The Vascular Architecture of the Different Forms of Small Intestinal Villi in the Rat (*Rattus norvegicus*)

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The vascular anatomy of the intestinal villi in the rat was studied by injection with Indian ink and silicone rubber. The vascular pattern in finger-leaf- and tongue-shaped villi is the same. One central arteriole divides into two marginal vessels, giving rise to a capillary net, which in turn collects into two paraaxial venues. In ridge-shaped villi there are multiple arterioles and venules. It appears that finger-shaped villi turn into leaf-shaped villi by lateral upgrowth of the lamina propria, and that ridge-shaped villi are also formed by upgrowth of the lamina propria between adjacent leaf-shaped villi.

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Many of the early hypotheses regarding the precise relationship of artery, capillaries, and vein in intestinal villi have been reviewed by Jacobson & Noer (7). Spanner (16) made an extensive study of the subject, comparing the pattern in different animals and man. Nevertheless descriptions in current reference books give imprecise and superficial accounts of the vascular supply of intestinal villi (2, 3, 5).

Following the introduction of jejunal biopsy techniques there was a renewed interest in the subject of villous morphology (13, 11, 6). Several recent papers (10, 9, 12) have described studies of the intestinal vasculature of rats and monkeys, but these have taken no account of the variations in villous architecture.

The shape of intestinal villi in the upper small intestine of a local strain of laboratory rats progresses from ‘fingers’ at birth, to ‘leaves’ and finally ‘ridges’ in the adult. These changes are always most marked proximally and less marked distally (1). The object of this investigation was to study the anatomy of the blood vessels in these different forms of intestinal villi.

MATERIALS AND METHODS

A local strain of laboratory albino rats (*Rattus norvegicus*) was studied. Initially, because of the relative ease of handling, young adult rats weighing 200-300 grams were used. Subsequently studies were extended to younger and older animals.

Under pentobarbitone anaesthesia, the aorta and superior mesenteric vein were cannulated.

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with polyethylene tubing. Initial studies were made by the aortic injection of Indian ink. Subsequent studies were made using silicone rubber (14, 15, 4). Both ‘RTV’ (Silicone Products Dept., General Electric Co., Waterford, New York, USA) and ‘Microfil’ (Canton Biomedical Products, Canton, Mass., USA) silicone rubber were used. These were mixed and cured according to the makers’ instructions. The vascular system of the intestine was flushed through with heparinized saline till the intestine blanched and the mesenteric vessels and effluent fluid were colourless. Silicone rubber was then injected by the aortic or venous catheter. When filling was complete, both tubes were clamped and curing allowed to proceed at 4°C. After curing, the small intestine was removed, opened, pinned on wax and cleared by immersion in increasing concentrations of glycerin.

At times, after completion of the rubber injection, the intestine was distended with 10 per cent formalin. This enabled groups of villi and the submucous vessels to be seen more easily. In some experiments, one coagulated rubber solution was injected arterially and another venously, to differentiate the arterial and venous supply to the villi. In other experiments a loop of small intestine was opened, and the flow of dye into and through the villous vessels was observed through a dissecting microscope.

For photography specimens were pinned on a black background, under glycerin. For general views of villi, photographs were taken through one eye piece of a Bausch and Lomb dissecting microscope, using a Nikkon F 35 mm camera, with a bellows extension and a Micro Nikkor 52 mm lens. For higher magnifications pictures were taken through a Spencer AO trinocular microscope with 35 mm camera attachment and Carl Zeiss objectives (16 mm and 45 mm) with built in iris diaphragm. In some cases the field was flattened by putting a glass coverslip over the villi. In other cases individual villi were dissected out and mounted on a glass slide. Photographs were taken on Ilford ‘Pan F’ film developed to give maximum contrast.

Fig. 1. Leaf-shaped villus from young adult rat injected intra-arterially, showing early vascular filling. (a) central arteriole, (m) two marginal vessels (×210).

Fig. 2. Leaf-shaped villus from same preparation as in Fig. 1, showing beginning of the capillary network (c). Other symbols as for Fig. 1 (×210).

Fig. 3. General view of leaf-shaped villi from young adult rat showing central arterioles and well-filled capillary network. Symbols as for Fig. 1 (×60).
RESULTS

In studies of leaf-shaped villi, when the vessels were observed during filling, the dye was seen to flow first up a central arteriole and then divide at the tip into two vessels running along the margin of the villus in its long axis (Fig. 1). From these marginal vessels a capillary net arises (Figs. 2 and 3). The marginal vessels lie in close apposition to the base of a line of columnar epithelial cells. The bases of the other columnar cells are related to the capillary net, but it is clear that not all cells are in direct contact with a capillary, since the bases of groups of five or more cells are seen surrounded by a capillary loop (Fig. 4). On either side of the villus, at a variable point, but often about midway between the tip and the base, the capillaries collect together to form, usually, two venules (Fig. 5), which then pass to a larger submucous vein (Fig. 6). In young animals with tongue-shaped villi (Fig. 7) and in very young animals with finger-shaped villi (Fig. 8) exactly the same arrangement exists.

