Embryonic Origin of the Caudal Mesenteric Artery in the Mouse

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ABSTRACT

It is commonly held that the caudal mesenteric artery (CaMA, or inferior mesenteric artery in humans) arises in the same manner as the celiac and cranial mesenteric artery (CrMA, or superior mesenteric artery in humans), i.e., from the remodeling of the vitelline system of arteries that surrounds and supports the yolk sac. Conflicting evidence about the precise manner in which the CaMA arises was presented in studies of the luxate syndrome (Carter: J. Genet. 1954;52:1–35) and sirenomelia (Schreiner and Hoornbeek: J. Morphol. 1973;141:345–358) in the mouse. These studies suggested that the CaMA arises from the remodeling of the medial umbilical arterial roots. Later studies of blood vessel development in the hindlimb of the Dominant hemimelic mouse (Gest: Anat. Rec. 1984;208:296; Anat. Rec. 1987;218:49A; Gest and Roden: Anat. Rec. 1988;220:37–38A) also supported the results of the previous studies. The present investigation tests the hypothesis that the CaMA arises as a result of the regression and remodeling of the medial umbilical arterial roots. Vascular corrosion casts of 9.5-13.5-day-old mouse embryos were observed by scanning electron microscopy (SEM). The results of the present investigation agree with the aforementioned studies. The medial umbilical roots initially conduct the blood to the placenta. On days 10-12 the medial umbilical roots regress and remodel into the CaMA, while the lateral umbilical roots take over the blood supply to the placenta. On the basis of our results, we conclude that the CaMA arises from the medial umbilical roots and not from the remodeling of the vitelline system of arteries, as previously assumed. Anat Rec Part A 271A:192–201, 2003. © 2003 Wiley-Liss, Inc.

Key words: development; vascular corrosion casts; scanning electron microscopy; caudal mesenteric artery; medial umbilical roots

It is commonly assumed that during the development of the gut, the caudal mesenteric artery (CaMA, or inferior mesenteric artery in humans) originates from the vitelline system of arteries. It has been well documented that the celiac artery and the cranial mesenteric artery (CrMA, or superior mesenteric artery in humans) arise from the vitelline arteries, and most current embryology textbooks hold that the CaMA arises in the same manner (Hamilton and Mossman, 1976; Moore and Persaud, 1993; Sadler, 1995; Larsen, 1997; Carlson, 1999). Specifically, it is assumed that the vitelline arteries that initially surround and support the yolk sac and gut later remodel to form the celiac artery, CrMA, and CaMA in order to support the foregut, midgut, and hindgut, respectively.

Conflicting evidence about the precise manner in which the CaMA arises was presented in previous studies of the

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luxate syndrome (Carter, 1954) and sirenomelia (Schreiner and Hoornbeek, 1973) in the mouse. These studies suggested that the medial umbilical roots remodel into the CaMA, although this transformation was not thoroughly documented. Further evidence against the vitelline origin of the CaMA comes from investigations of the development of blood vessels in the hindlimb of the Dominant hemimelic (Dh) mouse (Gest, 1984, 1987; Gest and Roden, 1988). These studies revealed a pattern in the remodeling of the medial umbilical arterial roots that supports the earlier observations.

The present study tests the hypothesis that the CaMA does not develop from the vitelline system of arteries, but rather arises as a result of the remodeling of the medial umbilical arterial roots. Vascular corrosion casts of mouse embryos of 9.5–13.5 days gestation were prepared in order to trace the development of the CaMA and to thoroughly document the remodeling process whereby the medial umbilical arterial roots render the development of the CaMA.

MATERIALS AND METHODS

Preparation of Vascular Casts

Mouse embryos (BALB/C) of 9.5–13.5 days gestation were used in this study. Mice mated during the night and were checked for vaginal plugs each morning. Day zero in the life of the embryo was defined by the presence of a vaginal plug. Embryonic specimens were collected every 0.5 days from the uterus of an anesthetized mouse. The extraembryonic tissues were dissected away under a dissecting microscope, leaving only the embryo proper, umbilical vessels, and placenta intact.

The casting media used was Mercox CL-2R (Japan Vilene Co., Tokyo, Japan), which is available as a blue, red, or colorless liquid resin with a viscosity of 20 centistokes/sec at 25°C. Mercox was diluted with 20–30% methyl methacrylate monomer (Fluka AG, Buchs, Switzerland) to reduce the viscosity. The low viscosity allowed the resin to thoroughly fill the lumen of injected blood vessels (Hodde and Nowell, 1980). The Mercox was prepared by thoroughly mixing the base resin with catalytic paste and methyl methacrylate. The mixture was aspirated into a syringe, from which all air bubbles were carefully removed, and connected to a syringe pump. The use of a syringe pump had many advantages over injection by hand. As opposed to manual injection, the perfusion apparatus allowed control over intravascular infusion pressure while maintaining reproducible injections for each specimen (Christofferson and Nilsson, 1988).

Many previous investigators used the umbilical vessels as the injection site because the entire vascular system can be injected, with minimal damage to the specimen (Navarro et al., 1998). However, the fetal mouse umbilical vessels were very difficult to inject without damaging these vessels. Consequently, the injection needle was inserted through the placenta toward the attachment of the umbilical vessels, and the casting medium was injected at the base of the placenta as close to the umbilical vessels as possible. In the liquid phase, the injectant filled the vascular compartment and was allowed to polymerize overnight, thereby replicating the luminal compartment of the vascular system. The specimens were held overnight in glass vials filled with distilled water.

The obscuring parenchyma was digested and macerated by alternating 24-hr periods of immersion in distilled water and sodium hydroxide (15%). The specimens were contained in the same vials when immersed in either of the two media. Because of the fragile nature of the casts, extreme care was taken at all times when the immersion medium was changed. Digestion of the noninjected tissues was complete in 4–7 days, depending on the size of the embryo. After the final exposure to the sodium hydroxide, the specimens were rinsed three times in distilled water and dried at room temperature.

