Vascular Pattern of the Mammalian Ovary with Special Reference to the Three-Dimensional Architecture of the Spiral Artery

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Summary. Casts of blood vessels in the ovaries of the female rat, pig and monkey were made with methacrylate, dissected out under a dissecting microscope and observed in a scanning electron microscope (SEM). The ovarian arteries and their branches were characterized by the presence of a spiral configuration. The spiral course of the arteries, however, varied greatly in detail among the different species. The arteries in the pig and monkey ovaries had tightly spiraling configurations, while there was only an image suggestive of a spiral in the rat ovarian arteries. The former species showed a rich plexus of the spiral arteries in the hilus and medulla of the organ. Their branches straightened at the transitional region between the medulla and cortex but again showed spiral configurations in the cortex. Further, the arterial branches supplying the growing and mature follicles showed a much more marked extent to the spiral configurations as compared with those of the corpus luteum. In this paper morphological findings shall be discussed in correlation with their physiological implications.

Among the mammalian reproductive systems, the ovary is unique in the sense that the organ is simultaneously responsible for the elaboration of sexual hormones as well as the maturation of Graafian follicles and the ova contained within the follicles. It has been well documented that the ovarian vasculature can handily adapt to changes in the size and/or functions of the ovary (DELMANN et al., 1949; REYNOLDS, 1950; BURR and DAVIES, 1951). The principal artery supplying the ovary is the ovarian artery, derived from the abdominal aorta. The ovarian arteries and their branches are collectively called coiled arteries, spiral arteries or helicine arteries because of their tortuous courses. Their functional significance has been much disputed (CLARK, 1900; DELMANN et al., 1949; REYNOLDS, 1950; BURR and DAVIES, 1951; ORIBE, 1976; KANZAKI et al., 1982).

FARRE (1858) first described the spiral arteries in the human ovary (see DELMANN, 1949). Following this, spiral configurations of the ovarian arteries and their branches have been reported in the chicken (NALBANDOV and JAMES, 1949; ORIBE, 1976), rat (BASSETT, 1943), rabbit (REYNOLDS, 1950; BURR and DAVIES, 1951; DOS SANTOS-FERREIRA et al., 1974), pig (ANDERSEN, 1926) and human being (CLARK, 1900; DELMANN et al., 1949). These gross and light microscopic observations revealed that the coils of the ovarian arteries were present in the hilus, medulla and cortex. It is rather difficult to trace their entire course both in serial sections and with the naked eye, and the
morphological findings obtained with either technique remain at variance with each
other in certain respects. In stereoscopic radiographs of the human ovary, not all the
ovarian artery branches were sufficiently filled with an opaque substance (KARDON and
KESSEL, 1979). The difficulties in realizing a perfect injection to the ovary may be due
to the complex spiral configurations of the ovarian artery.

Concerning the architectures of the spiral arteries, only a few studies have thus far
been done on the mammalian ovary, probably because of the technical difficulties
mentioned above. Since the invention of the vascular corrosion casting/scanning
electron microscopic (SEM) technique by MURAKAMI (1971), this kind of study of
microcirculation has become widely attainable. Recently, the technique has been
effectively applied to the demonstration of vascular patterns of the ovary under normal
and various experimental conditions (KARDON and KESSEL, 1979; KANZAKI et al., 1982).
These observations, however, have been limited to the capillary networks around the
follicles and the corpus luteum, and have not referred to the spiral arteries at all. The
vascular corrosion casting/SEM technique (MURAKAMI, 1971; OHTANI and MURAKAMI,
1978), which makes possible a clearer discrimination of the vascular architecture than
do the macroscopic and light microscopic methods thus far employed, is evidently a
useful means toward elucidation of the distribution and arrangement of the ovarian
spiral arteries.

