The three-dimensional feto-maternal vascular interrelationship during early bovine placental development: a scanning electron microscopical study

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ABSTRACT

Both the fetal and maternal microvasculature of bovine placentomes was examined by scanning electron microscopy of vascular casts. So far the development of the vascular architecture of the bovine placentome in early gestation has only been studied 2-dimensionally due to technical difficulties arising from the fragility of the early placental blood vessels. Repeated experiments led to the selection of the microvascular corrosion casts presented here. The vasculature of the maternal compartment is supplied by large caruncular stalk or spiral arteries, which release short maternal stem arteries. In the 3rd month of gestation, these arteries branch into several arterioles at their base, thus providing the vascular framework for the lower part of the septal walls of the primary crypts. In the 4th month, due to progressive longitudinal growth of the stem arteries, branching into arterioles occurs not only at the base, but over the whole length of the stem arteries. These arterioles supply the capillary complexes of the septa which resemble the major part of the septal vasculature and face the secondary crypts. Further indentation results in the formation of tertiary crypt capillary complexes, encircling the earlier secondary unit. From the 6th month of gestation the architecture resembles the fully developed maternal placenta with stem arteries running directly to the fetal side to branch into 4 to 6 arterioles, which turn back to enter secondary and tertiary septa. Maternal venules, collecting the blood from the capillary bed of secondary and tertiary septa, converge onto stem veins leaving the caruncle via branches of the uterine vein. The fetal part of the placentome is supplied by the cotyledonary arteries, which branch into fetal stem arteries that are the tributary to single villous trees. Over their whole course towards the maternal side, these give off arterioles entering secondary villi. The tertiary or terminal villous vasculature consists of capillaries, which are organised in serial capillary loops. This system is progressively elaborated in the course of gestation. In the 4th month there are only finger-like loops, whereas from the 6th month large fan-like structures can be observed. In early gestation the maternal and fetal blood vessels meet predominantly in a countercurrent fashion, changing to the less efficient crosscurrent exchange when the tertiary unit develops. These results indicate the development of a highly elaborated fetomaternal villous-crypt exchange system, already established in the 1st half of gestation, thus meeting the increasing needs of the fetus.

Key words: Bovine placentation; early gestation; corrosion casts; vasculature.

INTRODUCTION

Implantation in the bovine species starts around d 18 and 19 post insemination (p.i.) (overview by Leiser, 1975) and is characterised by the formation of a synepitheliochorial (Wooding, 1992), caruncular-cotyledonary or crypt-villous interrelationship (Mossmann, 1987) starting about d 30 p.i. (Melton et al. 1951; Greenstein et al. 1958). Dependent on the development of the underlying vasculature, the degree

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of placentomal elaboration increases until parturition (around d 280 p.i.). This has been shown for the 2nd half of gestation where the degree of fetomaternal indentation and, hence, the anchorage of the chorion in the uterus (Leiser et al. 1998) is distinctly elaborated (Leiser et al. 1997*a*, *b*). Information regarding the origin and development of the microvessels and their architecture during early placentome formation is so far lacking. We therefore attempted to elucidate the development of both the maternal and fetal vascular systems in the early bovine placenta.

MATERIALS AND METHODS

Placentomes from 9 cows (5 per animal) were selected immediately after slaughtering and excision of the uterus. The crown-rump-length (CRL) of the fetuses was recorded and used to allocate them to 3 different gestational ages, 3 (8–12 cm CRL), 4 (16–23 cm CRL), and 6 (35–38 cm CRL) mo (according to Schnorr, 1996). The placentomal vasculature was rinsed by perfusion with phosphate buffer (30 s, 0.1 M, pH 7.3; anticoagulant: 1000 IU/l heparin; vasodilator: 1% procaine) either through fetal (branches of the umbilical artery) or maternal vessels (branches of the uterine artery). Subsequently liquid plastic compounds (Batson no. 17 compound [Polysciences, Eppelheim, Germany] or Mercox CL-2R [Nordwald, Hamburg, Germany]) were freshly prepared and instilled. The procedure of casting and specimen preparation has been described in detail (Leiser & Kohler, 1983; Krebs et al. 1997; Leiser et al. 1997*b*). Finally, the casts were examined with a scanning electron microscope (Zeiss DSM 940, Oberkochen, Germany). Measurements of vessel diameter were made using on-screen callipers and the data were described by mean and range.

For comparison with histology, the fetal and maternal vasculature of additionally buffer perfused placentomes was injected with Indian ink (green [fetal blood vessels] and red [maternal vasculature] drawing ink, Rotring, Hamburg, with bovine serum: 1:1). The placentomes were then immersion fixed in 4% buffered formaldehyde (pH 7.3) for 3 d. After dehydration in a graded series of ethanols and embedding in Epon, 150 μm sections were obtained with a Polycut microtome (Leica) and examined without staining.

Rationale for the use of vascular corrosion casts

The basic principle is that the blood vessels intimately adjoin the single layered epithelium of the caruncle and the cotyledon thus following every contour of the tissue surface (Leiser & Koob, 1992). Therefore, a maternal crypt is formed by a vascular crypt, the surrounding stroma and the uterine epithelium (Wooding & Flint, 1994). Correspondingly, a fetal villus consists of its vascular villous tree, stroma components and the covering trophoblast (Leiser et al. 1998). The fetal villous and maternal septal or cryptal, microvasculature, respectively was classified according to established criteria (Leiser et al. 1997*a*, *b*). The different vessel types were distinguished by the shape of the impressions of protruding endothelial cell nuclei on the casts (Leiser & Kohler, 1983; Leiser et al. 1989). These impressions were deep and spindle-shaped in arteries, shallow and spindle-shaped in arterioles, long and oval in veins, just oval in venules and round in capillaries.

RESULTS

Relation of general maternal and fetal vascular components to the whole placentome

The typical mushroom-like form (Fig. 1*a*) with a caruncular stalk (Fig. 1*b*) of the bovine placentome was already present in the 3rd mo of gestation. The vasculature of the maternal caruncle consisted of a base with projecting blood vessels of fetally-oriented septa which formed vascular crypts (Figs 1*a*, 2*a*, *b*). These crypts were indented by chorionic villi, resulting in a villous-crypt fetomaternal relationship of the placentome. The vessels in the core of maternal septa and fetal villi were stem arteries and veins, or the primary structure, which ramified into arterioles and venules of intermediate septa and villi. These were the secondary structures, which supplied blood to or from the tertiary structures, which were the terminal capillaries of septal and villous placentomal parts (Figs 1*a*, 2*a*, 5*e*, 7*b*). The relation of tissues and corresponding microvasculature is summarised in Table 1. The measurements of vessel diameters from the 3rd to 6th mo of pregnancy are summarised in Table 2.

