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The uterine vascular system of the golden hamster and its changes during the oestrous cycle*

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INTRODUCTION

The vascular pattern of the hamster uterus was first described by Orsini (1957). However, her description of the non-pregnant vasculature was limited to that of the mesometrial region, because she principally dealt with the organisation of the vessels in the mesometrium during pregnancy. We have therefore, extended our study to elucidate the microvascular architecture in the female reproductive organs of the golden hamster following on the studies of the branching patterns of the large vessels supplying them (Michel, 1959; Del Campo & Ginther, 1972; Ogura, Nishida & Mochizuki, 1985).

Golden hamsters exhibit regular oestrous cycles with ovulation every four days, as do some other species of laboratory rodents. Since, during the oestrous cycles, the hamster uterus exhibits cyclic histological changes under the control of the ovarian hormones (Harvey, 1964; West, Norman, Sandow & Brenner, 1978; Sandow, West, Norman & Brenner, 1979; Brandon & Evans, 1983), the vascular system in the uterus may also be expected to show structural changes according to the stages of the cycle.

The intention of this study is, therefore, to confirm not only the general pattern of the vascular system in the hamster uterus but also its changes during the oestrous cycle by using the corrosion vascular casting method.

MATERIALS AND METHODS

Animals

Forty three adult virgin CBN hamsters (*Mesocricetus auratus*), weighing 114–157 g, were used in this study. They were housed with food and water available *ad libitum* in a lighting cycle of 14 hours light (onset 05.00) and 10 hours darkness. The vaginal discharge was examined each morning. The discharge of the morning of Day 2 is extremely consistent in appearance and can easily be distinguished from those of other days by its high mucosity and adhesiveness. Day 2 of the cycle represents the day following the dark period during which ovulation occurred. Day 1 to Day 4 of the hamster cycle roughly correspond to pro-oestrus, oestrus, dioestrus I (metoestrus) and dioestrus II (dioestrus), respectively, as seen in those strains of laboratory rat and mouse which exhibit a four days oestrous cycle.

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Vascular casts

Three to eight animals were prepared for every morning (11.00) and evening (19.00) on each day of the four days during the oestrous cycle. The animals were anaesthetised by an intraperitoneal injection of pentobarbital sodium. The thorax was opened and 1000 i.u./kg heparin was injected into the right ventricle; an incision was made into the left ventricle, through which the ascending aorta was rapidly cannulated with polyethylene tubing. After incising the caudal vena cava to allow blood to escape, Ringer's solution was perfused (10–15 ml/min) until fluid draining from the vena cava was free of red blood cells. The peritoneal cavity was not opened during the course of this procedure. The methyl methacrylate casting medium was prepared according to the method of Murakami (1975). The medium was infused via the same cannula at a rate of 5–10 ml/min. The injection was performed by hand and no attempt was made to measure the applied pressure. On completing this injection, the descending aorta and caudal vena cava were clamped with haemostats. The animals were immersed in hot water (50–70 °C, 4 hours), and then their caudal halves were transferred to 10% sodium hydroxide solution (50 °C, overnight). After washing in warm water, the cast of the reproductive organs was removed and dried. For the preparations of transverse or longitudinal sections, some pieces of the cast of the uterine horns were frozen in distilled water in disposable polypropylene syringes. Thus the cast could be cut in the appropriate planes using a fretsaw. After drying on filter paper they were fixed on stubs with silver paint. The specimens were gold-sputtered with an Eiko IB-3 ion sputter and were observed with a Hitachi S-430 scanning electron microscope at 5–15 keV.

RESULTS

General pattern

A scheme of the distribution of the vascular system in the hamster uterus is shown in Figure 1. A scanning electron micrograph (Fig. 2) shows the vascular pattern in the transverse section of a cast corresponding to Figure 1. The uterine horn was vascularised by the uterine artery which ran parallel to the longitudinal axis of the uterus. Five to seven, and rarely more than ten, segmental arteries arose vertically from the uterine artery. The segmental arteries usually took a slightly tortuous course, giving rise to 'arcades' (Orsini, 1957) that anastomosed with the adjacent segmental arteries to make an arterial network in the mesometrium. Another fine arterial system was derived from this arterial network. In this way the arterial system was divided into two main divisions, namely, the circumferential division and the medial arterial division.

The circumferential division, which nourished most of the uterine tissues, took much of the blood from the segmental arteries. These arteries further gave off a number of small arcades to make a finer network of small arteries. Just before this reached the mesometrial border of the circular muscle layer many circumferential arteries were derived at regular intervals from this arterial network. Dorsally and ventrally, these arteries entered the space between the circular and the longitudinal muscle layers. They followed a tortuous course in the direction of the antimesometrial border of the uterus and on approaching the termination of this border, these arteries gradually became straight and decreased in diameter. While the circumferential arteries sent no branches to adjacent circumferential arteries, they made a minor connection with the arteries coming from the opposite side on the antimesometrial border.