In the present study, the vascular corrosion casting/SEM technique combined with
dissection of casts was applied in the ascertainment of the entire course of the ovarian
arteries in certain mammals. SEM photographs were taken exclusively at lower
magnifications. This paper describes the vascular architecture of the ovarian spiral
arteries in correlation with their functional significance.

MATERIALS AND METHODS

Ovaries of rats, pigs and monkeys engaged in full reproductive activity were employed
in the present study. Pig ovaries were taken immediately after the animals were killed
at a slaughterhouse. Each ovary was thoroughly perfused through the cannulated
ovarian artery under manual pressure with a heparinized physiological saline. Non-
pregnant monkeys and rats were anesthetized with sodium pentobarbital (25 mg/kg)
and the abdominal cavity was exposed. The cannula was inserted retrogradely into the
abdominal aorta below the origin of the ovarian arteries. One ligature of silk surgical
thread was placed around the lower part of the abdominal aorta, while another ligature
was placed around the aorta above the left renal artery (FORSSMANN et al., 1977). The
animals were then thoroughly perfused through the cannulated aorta with the same
saline.

After the organs became completely pale with the saline perfusion, Mercox-resin
(Dainihon Ink Co. Ltd) containing 20% methyl-methacrylate (OHTANI and MURAKAMI,
1978) was slowly injected through the same route with minimal pressure until resin
flowed from the ovarian vein. The ovaries were immersed for 2-3 hrs in a warm bath
(about 60°C) in order to accelerate polymerization of the injected resin. They were
corroded in a detergent solution containing sodium hypochloride for 6-12 hrs at room
temperature and then thoroughly rinsed in tap water.

The vascular casts were dehydrated in an ascending ethanol series, dried with the
critical point method and dissected with sharpened needles and forceps under a
dissecting microscope. They were then mounted on aluminium specimen holders (32
RESULTS

The mammalian ovary has a thick peripheral zone or cortex which surrounds the medulla or zona vasculosa. Numerous dense networks of capillaries surrounding the follicles and the corpus luteum are situated in the cortex, while a plexus of arteries and veins are present in the medulla. The ovarian arteries penetrate at the hilus into the medulla, from which their branches run radially toward the cortex. In the present study, casts of the ovarian arteries and their branches have been dissected carefully under a dissecting microscope and examined by SEM. The distinction between arterial and venous divisions has been made on the basis of the following criteria (KARDON and KESSEL, 1979): the arteries show a tortuous configuration and have fusiform depressions on the surface of the casts, while the veins show a rather straight configuration and possess rounded, shallow depressions. Three-dimensional architectures of the ovarian arteries and their branches vary greatly not only from species to species but also from region to region of the ovary. This paper shows mainly a lower magnification of SEM images of the ovarian vascular casts in certain mammalian species.

Fig. 1. SEM image of an ovarian vascular cast of the rat ovary. The branches of the ovarian artery (A) display either straight or slightly undulated courses. V ovarian vein. ×25
The rat

Figure 1 shows a SEM image of a vascular cast in the rat ovary. Numerous capillary networks surrounding the follicles are present on the surface of the ovary. The ovarian artery from the abdominal aorta runs in a generally straight course, but tends to become somewhat tortuous as it approaches the hilus. The branches of the artery display either straight or slightly undulated courses (Fig. 13).

The pig

Figure 2 shows a macroscopic picture of the vascular cast in the pig ovary. In this specimen, vascular casts surrounding the follicles and the corpus luteum have been partly removed in order to trace the ovarian artery and its branches. Since the pig ovary is large in size and its arteries have correspondingly large diameters, it is relatively easy to dissect the ovarian artery and its branches under a dissecting microscope. After gross observations of the ovarian vascular casts, the same casts were investigated in detail by SEM. At the hilus, the ovarian artery is divided into two to four first-order branches which have a large diameter and show a tightly spiraling configuration (Fig. 2, 3). Additional small branches with similar configurations also arise from the same artery and run toward the uterine tube. The coiling observed in the first-order branch persists toward the medulla of the ovary. It appears that the spiral arteries in the medulla form more complicated vascular networks as compared