SEM of the Vascular Casts

The casts were mounted on aluminum stubs and sputter-coated in a Polaron (East Sussex, UK) E5100 sputter coater. A gold coat with a thickness of 30–40 nm is considered sufficient. The specimens in this investigation were coated for 2 min and then cooled for 30 sec. To ensure ample coating, the specimens were tilted 45° and coated again for 90 sec. If necessary, to prevent charging, the specimens were coated again using the above procedure. No adverse changes were observed in the casts as a result of the sputter coating. Because our study was concerned with patterns of developing blood vessels, which are revealed at a relatively gross scale, the relative thickness of the sputter coating did not hinder our investigation.

Scanning electron microscopy (SEM) is considered an excellent technique for the study of replication casts because it combines a large depth of focus with a superb clarity of visualization (Dollinger and Armstrong, 1974). Additionally, SEM of casts of embryonic vascular systems has become a standard method for studying the fine details of blood vessels (Navarro et al., 1998). All of the specimens in this study were examined at an accelerating voltage of 10 kV with an Amray (Bedford, MA) 1000-B scanning electron microscope. Voltages $>$ 15 kV may damage the specimen because overexposure to the beam will cause craters to develop on the surface (Burger et al., 1984). Specimens aged 9–13.5 days (separated by .5-day intervals) were photographed on Polaroid (Waltham, MA) 4x5 Land Film (Type 55, POS/NEG). Photographs were taken from various angles and orientations to best discern the vessel patterns and reveal the relationships among them.

RESULTS

The terminology used in the literature for the roots of the umbilical arteries varies. The terms "primary," "ventral," and "medial" have been used for the earliest-appearing ventral branches from the dorsal aorta that reach the placenta as umbilical arteries (the paired umbilical roots fuse to form a single umbilical artery in the mouse). The terms "secondary," "dorsal," "dorsolateral," and "lateral" have been used for the later-appearing arteries forming the umbilical arteries. In this report, we refer to the umbilical roots as medial and lateral, based upon their relative positions during development. Figure 1 summarizes the observed development of the medial and lateral umbilical roots and the CaMA. As the lateral umbilical roots form and replace the umbilical arterial supply initially provided by the medial umbilical roots, the medial roots regress to become the CaMA.

Photomicrographs of a 9.5-day-old embryo (Fig. 2) show that there are two unfused dorsal aortae whose caudal ends continue ventrally as the left and right medial umbilical roots. At the junction of the omphalomesenteric artery and the medial umbilical roots, the medial umbilical roots unite to form the single umbilical artery that is

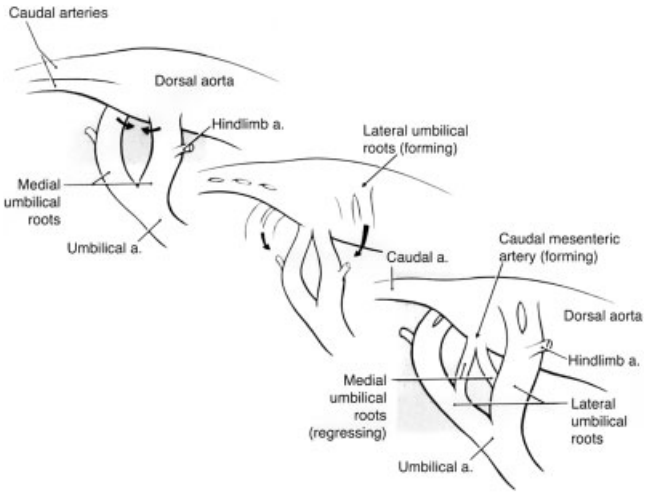

Fig. 1. Diagram of the formation of the lateral umbilical roots, the resulting regression of the medial umbilical roots, and their proximal fusion to form the caudal mesenteric artery.

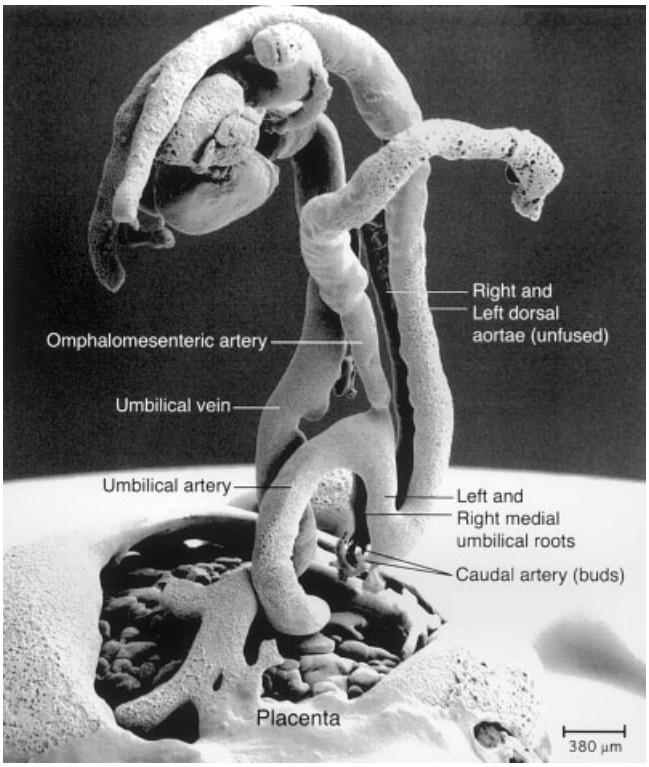

Fig. 2. Cast of a 9.5-day-old mouse embryo as seen from the left side. The two unfused dorsal aortae terminate by continuing as the right and left medial roots. Caudal arterial buds can be seen at the junction between the dorsal aorta and the medial root. The omphalomesenteric artery can be seen arising at the union of the medial umbilical roots that forms the single umbilical artery.

normally present in mice (as opposed to humans, in which the fetal-placental circulation normally consists of two umbilical arteries). Caudal artery buds are seen to arise from the point at which the dorsal aortae bend ventrally and cranially to continue as the medial umbilical roots.

