[Proceedings of the Iowa Academy of Science](https://scholarworks.uni.edu/pias)

Volume 64 | Annual Issue Article 89

1957

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James J. Prestage
State University of Iowa

H. W. Beams
State University of Iowa

The Structure of Renal Corpuscle in the Sparrow, *Passer domesticus domesticus*, as Revealed by the Electron Microscope[1]

By James J. Prestage[2] and H. W. Beams

Introduction

Light microscope studies on the structure of the renal corpuscle have been made by numerous investigators. Among these were Bowman (1842), Vimtrup (1928), von Mollendorff (1928), Bargmann (1929), Zimmermann (1929), McGregor (1929), Bensley and Bensley (1930), and many others. A diversity of opinions arose concerning the details of structure of the mammalian renal corpuscle which was to remain, to a certain extent, the legacy of the electron microscopists. Among the electron microscopists who studied the structure of the mammalian renal corpuscle were Pease and Baker (1950), Dalton (1951), Oberling, Gautier and Bernhard (1951), Hall, Roth and Johnson (1953), Jones (1953), Rinehart, Farguhar, Jung and Abul-Haj (1953), Reid (1954), Hall and Roth (1954), Mueller, Mason and Stout (1955), and Pease (1955). Some of the points of disagreement on the structural features of the renal corpuscle are: (1) basement membrane of Bowman's capsule, (2) epithelium of Bowman's capsule, (3) epithelium of the glomerulus, (4) basement membrane of the glomerulus, and (5) endothelium of the glomerulus.

Since studies with the electron microscope on the vertebrate renal corpuscle have been limited to mammals it seemed of interest to attempt an analysis of the bird's renal corpuscle by this method.

Materials and Methods

The birds, *Passer domesticus domesticus,* used as experimental animals were anaesthetized with chloroform. An incision along the midventral line exposed the visceral organs which were pushed aside so that the kidneys could be removed. The kidneys, when removed from the depressions formed by the vertebrae and the ilia, were placed on a slide, and with the aid of a dissecting microscope the lobules which make up the lobes were teased apart and cut into smaller pieces. The

[1]Aided by a Grant (RG-4706) from the National Institutes of Health, United States Public Health Service.

[2]Recipient of a Fellowship from the National Medical Fellowships, Inc., through funds appropriated by The National Foundation for Infantile Paralysis. Thanks are due Dr. T. C. Evans for permitting us the use of the electron microscope.

tissue was fixed for thirty minutes in 1% osmium tetroxide solution, buffered at a pH of 7.2. Following fixation the tissue was washed in distilled water, dehydrated in graded concentrations of alcohol ranging from 35% to 100%, and infiltrated with a mixture of 71% N-butyl methacrylate and 29% methyl methacrylate treated with the catalyst, Luperco. After polymerization, the tissue was sectioned with an International Rotary Microtome, placed on specimen grids covered with a thin celloidin film, and examined with an RCA EMU-2B electron microscope.

The terminology used in this paper has been adopted from the studies of Hall *et al.* (1953) and Mueller *et al.* (1955). Refer to the key of terminology.

Results

The basement membrane of Bowman's capsule as revealed by this study is dense and homogeneous in nature (Figures 1 and 2 BC). The membrane appears as a single layer with a thickness ranging from 750 Å to 1,240 Å. The laminated appearance of the basement membrane previously described by Mueller *et al.* (1955) was not observed in this material.

Attached or adjacent to the inside wall of the basement membrane of Bowman's capsule (BC), there is a single layer of epithelial cells which appear in some micrographs to be separated from it (Figure 4 EBC), but in other micrographs such a separation cannot be discerned. (Figure 1 EBC). This layer of epithelial cells is continued from the epithelium of the uniferous tubule, and is described by Mueller *et al.* as being continuous with the cells of the podocyte (PG). The typical nucleus of an epithelial cell of Bowman's capsule is oval in shape. The nuclear membrane appears as a single line and has a thickness of approximately 200 Å. Mitochondria (M) in the epithelial cells of Bowman's capsule (EBC) are characterized by an internal structure similar to that described in the mouse by Palade (1952).

In Figures 2, 3, and 4 there can be seen areas along the basement membrane of the glomerulus (BMG) where the podocyte (PG) appears to be a continuous layer through the extension of its cytoplasmic processes (PC). There are some projections from this layer that do not reach that portion of the podocyte cell containing the nucleus and these are referred to as foot processes (Figures 1, 2, 3, and 4 PFP). These processes vary in width from approximately 800 Å to 4,000 Å, and in height from approximately 1,450 Å to 5,600 A. Open spaces are observed between the foot processes and where the foot processes fail to make contact with that portion of the podocyte cell containing the nucleus. The podocyte cells have large nuclei which appear frequently to be oval in shape (Figures 1, 2, 3, and 4 PN). Their membranes are approximately 200 Å in thickness.