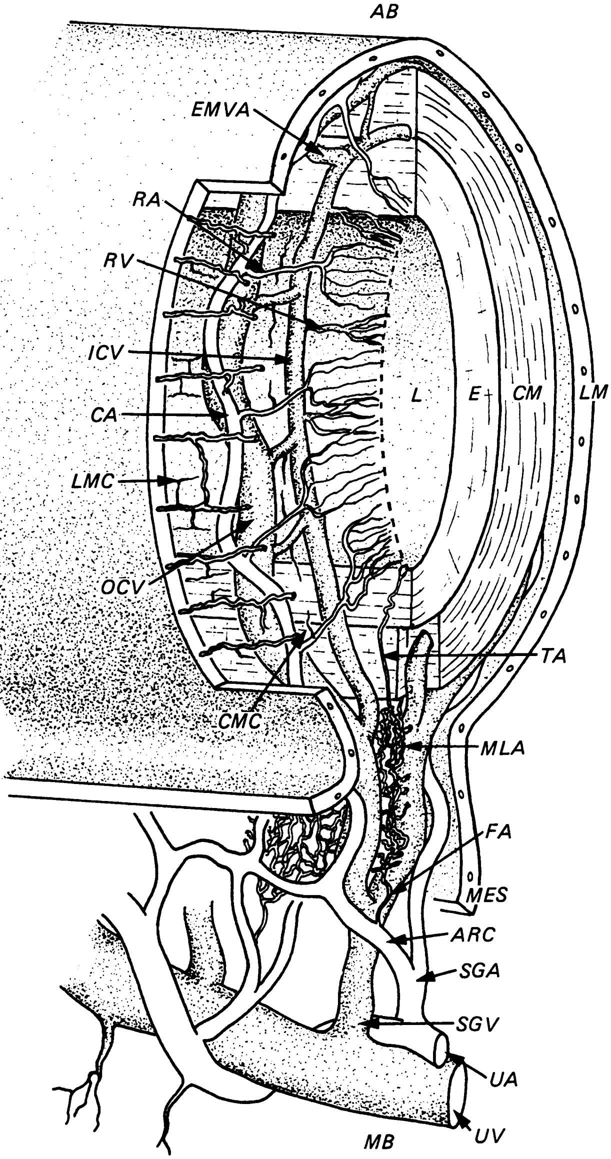


Fig. 1. Scheme of the vascular system of the hamster uterus. *AB*, antimesometrial border; *ARC*, arcade; *CA*, circumferential artery; *CM*, circular muscle layer; *CMC*, circular muscle capillary; *E*, endometrium; *EMVA*, endometrial–myometrial venous anastomosis; *FA*, feeder artery; *ICV*, inner circumferential vein; *L*, lumen; *LM*, longitudinal muscle layer; *LMC*, longitudinal muscle capillary; *MB*, mesometrial border; *MES*, mesometrium; *MLA*, medial longitudinal anastomosis; *OCV*, outer circumferential vein; *RA*, radial artery; *RV*, radial vein; *SGA*, segmental artery; *SGV*, segmental vein; *TA*, terminal artery; *UA*, uterine artery; *UV*, uterine vein.

From the circumferential arteries markedly coiled arterioles arose to run towards the serous surface. These vessels were arranged longitudinally and gave rise to capillaries which supplied the outer longitudinal muscle layer (Fig. 3). The inner circular muscle layer was supplied by capillaries which originated from the circumferential or the radial arteries. These capillaries showed a very coarse distribution in contrast to the elaborate network in the longitudinal muscle layer (Fig. 4).

