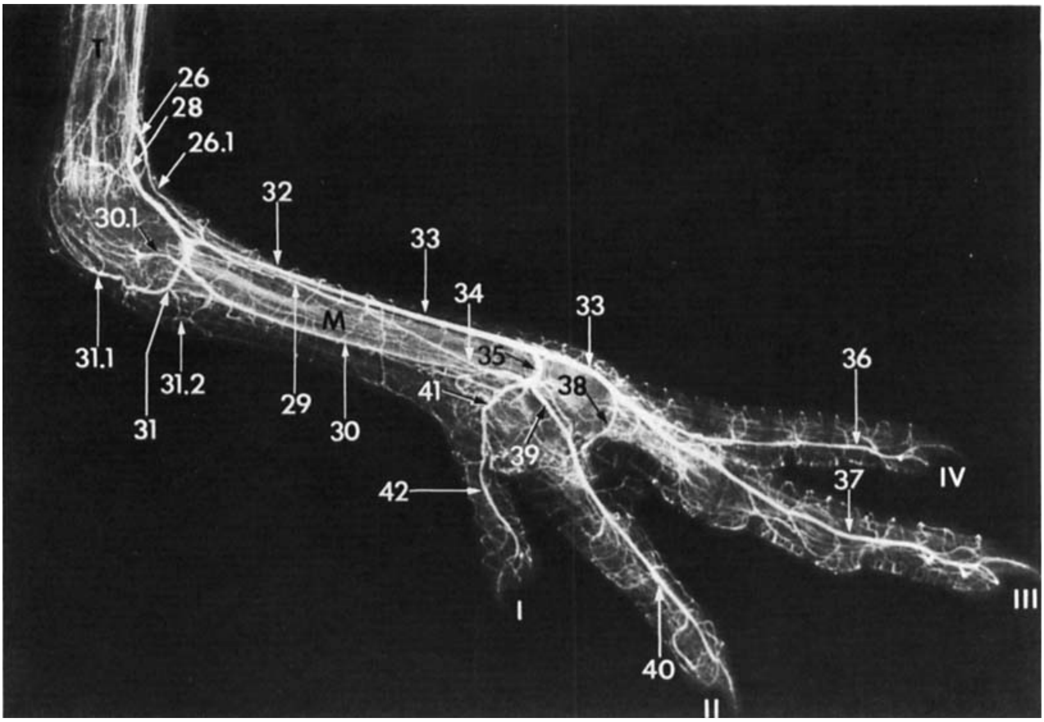

Fig. 9. Lateral radiograph of the hatchling left foot.

the same level as the profunda femoris artery, coursed cranially and medially. At the midthigh level a small artery, the caudal femoral (12), emerged from the ischiatic artery and passed caudally to terminate in the superficial soft tissues. The popliteal artery (13) is the continuation of the ischiatic artery beyond the origin of the caudal femoral artery.

The comitans nervi ischiatica artery (14), which originated from the popliteal artery just distal to the femoralis caudalis artery, was a caudally directed branch to the distal part of the thigh. At the midthigh level, a large branch of the popliteal artery, the middle femoral nutrient artery (15), emerged just distal to the comitans nervi ischiatica artery and passed cranially and distally to the femur.[7] The popliteal artery ran distally to terminate by bifurcating into the caudal and the cranial tibial arteries. The caudal tibial artery (16) arose just proximal to the distal femur where it passed to the dorsal surface of the proximal leg and terminated as multiple deep and superficial branches as well as tiny anastomosing recurrent branches to the profunda femoris artery.

The cranial tibial artery (17), the larger terminal branch of the popliteal artery, appeared to be a continuation of the popliteal artery. It passed ventral to the knee and proximal part of the tibia, and coursed distally spiraling around the tibia to acquire a lateral and finally an anterior location along the distal part of the tibia. The first branch of the cranial tibial artery, the inferior femoral nutrient artery (18), traveled craniolaterally from the cranial side of the cranial tibial artery to the distal portion of the posterior third of the femur. The inferior femoral nutrient artery bifurcated into a small ascending branch, which ran proximally giving branches to the distal part of the femur, and a genicular branch (18.1) to the periarticular soft tissues. The second branch of the cranial

[7]Both Nishida (1963) and Fitzgerald (1969) label this the superior femoral nutrient artery; we believe it to be more appropriate to call this artery the middle femoral nutrient artery.

tibial artery, the medial tibial artery (19), arose on the cranial surface of the cranial tibial artery at the level of the proximal part of the tibia. The medial tibial artery supplied small muscular and superficial branches to the proximal and middle portions of the anterior part of the leg. Several small, proximally directed branches originated from it as it turned distally, to be distributed to the proximal part of the leg. The genu suprema artery (20) had its origin from the cranial side of the medial tibial artery as it passed caudally over the proximal aspect of the tibia. It passed proximally and cranially to the anterolateral aspect of the femur, where it divided into several superficial branches, some of which appeared to anastomose with branches of the middle femoral circumflex artery.[8] A small artery, the peroneal artery (21), arose from the cranial surface of the cranial tibial artery and passed craniolaterally around the tibia, where it divided into a large ascending articular branch (21.1) to the knee, a small transverse branch (21.2) to the soft tissues, and two large descending branches (21.3) to the anterolateral muscles. A small, caudally directed artery, the ramus tibialis artery (22), arose from the dorsal surface of the cranial tibial artery at the same level as the peroneal artery. This artery turned to run distally parallel to the tibia near its caudomedial border where it gave deep muscular branches. It appeared to anastomose near the hock with ascending branches of the caudal medial metatarsal artery (31.1). The ramus fibularis artery (23) originated from the dorsal surface of the cranial tibial artery approximately one-third of the way down the tibia. This artery traveled distally in the dorsal soft tissues and appeared to anastomose with descending branches of the medial tibial artery (19). The lateral tibial artery (24) arose just distal to the origin of the ramus fibularis artery. It coursed distally and caudally in the leg where it terminated by anastomosing with ascending branches of the lateral recurrent tibial artery (27) in the lateral part of the hock. The cranial recurrent tibial artery (25) originated on the anterior aspect of the cranial tibial artery just proximal to the midtibia and coursed cranially, bifurcating into ascending and descending branches.[9] The rete tibialis arteriosus (R) took part in a looping anastomotic network between the cranial tibial artery and the metatarsal arteries on the anterior aspect of the hock. Additional tiny branches were distributed distally to the cranial surface of the metatarsus.