Clear evidence as to whether or not the podocyte layer is a syncytium has not been found by the study of the present material.

The basement membrane of the glomerulus in this material is well demonstrated because of the difference in density between it and the bordering layers, *i.e.*, the epithelium and endothelium of the glomerulus, are in close apposition with the basement membrane, and as a result of such a relationship this membrane may appear to serve as the basement membrane of both layers. It is 600 Å to 1,240 Å in

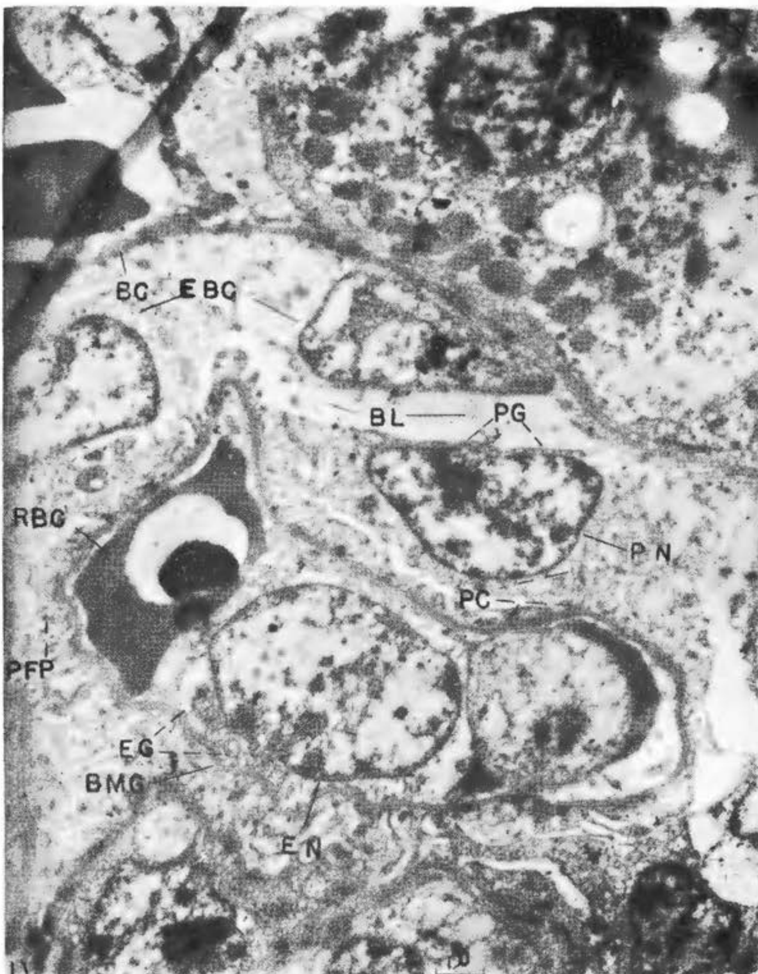

PLATE I

Figure 1. Portion of an oblique section of Bowman's capsule and the glomerulus. The capillary has within its lumen a blood cell and two endothelial cells.

thickness and appears to be composed of a single layer of homogeneous material.

Electron micrographs of the glomerulus in the sparrow reveal the presence of an endothelium layer (Figures 1, 2, 3, and 4 EG). The membrane of an endothelial nucleus is approximately 150 Å in thickness. In some micrographs the cytoplasm of the endothelial layer appears to be homogeneous, in others it appears to have a net-like structure. In several electron micrographs erythrocytes may be seen in the lumina of capillaries (Figures 2, 3, and 4 RBC). The erythrocytes are too dense to display the nature of their cytoplasmic struc-

