COMPARATIVE HISTOLOGY OF THE KIDNEY OF DOMESTIC ANIMALS

By

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A THESIS

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ABSTRACT

This study was undertaken to provide a more or less complete and up-to-date description of the microscopic structures of the kidney of the domestic animals. Studies were made on sixty-nine domestic animals of seven different species, the pig being chosen as a type.

The tunica fibrosa of the kidney capsule in domestic animals was two-layered except in the cat, where only one layer was present. The outer layer of the tunica fibrosa consisted of dense collagenous and a few elastic fibers and the inner layer was formed by loose collagenous and reticular fibers, with smooth muscle fibers present in all animals except the cat. In the sheep and goat, and to a lesser extent in the ox, the muscle fibers were very numerous and appeared to form a distinct muscular layer.

The juxtamedullary renal corpuscles in the horse (191μ), pig (156μ), dog (124μ), and cat (106μ) were larger than the cortical ones, which were 178μ, 137μ, 122μ, and 96μ, respectively. The juxtamedullary renal corpuscles in the ox (173μ), sheep (147μ), and goat (157μ) were smaller than the cortical ones, which were 181μ, 153μ, and 158μ, respectively. The juxtaglomeruli were larger than the cortical ones

in the pig, horse, dog, and cat; whereas in the ox the reverse was true. In the sheep and goat no appreciable difference was noticed between the size of the juxtamedullary glomeruli and those of the cortical ones.

The juxtaglomerular apparatus in all animals contained some spindle-shaped smooth muscle cells of the media of the afferent arteriole along with the usual myoepitheloid cells. In the goat and dog, the juxtaglomerular cells were more numerous than in the pig.

As compared with the pig (45μ), the diameter of the proximal convoluted tubule was greater in the horse (56μ), ox (50μ), and goat (48μ); equal in the sheep (45μ); and smaller in the dog (39μ) and cat (41μ).

The brush border was found to form a cluster from each individual cell in the proximal tubule of the pig kidney, whereas in other animals they were uniformly arranged along the luminal border of the cells. The basal striations were more distinct in the dog. Fat globules were observed in the proximal tubule of the cat and dog.

The maculae densae in all animals were single-layered except in the horse, in which they were found to be stratified.

The papillary duct was lined by both simple and transitional epithelium in all animals except the dog, in which the papillary duct

was lined by simple columnar epithelium only. Openings of the papillary duct on the papilla were observed in all animals studied.

The interstitial spaces of the kidney contained reticular fibers, a few collagenous fibers, fibroblasts, histiocytes, and mast cells in all animals except in the dog and cat, where mast cells were absent.

The intertubular cell groups or Becher's cells were present in the interstitial spaces in the cortical region, especially in the close neighborhood of Bowman's capsule, the cortical arteries, and arterioles in all animals except the cat, in which they were absent. These cell groups were more numerous in the ox and horse than in the pig, and less numerous in the sheep, goat, and dog. The cell groups near the arteries were larger than those located elsewhere. The cells were mostly polygonal with faintly eosinophilic cytoplasm and darkly stained nuclei. The cells were larger and more eosinophilic in the ox than those of the pig.

The cell unit of Goormaghtigh was found to be situated in the triangular space between the afferent and efferent arterioles, and the macula densa in all animals without any species variation.

The following findings are thought to be reported for the first time, or are contrary to the work of recent investigators:

1. Smooth muscle cells in the capsule of the horse, goat, pig, and dog.

2. Intertubular or Becher's cells in the horse, ox, sheep, goat, pig, and dog, but absent in the cat.

3. A stratified macula densa in the horse.

4. Mast cells in the interstitial spaces of the kidney of all species except the dog and cat.

5. Larger cortical than juxtamedullary renal corpuscles in the ox, sheep, and goat.

6. Larger cortical than juxtamedullary glomeruli in the ox, and equal or slightly larger ones in the sheep and goat.

7. Brush borders in clusters at the apices of the cells of the proximal tubule in the pig.

8. Transitional epithelium extending varying distances into the papillary ducts of all animals except the dog.

9. Papillary duct openings on the papilla of all animals investigated.

10. The cell unit of Goormaghtigh in all the species in this investigation.

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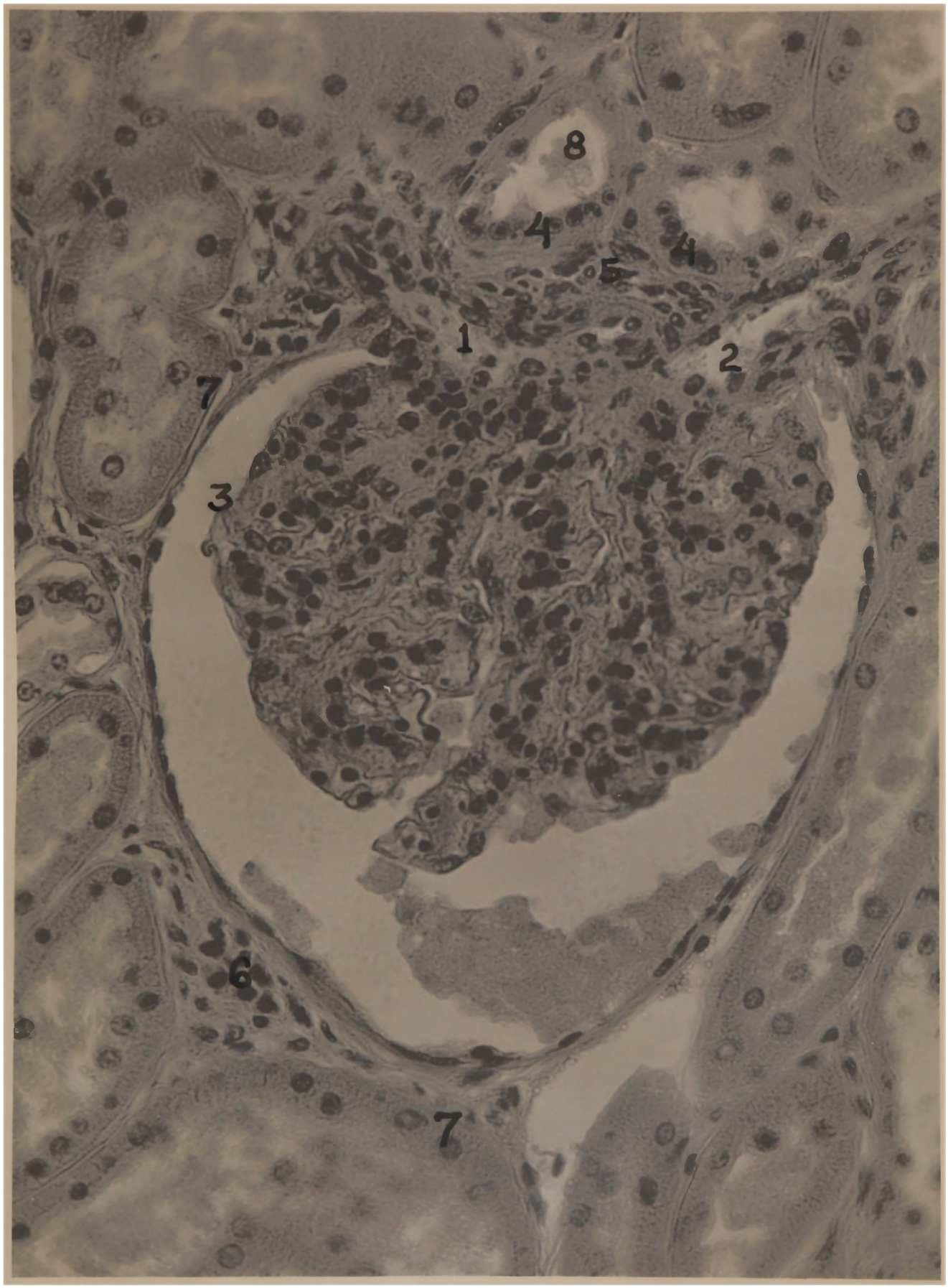
Photomicrograph of afferent (1) and efferent arterioles (2), renal corpuscle (3), unusual double maculae densae (4), cell unit of Goormaghtigh (5), Becher's cells (6), proximal tubule with basal striations (7), and the distal tubule (8). H. and E. 420x. Six-year-old cow.