The cranial tibial artery terminated at the level of the distal portion of the tibia by bifurcating into two arteries; the larger of the two was the medial tarsal artery (28), which traversed the anterior surface of the hock and continued to become the dorsalis pedis artery, and the smaller was the lateral tarsal artery (26). On the anterior surface of the tarsus the latter artery bifurcated into a descending branch (26.1) and a laterally directed branch, the lateral recurrent tibial artery (27), which ascended laterally and cranially to anastomose with a branch of the lateral tibial artery.

The medial tarsal artery terminated as three branches. The caudo-medial metatarsal artery (31) passed medially and posteriorly to bifurcate, sending one branch (31.1) proximally to anastomose with the ramus tibialis artery and a second smaller branch distally; the caudolateral metatarsal artery (30) descended laterally on the volar surface of the metatarsus; the dorsalis pedis artery (32) descended on the dorsal surface of the metatarsus. The caudolateral metatarsal artery (30) gave rise to a large proximal branch (30.1), which ascended to anastomose with branches of the lateral recurrent tibial artery. The caudolateral metatarsal artery continued on the volar surface of the metatarsus, where it anastomosed distally with the perforating metatarsal artery (35).

The dorsalis pedis artery (32) was the main continuation of the medial tarsal artery. Proximally, a descending branch (26.1) of the lateral tarsal artery terminated by joining the dorsalis pedis artery on its cranial surface at the level of the proximal metatarsus. The dorsalis pedis artery continued on the dorsal surface of the metatarsus as the major artery, until it bifurcated approximately half way down the metatarsus into a larger craniolateral metatarsal artery (33) and a smaller inconstant branch called the craniomedial metatarsal artery (34). The dorsalis pedis ar-

[8]Nishida (1963) describes an anastomosis between the genu suprema artery and the femoralis artery. Although these arteries were closely approximated, we did not identify their anastomosis.

[9]Nishida (1963) describes the cranial recurrent tibial artery as the next branch of the cranial tibial artery after the ramus fibularis artery. We found the cranial recurrent tibial artery to originate after origin of the lateral tibial artery.

tery gave off numerous branches, which coursed circumferentially to the superficial soft tissues of the metatarsus.

There was a small accessory (descending) branch (29) of the dorsalis pedis artery that ran parallel to it and continued distally to approximately the level of the origin of the craniomedial metatarsal artery. In some specimens (Fig. 5), it terminated in the superficial soft tissues; while in others (Fig. 9), it anastomosed with the dorsalis pedis artery to continue as the craniomedial metatarsal artery.[10] The craniomedial metatarsal artery coursed distally beyond the level of the perforating metatarsal artery where it appeared to supply branches to the proximal parts of the second and third digits.[11]

The craniolateral metatarsal artery was the major terminal continuation of the dorsalis pedis artery. A large perforating metatarsal artery (35) originated from the craniolateral metatarsal artery at the level of the distal metatarsus. The craniolateral metatarsal artery continued over the dorsum of the phalanges, where it terminated by trifurcating into the lateral digital artery (36) to digit IV, the medial digital artery (37) to digit III, and the lateral plantar metatarsal artery (38) to the proximal aspect of digit II. Each digital artery supplied numerous circumferential branches to the superficial soft tissues along its entire length. The perforating metatarsal artery (35) arose from the plantar surface of the craniolateral metatarsal artery (33) and coursed ventrally to participate in the formation of an anastomosing arch with the caudolateral metatarsal artery (30). It gave origin to the middle plantar metatarsal artery (39), which terminated as the second digital artery (40), supplying digit II, and the medial plantar metatarsal artery (41) with its terminal branch, the first digital artery (42), supplying digit I.

Arterial anatomy of the embryo

Development of the aortic arches (Figs. 10–17)

Prior to day 10 the aortic arches could not be distinguished adequately in our specimens. Three aortic arches were clearly seen on day 10 (Figs. 10,11). These represented the right third aortic arch (3) and the right and left fourth aortic arches (4R, 4L). The right and left brachiocephalic arteries (BC) took origin from the right third aortic arch.[12] This remained the predominant pattern from day 10 (HH36)[13] through day 15 (HH41), at which point the right third aortic arch merged with the right fourth aortic arch. By day 17 (HH43), two separate right aortic arches were no longer discernable. The left aortic arch was still present at this stage. By day 18 (HH44, Fig. 13), the left fourth aortic arch was seen to atrophy and the arch pattern then assumed the appearance found in the hatchling.

Development of the visceral vessels

On day 10 (HH36, Fig. 10A), the predominant branches of the abdominal aorta (A) were the unpaired cranial mesenteric artery (CrM) and the paired vitelline arteries (V). The cranial mesenteric artery was the major proximal branch, which in some embryos approached the diameter of the abdominal aorta. It supplied the yolk sac and the abdominal viscera, which at this stage were located outside of the abdomen. The abdominal aorta bifurcated into a large left and a smaller right vitelline artery, which supplied the vitelline membranes (Fig. 10B).

By day 12 (HH38, Fig. 12), the cranial mesenteric artery and the right vitelline artery both had diminished in size in comparison to the abdominal aorta and the left vitelline artery. By day 17 (HH43), the cranial mesenteric artery was very small approximating the size seen in the hatchling. The right vitelline artery was nearly atrophied and the left vitelline artery predominated.

By day 18 (HH44, Fig. 13), the right vitelline artery had almost disappeared. The left vitelline artery continued a short distance beyond the origin of the ischiatic artery (I), where it terminated abruptly. At this stage only a small amount of blood continued to supply the vitelline membranes. In the hatchling, the left vitelline artery appeared as a tiny strand originating from the ischiatic artery.

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[10]There are two proximal branches of the dorsalis pedis artery, which Nishida (1963) describes as terminating as digital arteries. These were not seen in our specimens.

[11]Nishida (1963) indicates that the craniomedial metatarsal artery gives rise to metatarsal I artery and terminates as the medial digital artery. This was not seen in our specimens.

[12]This differs from Romanoff's (1960) description whereby the right and left subclavian arteries originated, respectively, from the right and left aortic arches.

[13]HH36, HH41, etc., signify stages of Hamburger and Hamilton [1951].