In the 10-day-old embryo, photomicrographs (Figs. 3 and 4) depict the changes in the umbilical roots as the hindlimb arteries develop. By this stage, the two dorsal aortae have fused and the caudal arteries have undergone considerable development but remain unfused. Hindlimb arteries can be seen branching from the medial umbilical roots to form their associated arterial plexus (Fig. 4). The lateral umbilical roots begin as primitive outgrowths from the dorsolateral aspects of the dorsal aorta. Figure 3 shows the right lateral umbilical root as it forms as an outgrowth of the dorsal aorta and anastomoses with the hindlimb plexus.

The developmental events that occur in a 10.5-day-old embryo are exemplified in Figures 5–7. At this stage, the medial umbilical roots are regressing, while the lateral umbilical roots are developing and enlarging. The caudal arteries have fused, while the hindlimb plexuses have increased in complexity (Fig. 5). As seen in Figure 6, the left lateral umbilical roots originating from the dorsal aorta have remodeled into two vascular channels that eventually fuse to create one large-caliber lateral umbilical root. The lateral umbilical root still connects and anastamoses with the hindlimb arteries, as shown in Figure 5. During this developmental stage, the caliber of the lateral umbilical roots is greater than that of the medial umbilical roots, hence the lateral umbilical roots are conducting a larger proportion of the blood flow to the umbilical artery (Fig. 7).

The 11-day-old embryo is characterized by continued enlargement of the lateral umbilical roots and continued regression of the medial umbilical roots (Figs. 8 and 9). By the end of day 11, the proximal medial umbilical roots have regressed and remodeled to the extent that they have fused at their proximal origin from the ventral aspect of the dorsal aorta, thus marking the earliest appearance of the CaMA. At 11 days, the distal medial umbilical root elements are regressing and remodeling into the single arterial channel and the branches of the CaMA (Figs. 10 and 11).

Photomicrographs of a 12-day-old embryo show that the medial umbilical roots have regressed and remodeled into the CaMA and its associated arterial plexus. Concomitantly, the lateral umbilical roots, now more correctly termed the common iliac arteries, are fully developed and form the vascular channels that unite to supply the umbilical artery as well as the hindlimb (Fig. 12).

In the 13-day-old embryo, the hindgut plexus has continued to develop and acquire vascular contributions from the left and right lateral umbilical roots (common iliac arteries). Regression of the medial umbilical roots and their remodeling into the CaMA is complete at this stage of development (Fig. 13).

By 13.5 days, the foregut, midgut, and hindgut vasculature is apparent as the celiac artery, CrMA, and CaMA, respectively. Figure 14 depicts the relative relations of these blood vessels and the areas they supply. Specifically, the celiac and CrMA are ventral branches of the dorsal aorta. The CaMA is also a ventral branch from the dorsal aorta, but originates immediately cranial to the branching of the left and right common iliac arteries (originally lateral umbilical roots). The CaMA is seen to course ventrally and caudally to supply its branches to the hindgut plexus, which lies between the two common iliac arteries (lateral umbilical roots).

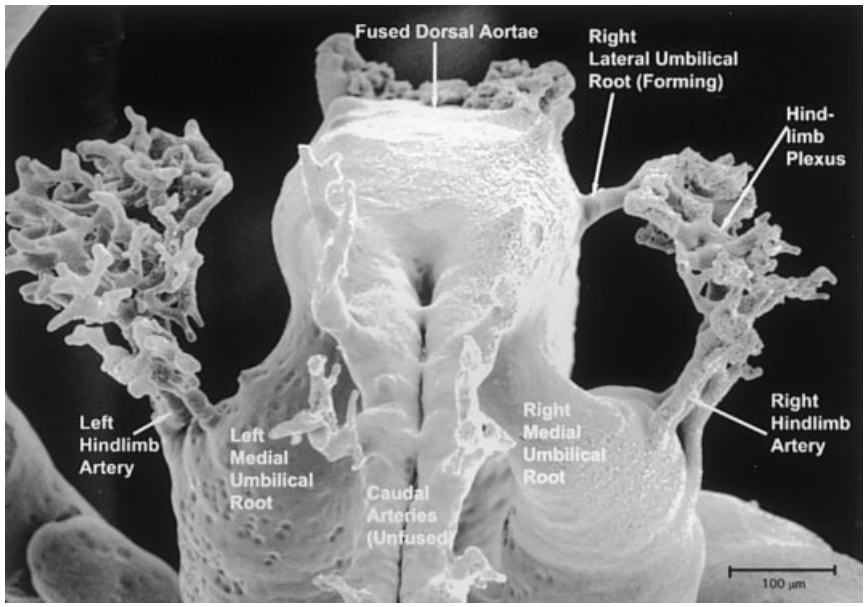

Fig. 3. Caudal view of a 10-day-old mouse embryo. The dorsal aortae have fused, while the caudal arteries have continued to elongate and are beginning to fuse. Right and left medial umbilical roots represent large ventral continuations from the caudal end of the dorsal aorta. Notice the hindlimb arteries that project from the medial roots and form their associated hindlimb arterial plexus. Also, note how the primitive lateral root begins as a bud from the dorsal aorta and coalesces with the hindlimb plexus.