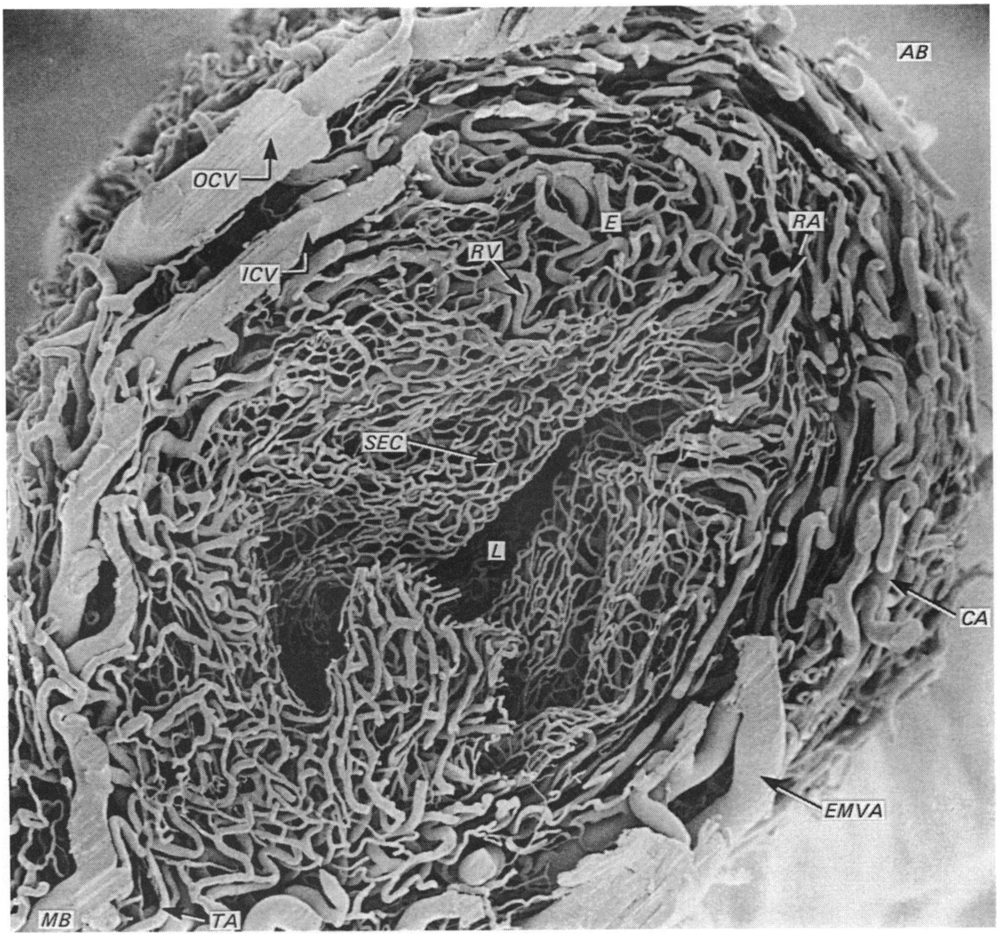
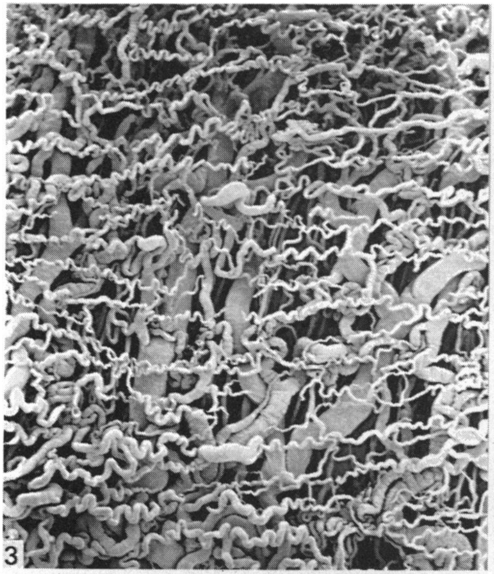
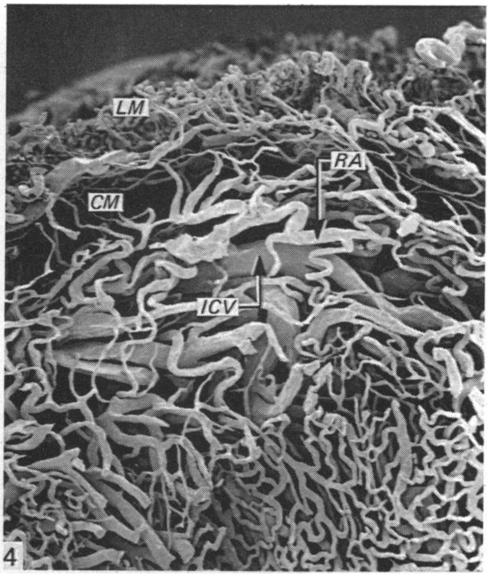


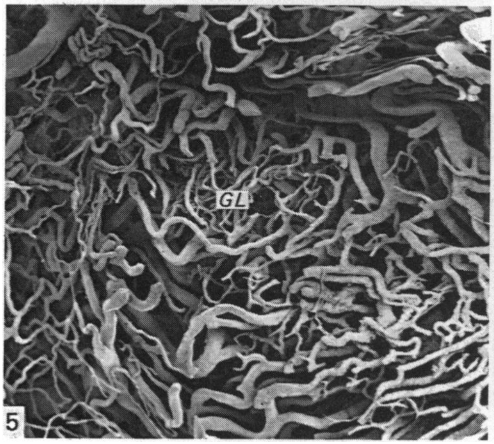
Fig. 2. Transverse section of a cast made on the evening of pro-oestrus. *SEC*, subepithelial capillary. For other abbreviations, see legend to Figure 1. ×44.

The circumferential arteries gave rise to the other set of branches, the radial arteries, towards the inner portion of the uterus. The radial arteries penetrated the inner circular muscle layer and then reached the basal border of the endometrium. At this marginal region of the endometrium, they gave a few branches which took a circular course but never completely surrounded the endometrium (Fig. 4). From these circular branches arose many small arteries arranged radially throughout the endometrium. They terminated in the subepithelial capillary plexus. In the endometrium some capillaries derived from the radial arteries formed incomplete basket-like structures (Fig. 5). These capillaries probably supplied the endometrial glands, judging from their position in the endometrium and from the volume of the basket-like structures.