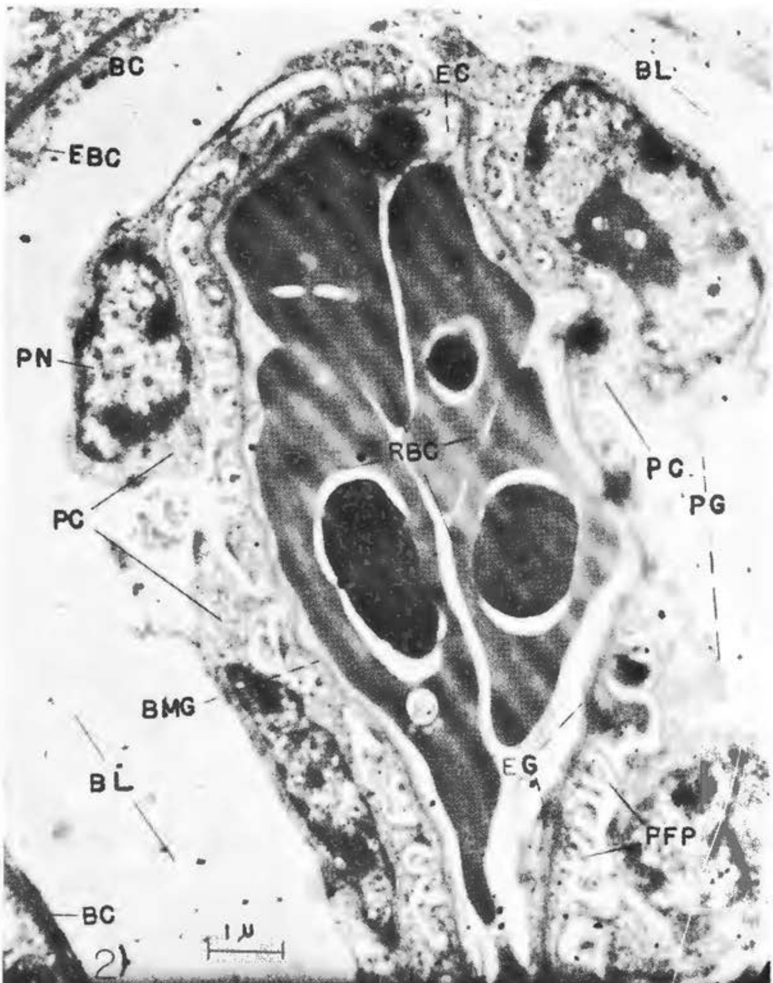

PLATE II

Figure 2. An oblique section of a capillary showing blood cells within its lumen. Podocyte cells surround the basement membrane of the capillary. In the lower and upper left hand corners and the upper right hand corner portions of Bowman's capsule are seen.

ture. Their nuclei, also, are sufficiently dense to mask the details of their ultramicroscopic structure.

Discussion

Since the classical studies of Bowman (1842), it has been known that the basement membrane of the renal corpuscle was continuous with that of the uriniferous tubule. Following Bowman's observation, numerous investigators have studied the basement membrane

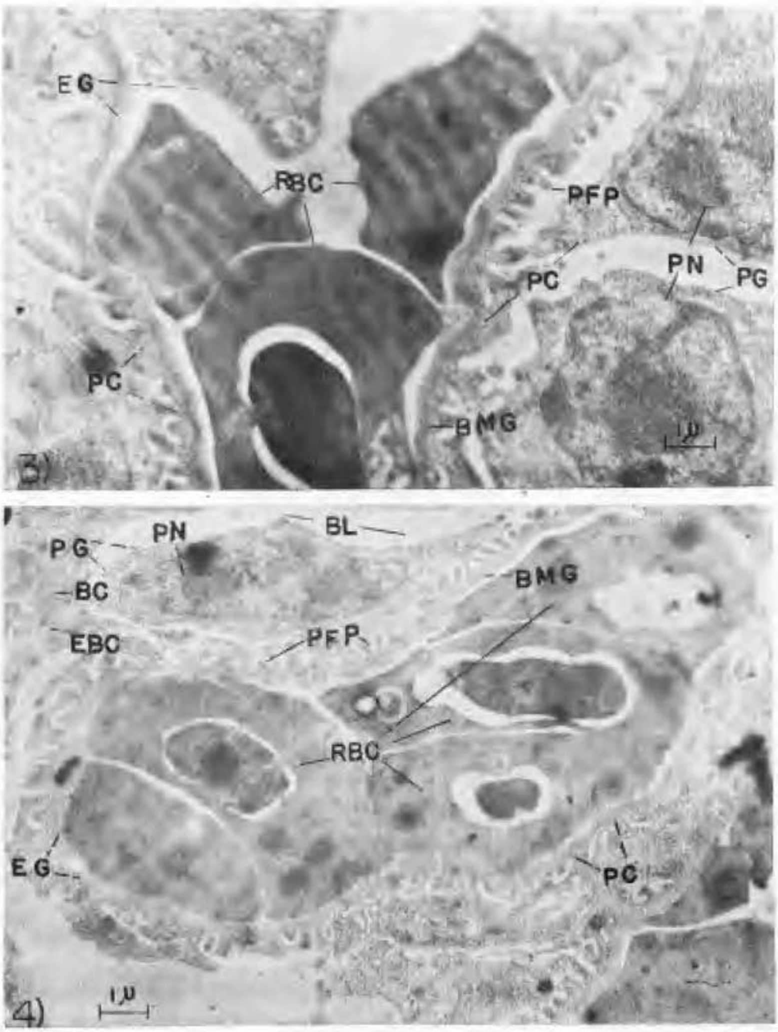

PLATE III

Figure 3. Portion of a glomerulus showing blood cells and parts of three podocyte cells.
Figure 4. A tangential section of a capillary surrounded by podocyte foot processes and a podocyte cells. Blood cells are within the lumen.