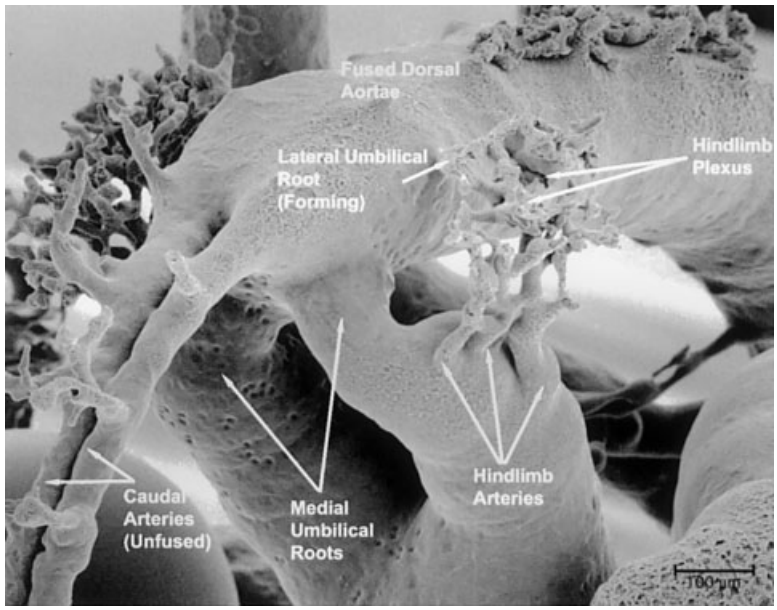

Fig. 4. Right lateral view of a 10-day-old mouse embryo. The caudal arteries remain unfused, while the medial roots can be seen to originate at the termination of the dorsal aorta. Hindlimb arteries are clearly seen to branch from the medial root and form the hindlimb plexus. Note that the lateral root begins as a sprout from the dorsal aorta and continues to the hindlimb plexus.

DISCUSSION

Previous studies of the embryonic development of vascular patterns have relied upon techniques such as the reconstruction of serial sections, or the injection of inks or dyes and clearing. In this context, it is enlightening to consider the comments of Senior (1919, p. 60–61), who stated: "The reconstruction of vascular plexuses in wax, using every second or fourth section as the case may be, is somewhat difficult. The practice followed has been to unite the parts of the adjacent plates which fit after careful adjustment and to remove those which do not join. In this way the plexus represented in the reconstruction is

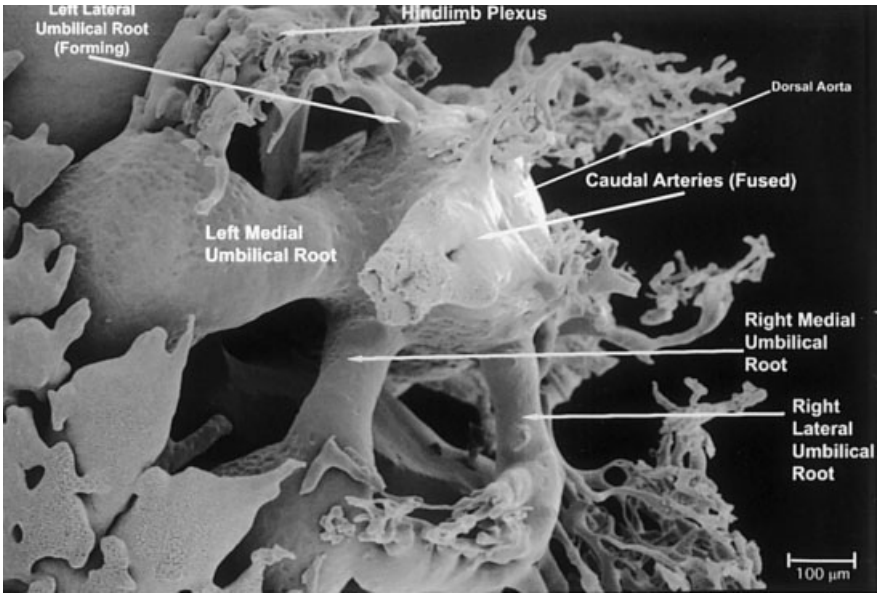

Fig. 5. Caudal view of a 10.5-day-old mouse embryo showing the continued formation of the lateral umbilical roots while the medial umbilical roots begin to regress. The caudal arteries have fused by this stage. The distal end of the caudal arteries has been dissected away to reveal the medial umbilical roots. Note the continued proliferation of the hindlimb plexus and the increasing caliber of the lateral umbilical roots.

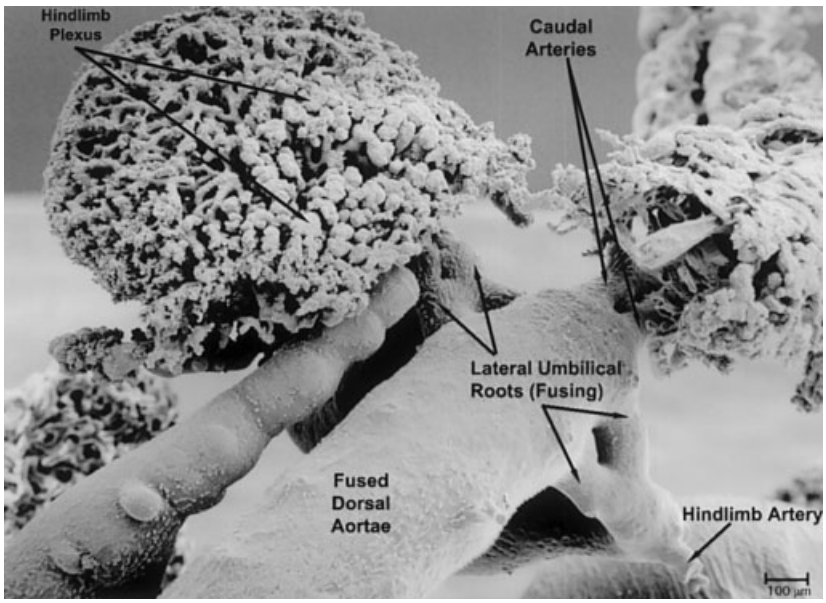

Fig. 6. Dorsal view of a 10.5-day-old mouse embryo. Note the completely fused dorsal aorta and the fusing lateral umbilical root buds forming a single root on each side. The left hindlimb plexus has been dissected away to reveal the connection between the lateral root and the hindlimb artery. Also, note the extremely proliferated right hindlimb arterial plexus supplying the rapidly developing hindlimb tissues.

