Scanning Electron Microscopy of the Renal Corpuscle of the Mesonephros in the Lamprey, *Entosphenus japonicus* Martens

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Summary. The renal corpuscle of the lamprey mesonephros was studied under the scanning electron microscope.

Bowman's capsules with individual spaces are chockshaped sacs closely packed together along a medial artery. The lateral walls of the capsules are apposed to those of neighbouring capsules.

Glomerular capillaries from the medial artery extend radially between the apposed walls of neighbouring Bowman's capsules. Bulgings of capillaries into the capsular space are associated with mesangial folds of the capsular epithelium.

The transitional zone of the visceral layer with podocytes and the parietal layer of squamous epithelium is bounded by linearly arranged rod-shaped epithelial cells. Apertures of the urinary tubule are lined by cells equipped with a fascicle of cilia.

Key words: Mesonephros – Lamprey – Renal corpuscle – Scanning electron microscopy.

Introduction

The mesonephros in the lamprey has an elongate renal corpuscle (for ref. see v. Möllendorf, 1930; Fontaine, 1958; Gérard, 1958; Forster, 1961 a.o.).

Histological examination (Forster, 1961; Hickman and Trump, 1969; Andrew and Hickman, 1974) has indicated that the glomeruli in *Lampetra fluviatilis* are fused to form one large glomus lying in a common urinary space, from which some urinary tubules emerge. According to the work of Youson and McMillan (1970) in ammocoetes and adult lampreys (*Petromyzon marinus*), the glomus is formed by a large number of lobed glomeruli. Dilated ends of urinary tubules are interposed between each pair of capillary lobes. However, the authors have not referred to the space continuity between neighbouring capsules.

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Many scanning electron microscope studies have revealed the threedimensional shape of the podocyte and the pattern of the glomerular capillary of some vertebrates in adult (Buss and Krönert, 1969; Arakawa, 1970, 1971; Fujita et al., 1970 a.o.) or in neonate (Buss, 1970; Miyoshi et al., 1971).

Electron microscope observations (Miyoshi, 1970; Youson and McMillan, 1970) have shown that the cellular constitution of the mesonephric glomerulus in the lamprey is very similar to that of other vertebrates, though the podocytes are primitive in shape.

The present study was undertaken to clarify the three dimensional relations between the glomerular capillary and the Bowman's capsule of the lamprey mesonephros under the scanning electron microscope.



Fig. 1. A longitudinally cut surface of a renal corpuscle. MA medial artery. The urinary spaces partitioned by walls (W) from individual Bowman's or capsular spaces (CS). AA Openings of afferent arterioles on the inner surface of the artery. U Urinary poles. EA efferent arteriole. $\times 210$

Fig. 2. A cross-section view of a corpuscle. The urinary space is subdivided into lunar or triangular compartments of Bowman's capsules. Winding capillary swellings (C) on the capsular walls extend from the arterial portion toward the peripheral area. *PE* peritoneal wall. $\times 210$

Fig. 3. A close-up of the boxed area of Figure 2. The wall (*W*) separating two compartments contains numerous capillaries (*C*). Some capillaries empty into a large efferent arteriole (*EA*). *T* urinary tubule. \times 530



Materials and Methods

Adult lampreys, *Entosphenus japonicus* Martens, of about 200 gm and 600 mm length were used in the present study. The animals were obtained from the Shinano River (Japan) in winter as they were migrating from the sea.

The lampreys were fixed by perfusing (Maunsbach, 1966) 200 ml of fixative via the aortic bulb. The fixative used was 2.5% glutaraldehyde buffered to pH 7.4 with 0.1 M phosphate containing 50 ppm CaCl₂.

The slender mesonephros was cut into pieces about 5 mm long, some of which were trimmed to expose the cut surface of the renal corpuscle in the longitudinal plane. The specimens were dehydrated with a series of graded acetones and transferred into iso-amylacetate. Drying of the specimens by the critical point method of CO_2 (Tanaka, 1972) was followed by coating with carbon and gold.

Observation and photography were performed in a Hitachi SSM-2 type scanning electron microscope.

Results

On longitudinally cut surfaces through the medial artery (Fig. 1), partitioned urinary spaces are arranged in a row along a furrow of the cut-open artery. The compartments, which correspond to spaces of Bowman's capsules, are almost rectangular troughs. They are about $100 \,\mu\text{m}$ in width and $250 \,\mu\text{m}$ in length, while their depth varies by sections.

On transversely cut surfaces (Fig. 2), the renal corpuscle appears as a round structure. The medial artery is situated near the peritoneal wall. The urinary space is septated into five or six compartments by walls radiating from the arterial portion toward the peripheral margin of the corpuscle. All the compartments are arranged around the artery like the segments of a fan or an orange.

The largest part of the visceral layer of Bowman's capsule is rough due to the presence of many swellings of capillaries and podocytes. The parietal layer is smooth. The round aperture of the urinary tubule is seen in the parietal layer (Fig. 1).