Development of the arterial anatomy of the upper limb

At day 4.5 (HH26, Fig. 14), there was a single dominant artery, the axial artery (a′), traversing the middle of the upper extremity. Distally, this artery terminated as a capillary network (c′). Proximally, two additional major arteries were identified; one (t) was directed caudally to the thoracic wall and the other (c) craniolaterally to the shoulder where it branched into a capillary network.

By day 5 (HH27, Fig. 16), the axial artery that traversed the middle of the limb bud, bifurcated distally. At this time two unnamed arteries were observed: a major artery (t) to the thoracic wall and a dominant branching artery (c′′) to the proximal part of the shoulder. The capillary networks that served as the terminal distribution of these vessels were no longer apparent.

By day 7 numerous branching arteries supplying the developing upper limb were seen. In the thorax there were four major branches that descended to supply the thoracic wall. These resembled the pattern seen in the hatchling. Numerous ascending branches to the shoulder, which resembled the humeral circumflex arteries, were seen. At this point, the arterial pattern to the proximal and distal portions of the wing resembled that of the hatchling. The relationship of these arteries to the adjacent musculature could not be defined.

Development of the arterial anatomy of the lower limb

At day 4.5 (HH26, Figs. 14, 15) the distal part of the abdominal aorta (A) trifurcated into two large, laterally directed arteries, the vitelline arteries (V), and a large sacral artery (A′). In its course, the latter artery located in the midline supplied approximately 10–15 branches to caudal segments.

The vitelline arteries gave origin to a large central artery, the axial artery (a), which traversed the limb where it bifurcated distally. A capillary network supplying the soft tissues of the thigh, leg and foot was present. No large branches of the axial artery were seen. Approximately three vertebral segments cranially, a small laterally directed capillary plexus (ce) originated from the abdominal aorta and passed to the cranial aspect of the proximal part of the thigh. No single vessel predominated.

By day 5 (HH27, Fig. 16), the single axial vessel that traversed the hind limb bifurcated distally. At this stage, a single large caudomedially directed artery (ca) was seen to emerge at the junction of the proximal and middle thirds of this vessel. A second dominant artery (cr), originating on the cranial aspect of the axial artery at junction of the middle and distal thirds was directed craniomedially. An artery that resembled the external iliac artery of the hatchling emerged from the capillary plexus on the cranial aspect of the proximal part of the thigh. This vessel was clearly the dominant artery supplying the cranial aspect of the proximal part of the thigh; it ended by sending branches to the proximal soft tissues of the thigh.

By day 7 (HH31, Fig. 17), the well-developed central artery (i) sent numerous branches to the soft tissues of the thigh and continued to the leg and foot, where it supplied branches to the digits. The external iliac artery persisted as a dominant vessel to the cranial aspect of the proximal part of the thigh, giving off numerous discrete arteries to supply the soft tissues on the cranial side of the thigh. Between days 4.5 and 8, the hind limbs became increasingly dominant in size with respect to the tail.

By day 8 (HH34), the ischiatic artery and its tributaries resembled the pattern seen in the thigh and leg of the hatchling. In the metatarsus, a large cranially directed artery and a smaller lateral artery traversed the metatarsus and formed what appeared to be a metatarsal arch, resembling the hatch-

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Abbreviations

Abbreviations for Figures 10–13

A	aorta
BC	brachiocephalic arteries
C	celiac artery
CrM	cranial mesenteric (umbilical) artery
EI	external iliac artery
I	ischiatic artery
MS	medial sacral artery
S	shell
V	vitelline artery (R, right; L, left)
Y	yolk
3	3rd aortic arch, right
4	4th aortic arch (R, right; L, left)

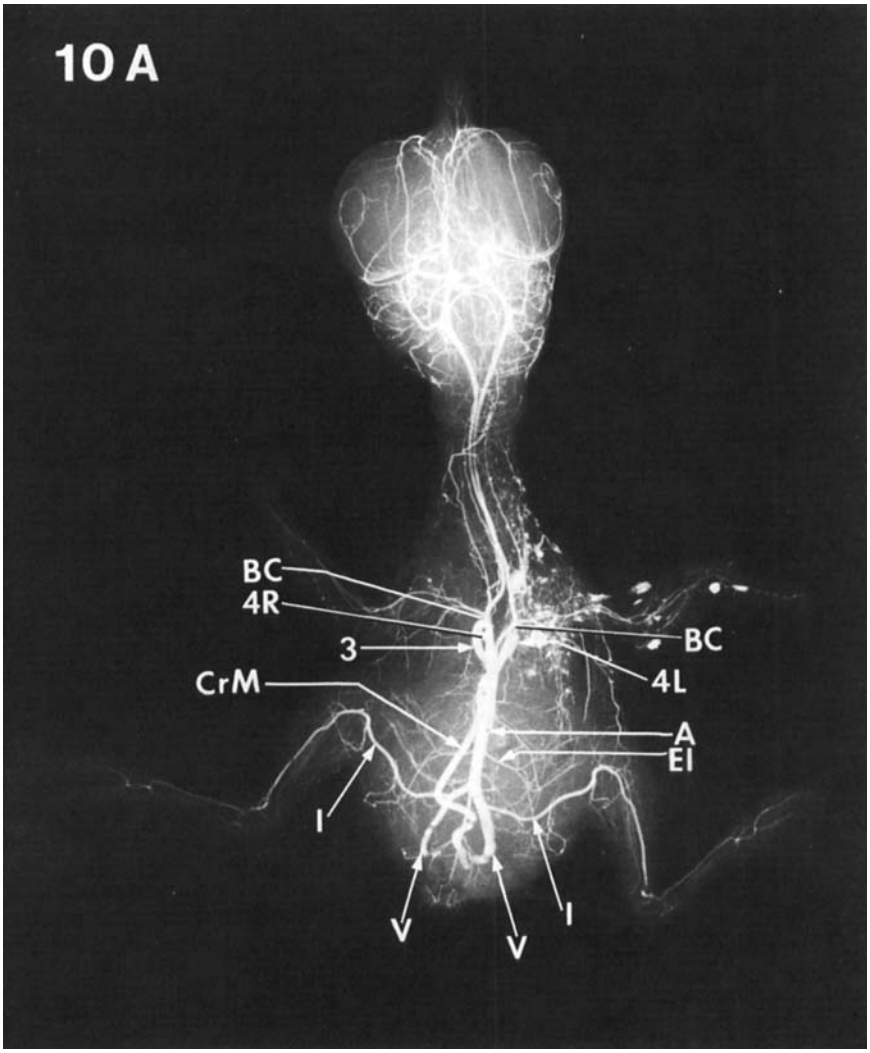

Fig. 10A. Anteroposterior radiograph demonstrating the developing arteries of the 10-day embryo.

ling's caudolateral and craniolateral metatarsal arteries. An artery, which bifurcated almost immediately sending branches to both sides of digit I, was seen to emerge from this arch. Farther distally, a second artery emerged which sent branches to the cranial and caudal aspects of digit II and a branch to the caudal aspect of digit III. Three branches emerged from the most cranial aspect of the arch and supplied the cranial aspect of digit III and the cranial and caudal aspects of digit IV.