probably less dense than that occurring in the embryo. The reconstruction, in fact, reproduces the spirit rather than the letter of the original." In the present study, we initially employed the standard technique of ink injection and clearing as described by Seichert and Rychter (1971), but found that this method did not adequately reveal the intricate branching and communication of developing blood vessels (see Fig. 11). Therefore, other preparation techniques for accurately and completely revealing blood vessel patterns were sought.

The technique of vascular corrosion casting was first introduced by Taniguchi et al. (1952, 1955) as an improved method for displaying the three-dimensional architecture of blood vessels. Over 20 years ago, Hodde and Nowell

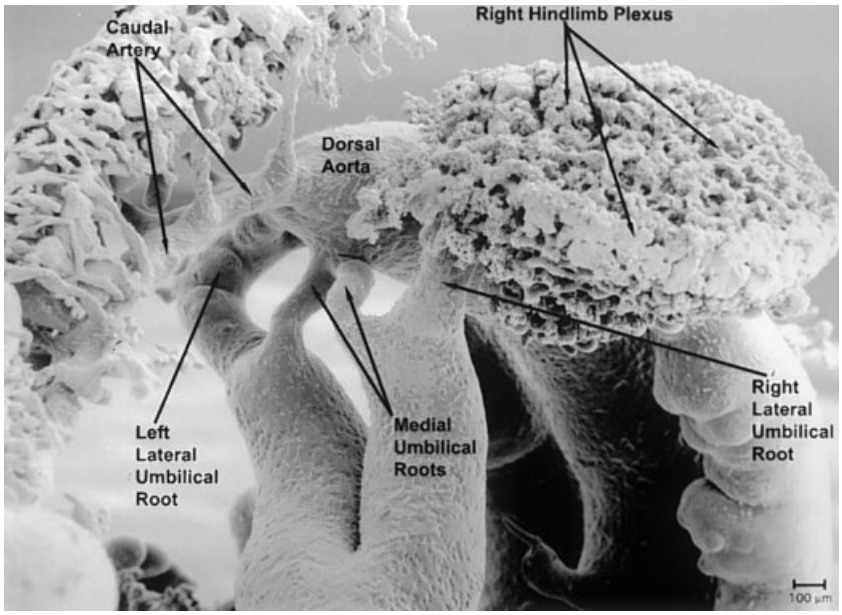

Fig. 7. Right oblique caudal view of a 10.5-day-old mouse embryo. The lateral umbilical roots are still connected to the increasingly complex hindlimb plexus. The medial umbilical roots have undergone considerable regression and are of smaller caliber than the lateral umbilical roots.

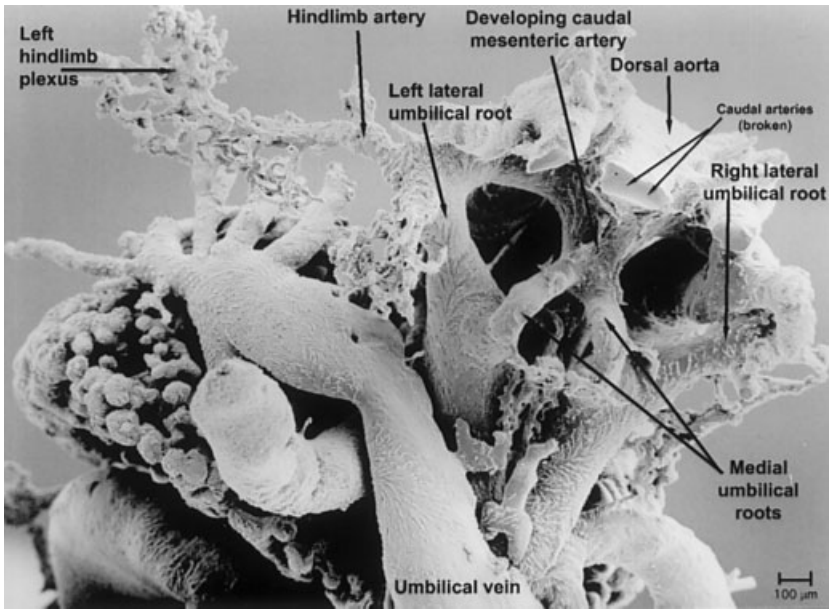

Fig. 8. Caudal view of an 11-day-old mouse embryo. The lateral umbilical roots are well developed, while the medial umbilical roots have considerably regressed. The proximal fusion of the medial umbilical roots represents the earliest stage of the development of the caudal mesenteric artery. Note the elongated hindlimb artery that supplies the hindlimb plexus. The caudal arteries have been removed by dissection.

