Structure of the Rete Mirabile in the Kidney of the Rat as Seen with the Electron Microscope

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PLATES 33 AND 34

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ABSTRACT

Electron micrographs of the rete mirabile in the medulla of the rat have revealed that the endothelium of the afferent and efferent vessels are markedly different in fine structure. The venous capillaries returning blood from the papilla are lined with a fenestrated endothelium much like that in the peritubular capillaries of the kidney. The arterial capillaries delivering blood to the papilla have an unperforated lining of overlapping endothelial cells with extremely irregular tapered margins. It is pointed out that the organization of particularly the latter vessels suggests that the functional capabilities of these retia go beyond those of a simple diffusion countercurrent exchanger.

INTRODUCTION

Fawcett and Wittenberg (1) have recently reported on the dimorphism of the afferent and efferent capillaries in the rete mirabile of the swim bladder of *Opsanus tau*. They have found the afferent capillaries to be lined with an endothelium varying in thickness from 2 to 4 μ; the efferent capillaries also have areas this thick, but are characteristically lined by a fenestrated endothelium varying in thickness from 10 to 70 mμ. At the thinnest points the continuity of the cell is maintained by a membrane representing solely the fused membranes from the opposite sides of the cell; actual pores are not seen. These observations extend with the electron microscope the findings of previous workers who have reported in some instances differences in the thickness of the endothelium of the efferent and afferent vessels in the retia mirabilia of the swim bladder of other species (Woodland (2), Fänge (3), Rauther (4)). Haldane (5), in remarks based on Woodland's observations, implies that this difference is the rule, but this does not accurately reflect Woodland's report, which notes the condition in only one species.

The bundles of vessels (vasa recta) traversing the inner stripe of the outer zone of the medulla in the kidney of mammals (Figs. 2 and 3) are also fully developed retia mirabilia conjugata (retia with two directional flow) (Longley and Burstone, unpublished observations). It was possible to conclude this on the basis of a striking difference in histochemical activity between the efferent and afferent vessels in the medullary vascular bundles of the rat. In this species the vessels afferent with respect to the papilla (the *efferent* arterioles of the juxtamedullary glomeruli, or arteriolae rectae spuriae) histochemically show intense esterase activity in their endothelium, but the efferents show none; differentially stained by this method the tendency to a regular pattern of intermixing of the two types is dramatically apparent.

This structural similarity between the swim bladder rete in fish and the mammalian renal rete of course suggests similar functional activities in the two locations. Scholander (6) has extensively discussed the countercurrent exchange possibilities of the swim bladder rete; recent experimental work indicates that similar functions are performed by the medullary vascular bundles in rats (7).

OBSERVATIONS

In this further study of the medullary rete in the rat, thin sections have been examined by electron microscopy. The material was fixed in

veronal-acetate buffered osmium tetroxide (8), dehydrated in alcohol, and embedded in 1:7 methyl:butyl methacrylate. A structure scarcely distinguishable from that of the rete of the *Opsanus* swim bladder as described by Fawcett and Wittenberg has been revealed.

The afferent esterase-active vessels are lined by an endothelium ranging in height from 0.2 to 4.7 μ (Fig. 1). These cells frequently overlap broadly, as do endothelial cells in capillaries of bone marrow (9), heart (10), and lung (11). The free edges of the underlying cells are perhaps dentate or filiform, since small bodies which are apparently cross-sections of cytoplasmic extensions are frequently seen between an overlying endothelial cell and the capillary basement membrane (Fig. 5). This seems to be similar to the condition described by Parks (12) in the hepatic sinusoids. The cytoplasm of the endothelial cells contains moderate numbers of small mitochondria, usually at least 0.2 μ wide but rarely more than 1 μ long (Fig. 5). Vesicles about 60 mμ in diameter similar to those that other observers (9, 10, 13) have associated with "cytopempsis" or "pinocytosis" are frequently seen (Fig. 5). The cytoplasm of adjacent cells frequently differs markedly in density, chiefly as a result of closer packing of the elements of the ergastoplasm in the denser cells (Fig. 1). Fine filaments are usually seen in the cytoplasm of the less dense cells (Fig. 5). The free surface of the cytoplasm of the denser cells frequently extends microvilli into the capillary lumen. Since the cytoplasm of any individual cell tends to be of uniform density, there is some possibility that there are two types of endothelial cells in these vessels. Nuclei are seen in about half the cross-sections of afferent vessels. The "plasma membrane" of the endothelial cells is limited on the outside by a zone of low electron density from 30 to 40 mμ wide. This separates the cells from each other and from the electron-dense "basement membrane" which surrounds the vessel as a whole. The structure of the membrane is not clear but in some instances it appears fibrillar. Outside the basement membrane pericytes are sometimes seen closely applied to the vessel (Fig. 4). Within the lumen numerous red cells are usually seen embedded in a granular matrix of plasma protein (Fig. 1).