Maternal vasculature

In the early gestation placentomes (8–12 cm CRL, 3rd mo of gestation) the caruncular stalk arteries were showing a more spiral course than the corresponding veins (Figs 1*a*, *b*, 4). In the basal plate of the placentome or caruncle base (Fig. 1*a*) each ramified at right angles to maternal stem arteries and veins, respectively, which entered the main septa as a pair, and followed them up to about one third of the height

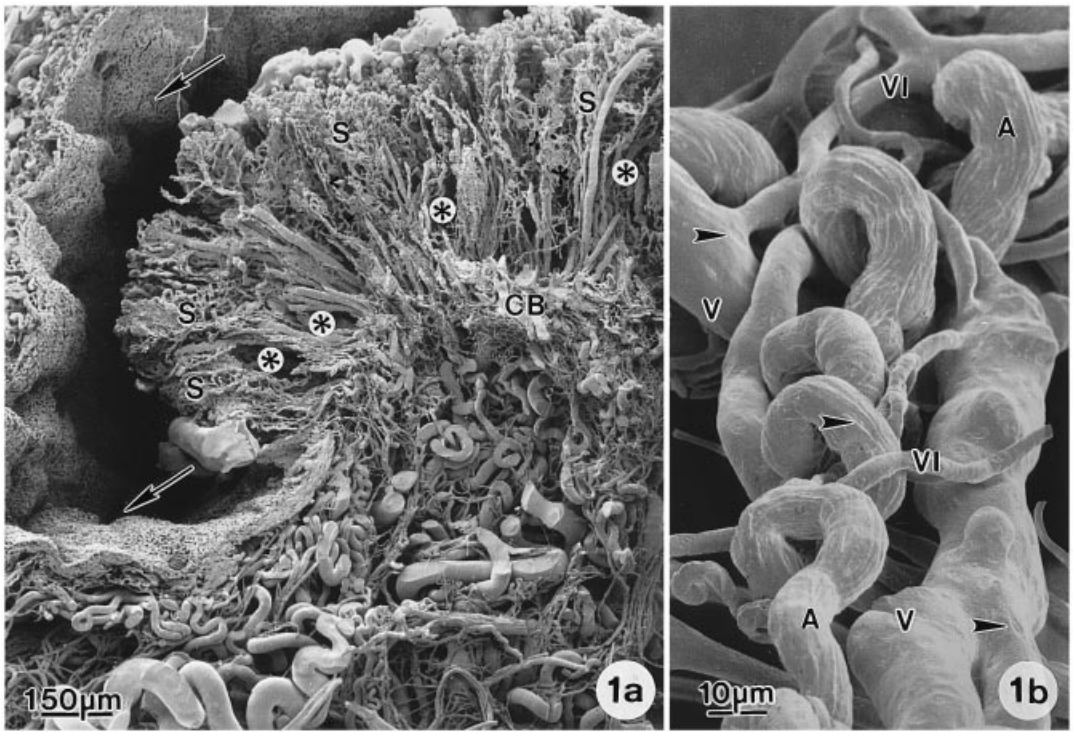

Fig. 1. Maternal vasculature. (*a*) Scanning electron micrograph of a cracked, laterally viewed maternal vessel cast of bovine endometrium; fetus of 8 cm CRL. Overview of the intercaruncular vasculature (arrows) which extends from the stalk (below right) to the body of caruncular vasculature of placentome (top right). Note spiral arteries running from the caruncle stalk into the base of the caruncle (CB). Blood vessels of main septa (S) and primary crypts (asterisks) are indicated. (*b*) Detail of a caruncle stalk, fetus of 23 cm CRL. The coiling of the spiral artery (A) contrasts with the veins (V) and venules (Vl) which are straighter and have a relatively larger diameter. Impressions of endothelial perikarya can be observed (arrowheads).

of the caruncle (Figs 1*a*, 2*a*). Therefore, these stem vessels built up a sector of the main septum which was the wall of a primary crypt (Figs 2*a*, 4). With the ramification of the stem vessels into arterioles and venules (Fig. 2*b*) intermediate septa were formed, which as walls of secondary crypts could reach almost to the top of the caruncle (Figs 1*a*, 2*a*, *c*, 3, 4). Several venules (3–4), sometimes anastomosing with each other, accompanied a single arteriole (Figs 2*a*, *c*, 4). The arterioles ran in the centre of intermediate septa, whereas the venules were located in the periphery (Fig. 2*c*). The average venule diameter of 35 µm was exceeded in branching points of the crypts (35–65 µm) (Fig. 2*b*). Along intermediate vessels there were many ramifications leading to a terminal capillary complex (Fig. 2*a*, *b*) which bordered the secondary crypts as a vascular tuft (Figs 2*a*, 3). With higher magnification, this tuft at the rim of the septal system showed serially linked, anastomosing and winding capillary loops with distinct dilations (Figs 2*d*, 3, 4), which were seen to be related to rather primitive tertiary crypts when viewed from the fetal side of the placentome (Fig. 3).

Up to midgestation (35–38 cm CRL or 6th mo of pregnancy) the maternal vascular system of bovine placentomes developed until similar appearances to those at near term were achieved (see Leiser et al. 1997*a*, *b*). The stem vessels which ran to the convex side of the placentomal surface also branched, the average diameter increased (artery: 146 µm; vein: 276 µm), and the length was distinctly elongated (Figs 5*a*, 6). Along their way, the stem arteries and veins, which were usually centred as a pair in the main septae (Figs 5*b*, 6), increasingly gave off arterioles (Fig. 5*a*) and venules (Fig. 5*e*). Most of these vessels could be seen close to the fetal surface, together forming 'weeping willow'-like structures (Figs 5*c*, 6). Hence, depending on the number of arterioles and venules (which were the core of intermediate septa), there were only a few and indistinctly formed secondary crypts close to the caruncular base as seen on a cross-section of the cast (Fig. 5*b*) whereas, on the opposite side of placentome, secondary crypts were numerous (with 4–6 surface arterioles) and thus identical with the deep indentations seen in the weeping willow (Fig. 5*c*). Secondary crypts appeared as marginal niches from primary crypts (Fig. 5*a*, *c*). The border of this cryptal system, a dense tuft of capillaries in columnar form in a maternofetal orientation (Fig. 5*a*) and as large as the width of primary crypts (Fig. 5*a*, *b*), was developed from the 3rd to the 6th mo of gestation. Viewed at higher magnification, these capillaries represented complexes linking the ramifications of the inter-