In older animals the leaf-shaped villi become still broader and may be termed ridges. Careful study, however, shows that all stages can be seen from individual separate leaves (Fig. 3) to complete ridges. The first stage appears to be a raised connecting band filled with a capillary network joining two or more leaves (Figs. 9 and 10). Later stages, which may be seen more proximally in the same animal, or in older animals, show a higher connecting band which gradually fills up the spaces between the tips of the ‘leaves’ (Fig. 11). At this stage it is clear that each leaf, though joined to its neighbour, still retains its basic vascular pattern.

Fig. 4. Leaf-shaped villi from adult rat injected with Indian ink and viewed in combined transmitted and reflected light. Note that the bases of the epithelial cells are not all in direct apposition to the vascular network. Symbols as for Fig. 1 (×200).

Fig. 5. Leaf-shaped villus from adult rat injected intra-arterially, showing capillary net forming the two paraxial veins (v). Other symbols as for Fig. 1 (×210).

Fig. 6. Leaf-shaped villus from adult rat. White silicone rubber injected intra-arterially fills the central arteriole and marginal vessel on the left. Red silicone rubber injected intravenously fills the marginal vessel (m) on the right, the capillary net (o), the three venules (v), and the submucous vein (sv). The presence of three venules is unusual, the two on the left drain directly into the submucous vein. The vessel (s) is posterior and does not belong to this villus. The marginal vessel (m) on the left appears to drain directly into the left-hand venule (×210).
Fig. 7. Three-week-old rat injected intra-arterially showing tongue-shaped villi broader at the base than at the tip. The same basic vascular anatomy exists as in the case of the older animals with leaf-shaped villi (×65).

Finally, in still older animals ridge-shaped villi are found, where the luminal surface is more or less a straight edge (Fig. 12). The vascular supply of these ridges still follows the basic pattern originally present in the leaf-like villi before they were joined together.

DISCUSSION

The vascular anatomy of the leaf-shaped villi of the rat, as described here, conforms with the ‘fountain’ Pattern of Mall (8) and with the descriptions of Spanner (16), Nylander & Ole- rud (10), and Mohiuddin (9).

The identity of the vasculature in finger-, tongue- and leaf-shaped villi strongly suggests that in the development of these forms from the finger-like structures of the foetus, one finger-like villus turns into one leaf-like villus. It appears that the first change in a ‘finger-like’ villus is a broadening at the base, while the tip remains the same, producing a ‘tongue-shaped’ structure (Fig. 13B). This broadening subsequently extends along the length of the villus producing a ‘leaf-shaped’ structure (Fig. 13C). The fact that leaf-shaped villi with two arterioles do not usually occur, would appear to rule out the possibility that leaf-shapes are formed by the lateral fusion of finger-shaped villi.

The vascular pattern in short ridges, where there are two arterioles and four venules, strongly suggests that these short ridges are formed from two leaves. The vascular pattern of longer ridges, where there are multiple arterioles, suggest that they are formed from a number of leaves. All stages from separate leaves (Fig. 13D) through leaves connected by bands of increasing height (Fig. 13E & F) to complete ridges (Fig. 13G) are found. This indicates that the ridge arises by the upgrowth

Fig. 8. Finger-like villus from a 15-day-old rat injected intra-arterially showing central arteriole (a), marginal vessels (m), some filling of the capillary net (c), and the venule (v) on one side (×175).

Fig. 9. Adult rat injected intra-arterially. Two leaves joined together by a low connecting band. There are two arterioles (a) and four venules (v) (×80).
of the lamina propria between the leaves.

The observation that not all the absorptive epithelial cells are directly related to a capillary vessel raises the problem of how substances pass from such epithelial cells to the capillary bed? The answer to this problem must await further study.

In some experiments it was noticed that during injection into the arterial catheter, dye flowed almost immediately from the venous catheter. This could have been due to preferential flow through a small segment of intestine, or to some form of arteriovenous shunt as described in some other animals by Spanner (16). Definite proof of the existence of a shunt could not be obtained, although in the villus depicted in Fig. 6 the marginal vessel on the left appeared to connect directly with the
venule. Further investigation of this aspect of the intestinal circulation in the rat would be of interest.

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