By day 10 (HH36, Fig. 10A), the arterial pattern to the thigh, leg, and digits was almost identical to that seen in the hatchling.

DISCUSSION

The arterial pattern observed in the hatchling was remarkably constant among the animals studied. When our observations differ from those of others, the differences are indicated by the footnotes. Some of these variations may reflect species or strain differences, while others may be related to the age

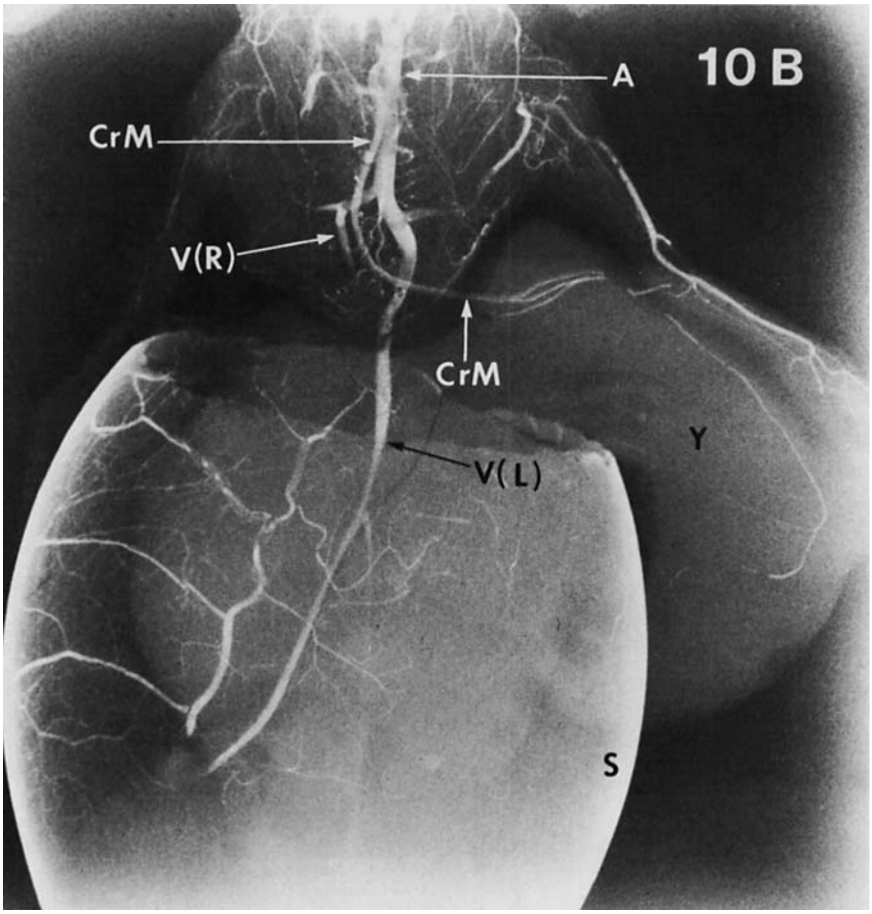

Fig. 10B. Anteroposterior radiograph showing the cranial mesenteric (umbilical) artery supplying the yolk sac and the vitelline artery supplying the vitelline membranes.

differences between our specimens and those reported elsewhere. We were unable to opacify the renal and gonadal arteries in any of our animals. This may be due to the young age of our embryos. It is also possible that the renal portal system contributes the predominant blood flow to these organs in the embryo hatchling and that the renal arteries carry too little blood to be visualized by our method.

In our specimens we identified an anastomosis between the terminal ventral branches of the internal thoracic artery and the ascending branches of the femoral circumflex arteries, as well as anastomoses between the terminal dorsal branches of the internal thoracic artery and the cranial glutealis artery. These anastomotic pathways have not been described previously. Since most detailed arterial descriptions have been of either the upper or lower extremity, but not both, and since these anastomotic pathways are extremely small, it may be that they were overlooked during anatomical dissection.

Most authors use the term umbilical artery (Fitzgerald, 1969; Nishida, 1963) interchangeably with pelvina interna artery (Fitzgerald, 1969; Kaupp, 1918; Lucas and Stettenheim, 1972) and indicate it to be a branch of the external iliac artery. Our interpretation is that the umbilical artery is synonymous with the embryonic cranial mesenteric artery; its large size in the early embryo and the gradual decrease in caliber as the embryo matures is consistent with this interpretation. We have also shown that the artery that becomes the cranial mesenteric artery of the hatchling, in fact provides the