The walls common to the neighbouring Bowman's capsules are formed by two adjacent visceral layers. Between the two layers are seen many furrows, or round caves, of similar thickness (about $15 \,\mu$ m), representing glomerular capillaries cut open (Figs. 1–4). Neither communicating pores nor epithelial continuity have been found between neighbouring Bowman's capsules.

Glomerular capillaries of the visceral layer give rise to slender swellings of almost uniform size (about $15 \,\mu m$ thick). The swellings with numerous windings and mutual anastomoses extend radially from the arterial portion toward the margin of the corpuscle (Figs. 1, 2, 7).

Cross-sections of glomerular capillaries show thin folds of the visceral layer, connecting the capillaries to the wall of Bowman's capsule (Figs. 2, 3, 5). The folds are a primitive type of mesangium of the glomerular capillaries.

Podocytes on the visceral layer consist of perikarya, large cytoplasmic processes and thin foot processes as do the cells in mammals.

The podocytes on the capillary swellings are fusiform (Figs. 4, 7). The cells and their large cytoplasmic processes cover the capillary swellings so densely that fine foot processes are not easily observed. The beaded arrangement of spherical cells as seen in sections (Miyoshi, 1970) may represent cross-sectioned profiles of densely packed podocytes.



Fig. 4. Inner surface of the visceral layer. The capillary swellings (C) form anastomoses (arrows), and are densely covered with fusiform epithelial cells. ×1100

Fig. 5. Podocytes in the intercapillary area. The cell body is fusiform or star-shaped, from which threadlike or membranous processes (*) emerge. Fine lace of finger-like processes are foot-processes (FP). Free surfaces of the cells are covered with granular projections. \times 5200



Fig. 6. High magnification of a cut-surface of the apposed wall of neighbouring Bowman's capsules. Furrows (CL) in the wall are capillaries cut open longitudinally. The capillary bulgings on either side of the wall are associated with mesangial folds of visceral epithelium (arrows). C capillary swelling. $\times 1300$

Fig. 7. Transitional area between parietal layer (P) and visceral layer (V), where capillary swellings (C) and podocytes are seen. Thin rod-like cells (arrows) in a successive arrangement line the boundary of the two layers. Small arrows: cilium $\times 1000$



Fig. 8. A surface view of the parietal layer. Penta- or hexagonal cell surfaces are tightly paved. Free surface of each cell is rough with numerous globular projections and equipped with a cilium. $\times 2200$

On the flat wall between capillary swellings, the podocytes are loosely arranged. Most of the cells are fusiform, but flattened stellate cells are also present (Fig. 5). Very thin processes sometimes extend over many cells to far distant areas (Fig. 4).

The podocytes in the area adjoining the parietal layer are usually thin. The transitional area of the two layers is lined by a successive arrangement of thin rod-like cells (Fig. 7).

The foot processes at the margins and the tips of large processes (Fig. 5) are finger-like in shape and almost similar in size (about $1 \mu m \log and 0.1 \mu m$ thick).

The free surfaces of the podocytes are usually granulated and studded with numerous globular projections measuring about $0.2 \,\mu\text{m}$ in thickness, the latter exhibiting local concentrations on the cells (Fig. 5). A cilium is sometimes observed on the perikarya of podocytes (Fig. 7).

The urinary pole of Bowman's capsule, a funnel-like structure, is shown in Figure 1. The parietal layer in the vicinity is flat with a tight pavement of penta- or hexagonal cell surfaces (Fig. 8). The central portion of each cell surface bears a cilium (about $10 \,\mu m \log$) (Fig. 8).

Discussion

The present study clearly demonstrates that the urinary space of the lamprey renal corpuscle is partitioned into compartments of Bowman's capsules. No perforation

has been seen in the partitioning walls. The Bowman's capsules in the lamprey which represent dilated end sacs of nephrons (Youson and McMillan 1970) do not communicate.

Youson and McMillan's (1970) reconstructions of the corpuscle have shown that the dilated end of the tubule lies between a pair of loops consisting of anastomosing networks of capillaries. Furthermore, the authors pointed out the existence of capillaries which penetrate Bowman's capsules, forming anastomoses between capillary loops.

The present observation showed development of capillary nets on the entire surface of the visceral layer. There was no local difference of capillary development on anyone of Bowman's capsules. The capillaries which bulged into the space of Bowman's capsules were necessarily associated with mesangial folds of the visceral layer. Therefore, the findings indicate that the glomerular capillaries extend through slit-like spaces between neighbouring walls of Bowman's capsules. Capillary penetration of Bowman's capsules was not seen in the present study.

The podocytes were primitive in shape as mentioned previously (Miyoshi, 1970; Youson and McMillan, 1970). Dense arrangement of perikarya and occurrence of irregularly shaped processes, particularly membranous processes, resemble developing epithelial cells in mammals (Suzuki, 1959; Simon and Chatelanat, 1969; Buss, 1970; Miyoshi et al., 1971).

The described gradual transition from squamous cells to spherical and columnar podocytes (Youson and McMillan, 1970) may be due to the presence of cross-sectioned profiles of the lining cells on the boundary between the parietal and the visceral layer in the present study.

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