The second arterial system, the medial arterial division, arose from the segmental arteries or the arcades as 'feeder arteries' (Orsini, 1957). The feeder arteries took a slightly tortuous course in the mesometrium, running towards the uterine horn (Fig. 6). They became more tortuous and coiled as they approached the circular muscle layer. The vessels formed a 'medial longitudinal anastomosis' (Orsini, 1957) in the mesometrial border of the circular muscle layer (Fig. 6). This anastomosis was recognised as a mass of small arteries wedged between the ventral and dorsal







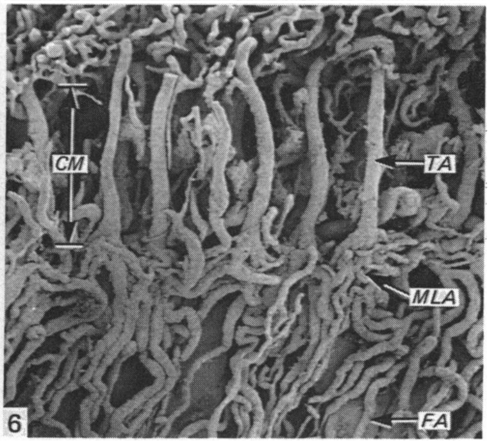


Fig. 3. The serosal aspect of the longitudinal muscle. Most of the small arteries and capillaries run along the long axis of the uterus. ×42.

Fig. 4. Uterine wall in a transverse section. Note the coarse distribution of capillaries in the circular muscle layer (*CM*) in contrast to those in the longitudinal muscle layer (*LM*). Inner circumferential vein (*ICV*) forms a long arch while a branch of the radial artery takes shorter circular courses in this area (*RA*). ×55.

Fig. 5. A basket-like structure of capillaries demonstrating the vasculature of a uterine gland (*GL*). ×58.

Fig. 6. Longitudinal section cut in the mesometrial–antimesometrial plane. The elements of the medial arterial division, the feeder arteries (*FA*), the medial longitudinal anastomosis (*MLA*) and the terminal arteries (*TA*) are fully exposed. *CM*, circular muscle layer. ×45.

circumferential arteries or veins. A row of straight and somewhat enlarged arteries was derived from this anastomosis at regular intervals (Fig. 6). They were named 'terminal arteries' by Orsini (1957).

After penetrating the circular muscle layer, the terminal arteries passed into the mesometrial portion of the endometrium (Fig. 2). They usually showed a corkscrew appearance, the twist of which was attenuated as they came close to the uterine lumen. They did not exhibit any obvious ramification before they broke up into the subepithelial capillary plexus of the mesometrial side.

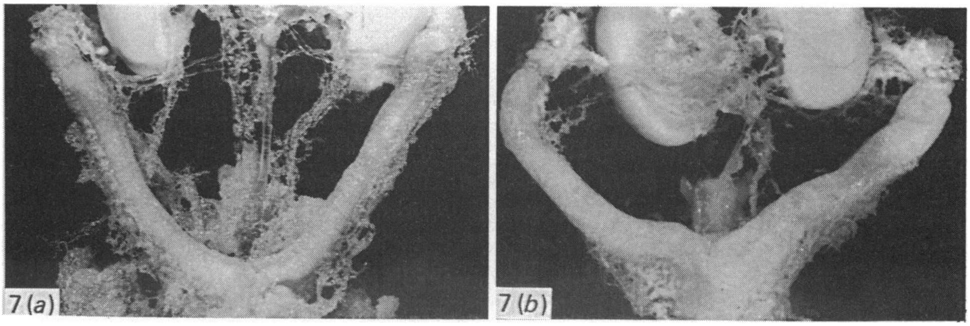


Fig. 7. (*a–b*). Ventral view of whole intact casts of the female reproductive tract of the hamster. (*a*) Evening of dioestrus I. (*b*) Evening of pro-oestrus. Note the symmetrical 'V' appearance on the evening of dioestrus I. × 1·5.