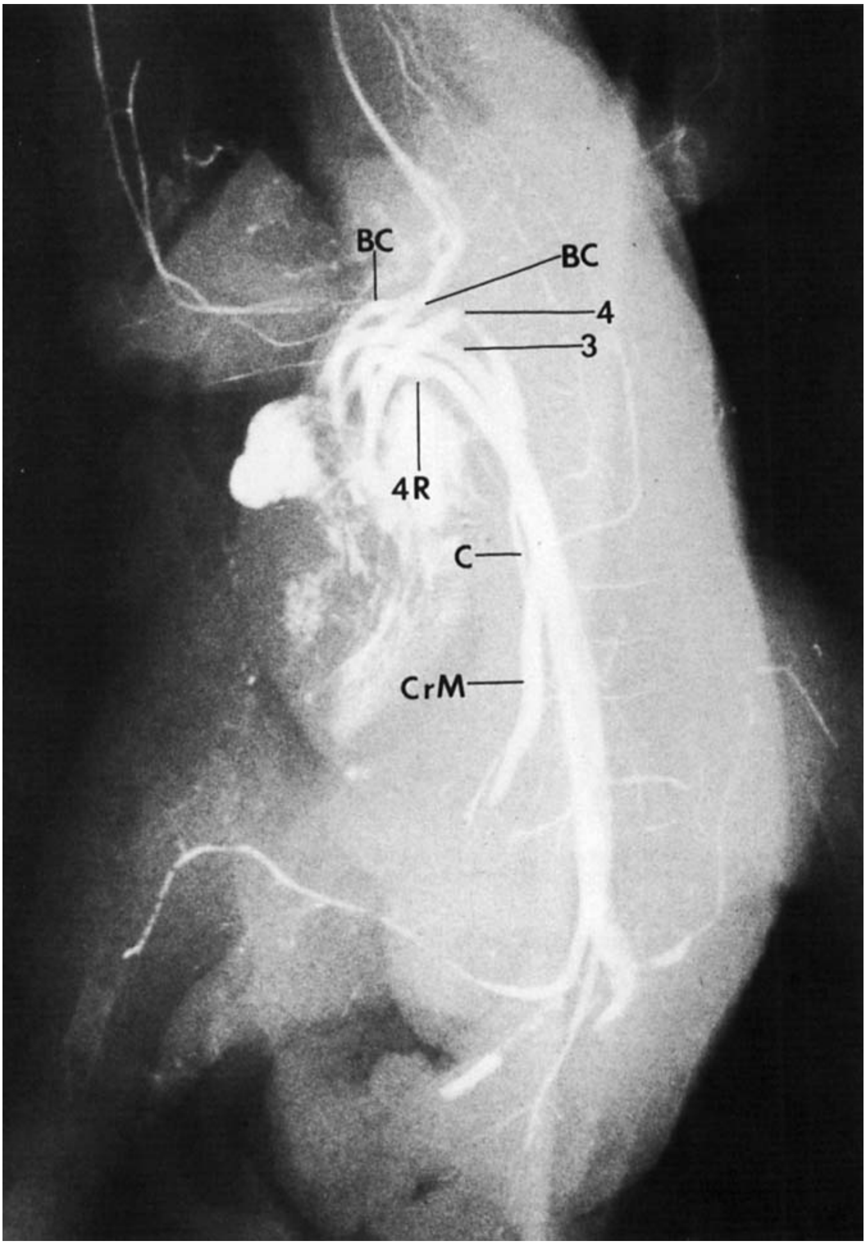

Fig. 11. Lateral radiograph demonstrating the developing arteries of the 10-day embryo.

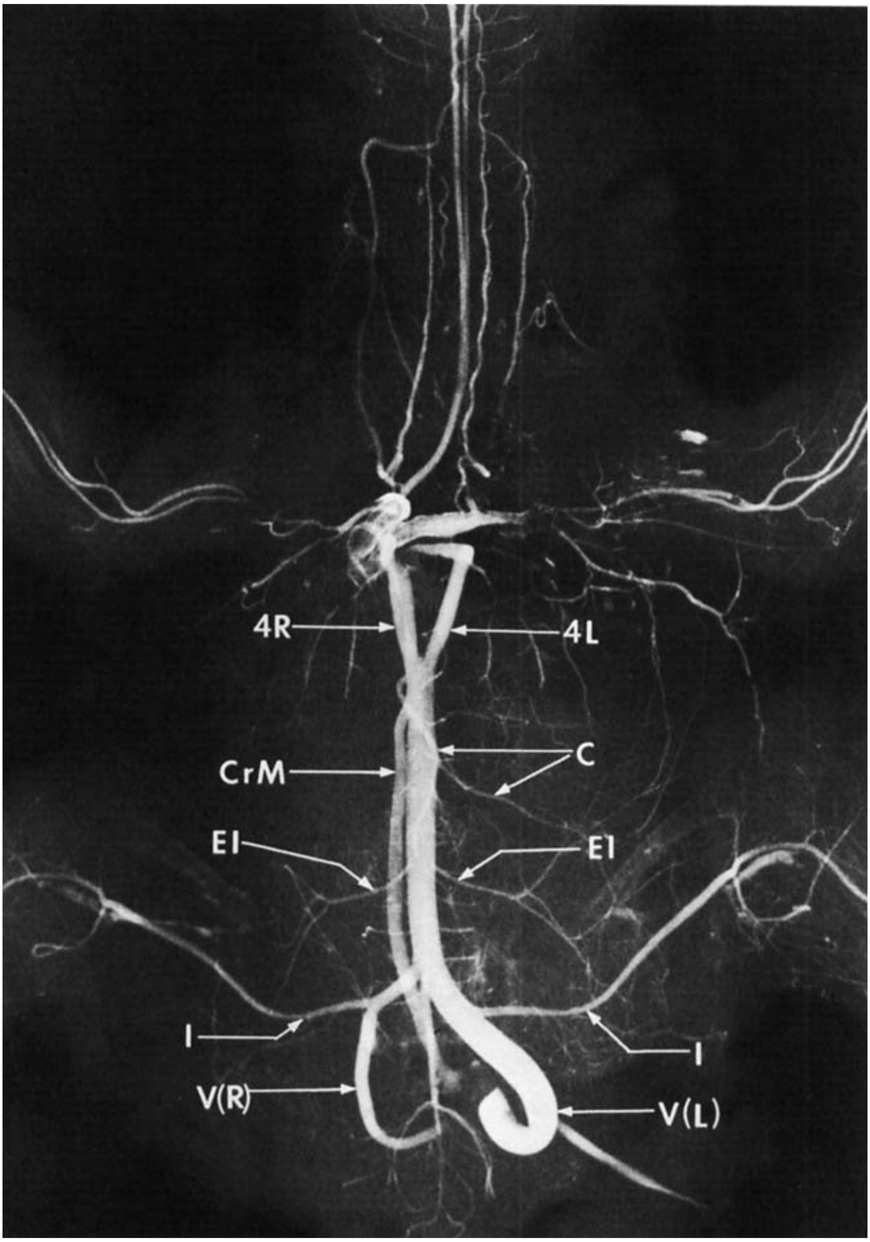

Fig. 12. Anteroposterior radiograph demonstrating the developing arteries in the body of the 12-day embryo.