(1980, p. 89) wrote that SEM combined with corrosion casting is "an established means of investigating such phenomena as the three-dimensional aspects of branching and anastomosing. . .vascular pathways. . .all of which are obscured by surrounding parenchyma. . ." Yoshida and Chiba (1992, p. 457) noted that "[s]canning electron microscopy (SEM) of vascular corrosion casts has become a standard method for studying the fine distribution of blood vessels in many organs and tissues. However, there are few reports of prenatal microvasculature of experimental animals. This may be due to the extreme difficulty in handling delicate capillaries and the methacrylate resin casts of embryonic animals." The present authors will attest to the difficulty of handling the vascular corro-

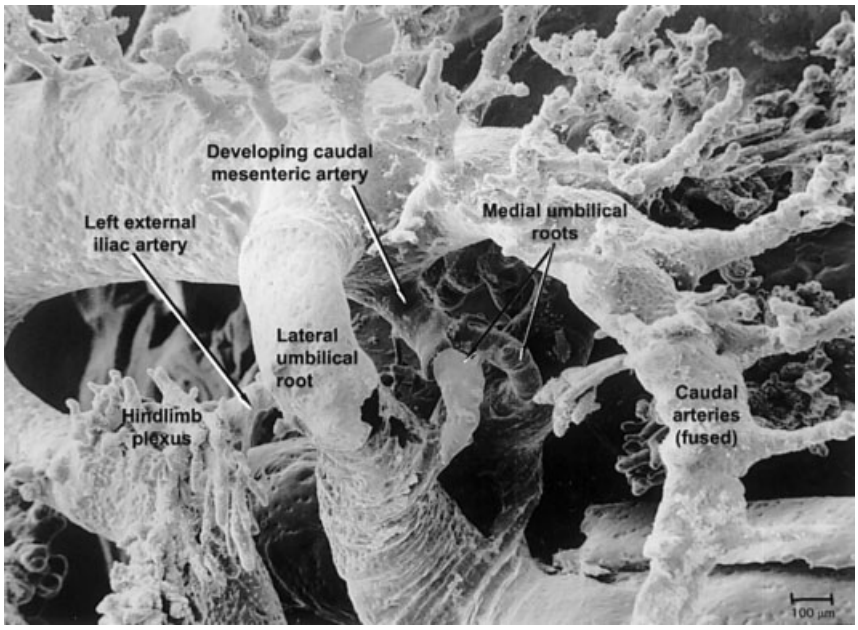

Fig. 9. Left lateral view of an 11-day-old mouse embryo. Note the reduced medial roots and their small caliber as compared to the well-developed lateral roots. The caudal arteries have fused completely by this stage, and the hindlimb artery and associated hindlimb plexus are readily visible.

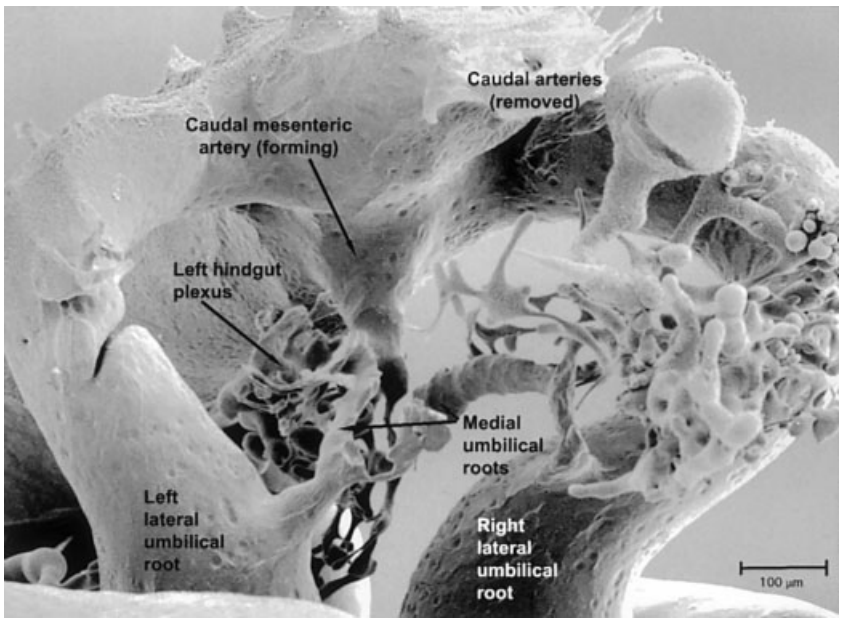

Fig. 10. Caudal view of an 11-day-old embryo. The lateral umbilical roots are well developed and of large caliber. The medial umbilical roots have regressed considerably and are remodeling to form the caudal mesenteric artery and associated hindgut arterial plexus. The caudal artery and the hindlimb plexus have been dissected away to reveal the hindgut vasculature.

sion casts of developing mice, but it is our belief that these investigational methods allowed the patterns of vessel development, especially CaMA development, to be documented at sequential stages of embryonic development.

The fundamental design of corrosion cast studies includes filling the compartment of interest with a liquid, which subsequently solidifies in the system, thereby creating an "injection replica." The surrounding tissue is corroded away, leaving only the replica of the compartment. After the specimens are dried and dissected, they are rendered conductive and mounted on stubs for SEM (Hodde and Nowell, 1980). In the present study, vascular

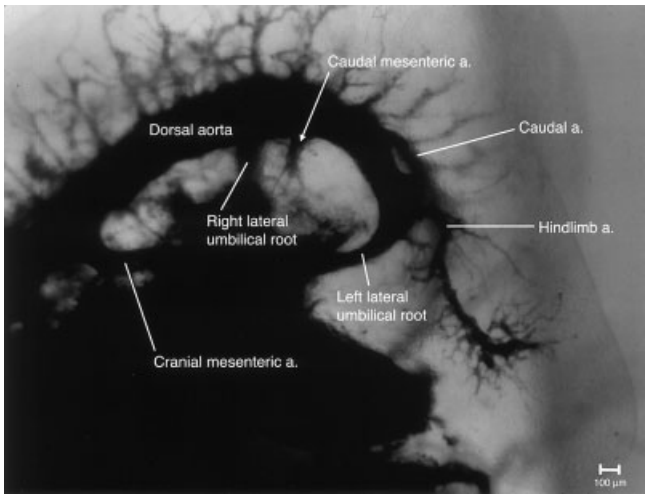

Fig. 11. Left oblique dorsal view, looking caudally, of an 11.5-day-old mouse embryo prepared by ink injection and clearing. Connections between the caudal mesenteric artery and the lateral umbilical roots are difficult to discern.

corrosion casts made from mouse embryos (9.5–13.5 days old) were observed and photographed using SEM. Our observations were focused on the development, remodeling, and regression of the medial umbilical arterial roots. This method was deemed most appropriate because vascular corrosion casting allows visualization of the three-dimensional nature of vascular channels, and permits a high-magnification study of surface detail (Burger et al., 1984).