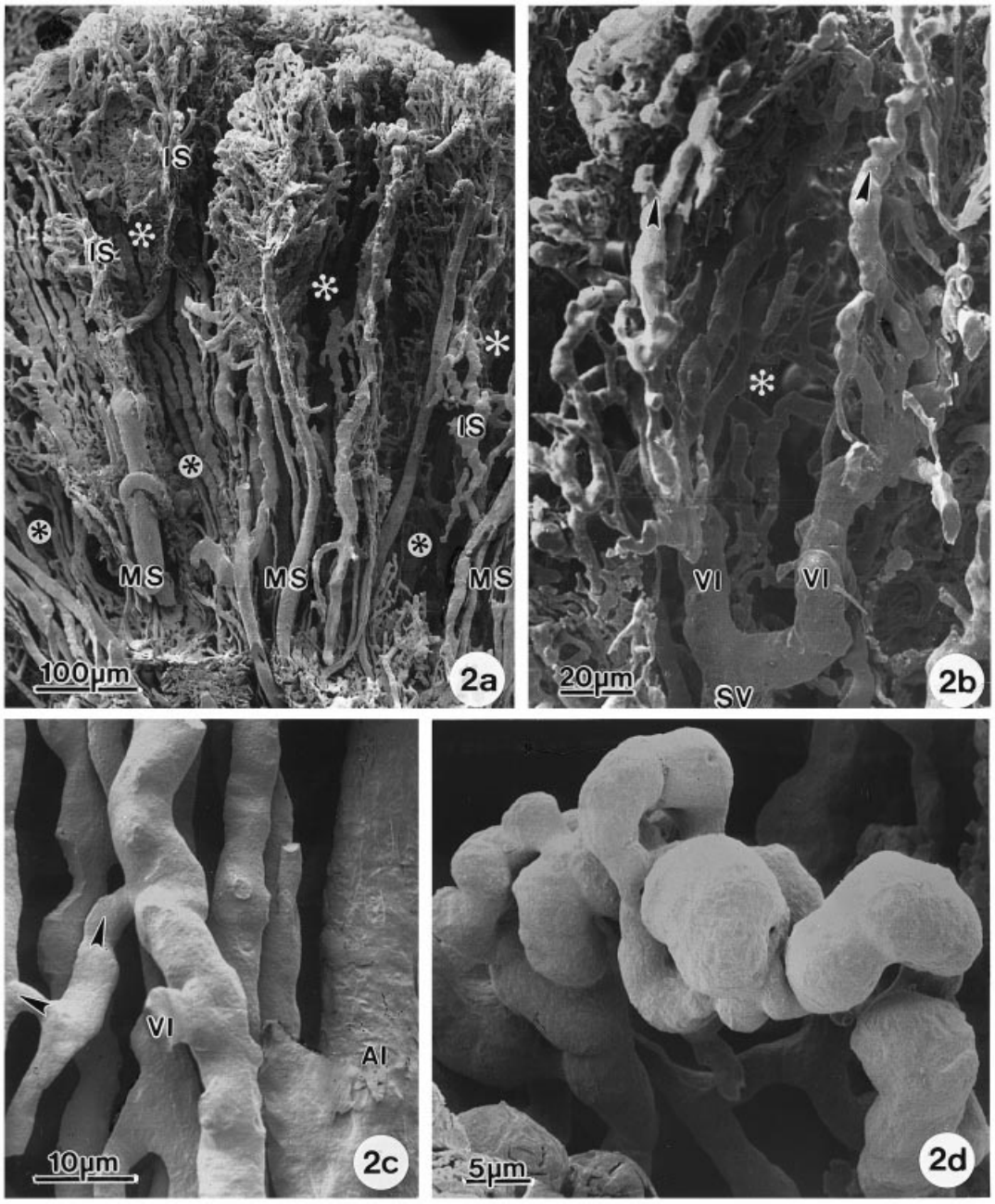

Fig. 2. Caruncular vasculature of 8 cm CRL fetus. (*a*) Main vascular septa (MS), mostly consisting of arterial and venous stem vessels which reach from the caruncle base up to about one third of the height of caruncle, form the walls of primary vascular crypts (small asterisks). Intermediate septa (IS), containing arterioles and venules, extend almost to the top of caruncle, thus providing the vascular framework for the secondary crypts (large asterisks), which are bordered by relatively small superficial complexes of terminal capillaries. (*b*) Higher magnification of the central area of *a*. A stem vein (SV), branching into 2 venules (Vl) gives rise to a secondary vascular crypt (asterisk) which is formed by the secondary septa and their adjacent terminal capillary complexes (arrowheads). (*c*) Detail of the microvasculature of a secondary septum showing one arteriole (Al) which is accompanied by several, parallel partly anastomosed (arrowheads) venules (Vl). (*d*) Terminal capillary loops clearly displaying sinusoidal dilations.

mediate septal arterioles and venules (Fig. 5*a*) and were arranged in a centrifugal way around the axis of the stem vessel pair (Figs 5*b*, 6). At the surface of these complexes, distinct tertiary crypts were formed, together appearing as a honeycomb-like system (Fig. 5*c*, *d*). Sinusoidal dilations on terminal capillaries were still a frequent phenomenon.

Fetal vasculature

The fetal vasculature of the bovine placentome could not be prepared by the method of vessel casting in very early placentation in this study (see Discussion) and therefore only stages from 16 to 38 cm CRL or 4th to 6th mo of gestation are shown.