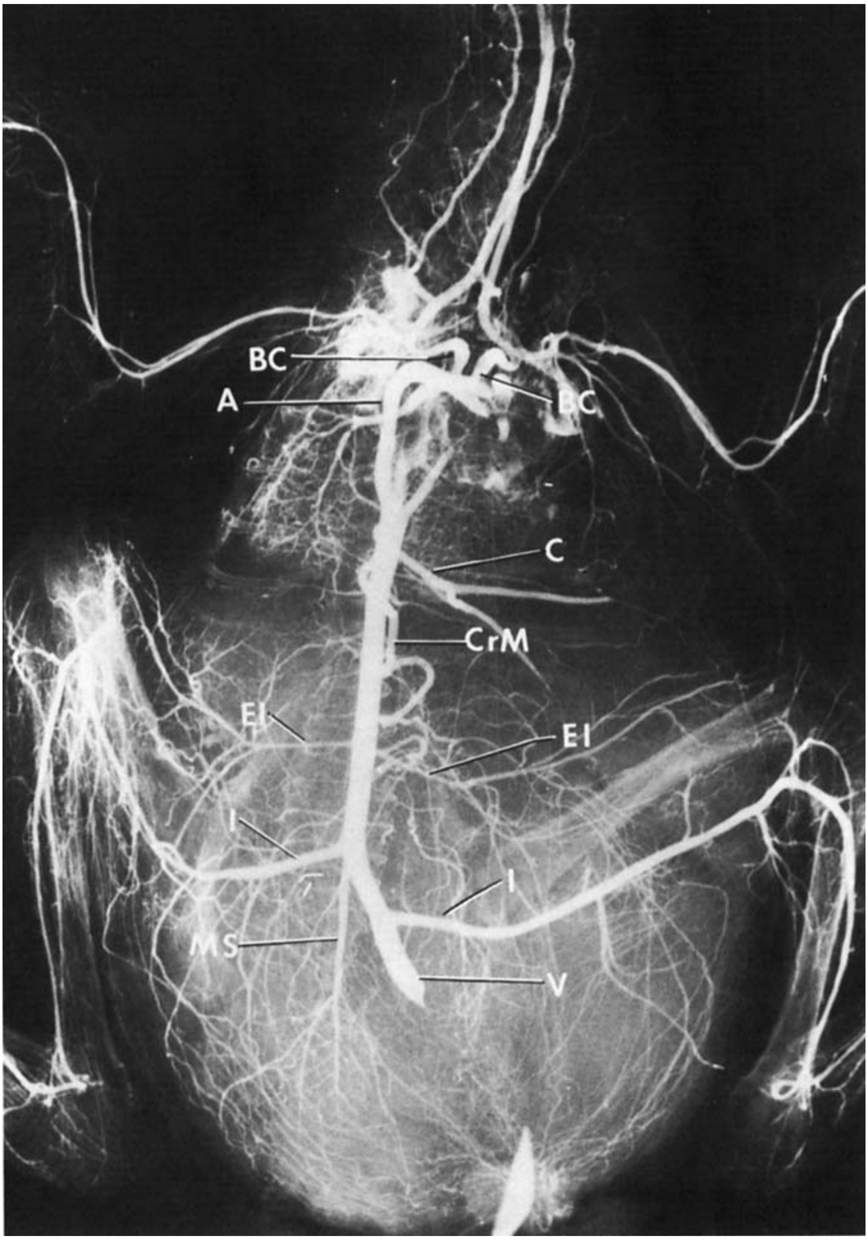

Fig. 13. Anteroposterior radiograph demonstrating the developing arteries of the 18-day embryo.