The foundational works of Lockwood (1885), Hochstetter (1890), Mall (1891), Ravn (1894), and Frédéric (1897) established the concept that the vitelline system of arteries remodels to form the celiac, superior mesenteric, and inferior mesenteric arteries. The origin of these three arteries as ventral branches from the dorsal aorta has been supported by the work of Tandler (1903), Broman (1908), Felix (1910), Tada (1956), and Barth et al. (1976), and is accepted by most textbooks of embryology (Keibel and Mall, 1912; Hamilton and Mossman, 1976; Moore and Persaud, 1993; Sadler, 1995; Larsen, 1997; Carlson, 1999).

In addition, most observers of the formation of the umbilical arteries have concluded that the primary or medial umbilical roots regress and disappear completely during development, following the establishment of the lateral umbilical roots (Tandler, 1903; Broman, 1908; Senior, 1919; Dawson, 1922). It is quite interesting to note, in the light of our present observations, the following comment by Dawson (1922, p. 334): "The umbilical arteries are regarded as caudal precocious members of the vitelline series."

In his studies of the luxate syndrome in mice, Carter (1954) observed the vascular development of the hindgut and umbilical vessels, using the method of reconstruction of serial sections. Specifically, he examined and reported on the events involving hindlimb and hindgut development of mouse embryos aged 10–15 days. He observed that up to day 10.5, the medial umbilical roots are the primary vascular channels supplying the single umbilical artery in mice (as opposed to humans, who normally have two umbilical arteries). The paired lateral umbilical roots form and replace the regressing medial umbilical roots. Eventually, the lateral umbilical roots become the common iliac arteries and supply all fetal blood to the umbilical artery, as well as the hindlimb. Furthermore, Carter states that between 10.5 and 11.5 days of development the medial umbilical roots regress and remodel into the CaMA. Carter's description of the morphological changes of the umbilical artery occurring in the 10.5- and 11.5-day-old embryo agree with the results of the present investigation. He observed that in the 10.5-day-old embryo the umbilical artery originates from the ventral aspects of the dorsal aorta, and that the limb artery develops from the dorsolateral aspects of the left and right medial umbilical roots. These results agree with those of our study, and can be seen clearly in Figures 2–4.

Regarding the 11.5-day-old embryo, Carter (1954) observed extensive changes occurring in the vasculature of the limb and umbilical arteries, and noted that the lateral umbilical roots originate from the dorsal aorta and anastomose with the hindlimb arterial plexus. Once again, these observations agree with the present results (see Figs. 2–4). Carter (1954, p. 11) reported that "[d]uring the next few hours, these lateral arterial courses develop enormously, taking over almost the whole umbilical blood flow, while the original paired (medial) umbilical arteries regress to a fraction of their erstwhile size." This description agrees with our observations in the 10.5- and 11.5-day-old embryos (Figs. 4–9). The lateral umbilical roots begin as small-caliber vascular channels that anastomose with the hindlimb vessels originating from the medial umbilical roots. The lateral umbilical roots enlarge to assume the role of the umbilical blood supply, replacing the medial umbilical roots. Concomitantly, the medial umbilical roots regress to become much smaller-caliber vessels.

Carter (1954, p. 23) noted that in the 12.5-day-old embryo "[t]he posterior mesenteric artery is all that remains in the adult of the primitive medial umbilical arteries." In the present investigation, we observed an 11-day-old embryo whose medial umbilical roots were simultaneously remodeling into the CaMA at its proximal end, and continuing to regress at its distal end. In the 12-, 13-, and 13.5-day-old embryos in our study, the medial umbilical roots had completely regressed and remodeled into the CaMA and its major branches of the hindlimb arterial plexus. By 13.5 days, the final vascular pattern is established. Our observations confirm the hypothesis that the CaMA arises from remodeling of the medial umbilical roots. At 13.5 days, the CaMA is situated on the ventral aspect of the dorsal aorta, located cranial to the left and right common iliac arteries (lateral umbilical roots).

The results of the present investigation, based upon SEM of vascular corrosion casts, agree with and confirm the observations of Carter (1954), who used reconstructions of serial sections. The medial umbilical roots initially conduct the blood to the placenta. From day 10 to day 12, the medial umbilical roots regress as they are replaced by newly formed lateral umbilical roots. However, instead of completely disappearing, the medial umbilical roots remodel into the CaMA. We therefore conclude that, contrary to commonly held concepts of gut blood-vessel development, the CaMA arises from the medial umbilical roots and not from the remodeling of the vitelline system of arteries.