of renal corpuscles from a wide variety of mammals in hope of learning more about its structure.

Bowman spoke of it as being a simple, homogeneous and perfectly transparent membrane, in which no structure could be discerned. Through the years Bowman's interpretation has had many supporters, among whom were Zimmerman (1929), McGregor (1929), Bensley and Bensley (1930), and others. Contrary to the interpretation of Bowman has been that of Volterra (1928), who contends that the basement membrane is composed of a lamellar reticular connective tissue which shows a network of fine argyophile fibers.

With the electron microscope Dalton (1951) observed the basement membrane of Bowman's capsule in the mouse to be homogeneous whereas Mueller *et al.* (1955) observed it to be laminated. In this study, the basement membrane of Bowman's capsule is observed to be homogeneous in nature supporting the earlier interpretation of Bowman and the more recent interpretation of Dalton.

Like the basement membrane of the renal corpuscle, the epithelium of Bowman's capsule is continuous with the epithelium of the uriniferous tubule (Bowman 1842). The basal cell membrane of the epithelium of Bowman's capsule, according to Mueller *et al.* (1955), is adjacent to but not a part of the basement membrane of Bowman's capsule. In this study such a relation between the epithelium and basement membrane of Bowman's capsule is discernable in some micrographs but, as previouly mentioned, this relationship is not consistently observed. It may be that the epithelial cells are so firmly attached to the underlying basement membrane that the two structures cannot always be distinguished from one another.

The podocyte, or epithelial cell of the glomerulus, is the most controversial structure in the renal corpuscle. Gerlach (1848) concluded from his studies with injected material that the capillaries were separated from the capsular space by cells which formed a layer over the tips and crevices of the glomerular lobules. Since the studies of Gerlach a tremendous amount of investigation has been carried out on this topic and consequently numerous interpretations have been expressed. With the light microscope these interpretations have varied from the podocyte being "a layer of not very well defined cells with spherical nuclei" (Ludwig 1872), to the podocyte forming a radiating protoplasmic network on the surface of the capillaries (von Mollendorff 1928).

Electron microscope studies have presented a variety of interpretations of the structure of the podocyte epithelium and its relation to the basement membrane of the glomerulus. Pease and Baker (1950) pose the possibility of the glomerular epithelium being a continuous layer, a view which is also adopted by Dalton (1951) and

Reid (1954). However, studies by Hall and Roth (1954), Mueller *et al.* (1955) and Pease (1955) expressed the view that the epithelial cells in the adult are specialized and lack contiguous borders.

Considerable discussion has been focused upon the cytoplasmic projections extending from the podocyte cells toward the basement membrane. Views pertaining to the origin and termination of these projections, as well as the foot processes with which they may be associated, have been advanced by Pease and Baker (1950), Oberling *et al.* (1951), Rinehart *et al.* (1953), Mueller *et al.* (1955) and Pease (1955).

In the present observations, the cytoplasm overlying the basement membrane appears variable in thickness, but always present. It is most conspicuous in those regions where cytoplasmic projections from the podocyte cells occur. It seems likely that the apparent projections from the basement membrane are also derived from the podocyte cells. It can be observed that when cytoplasmic projections extending from a podocyte maintain contact with the basement membrane for some distance, no other processes are seen in that area. This indicates a contiguity between the podocyte epithelium and the basement membrane of the glomerulus.

Three schools of thought exist with regard to the basement membrane of the glomerulus: (1) Mueller *et al.* (1955), among others, stated that the basement membrane of the uriniferous tubules expands as Bowman's capsule, and covers the capillary endothelium as the only basement membrane found in the glomerulus. (2) Hall and Roth (1954) assert that the basement membrane of the glomerulus (lamina densa) is of endothelial origin. (3) Jones (1953) concluded that there were two basement membranes and stated that "the normal glomerulus consists of complex loops of capillaries having their own delicate basement membrane. An epithelial basement membrane and the covering glomerular epithelium extend around Bowman's capsule and are reflected over the capillary loops."