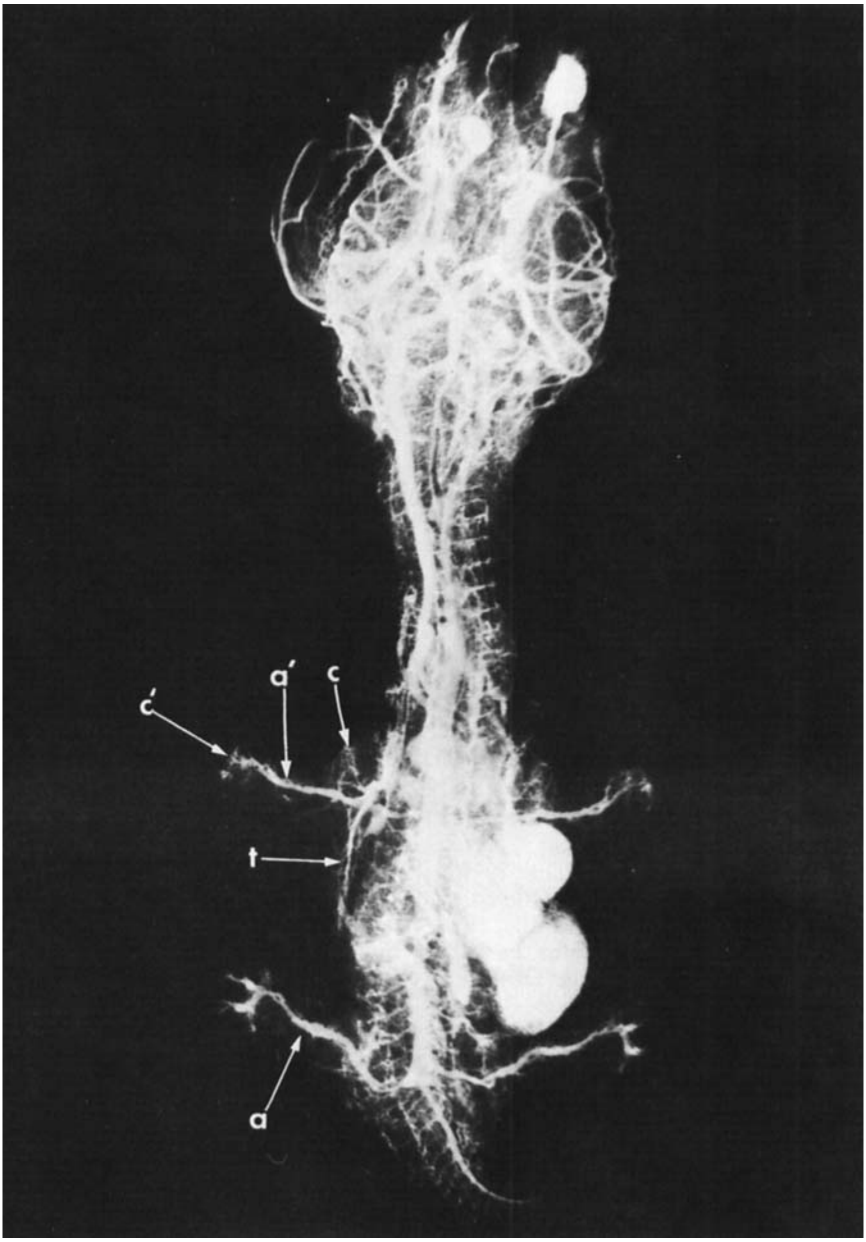

Fig. 14. Anteroposterior radiograph demonstrating the developing arteries in the body of the 4.5-day embryo.

Abbreviations

Abbreviations for Figures 14–17

I–IV	digits
A	abdominal aorta
A'	midline sacral artery
a	axial artery (lower extremity)
a'	axial artery (upper extremity)
c	capillary network (proximal)
c'	capillary network (distal)
c''	embryonic artery to the shoulder
ca	caudomedial branch of axial artery (lower extremity)
ce	capillary plexus (proximal)
clm	caudolateral metatarsal artery
cr	cranial branch of axial artery (lower extremity)
crl	craniolateral metatarsal artery
ct	cranial tibial artery
ei	external iliac artery
i	ischiatic artery
t	thoracic artery
V	vitelline artery

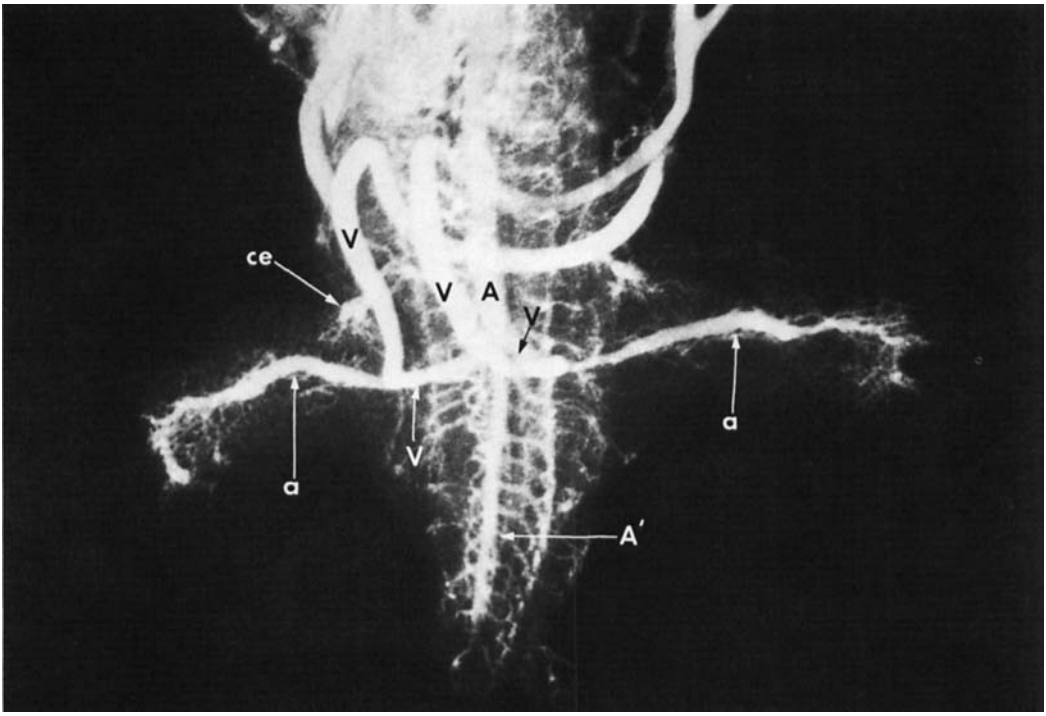

Fig. 15. Anteroposterior radiograph of the caudal part of the body demonstrating developing arteries in the 4.5-day embryo.

arterial supply to the yolk sac. This is in agreement with the findings of Gilchrist (1968). As demonstrated in Figure 10B, the left vitelline artery originating from the left ischiatic artery clearly supplies the vitelline membranes.

The arterial patterns in the upper and lower limbs of the chick embryo share some developmental similarities. In both pairs of limbs, a major axial artery forms from a diffuse capillary network. This is followed by the condensation of discrete arteries developing from proximal and distal capillary networks that merge with the axial artery. Disappearance of portions of these early arteries and replacement by secondary branches was noted. The detailed names of these arteries cannot be assigned with confidence, since our experimental method does not allow us to determine the exact relationship of an artery to the adjacent soft tissues. In the upper extremities at approximately day 7 of incubation and in the lower extremity at approximately day 8 of incubation, the pattern resembled that seen in the hatchling.

Some similarity exists between the development of the arterial pattern in the chick embryo and that in the human embryo. Senior (1919) analyzed the arterial development in the lower extremity of the human embryo between 12 and 22 mm CR (crown rump) stages of gestation. As in the chick embryo, a single axial artery and its incorporation into arteries developing in adjacent areas eventually results in the adult pattern. This development is consistent among individuals of a species. The pattern is so uniquely specific that Senior (1918–1919, 1929) and Pierson (1925) were able to attribute differences in the human adult pattern to the retention of normally transient embryonic vessels.