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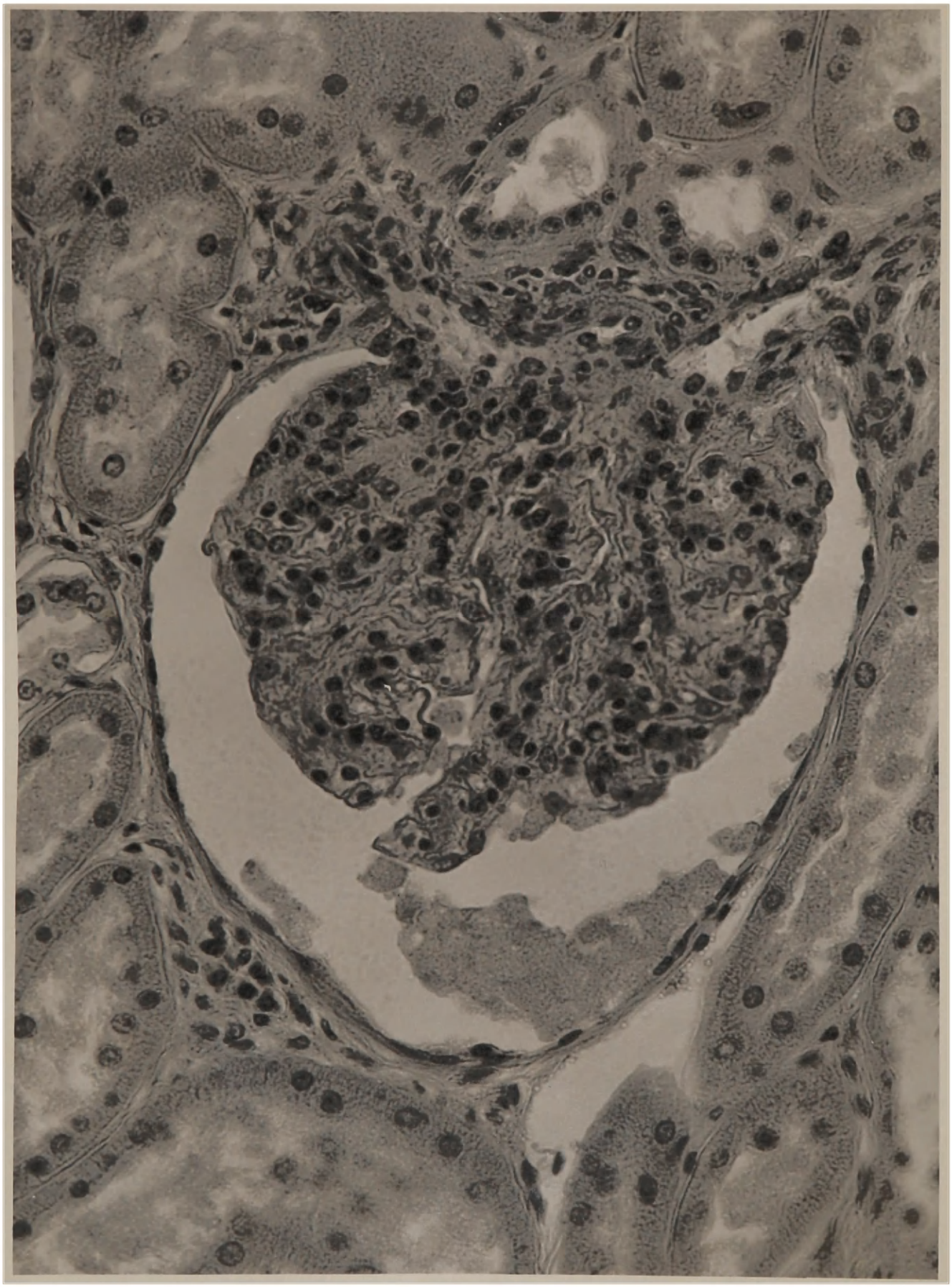