Table 1. *Terminology of bovine placentomal microvasculature*

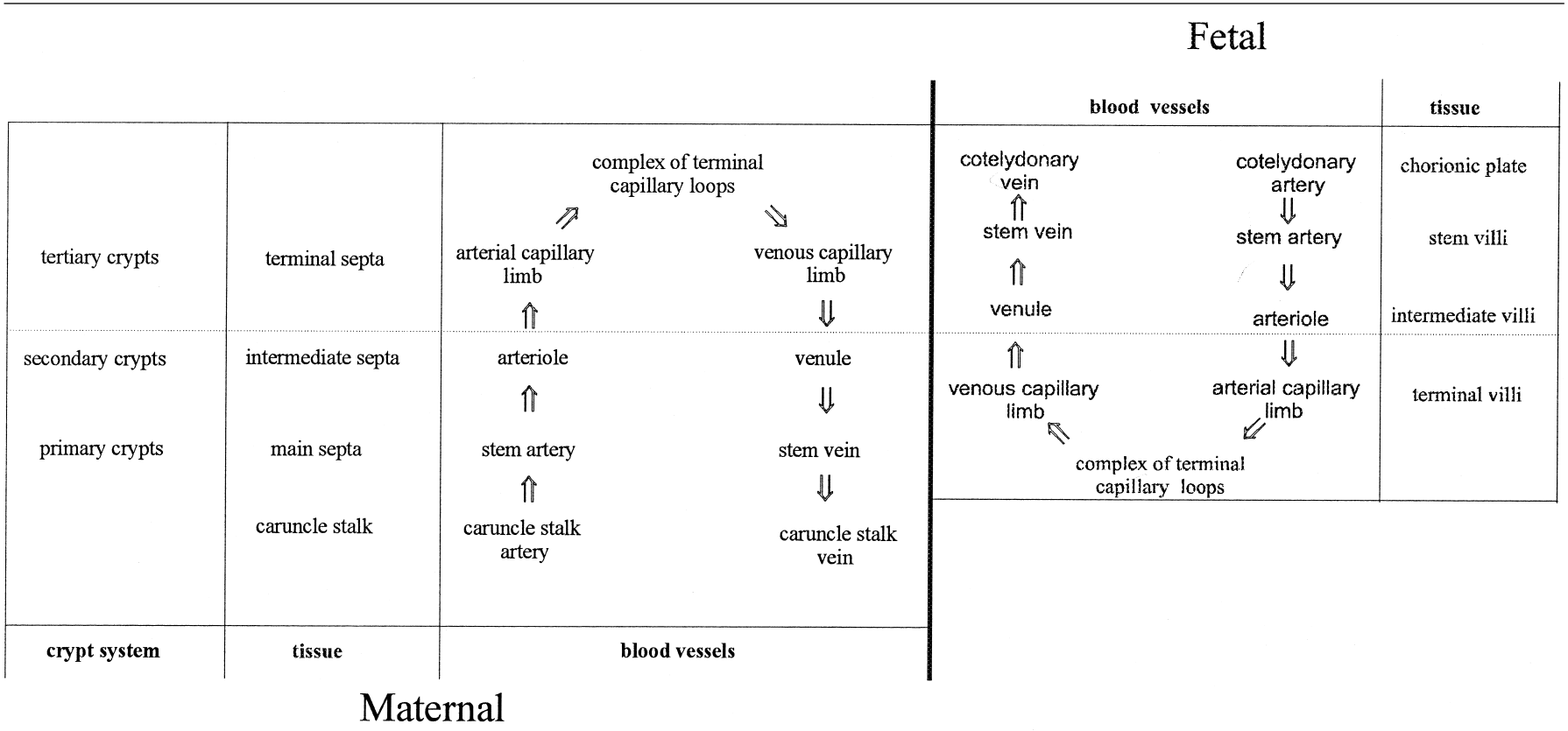

Table 2. *Vessel diameters*

Placentome	Maternal vasculature (gestational age)			Fetal vasculature (gestational age)	
Vessel type	~ 3rd month (8 cm CRL)	~ 4th month (23 cm CRL)	~ 6th month (36 cm CRL)	~ 4th month (23 cm CRL)	~ 6th month (38 cm CRL)
Stem arteries μm (mean)	88–105 (90)	108–300 (146)	143–263 (192)	108–145 (122)	107–214 (154)
Arterioles μm (mean)	40–60 (50)	57–101 (83)	90–130 (112)	25–63 (38)	32–50 (40)
Capillaries μm (mean)	18–23 (19)	13–23 (17)	14–28 (19)	8–14 (11)	7–12 (10)
Venules μm (mean)	15–58 (35)	40–83 (62)	38–120 (82)	30–90 (56)	35–45 (40)
Stem veins μm (mean)	98–125 (114)	260–300 (276)	168–270 (198)	104–160 (136)	108–276 (190)

n = 15 (per vessel type, compartment and gestational age).

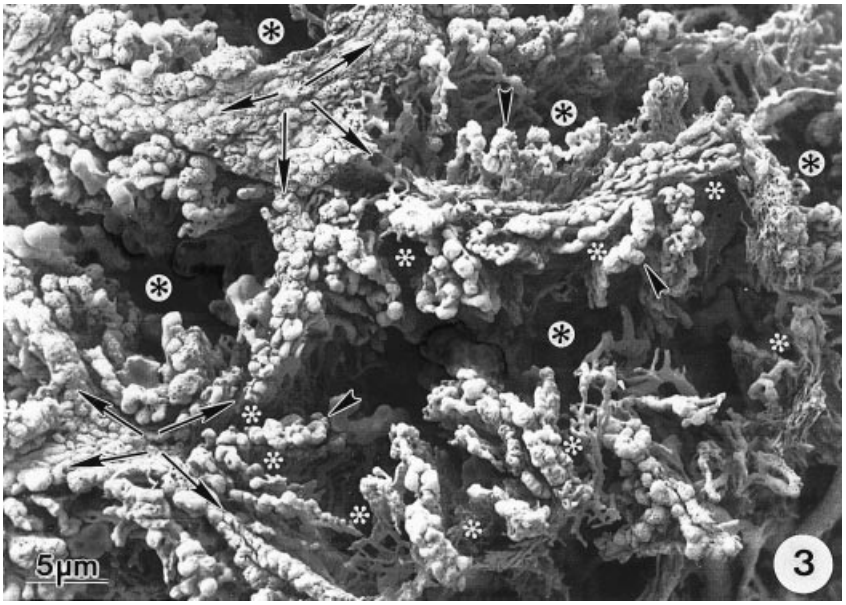

Fig. 3. Caruncular vascular cast viewed from the fetal side (8 cm CRL fetus). The top of caruncle which is covered with terminal capillary complexes allows insight into a vascular system of ramified primary (arrows) and secondary septa (arrowheads), enclosing primary (black asterisks) and secondary crypts (white asterisks).

Cotyledonary arteries of the chorionic plate, which were represented by 1–3 arteries with a straight course and branch at an acute angle supplied 1 placentome, whereas the 1–3 cotyledonary veins were thicker in diameter than the arteries and showed a rather winding course and variable-angled branchings. Many arteries and veins originated from these ramifying allantochorionic vessels and branched frequently before entering the vascular villous trees. From the base of the villous trees they were called stem vessels (Figs 7*a*, *b*). Villous trees on casts were easy to recognise not only by scanning electron microscopy (Fig. 7*b*) but also macroscopically since their length varied from 4 to 8 mm. Their orientation was fetomaternal.

The arterial and venous systems inside the villous tree ran in parallel thus being different from the allantochorionic vasculature outside the trees. The pairs of stem arteries and veins were oriented parallely in the centre of the stem villi (Fig. 7*c*) and gave off arterioles and venules in an irregular manner (Fig. 9). With progressing gestation, more than one stem vein developed to accompany a single stem artery.