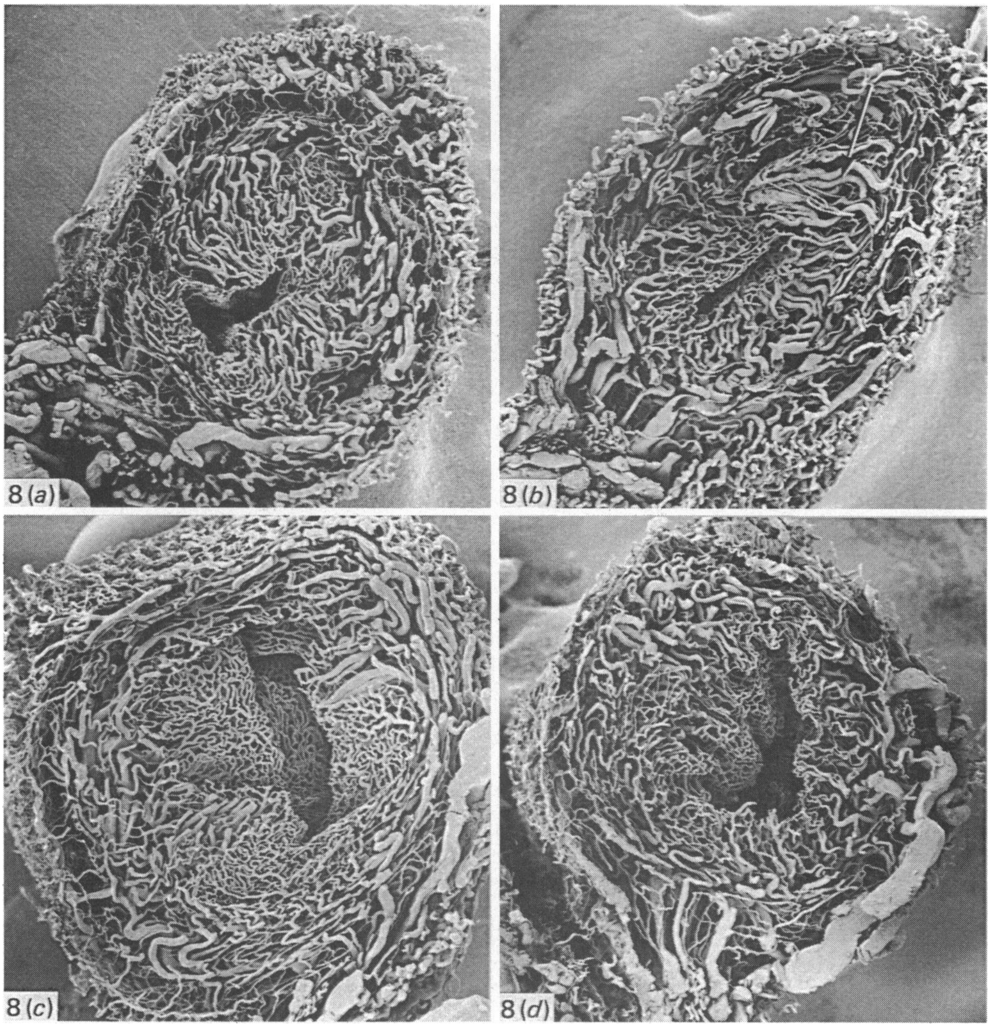


Fig. 8(*a–d*). Transverse sections of the hamster uterus. (*a*) Evening of dioestrus I. (*b*) Morning of dioestrus II. (*c*) Evening of dioestrus II. (*d*) Morning of oestrus. Compare also pro-oestrus in Figure 2. The radial vessels in the endometrium are evenly developed at dioestrus I. An arrow in (*b*) shows dilatation of the radial vessels in the antimesometrial area. × 24.

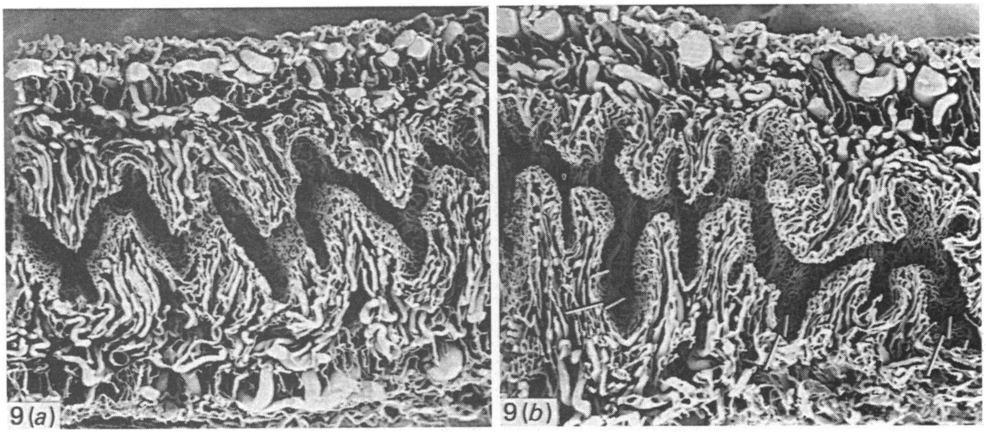


Fig. 9(*a–b*). Longitudinal sections cut in the plane which connects both lateral sides. (*a*) Evening of dioestrus I. (*b*) Evening of dioestrus II. The uterine lumen at dioestrus I shows a narrow zigzag line. In the evening of dioestrus II, several indentations are developed in the endometrium (arrows). × 24.

The venous system of the hamster uterus showed an arrangement almost similar to that of the arterial system. However, it differed distinctively from the latter in that there was no part of the venous system corresponding to the medial arterial division. Furthermore, the veins formed another circumferential plexus lying between the circular muscle layer and the endometrium, where the arteries did not take a continuous course around the uterus. These inner circumferential veins formed major anastomoses with the outer veins in the antimesometrial region of the uterus and additional anastomoses were found laterally between the tributaries among the two types of circumferential veins (endometrial–myometrial venous anastomoses) (Figs. 1, 2).

Changes in the vascular system during the oestrous cycle

A series of intact vascular casts of the whole reproductive tract during the four days cycle indicates that the casts of dioestrus I, especially in the evening, could be regarded as representing a standard pattern of the external appearance during the oestrous cycle. At dioestrus I, the right and left uterine horns presented a symmetrical 'V' appearance and were straight from the meeting point of the two wings to the cranial end connecting with the oviduct (Fig. 7*a*). From dioestrus II to oestrus, in contrast to dioestrus I, the left and right uterine horns were asymmetrically situated and showed various degrees of distension and inflection (Fig. 7*b*).