There has been increasing recognition of an association between arterial pattern anomalies and bony defects in human limbs

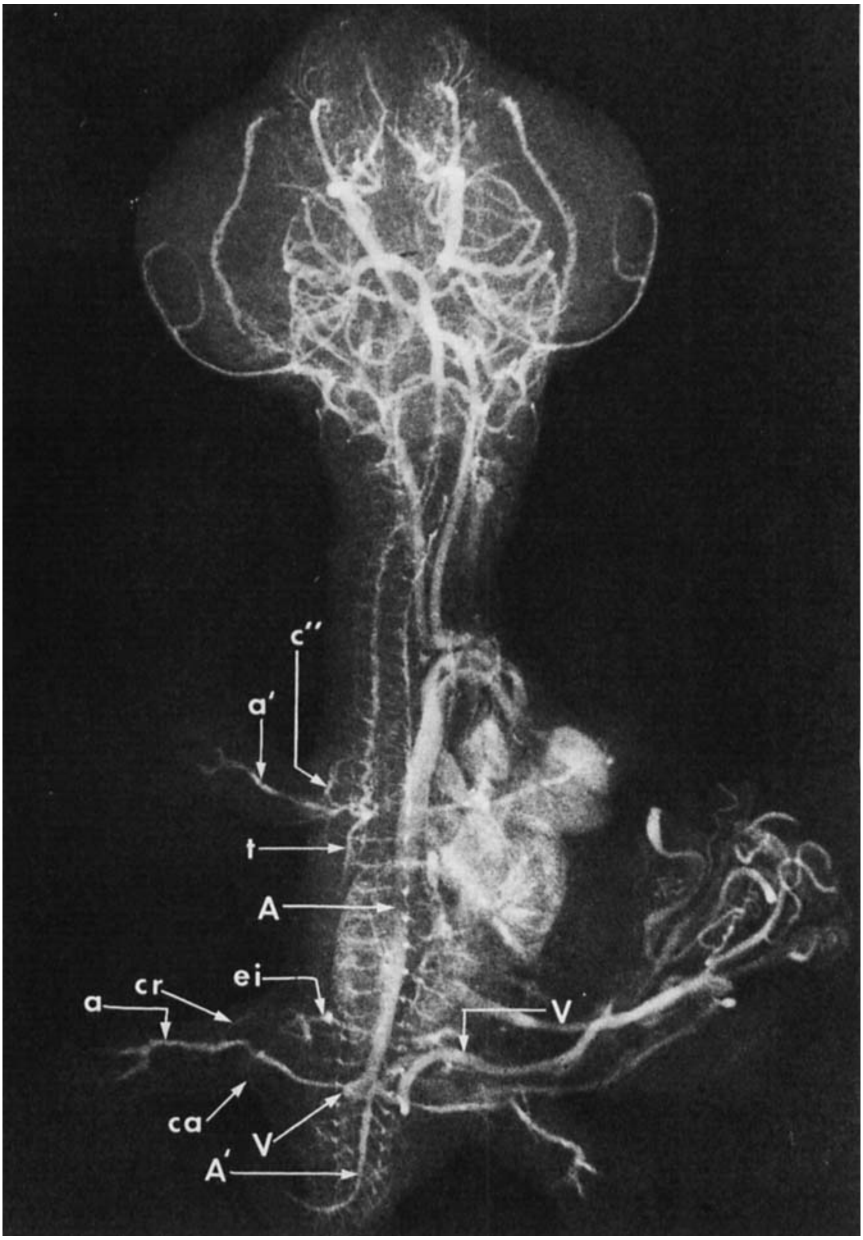

Fig. 16. Anteroposterior radiograph demonstrating the developing arteries in the body of the 5-day embryo.

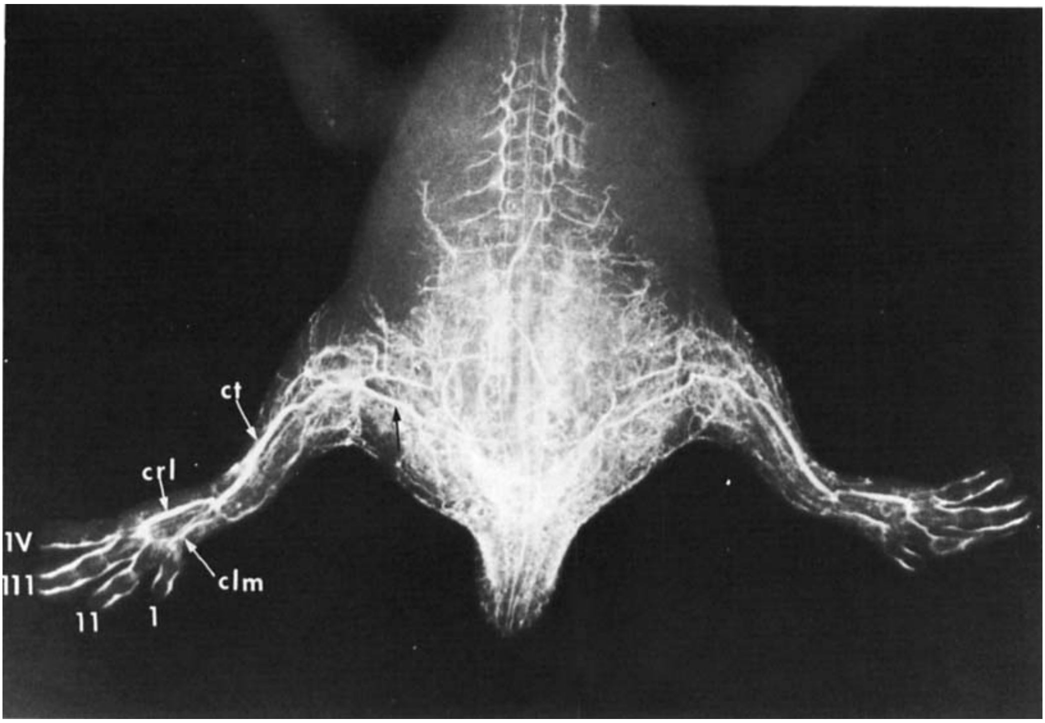

Fig. 17. Anteroposterior radiograph demonstrating the developing arteries in the caudal part of the body of the 7-day embryo.

(Atlas et al., 1980; Ben-Menachem and Butler, 1974; Blauth and Schmidt, 1969; Hootnick et al., 1980a,b, 1983b, 1984; Van Allen, 1981; Van Allen et al., 1982). We wish to develop an experimental model to study the significance of that association. The chicken embryo is advantageous for such studies because it is inexpensive, there is an extensive body of knowledge available regarding avian limb development, and there is ease of access to the embryo for experimental manipulation. The present study was designed to outline the development of the arterial pattern in the chicken embryo and to demonstrate the emergence of the hatchling pattern. The hatchling pattern must be defined in great detail in order to recognize minor variations resulting from experimental manipulation. The detailed arterial description in this study provides a basis for future experimental work.

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