As ramifications from the stem vessels, a single arteriole accompanied by several venules represented the core of an intermediate villus, which was short in relation to a stem villus (Fig. 7*c*). These arterioles branched into capillaries (arterial capillary limb) which supplied the terminal villi from their centre (Figs 5*e*, 7*c*, 8, 9). One terminal villus was composed of several capillary loops (2–4: Fig. 8) each about 400–700 μm long. These terminal villous capillaries were frequently arranged in parallel or in a slightly fan-like shape with many anastomoses. With progressing gestation, the loops were increasingly linked in a serial manner (Fig. 8). The terminal capillary loops converged to venous capillary limbs, which had a more peripheral position in the terminal villi when

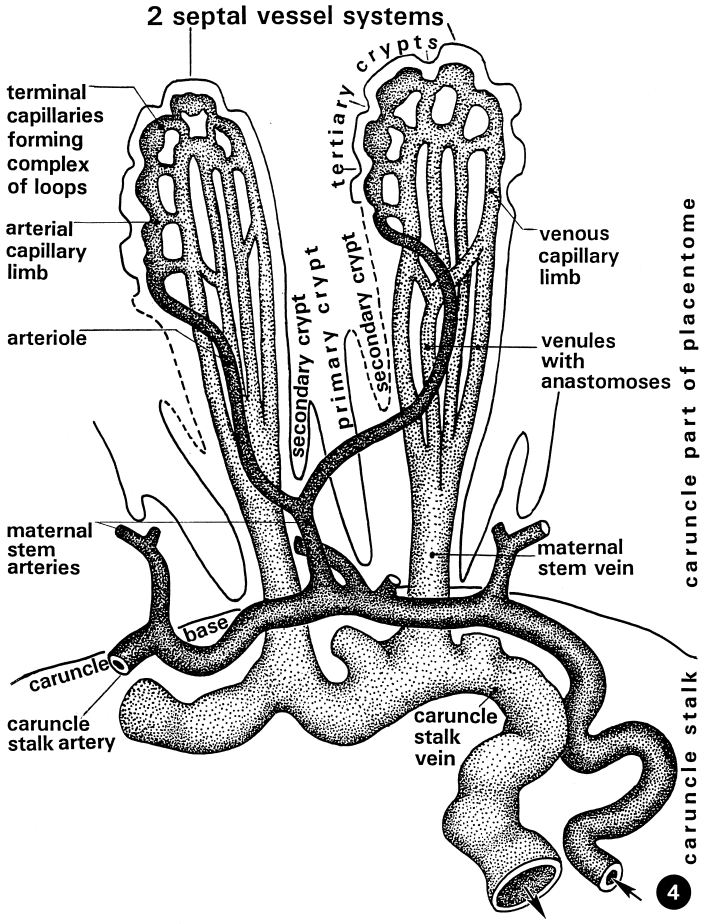

Fig. 4. Schematic drawing of the bovine maternal (caruncular) microvasculature of the placentome in the 1st trimester.

compared with the arterial capillary limbs (Figs 8, 9). Sinusoidal dilations of capillaries were rare, but occurred at sites of 'U turns' (Figs 8, 9). From the 4th to 6th mo of pregnancy, an increasing number of capillary 'vasa vasorum' were observed along the stem vessels.

DISCUSSION

Technical remarks

In early gestation (before 16 cm CRL, ~ 4th mo), casting of the fetal, cotyledonary vasculature was impossible due to the fragility of the blood vessels. The fetal mesenchymal tissues were very delicate at the beginning of gestation, so that extravasation of the casting resin occurred frequently, completely covering most of the remaining vessels. Even rinsing procedures with various fixatives and/or vasodilators did not improve the results. Indian ink histology was necessary to gain insight into the relation of fetal and maternal blood vessels, due to the transparency of the unstained thick sections. The dense microvasculature prevented this assessment in corrosion casts.

Implications of architectural changes

In the caruncle stalk vasculature of the bovine placentome 'spiral' arteries show a more winding course than the corresponding veins, but both are more distinct in early gestation than in later stages of pregnancy (Leiser et al. 1997*b*). Spiralling, therefore, seems to be essential at least in early placentation for curbing the blood pressure and flow in cattle in order to avoid compression of the delicate fetal villi as has also been discussed in man (Carter, 1975; Benirschke & Kaufmann, 1995). Of less importance may be the fact that this arrangement might also deform, as do 'bed springs', when the caruncle stalk becomes flexed by movements of the fetus and the mother (Leiser et al. 1997*b*).

The early *caruncular vasculature*, with its supply represented by stem and intermediate vessels (Leiser et al. 1997*a*), exceeds the working part by volume, the former guiding the blood from the caruncular base through the stem septa to the top of the intermediate septa (Leiser et al. 1997*a*). The latter includes the capillaries being active for exchange at the caruncular periphery (see also Fig. 1*a*).