The uterus at dioestrus I showed an oval shape in transverse section (Fig. 8*a*). The uterine lumen was generally slit-shaped and its sections showed few variations in size. The radial vessels, which did not exceed 30 μm in diameter, were evenly developed in the endometrium. The diameters of the circumferential arteries ranged from 50 to 60 μm and those of veins ranged from 90 to 100 μm. Another aspect of the uterine lumen could clearly be seen in the longitudinal sections, together with the well-shown appearance of the endometrial folds outlined by the subepithelial plexus (Fig. 9*a*). At dioestrus I, the lumen showed a marked narrow zigzag appearance along the long axis of the uterus as a result of the interdigitation between the two halves of the lateral endometrium. At the level of the subepithelium, many capillaries anastomosed freely to make a well-developed network. Some blind-ending vessels were visible in the plexus (Fig. 10*a*).

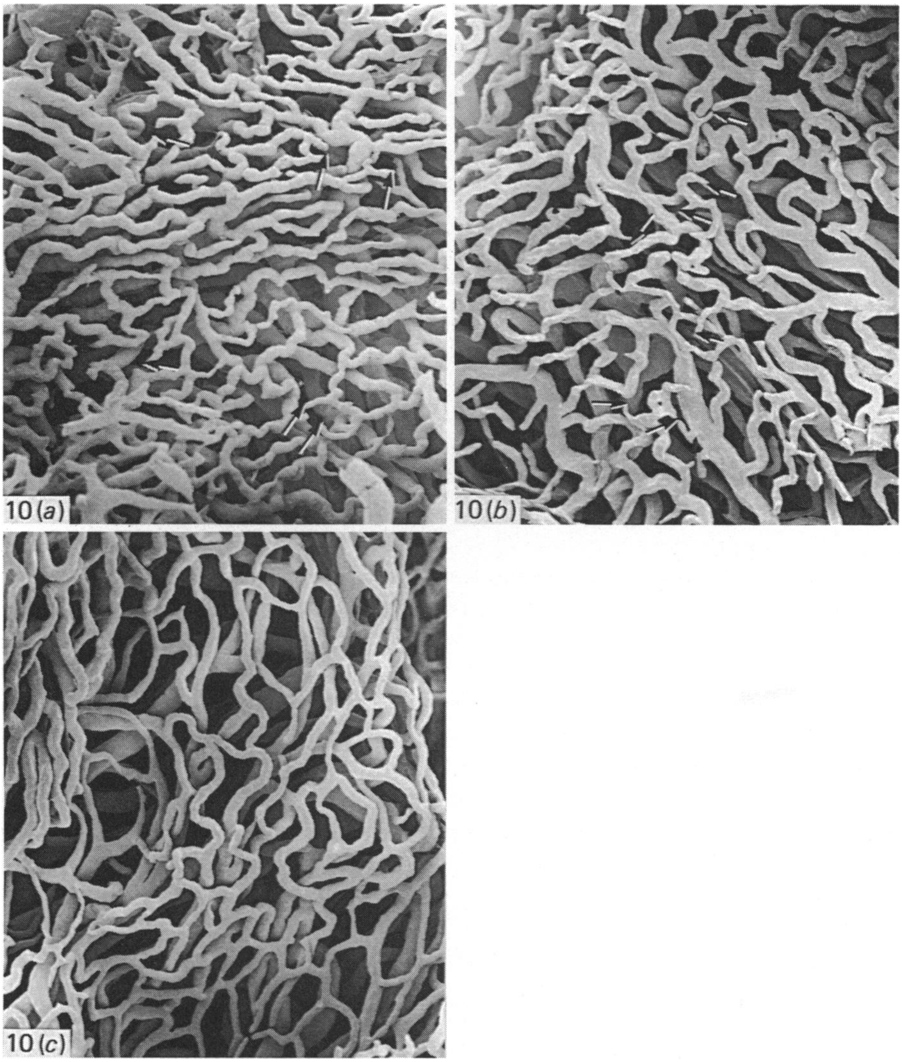


Fig. 10 (*a–c*). Vasculature of the subepithelial plexus on the luminal aspect. (*a*) Morning of dioestrus I. (*b*) Evening of dioestrus II. (*c*) Evening of pro-oestrus. Arrows indicate the blindly ending vessels. Note that such vessels are rarely seen on the evening of pro-oestrus. × 120.

In the morning of dioestrus II, no major changes were observed in the uterine vasculature except for dilatation of endometrial radial vessels in the antimesometrial area (Fig. 8*b*). Commonly these were about 40 μm in diameter.

On the evening of dioestrus II, a series of changes began in the uterine vasculature. A transverse section of a cast at this period is shown in Figure 8*c*. The uterus was distended in all directions and became almost circular in outline and the uterine wall was much thinner. The lumen was no longer slit-shaped but was complicated by endometrial folds protruding at random into the lumen. Most vessels of the circumferential division were enlarged at this period. Their diameters ranged from 60 to 70 μm for the circumferential arteries and from 100 to 130 μm for the circumferential veins. A longitudinal section showed the great increase of the luminal volume and indicated that this feature was caused not only by the dilatation of the uterus but also by the development of the rounded indentations extending into the endometrium (Fig. 9*b*). The previous interdigitation of the endometrium of both sides had disappeared completely. The subepithelial capillary plexus still showed some blindly-ending vessels and had slightly coarser meshes (Fig. 10*b*).