The efferent capillary of the rete stands in strong contrast to the afferent just described. Although the endothelial cells may have substantial thickness, they characteristically show the tenuous fenestrated structure known in many other sites (14–20). The thin cytoplasm, some 40 mμ thick, is frequently interrupted entirely, and the continuity of the cell is maintained, as in the rete of *Opsanus*, only by the fused membranes from the two sides of the cell (Fig. 6). Pores such as those described in the endothelium of the glomerular vessels (21, 22) have not been seen. The interruptions of the cytoplasm are sufficiently regular so that in section the endothelium frequently has a beaded appearance. The "beads" are about 35 to 70 mμ in length and are usually separated from each other by about half this distance. In the thicker portions of the cells small mitochondria about 0.4 μ across are seen. Since they rarely exceed this dimension it must be assumed that they are nearly spherical. Endothelial nuclei are seen only in about one-fifth as many cross-sections as in the afferents. Small vesicles similar to those seen in the afferents are also found. A zone of low electron density separates the cells from their basement membranes and from each other (Fig. 6).

Concerning the relation between the vessels, as suggested before there is a tendency for the afferents to be surrounded by efferents, and *vice versa*. Since the best understood functional capacity of the rete mirabile is its ability to facilitate exchange between the fluids of opposing directions of flow in the two sets of capillaries which comprise them, it is interesting to note that the apposition of the rete vessels, though it may occasionally be very close, is not generally especially intimate. Interstitial spaces appear to be moderately extensive and contain numerous interstitial cells and extracellular spaces.

CONCLUSIONS

The structural resemblance already noted with the light microscope between the retia mirabilia of the swim bladder of fishes and in the mammalian kidney has now been shown to extend to their submicroscopic structure. The probability that they are also very similar in function seems more likely than ever. In addition to their capacity for countercurrent exchange, it is reasonable to suggest, since the structural characteristics observed in the retia examined go considerably beyond those required for efficient passive exchange of diffusible materials between the two sets of vessels, that an even more complex explanation of their physiological role will be necessary before the latter is fully understood. Specifically, the endothelium, particularly of the arterial capillaries,

may be able to modify their permeability so as to regulate the molecular and ionic species subject to countercurrent exchange. Should the endothelium be able to transport actively any substance into the blood flowing through the arterial capillaries, then for that substance the countercurrent diffuser would become a countercurrent multiplier, able to contribute not only to the maintenance of, but to the creation of, the hyperosmolarity of the renal papilla (23).