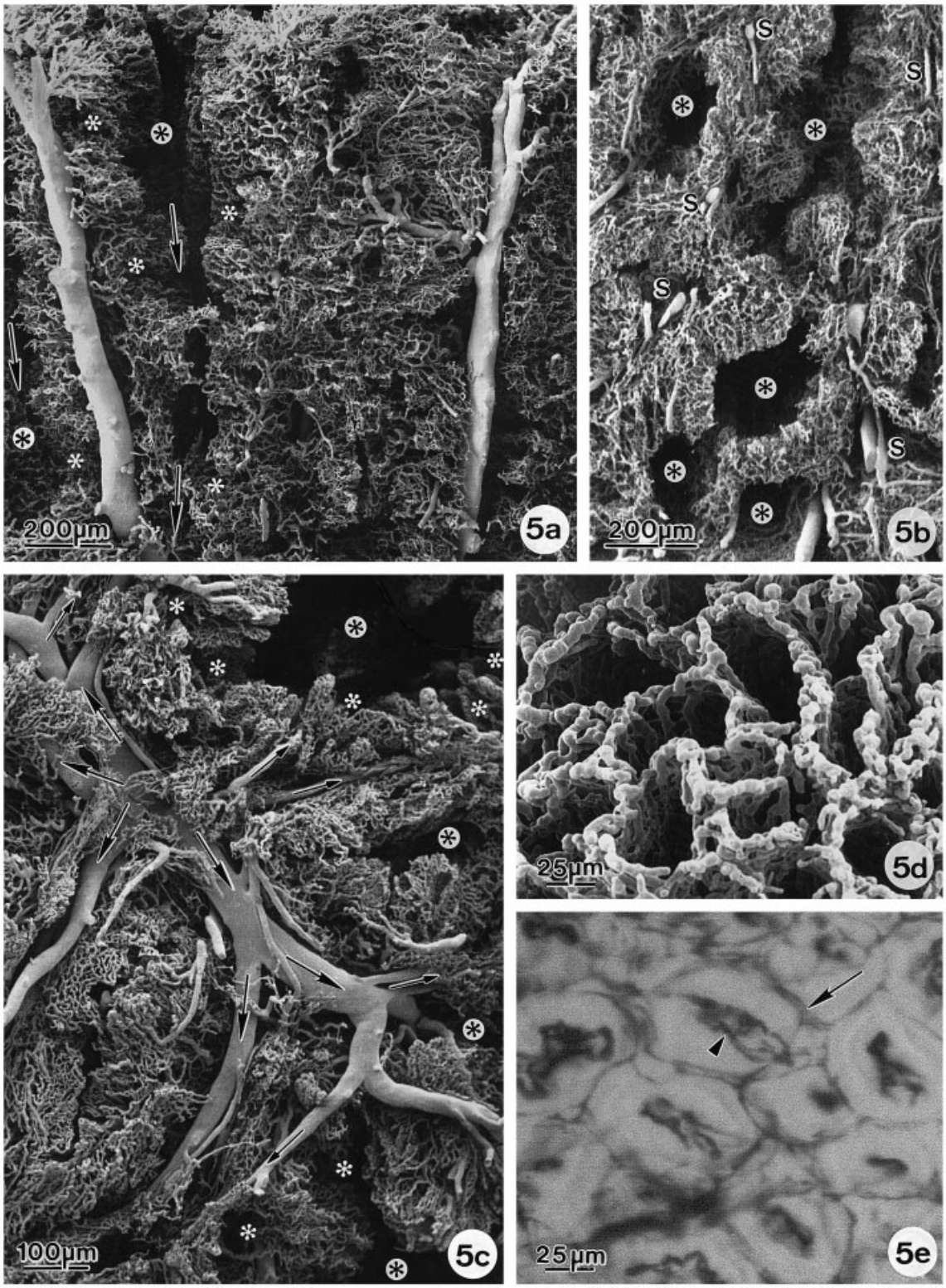

Fig. 5. Maternal vasculature of 36 cm CRL fetus. (*a*) Lateral view of a cracked arterial cast of the caruncle. Two maternal stem arteries, each running in the centre of a main/primary septum from the base (below) to the top of a placentome (above), ramify into the arterioles (most of them broken) of the secondary vascular crypts (white asterisks; arrows indicate orientation of fetal stem villi) which supply the large terminal capillary complex. Primary vascular crypts are indicated by black asterisks. (*b*) Horizontally cracked caruncular cast from the same animal. Primary crypts (black asterisks) are surrounded by the rough reticulum of the capillary complex. Inside this complex, conspicuous stem vessels (S) mark the centres of main (primary) septa. (*c*) Caruncle vasculature with view of the fetally oriented surface. A stem artery branches into centrifugally oriented ramifying arterioles (large arrows) which with a bend of about 90° reach into intermediate septa (small arrows) and ultimately supply the terminal capillary complex. This resembles the branching pattern of a 'weeping willow'. Note the primary (black asterisks) and secondary crypts (white asterisks). (*d*) Higher magnification of the caruncular microvasculature. The terminal capillary

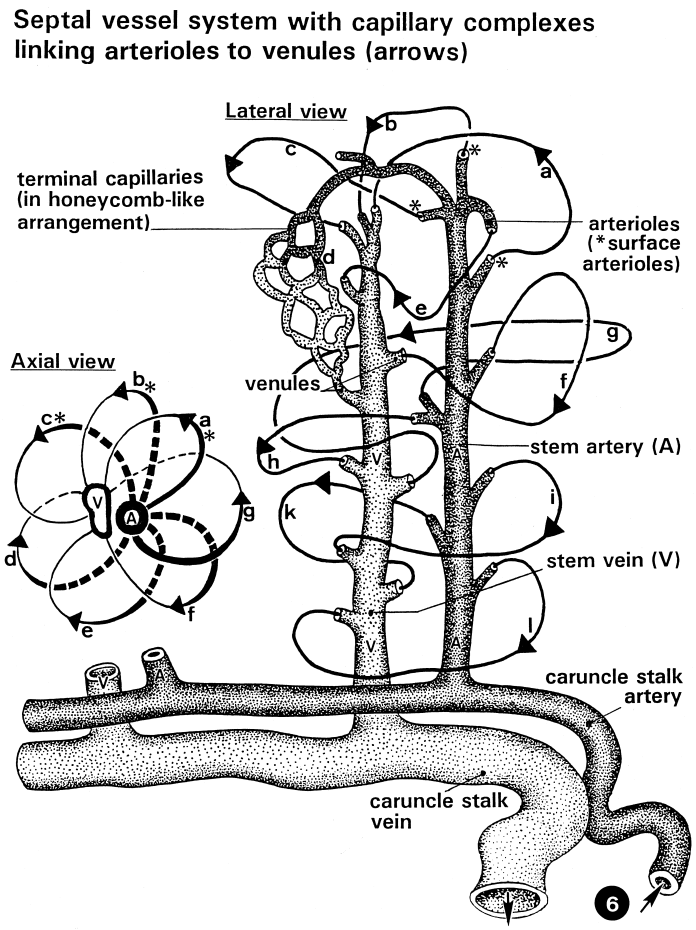

Fig. 6. Schematic drawing of the bovine maternal microvasculature of the placentome in the 2nd trimester. Arrangement of capillary complexes (*a–l*) in fetomaternally directed (left) and lateral (right) views with respect to the axis of a main septum.

The fact that stem arteries and veins of the supplying part are relatively short in the lower third of the caruncle and intermediate arterioles and venules reach up almost to its tip, a 'vascular frame' is given in early pregnancy which allows these arterioles and venules to turn into branches of stem vessels in the middle of gestation (Fig. 6). In early gestation, these branched stem vessels are the basis of many newly growing intermediate arterioles and venules which transport the blood to the fetal side of the placentome and distribute it in a 'weeping willow' pattern, thus providing a relatively short link from the stem vasculature to the capillaries (Fig. 6). This vascular system continues as a basic ramification principle for the second half of pregnancy, since only length and ramification density of vessels will change when compared with the increasing size ($\times 3$) of the placentomes (Tsutsumi, 1962; Leiser et al. 1997*a*).