At pro-oestrus, the vasculature of the myometrium and the endometrium showed a similar pattern to that previously observed at the preceding period. The cross-cut plane in Figure 2 shows the further enlargement of the radial and circumferential vessels. The circumferential veins, above all, were greatly distended and had diameters of over 200 μm. While the intercapillary spaces of the subepithelial plexus were still distended, blind-ending capillaries were no longer visible (Fig. 10*c*).

On the morning of oestrus, the uterus again decreased in diameter, although it remained rounded in the section selected for the photography (Fig. 8*d*). No dilatation of the radial vessels was found in the endometrium except in the antimesometrial area. The lumen was less dilated, and the zigzag appearance of the lumen was already partly restored by the interdigitation of folds of the endometrium. On the evening of oestrus, casts showed an appearance almost similar to that seen at dioestrus I.

No major changes were observed in the vascular pattern of the medial arterial division. Although the terminal arteries varied in the degree of their coiling according to the thickness of the endometrium and myometrium, they did not show any distension, even at pro-oestrus (Fig. 2).

DISCUSSION

General pattern

Two main divisions, the circumferential and medial arterial divisions, were found in the vascular system of the hamster uterus, as previously described by Orsini (1957). She reported that primary and secondary segmental arteries or arcades could be distinguished. In this study, however, it was difficult to distinguish the secondaries from the primaries because of a consistent gradation between larger and smaller segmental arteries or arcades. The rat has no arcades (Orsini, 1957), few arcades (Young, 1951) or one arcade (Holmes & Davies, 1948) between any two neighbouring segmental arteries. No arcade-like structures are observed in other species such as guinea-pigs, mice, rabbits and chinchilla (Orsini, 1957). The roles of arcades remain to be determined, but they seem to be able to control the blood flow between the segments of the uterus and probably between the conceptuses during pregnancy.

Although the vascular structure of the circumferential division in the hamster uterus is essentially similar to that of the rat, a characteristic type of vessel can be distinguished; these are the circular branches of the radial arteries. They are involved in the formation of the plexus at the base of the endometrium along with the inner circumferential veins. The radial arteries of the rat have few circular branches, so that the inner circumferential vein is the only component of the plexus (Williams, 1948; Young, 1951; Rogers & Gannon, 1981). No plexus of this kind is visible in either guinea-pigs (Bacsich & Wyburn, 1940) or rabbits (Reynolds, 1949).

The arterial systems corresponding to the medial arterial divisions have also been reported in rats (Williams, 1948; Young, 1951; Rogers & Gannon, 1981; Takemori *et al.* 1982) and rabbits (Reynolds, 1949). In all species, these arterial systems are known to supply an increasing amount of blood to the placenta as pregnancy advances. In the hamster, this division shows several characteristics in its branching and distribution. First, the vessels of this division arise from the segmental arteries or arcades closer to the uterine artery in the hamster than in the rat. Secondly, they make a large medial longitudinal anastomosis lying along the mesometrial border of the uterus. This vascular anastomosis takes part in the formation of the 'vascular knot' during pregancy (Orsini, 1957), which has been considered to be a structure for lowering the maternal blood pressure before blood reaches the labyrinth. This conglomerate structure of the arteries may also serve to control the blood pressure in a non-pregnant period. However, it seems more probable that it is a partly preformed structure, allowing the vascular knot to be completed within such a short period of pregnancy (15–16 days). Thirdly, the terminal arteries hardly bifurcate before they reach the subepithelial capillary plexus in the hamster, whereas the vessels repeatedly bifurcate in the rat to form the 'mesometrial triangle' in the mesometrial region of the endometrium (Williams, 1948; Young, 1951; Rogers & Gannon, 1981; Takemori *et al.* 1982). Although the number of terminal arteries is much less in the hamster than in the rat, an equal number (1–3) of placental arteries develop from them in both species (Holmes & Davies, 1948; Orsini, 1957; Takemori *et al.* 1985).

Changes in the vascular system during the oestrous cycle

Changes in the vascular structure of the hamster uterus at the various stages of the oestrous cycle were studied with corrosion casts sectioned in the transverse or longitudinal planes, and also by using whole casting preparations to observe the external appearance of the uterus. Neither the destruction nor the reconstruction of the vessels were observed during the oestrous cycle in the hamster, as was seen in the rat (Williams, 1948; Young, 1951; Rogers & Gannon, 1981; Takemori *et al.* 1982) and guinea-pig (Bacsich & Wyburn, 1940). However, very noticeable changes were found in the three dimensional arrangement of the vascular system. These changes of the vessel spacing were closely related to those of the external form of the uterus and the shape of the lumen.