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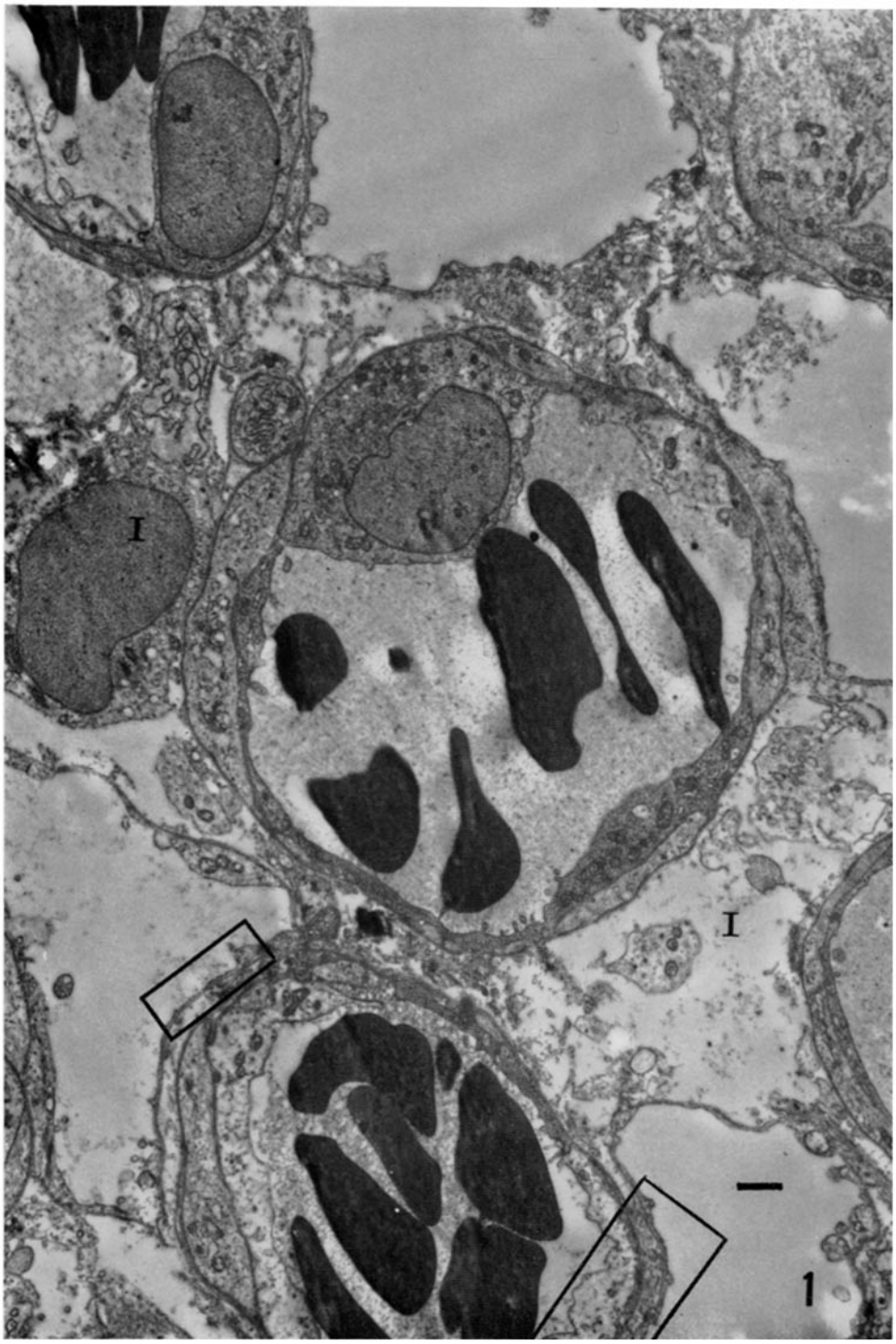
Explanation of Plates

Magnification of each electron micrograph indicated by marker representing 1 μ.

Plate 33

Fig. 1. Cross-sectional view of small area from medullary vascular bundle of rat. Figs. 2 and 3 provide orientation. The thick walled vessels, usually containing red cells and a dense granular plasma precipitate, are branches of afferent arterioles of juxtamedullary glomeruli. The entire blood supply of the two innermost zones of the kidney arrives through these vessels. Intimately intermingled in the bundles with vessels of this type are venous capillaries, appearing here as nearly empty, somewhat collapsed, thin walled vessels. Red cells are rarely observed in these. Interstitial spaces and cells (*I*) make up a significant part of the area seen. Black rectangles outline areas shown at greater magnification in Figs. 5 and 6.



(Longley *et al.*: Structure of rete mirabile in kidney)