The capillaries, or working part of the early caruncular vasculature, are conspicuously poorly developed, enclosing a small layer on top of the septal system with as yet little formation of tertiary crypts (Fig. 4). The capillaries inside the terminal septa are directly adjacent to the extremely short fetal villosity, which guarantees a short interhaemal distance for transplacental exchange. The large surface, due to the winding course and sinusoidal dilations of these capillaries, favours substance transfer. Sinusoids located near the septal tips may slow the blood flow, providing a specific opportunity for maternofetal exchange (Arts, 1961). This is also sustained by the fact that venules are especially thin-walled in early placentation (Björkman, 1954; Tsutsumi, 1962) and therefore easy to penetrate.

Up to the middle of pregnancy, the capacity for substance transfer is distinctly increased (Björkman,

loops of the tertiary septa are arranged in a honeycomb-like fashion, thus enclosing the tertiary crypts. (*e*) Micrograph of a combined fetomaternal Indian ink perfused histological section, 35 cm CRL fetus. Blood vessels of maternal tertiary crypts (arrow) surround fetal terminal villous capillaries (arrowhead) in a honeycomb-like fashion.

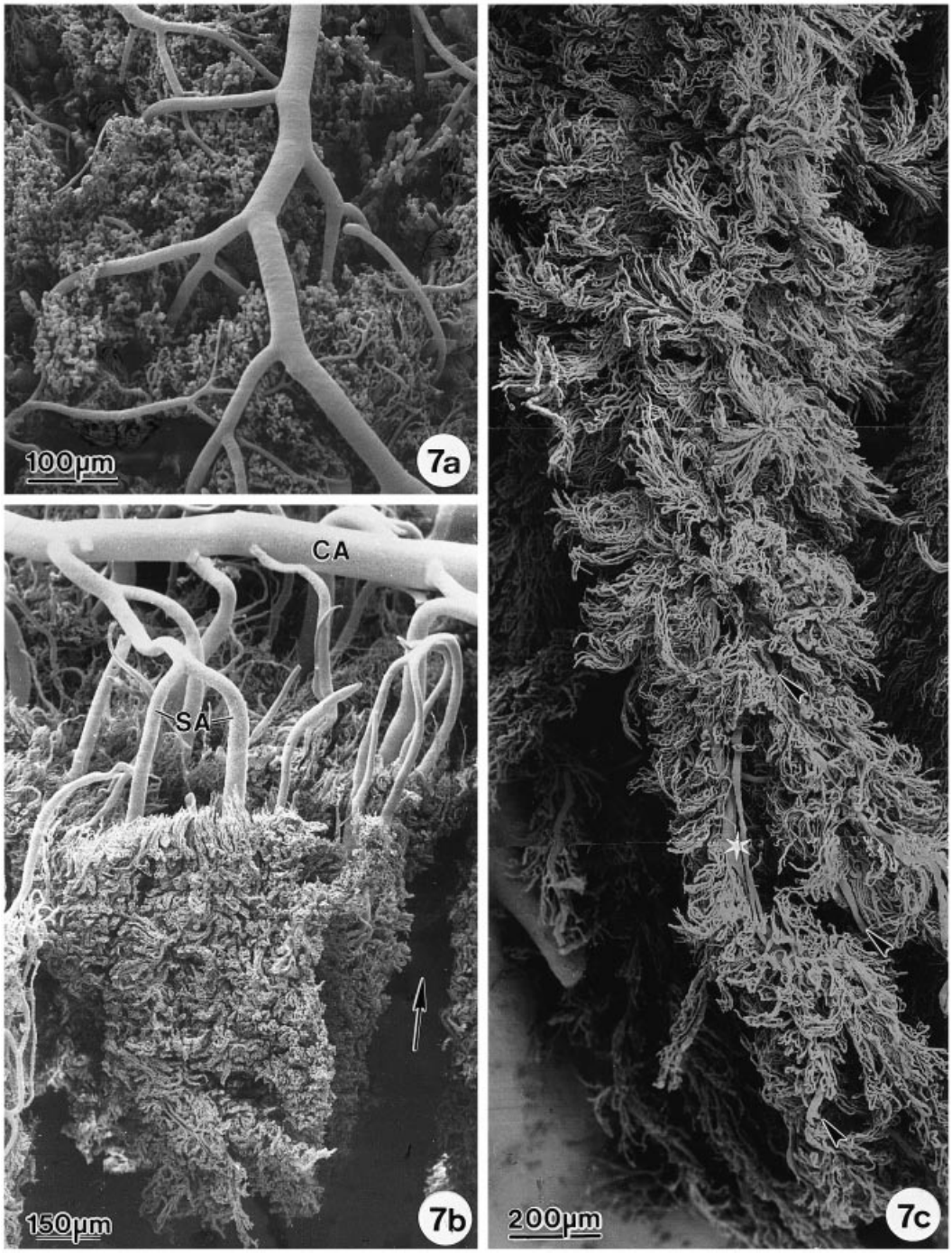

Fig. 7. Fetal vasculature. (*a*) Scanning electron micrograph of vessel cast showing the allantochorionic surface of a cotyledon or fetal part of a bovine placentome (16 cm CRL fetus). Stem arteries, ramifying from a cotyledonary artery of the chorionic plate, disappear in several capillary complexes which are not organised in the shape of villous trees at this time. (*b*) Scanning electron micrograph illustrating the branching pattern of a large cotyledonary artery (CA) into many smaller ones which are followed by stem arteries (SA); fetus of 38 cm CRL. The cotyledonary arteries bend from the chorionic plate into a straight uterine direction before reaching the centres of their conical villous trees. The intervillous space (arrow) corresponds to a caruncular septum. Note that the surface of these vascular trees consists of the terminal capillary complexes. (*c*) Micrograph of the tip of a villous tree (50 cm CRL fetus). The innumerable capillary loops of the terminal villi are missing in some places and therefore allow sight onto the stem vessels (star) as well as arterioles and venules (arrowheads).

1954) probably by the newly developing tertiary crypts, which are embedded in the large and dense capillary tuft located along the secondary crypts. Tertiary crypts are indented by tertiary villi of the cotyledon, a phenomenon which, besides substance transfer, results in anchoring of the bovine fetal placenta in the uterus (Leiser et al. 1998). All this increases progressively until the end of gestation (Leiser et al. 1997*a*,*b*).