At dioestrus I the uterine horns tend to be straight from the caudal end to the cranial tip that connected with the oviduct. In contrast, the uterine horns of other stages show many variations in shape. If the external form of the uterine horn represents the motility of the myometrium, it will be in a state of quiescence at dioestrus I and will become motile at dioestrus II. The motility of the uterus is known to be responsible for moving large numbers of spermatozoa through the uterus (Rossman, 1937; Genell, 1939).

In the microvascular system of the uterus, the visible changes first appear in the antimesometrial region of the endometrium on the morning of dioestrus II. At this stage the radial vessels in this area become larger, preceding the general dilatation of the uterine vessels at subsequent stages. This limited dilatation of the antimesometrial radial vessels has also been reported in rats (Williams, 1948; Young, 1951) and guinea-pigs (Bacsich & Wyburn, 1940) as 'antimesometrial hyperaemia' at comparable stages of oestrous cycles. From these previous studies, this type of hyperaemia seems to be related to the decidualisation of the antimesometrial stroma and to the antimesometrial attachment of the blastocyst. The same may be true in hamsters, since they show the same pattern of implantation and decidualisation as that in rats and guinea-pigs (Ramsey, 1982).

From the evening of dioestrus II to pro-oestrus, the uterus showed drastic structural changes. First, the general dilatation in the vascular system was observed throughout the uterus. This feature indicates the increase of the uterine blood volume. In rats and mice, the maximal uterine blood volume during oestrus has been reported by Brody *et al.* (1974) and many other workers.

Secondly, the luminal volume of the hamster uterus is greatly increased. It is well established that the lumen of the rat uterus is swollen from late dioestrus to pro-oestrus and begins to collapse at oestrus (Williams, 1948; Young, 1951; Roger & Gannon, 1981; Takemori *et al.* 1982). Despite the homology of this cyclic change in the hamster and the rat, there is a difference between these two species in the appearance of the endometrial folds that determine the shape of the lumen. In the rat, the increase in the lumen size occurs during the disappearance of the endometrial folds. In the hamster uterus the endometrial folds are well developed throughout the oestrous cycle and the increase of the luminal volume is achieved by the formation of indentations of various sizes into the endometrium. The increased luminal volume seems to result from the accumulation of the luminal fluid, which may be a consequence of the large uterine blood volume mentioned above. To examine the significance of the accumulation of the luminal fluid, Toner & Adler (1985) carried out an experiment in which they altered the fluid volume in cycling rats. They revealed that the intraluminal fluid has a strong influence on uterine contraction and a weak effect on trans-uterine sperm transport.

Thirdly, the intercapillary spaces of the subepithelial plexus extend as the stage advances. This may be due to the increase of surface area of the endometrium, which is caused by the development of the endometrial indentations. At pro-oestrus, most of the blind endings of the capillaries disappear and the complete capillary network is formed. This kind of vascular change has already been reported by Rogers & Gannon (1981) and Takemori *et al.* (1982) in the rat uterus, but its physiological significance has still not been elucidated. Since the subepithelial capillaries nourish the uterine epithelial cells, they may be closely related to the function and viability of these cells. In a study of the cyclic morphological changes of the hamster uterine epithelium, Sandow *et al.* (1979) observed the epithelial cells proliferating from dioestrus II to pro-oestrus and degenerating at oestrus. Since the epithelial cells show the maximal proliferation at pro-oestrus simultaneously with the formation of the complete capillary network, these capillaries may take part in the regulation of the cyclic morphological changes of the epithelial cells.

As described above, a series of marked changes in the vascular structure from dioestrus II to pro-oestrus is probably related to the physiological changes in the uterus, for example the high motility of the myometrium, the hyperaemia in the antimesometrial endometrium, the increase of blood flow and the proliferation of the epithelial cells. These types of physiological changes are mainly controlled by oestrogen, especially oestradiol (Bacsich & Wyburn, 1941; Williams, 1948; Reynolds, 1965; Brody *et al.* 1974; West *et al.* 1978). In the hamster, plasma oestradiol is kept at a high level from dioestrus II until its abrupt increase at pro-oestrus (Baranczuk & Greenwald, 1973). Probably, the three dimensional structure of the vessels in the hamster uterus is also controlled by oestradiol.

SUMMARY

The vascular pattern of the hamster uterus and its changes during the oestrous cycle were studied by using the corrosion vascular casting method. The vascular system of the hamster uterus has two main divisions, the circumferential division and the medial arterial division. The former consists of circumferential and radial vessels and supplies the major part of the uterus. In this system the arteries and veins run parallel to each other throughout the uterus except for the inner circumferential plexus to which veins are predominantly distributed. The latter division has a delicate arterial system which supplies the mesometrial area of the endometrium. It forms a conglomerate structure along the mesometrial surface of the circular muscle layer.

The arrangement of the vessels, especially those in the circumferential division, evidently changes during the oestrous cycle. From the evening of dioestrus II to the evening of pro-oestrus most of the circumferential and radial vessels are enormously dilated and subepithelial capillaries make an elaborate network without blind endings. These changes in the vascular structure are associated with those in the external and internal (or luminal) aspects of the uterus: the uterine horns are markedly swollen and the luminal surface becomes much more irregular due to the indentations in the endometrium. No new vascular formation is found in the uterus throughout the four days cycle.

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