Fig. 2. Macroscopic view of an arterial vascular cast of the pig ovary. The arteries show a tightly spiraling configuration at the hilus (H) and medulla (M), while the arterial branches interposed between the medulla and the cortex (C) display a straight course. CL corpus luteum. ×2.6
Fig. 3. SEM image of a cast of the ovarian artery at the hilus in the pig ovary. The ovarian artery is divided into two to four first-order branches with a slightly spiraling configuration. ×13

Fig. 4. Spiral arteries in the medulla of the pig ovary. They have more complicated vascular networks. ×16
Fig. 5. Arteries in the cortex of the pig ovary. The artery supplying the corpus luteum is large in diameter and runs in a slightly undulated course, while the arteries supplying the small follicles are small and show a tapering spiral configuration. ×16

Fig. 6. Arteries (A) supplying the large follicle in the pig ovary. They run in a spiraling course up to the follicles. C a capillary network surrounding the follicle. ×87
with those in the hilus (Fig. 2, 4). The arteries interposed between the medulla and the cortex generally run in a straight course. Near the cortex, the higher-order branches of the arteries are small in diameter and again show the spiral artery pattern (Fig. 5, 6). It is impossible to exactly trace arteries in the cortex under a dissecting microscope because of their small diameters. The arteries supplying the small follicles (probably primary and secondary follicles) are also small in diameter (about 40 μm) and show the pattern of the tapering spiral artery (Fig. 5). Those supplying the large follicles (mature follicles) have a medium diameter (about 170 μm), and take a spiraling course up to the follicles (Fig. 6). On the other hand, those supplying the corpus luteum are large in diameter (about 240 μm) and display either straight or undulated courses (Fig. 2, 5). In addition, the mature follicles and the corpus luteum have dense networks of capillaries (Fig. 6). From these findings, it is suggested that the mature follicles and the corpus luteum have a large amount of blood supply.

**The monkey**

The right and left ovarian arteries of the monkey are derived from the abdominal aorta immediately below the level of the origin of the renal arteries. Since they are very small in diameter and continue spiraling throughout their courses, it is rather difficult to make perfect vascular casts of the monkey ovary. The vascular perfusion

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**Fig. 7.** SEM image of the arterial vascular cast of the monkey ovary. The ovarian artery and its branches are characterized by the presence of a spiral configuration. \( H \) hilus, \( M \) medulla, \( C \) cortex. \( \times 18 \)

**Fig. 8.** The ovarian artery at the hilus of the monkey ovary. The artery is divided into two first-order branches with a slightly spiraling configuration. \( \times 12 \)
method according to FORSSMANN et al. (1977) enabled us to make satisfactory vascular casts in the monkey ovary. Figure 7 shows a SEM image of the vascular cast in the monkey ovary. The ovarian arteries running toward the ovarian hilus indicate a spiral configuration. At the hilus, the ovarian artery is divided into two first-order branches both of which have a large diameter and show a spiral configuration (Fig. 8). Coiling of the ovarian arteries continues into the medullary portion of the ovary (Fig. 7). They have relatively large diameters (150 to 230 µm). The medulla of the ovary is occupied by a complicated plexus of spiral arteries similar to that of the pig ovary (Fig. 7, 9, 10). The arteries running from the medulla to the cortex course relatively straight (Fig. 10, 11). In the ovarian cortex, the higher-order branches of the ovarian artery diminish in diameter and are seen to proceed toward the follicles in patterns of corkscrew twists (Fig. 12). The general arrangement of the arterial system in the monkey ovary is essentially similar to that of the pig ovary, but differs considerably from that of the rat ovary (Fig. 13).