Not only has the relation between the capillaries and the basement membrane been a subject of debate, but also the finer structure of the basement membrane. McManus (1950) believed that the glomerular basement membrane was composed of argyrophil fibers from both Bowman's capsule and afferent and efferent endothelium. Hall and Roth (1954) described the basement membrane of the glomerulus as being continuous, smooth, dense, and perhaps finely porous, whereas Dalton, Mueller *et al.*, expressed similar views by stating that the basement membrane of the glomerulus appeared to be a single homogeneous membrane. The views of these investigators on mammals are supported by the present investigation on birds.

The presence of endothelial cells was observed by von Mollendorff (1928), Zimmerman (1929) and many other investigators. The question as to whether or not these cells constituted a continuous layer arose and, as it was with other structures of the renal corpuscle, various opinions were expressed as to its true nature. Von Mollendorff and Bargmann (1929) expressed some doubt as to whether the endothelial cells completely lined the internal wall of the capillaries, whereas McGregor (1929) and Bensley and Bensley (1930) stated that the endothelium of the capillary was continuous. Among the electron microscopists, Pease and Baker (1950) contended that the glomerular capillary does not have a continuous endothelium, but evidence of a continuous endothelium has been found by Dalton (1951), Hall *et al.* (1953), Mueller *et al.* (1955), and others. In this study the endothelium was observed to be continuous.

With regard to filtration, Mueller *et al.* (1955) on the basis of their observations of the glomerulus in the fetus, concluded that the epithelial cells became specialized in the adult and are lifted from the basement membrane by the foot processes which permit filtration to occur without the filtrate being required to pass through the epithelial cells. They believed that the filtrate may be permitted to pass through the endothelium, through the basement membrane and then between the podocyte foot processes and under the trabeculae of the podocyte to arrive in the lumne of Bowman's capsule. This view is also shared by Hall (1955). Pease and Baker (1950) suggested that "the interdigitating ridges on the wall of the capillary provided strength particularly against bursting pressures, while allowing the wall to be maximally thin as an aid to diffusion." To the writers' knowledge, no other investigators of this topic have suggested or advanced an hypothesis pertaining to the filtration process.

As mentioned above, the basement membrane of the glomerulus in this study has not been found to be without some quantity of cytoplasm on its outer border. The cytoplasm covering the basement membrane is thought by present investigators to be of podocyte epithelial origin. If such be the case, the filtrate from the glomerulus would pass through this thin cytoplasmic covering and then under the podocyte cells to arrive in the lumen of the Bowman's capsule.

The structural features of the renal corpuscle as described for mammals are essentially the same as herein reported for birds.

Summary

1. Glomeruli of the sparrow's kidney were prepared for electron microscopic examination by fixing in 1% osmium tetroxide buffered at pH 7.2, embedding in methacrylate polymer, and sectioning at thicknesses ranging from 0.25 to 0.50 micron.

2. The basement membrane of Bowman's capsule was observed to be composed of a single, dense and homogeneous material, ranging from 750 Å to 1,240 Å in thickness.

3. The epithelium of Bowman's capsule was observed to be a single layer of cells lying attached to or adjacent to the basement membrane of Bowman's capsule.

4. A cytoplasmic layer, which was thought to be of podocyte epithelial origin, was observed to be continuous with the basement membrane of the capillary. Open spaces were observed between projections from the cytoplasmic layer covering the basement membrane and that portion of the podocyte cells containing the nuclei.

5. The glomerular basement membrane was observed to be composed of dense and homogeneous material, ranking from 600 Å to 1,240 Å in thickness.

6. The endothelium was observed to be continuous as the inner wall of the capillary.

7. Capillary lumina containing blood cells were observed. The cytological structure of these cells was not discernable.

8. In general, the ultramicroscopic structure of the bird's renal corpuscle is similar to that of mammals.

Key to Terminology

1. Basement membrane of Bowman's capsule .... BC
2. Epithelium of Bowman's capsule .... EBC
3. Epithelium of the glomerulus (podocyte) .... PG
4. Podocyte nucleus .... PN
5. Podocyte cell body .... PC
6. Podocyte foot process .... PFP
7. Basement membrane of the glomerulus .... BMG
8. Endothelium of the glomerulus .... EG
9. Endothelial nucleus .... EN
10. Endothelial cell body .... EC
11. Endothelial lining net work .... ELN
12. Capillary lumen CL
13. Lumen of Bowman's capsule .... BL
14. Erythrocyte .... RBC
15. Mitochondria .... M

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Department of Zoology
State University of Iowa
Iowa City, Iowa