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Dedicated to my Professor

Dr. M. L. Calhoun, D.V.M., M.S., Ph.D., Professor and Head, Department of Anatomy, College of Veterinary Medicine, Michigan State University, whose devotion to research, scientific achievements, and rich human understanding have been a never-ending source of inspiration.

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VITA

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INTRODUCTION

This investigation deals with a comparative study of the microscopic structures of the kidney of the horse, ox, sheep, goat, pig, dog, and cat. The pig has been chosen as a type because of the morphological similarity of its kidney to that of the human species. A detailed description of the microscopic structures of the kidney of the pig has been given, and a comparison has been made with the structures of the kidney of the rest of the animals mentioned above.

The microscopic structure of the kidney is of immense physiological and pathological value. There are many good textbooks of histology in the English language that deal with the normal structure of the human kidney. But there is none which describes the normal structure of the kidney of the domestic animals, except an English translation of Trautmann and Fiebigers' German textbook, "Fundamentals of the Histology of Domestic Animals." Although this book was translated, revised, and published in 1952, there is no mention of some of the very important structures of the kidney such as juxtaglomerular apparatus, macula densa, and intertubular cells. In certain places a description of the structures of the kidney has been made without mentioning the species, which creates confusion.

Tereg (1911) contributed a valuable chapter on the kidney of domestic animals in Ellenberger's textbook, "Handbuch der Vergleichende mikroskopischen Anatomie der Haustiere." But this was written long ago and many new structures have been discovered since then by various investigations on the kidney of man and laboratory animals.

Kunkel (1930) and Rytand (1938) made comparative studies of the number and size of the glomeruli of the kidneys of various domestic animals. These were valuable contributions, but the studies remained confined to a very limited field.

Langham and Hallman (1939), and Langham et al. (1942) made extensive studies of the microscopic structure of the bovine kidney, but they also left some of the important structures (juxtaglomerular apparatus, macula densa, and intertubular cells) of the kidney untouched.

Bloom (1954) gave a description of the normal structures of the kidney of the dog and cat in his book, "Pathology of the Dog and Cat." This description is based upon the work of various investigators, and certainly is of great value so far as the microscopic structures of the kidneys of the dog and cat are concerned.

Nowhere in the literature has there been found a more or less complete description of an up-to-date study of the comparative

histological structures of the kidney of the horse, ox, sheep, goat, pig, dog, and cat. This investigation was undertaken to contribute something towards this aspect of the science.

All microscopic studies were made under an ordinary light microscope, and hence the description of ultramicroscopic structures of the kidney of the domestic animals cannot be expected from this work. Electron microscopic study is necessary to reveal such structures, and the author hopes that some investigators will undertake that work in the near future. Further work also remains to be done on the reversal of the Golgi element in the macula densa, the granules of the juxtaglomerular cells, the nerve endings, and the lymph vessels. In spite of these omissions the author hopes that this paper will serve as a reference to biologists, physiologists, pathologists, histologists, and students of anatomy.

HISTORICAL BACKGROUND

The study of the mammalian kidney goes as far back as the fourth century B.C., when Aristotle (384-322 B.C.), a Greek philosopher, scientist, and founder of comparative anatomy, gave an illustrated description of the mammalian uro-genital system in his "Historia animalium." Aristotle called the kidney "the nephros" and the pelvis of the kidney "the cavity of the nephros." The ureter was called the "duct from nephros to cystis."