The fetal vasculature of the bovine placentome

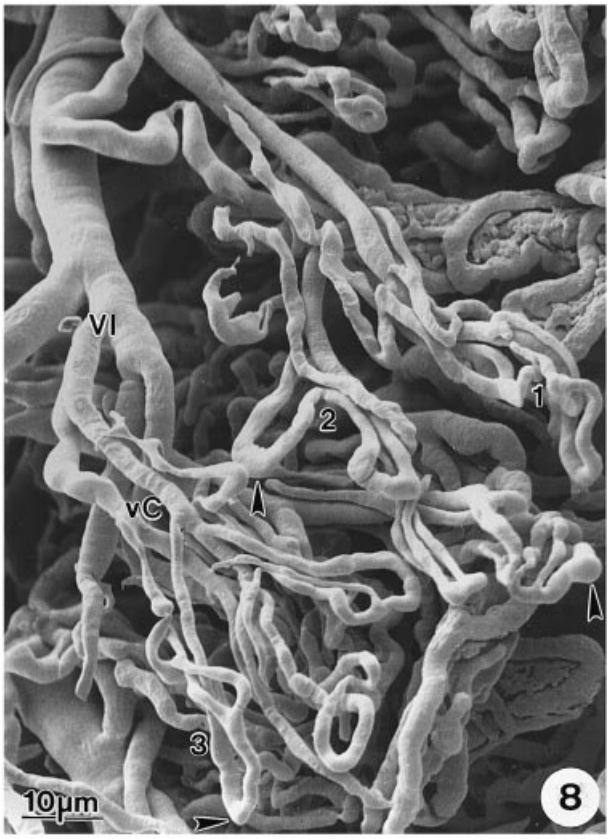

Fig. 8. Detail of a complex of serially-linked fetal capillary loops (38 cm CRL fetus). The capillary loops (1, 2, 3, …) each consisting of 2–4 terminal capillaries, converge to venous capillary limbs (vC), venules (Vl), and a stem vein (top left). Note some sinusoidal dilations of the capillaries (arrowheads).

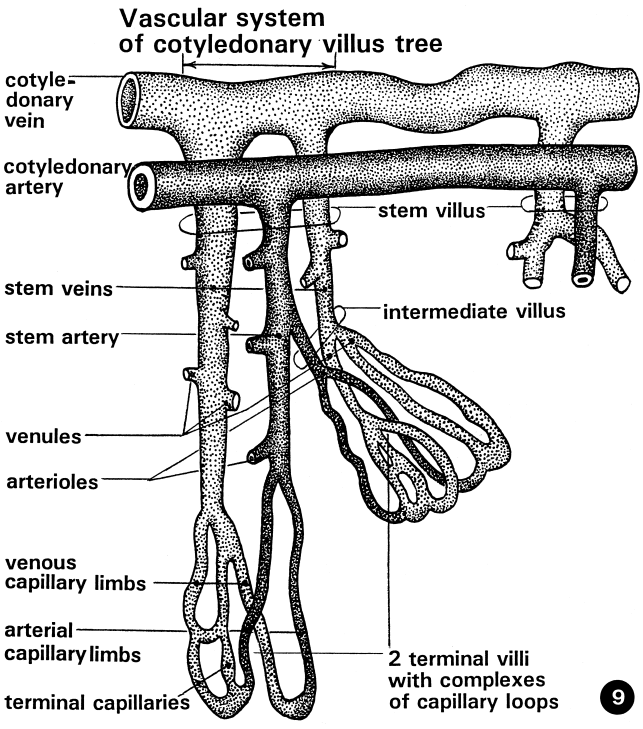

Fig. 9. Schematic drawing of the bovine fetal microvasculature of the placentome in the second trimester.

shows the same main characteristics as in later placentae by the first half of pregnancy (compare Fig. 9 with Leiser et al. 1997*a*, *b*). Conforming to the cryptal organisation of the caruncle primary, secondary, and tertiary villi develop, indenting these crypts. Differing from the caruncular vasculature, the vessels of the primary villous vasculature are distinctly isolated from each other when branching from the cotyledonary vessels. Hence, the stem vessels and their ramifications—arterioles and venules—from the beginning of their development almost completely follow the whole height of the placentome with a more central location for the arterial vessels and a peripheral one for stem and intermediate villous vessels. This provides the shortest distance from supplying vessels to the capillaries of the working part (Leiser et al. 1997*a*) where more of the transplacental exchange takes place, and results in a countercurrent blood flow interrelationship of the fetal and maternal vasculatures (see below).

The fetal capillary system of midgestation is characterised by its parallel anastomosed loops being relatively long in comparison with the size of the whole placentome (Fig. 9). They are already representing a rough 'framework' for the vasculature seen at term (see fig. 5*d* in Leiser et al. 1997*b*). Hence, in fulfilling the increasing need for placental exchange until term, the capillaries will shape into a typical fan-like, serially-linked arrangement of loops or complexes which are distinctly convoluted and show an abundance of dilations to aid blood flow (Leiser et al. 1997*a*, *b*). In general, slow blood flow should occur in the relatively wide-calibre venous capillary limbs and venules of terminal and intermediate villi and therefore could ameliorate conditions not only for diffusional O_2 or CO_2 exchange (Faber & Thornburg, 1983), but also for slow-transported solutes of the active placental exchange (Alberts et al. 1983). Substance transfer might also be facilitated by the vicinity of terminal vessels which are located peripherally along the villous axes.

Development of maternofetal blood flow interrelationship

The bloodflow interrelationship is mainly countercurrent in the relatively early placentation of the 3rd and 4th mo of gestation. The lack of most of the capillaries of the tertiary structure allows the stem and intermediate vessels both of the caruncular and cotyledonary parts of the placentome to meet in a countercurrent fashion (compare Figs 4 and 9). Thus one of the most efficient transplacental exchange

systems is established (Faber & Thornburg, 1983; Leiser & Kaufmann, 1994), substituting for the lack of capillaries very efficiently.

From the middle third up to the end of gestation, the mainly countercurrent (Tsutsumi, 1962) bloodflow interrelationship of the stem vessels is maintained, but its significance reduces with the development of tertiary crypts and interdigitating terminal villi. The fetal and maternal capillary complexes of the tertiary unit, where the majority of the exchange takes place are in a crosscurrent blood flow relation with each other (compare fig. 6 with fig. 12 in Leiser et al. 1997*a*). The crosscurrent exchange is considered to be not as efficient (see Faber & Thornburg, 1983), but (1) the combination of both systems, (2) the multiplication of the exchange surface (Baur, 1981) due to progressive capillary growth and (3) the vascular architecture displaying a short supplying component of the vasculature results in a placenta of relatively high substance transfer, especially when considering the ratio of fetal and placental weight, which is about 12:1 in cattle (Dantzer et al. 1988). Additionally, the presence of morphology independent exchange-promoting factors, such as vascular endothelial growth factor (Torry & Torry, 1997), may compensate for the reduced efficiency of the crosscurrent exchange condition.

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