PLATE 34

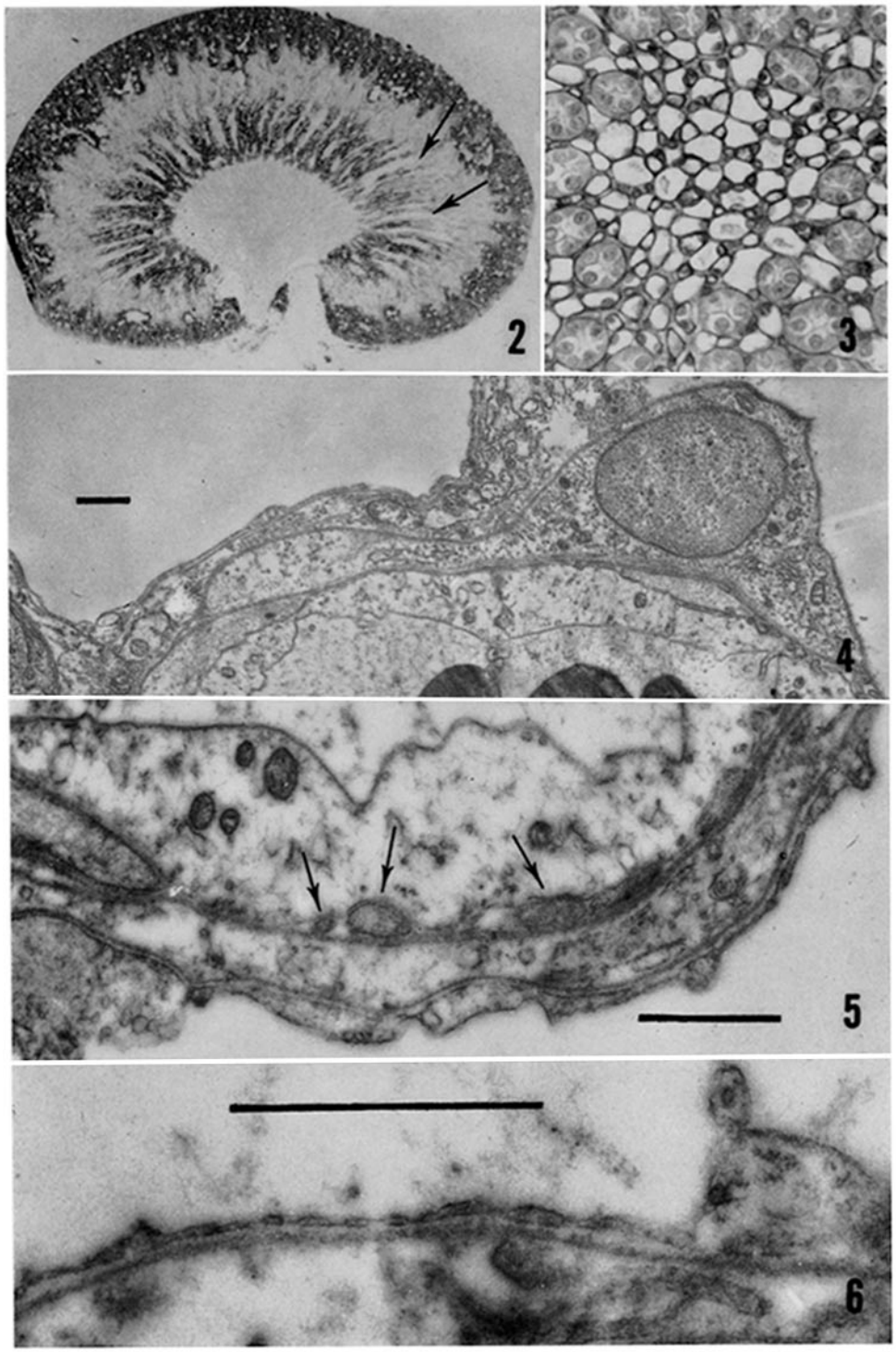
FIG. 2. Sagittal section of rat kidney stained to demonstrate zones of kidney. Medullary vascular bundles (arrows) are seen unstained crossing the inner stripe of the outer zone of the medulla. Succinic dehydrogenase. × 4.

FIG. 3. Cross-section of medullary vascular bundle as seen in the light microscope. In general the smaller vessels are the arterial capillaries, the larger empty ones the venous. Surrounding the bundles are seen sections of the straight segments of the distal tubules (thick ascending limbs) and possibly collecting tubules. At the level shown in this figure thin limbs are not conspicuously associated with the bundle. Note the tendency for arterial vessels to be surrounded entirely by venous vessels and *vice versa*, an arrangement favorable to efficient countercurrent exchange. Periodic acid–Schiff stain. × 325.

FIG. 4. Typical area of contact between arterial capillary (below) and venous capillary (above left). Intruding into the space between the vessels is a pericyte, an interstitial cell closely applied to the outside of the arterial capillary. At this magnification the separation between the endothelium and the basement membrane is visible in the venous capillary, and the beaded appearance of the endothelium in section can just be made out.

FIG. 5. Higher power view of the area marked at the bottom of Fig. 1. The arrows indicate cell processes lying between the basement membrane of an arterial capillary and an overlying endothelial cell. Notice the difference in density of cytoplasm. Below, separated from this vessel by about half a micron, is the wall of an adjacent venous capillary. Small vesicles may be seen in the cytoplasm here.

FIG. 6. Higher power view of the area in Fig. 1 marked by the small rectangle, showing the wall of a venous capillary. The beaded appearance of the endothelium is clearly shown. Geometric considerations indicate that the section is thin enough to establish that pores do not occur.



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