Aretaeus (early second century A.D.) gave a description of the kidneys which has led many anatomists to suspect that Aretaeus was aware of the existence of the papillary ducts (ducts of Bellini). Aretaeus considered the kidneys to be true glands, and compared them with the testes, probably because of the superficial similarity in shape. Aretaeus stated "their cavities are small and like sieves, for the percolation of the urine; and these have attached to each of the nervous canals, like reeds, which are inserted into the shoulders of the bladder on each side; and the passage of urine from each side of the kidneys to the bladder is equal."

Leonardo da Vinci (1452-1519), one of the greatest biological investigators of all time and an artist anatomist, made a valuable sketch of the outline of the urino-genital system.

Berenger (1470-1530) was very much interested in the vascular bed of the organs, and it was this interest that led him to an investigation of the form and function of the kidney. In his "Commentaria cum amplissimis additionibus super anatomiam Mundini" Berenger mentioned that he injected the renal blood vessels.

Vesalius (1543) gave an illustrated description of the male and female urino-genital system in his monograph "On the fabric of the human body." Vesalius' treatment of the kidney is inadequate. There is a crude discussion of the kidney in which the pelvis is described and represented as divided in two by a sievelike structure.

Eustachius (1520-1574) attacked Vesalius for having represented the kidney of the dog instead of that of the human. Eustachius described for the first time the cortical substance of the kidneys. He used magnifying lenses and injected vessels to aid his study.

Ruini (1599) gave an excellent description of the kidney in his monograph on the anatomy of the horse (Anatomia del Cavallo).

Ruysch (1638-1731), one of the most capable anatomists of the period, became famous for his injection technique and studies

of the renal glomerulus. The renal glomerulus was named "Glomerulus Ruyschiana" after him.

Bellini (1662) discovered the straight collecting tubules and the papillary ducts of the kidney, and hence the papillary ducts are also known as the ducts of Bellini. Malpighi (1659) went beyond this by demonstrating that the kidney was composed of those pyramidal masses of Bellini's tubules. These pyramids of the kidney are hence called pyramids of Malpighi. In addition, Malpighi observed the convoluted tubules, and, with the aid of injected specimens, noted that they commenced as inflated swellings or capsules containing a cluster of small blood vessels which in turn hang on the little arteries like "apples on a tree." These structures are now commonly referred to as Malpighian corpuscles. Malpighi was one of the founders of microscopic anatomy.

Ferrein (1693-1769) described the small groups of straight tubules radiating from the boundary zone of the renal pyramids into the cortex as the medullary rays. These medullary rays were once called Ferrein's pyramids. Ferrein also described the convoluted uriniferous tubules of the kidney.

Bertini (1772-1845) demonstrated for the first time the renal columns which are inward extensions of the cortical structure of

the kidney, between the renal pyramids. Hence these renal columns are also known as columns of Bertin.

Henle (1841) gave a detailed description of the loops of the uriniferous tubules of the kidney in his "Allgemeine Anatomie." These are called the loops of Henle.

Heidenhain (1834-1897) is remembered for his method of staining the cells of the kidney by injecting indigo-carmine into the blood.

Working with little more than a microscope and a dissecting needle, William Bowman (1842) first drew a picture of the single nephron that is remarkable close to present-day ideas of the renal functional unit.

The above description of the historical events is based on the work of Singer (1925), Castiglioni (1947), and Mettler (1947).

REVIEW OF LITERATURE

Gross Anatomy

Chauveau (1873) described the kidney of the ox as multipyramidal with well-defined external lobation having fifteen to twenty lobes in each kidney. Langham and Hallman (1939) found sixteen to thirty-two lobes in each kidney of the ox.