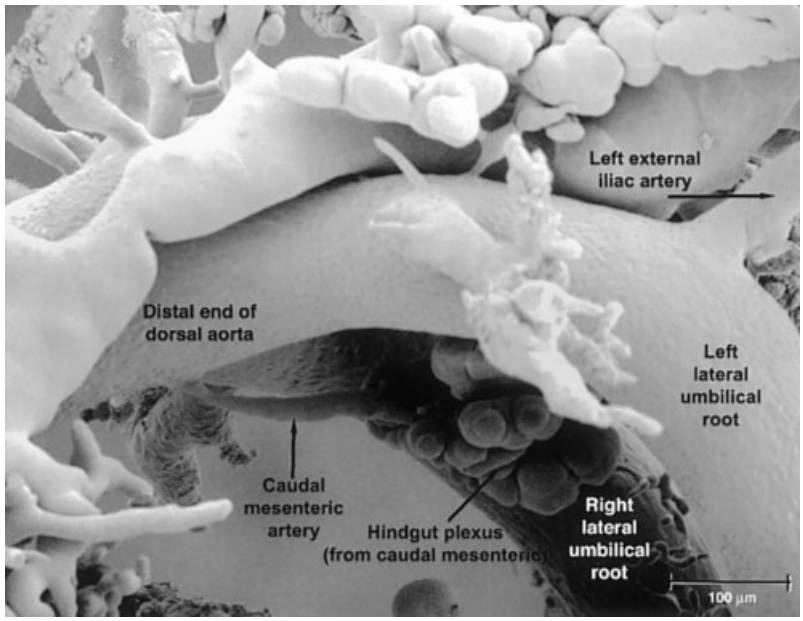

Fig. 12. Left lateral view of the hindgut vasculature of a 12-day-old mouse embryo. At this stage, the medial umbilical roots have completely regressed and remodeled into the caudal mesenteric artery and associated hindgut plexus. Note that the external iliac artery projects from the lateral root (common iliac artery) to supply the hindlimb tissues.

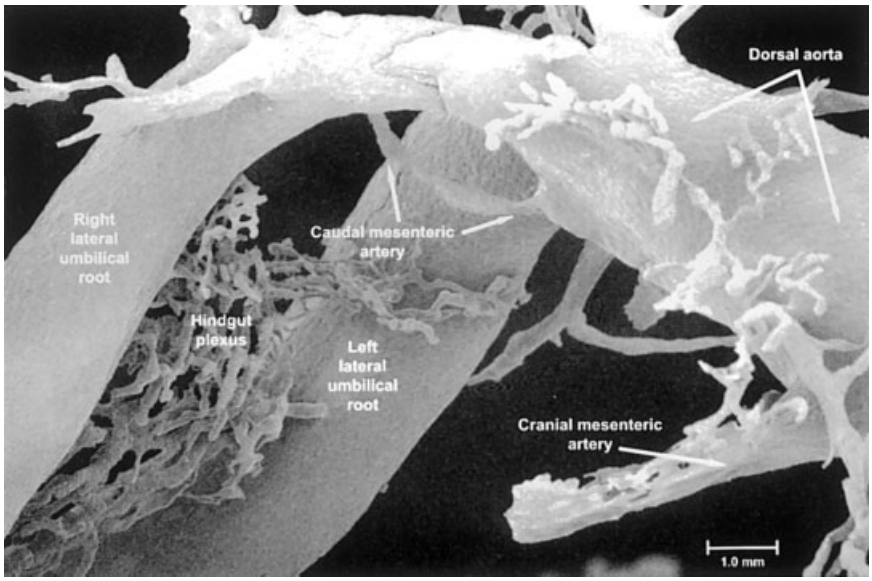

Fig. 13. Right lateral view of a 13-day-old mouse embryo from which much of the obscuring vasculature has been dissected away. The medial umbilical roots have completely regressed and have remodeled into the caudal mesenteric artery.

The results of the present study will further our understanding of the role played by the medial umbilical roots in the normal development of the CaMA, and may help to explain the causes of malformations that may result from abnormal medial umbilical root development. Carter (1954) observed such abnormal remodeling of the medial umbilical roots, and suggested that it may be related to kidney malformations. He further proposed that anomalies of the CaMA may be linked to ureteric kinks and hydronephrosis. We think it is possible that abnormal remodeling of the medial umbilical roots may result in ligamentous connections between the CaMA and the common iliac arteries, and these connections may cause constrictions in the ureters passing between these vessels during their development. Further studies of mouse strains such as the luxate and

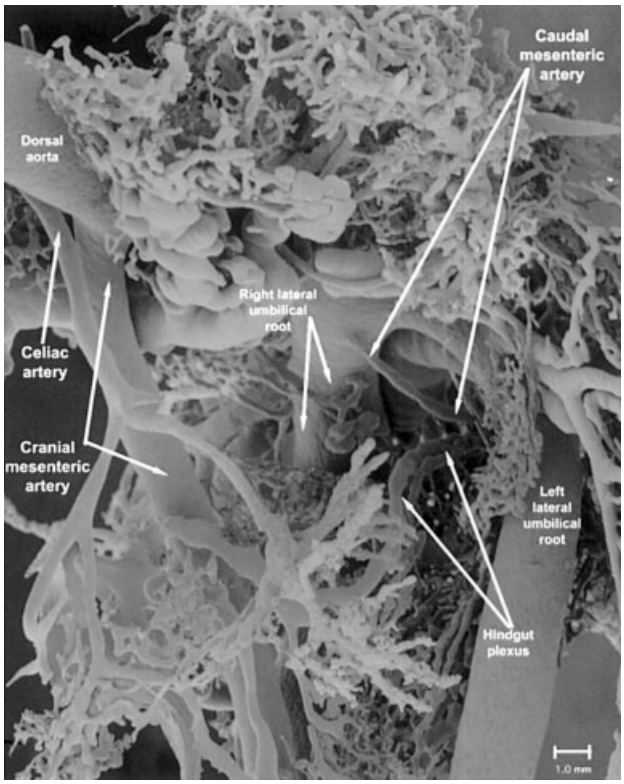

Fig. 14. Left oblique ventrolateral view of a 13.5-day-old mouse embryo. The foregut, midgut, and hindgut vasculatures are represented by the celiac, cranial mesenteric, and caudal mesenteric arteries, respectively. The celiac and cranial mesenteric arteries arise from the dorsal aorta. The caudal mesenteric artery arises from the dorsal aorta at the bifurcation of the right and left lateral umbilical roots (common iliac arteries). Note that the caudal mesenteric artery courses caudally to supply the hindgut plexus.

Dominant hemimelia may elucidate this possible relationship.

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