**DISCUSSION**

In general, the ovarian arteries arising from the abdominal aorta enter the hilus of the ovary and branch profusely as they course through the medulla. Their branches then penetrate radially into the cortex, where they break up into networks of capillaries (CLARK, 1900; ANDERSEN, 1926; BASSETT, 1943; BURR and DAVIES, 1951). A dense network of capillaries surrounds the mature follicles and the corpus luteum (DOS
Fig. 10. Vascular casts in both the medulla (M) and the cortex (C) of the monkey ovary. ×33

Fig. 11. Higher magnification of a part of Figure 10. An artery interposed between the medulla and the cortex runs in a straight course. ×40

Fig. 12. Higher-order branches of the ovarian artery in the cortex of the monkey. They proceed toward the follicle in the pattern of corkscrew twists. ×50
SANTOS-FERREIRA et al., 1974; KARDON and KESSEL, 1979; KANZAKI et al., 1982). However, details of the vascular patterns in the ovary vary greatly among different species of animals. Thus, the vascular system in the human (CLARK, 1900), monkey and pig ovaries are much more complex than the corresponding system in the rat. The ovarian arteries in the monkey and pig ovaries are usually characterized by tightly spiraling configurations, while there is only a suggestion of coil-like structures in rat ovarian arteries. The vascular pattern in the rabbit ovary as demonstrated by REYNOLDS (1950) and BURR and DAVIES (1951) showed intermediate configurations. The menstrual cycle (estrous cycle) of the human being and monkey is longer than that of the rat, the former being 28 days and the latter 4 days. Thus, it seems that the complex vascular system and marked coiling of arteries in the human and monkey ovaries are due to a longer menstrual cycle.

CLARK (1900) made an excellent three-dimensional reconstruction of the spiral arteries in the human ovary based on the reconstruction of two-dimensional images. In general, it is very difficult to perfectly trace the ovarian spiral arteries by means of light microscopic observations of serial sections. In the present study, a direct three-dimensional visualization of the ovarian arteries was possible through the use of the cast technique and SEM. Moreover, the finest distribution and arborization of the arteries could be revealed by this method.

The spiral arteries seen in both the hilus and the medulla formed a rich plexus of arterial networks. REYNOLDS (1950) postulated that the spirally arranged arteries in the ovary serve to decrease blood pressure from a high level in the ovarian artery to the low level of the effective osmotic blood pressure in plasma. From the present morphological findings, it is likely that the overall blood pressure in the stroma of the

**Fig. 13.** Diagram showing the arterial supply of the rat, pig and monkey ovaries. The arteries in the rat ovary display slightly undulated courses, while those in the pig and monkey ovaries show tightly spiraling configurations. H hilus, M medulla, GF Graafian follicle, CL corpus luteum.
Spiral Artery of the Mammalian Ovary

Ovary is regulated mainly by a plexus of spiral arteries, in particular, those situated in both the hilus and the medulla. The spiral arteries in the cortex supplying the various stages of follicles are smaller in diameter as compared with those in the hilus and medulla. The spiral arteries in the cortex may also play a role in decreasing blood pressure.

Contrary to the spiral configurations of the ovarian arteries, straight configurations were found in the arteries interposed between the medulla and the cortex and in those supplying the corpus luteum. It has been reported that the ovarian vasculature varies greatly in response to the changes in size of the ovary observed during the course of the reproductive cycle (Reynolds, 1973). The corpus luteum also demands a large amount of the blood flow for the elaboration of hormones (Bindon, 1969). In the present SEM observations, the corpus luteum was found to be supplied by either straight or slightly undulated arteries which broke up into a dense network of capillaries. It seems that the straight configuration of arteries is suitable for functions of the corpus luteum. In contrast, the arterial branches supplying the primary and secondary follicles were smaller in diameter than those supplying the corpus luteum, showing tightly spiraling configurations.

In conclusion, it is suggested that the spiral artery in the mammalian ovary plays an important role in the maturation of the follicle and the elaboration of hormones.

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