Chauveau (1873), Bremer (1944), Patten (1953), and Arey (1954) referred to the structure of the mammalian kidneys during intrauterine life. These authors described the presence of multilobar kidneys in the mammalian fetus with distinct superficial lobation.

Dixon (1931) described superficial lobation in the kidney of a young child, and sometimes, though much less distinctly, in the adult. Straus (1934) found the kidney of man to be multipyramidal and that of apes unipyramidal.

Grahame (1944a) and Smith (1951) described the kidney of the elephant as multipyramidal with distinct external lobation.

Elias (1944) and Sisson and Grossman (1953) described distinct pyramids in the kidney of the pig, although the external surface was quite smooth as in the case of unipyramidal kidneys.

Elias (1944) described the kidney of the horse, sheep, and goat as a unilobar organ similar to that of rodents. In the German shepherd dog, Elias stated that the pyramids of the kidney resembled those of the pig. In a great Dane dog, the pyramids were closely united; in the cat a simple, unilobar kidney with a simple pyramid was present.

Sisson and Grossman (1953) stated that the longitudinal section of the kidney of the horse presented a nonpapillated appearance. The inner central part of the medulla was formed by a concave ridge which was projected into the pelvis of the kidney. This projection was called a renal crest. The renal crest presented a number of small openings constituting the area cribrosa. In the ox these authors described distinct pyramids with their papillae projecting into the calyces minores. The renal columns were also very distinct. In the sheep, the renal crest was formed by the fusion of twelve to sixteen pyramids. Sisson and Grossman also described distinct papillae in the kidney of the pig. In frontal sections of the dog kidney, curved ridges proceeded dorsally and ventrally from the renal crest. Sections above or below the renal crest cut those ridges in such a manner as to give the appearance of conical papillae, producing a false impression.

Microscopic Anatomy

The Capsule

Chauveau (1873) described the enveloping tunic of the kidney of the horse as a fibrous membrane intimately united to the parenchyma of the kidney into which it sent many prolongations.

Tereg (1911) described the capsule of the mammalian kidney as composed of two easily separable layers. The inner layer was devoid of blood vessels. The outer layer contained blood and lymph vessels, and nerves. Tereg (1911) and Trautmann and Fiebiger (1952) described the presence of smooth muscle fibers in the deeper portions of the capsule of the kidney of the ox and sheep.

Möllendorff (1930), Maximow and Bloom (1952), and Smith and Copenhaver (1953) described the capsule of the human kidney as being composed of collagenous fibers and a few elastic fibers. Greep (1954) described the presence of a few smooth muscle cells in the capsule of the human kidney in addition to the usual collagenous and elastic fibers.

The Uriniferous Tubules

Greep (1954) described a uriniferous tubule as being composed of two segments, a secretory portion, the nephron, having the function

of elaboration of urine, and a collecting portion, the collecting tubule, to convey urine into the pelvis of the kidney. A uriniferous tubule in the human kidney was described as being 50 to 60 millimeters long, the secretory portion being 30 to 40 millimeters in length.

The nephron

Huber (1932) teased out individual nephrons from adult rabbit kidneys that had been subjected to acid maceration. Huber called the nephron the renal tubule which was considered to be made up of the renal corpuscle, the proximal convoluted portion with the medullary loop, the distal convoluted portion, and the junctional tubule.

The renal corpuscle. The renal corpuscles of the mammalian kidney were found to be spherical with a diameter varying between 100μ and 200μ (Huber, 1932, 1935). Langham and Hallman (1939) observed the diameter of the renal corpuscle of an adult bovine kidney to be 216μ in a fixed and stained preparation. They noted that the size of the renal corpuscle increased with the advancement of age, reaching a maximum in a fully grown individual. Smith and Copenhaver (1953) and Greep (1954) described the diameter of the renal corpuscle of the human kidney as being close to 200μ.

The glomerulus of the mammalian kidney was studied from time to time by various investigators. The results of their investigations showing the number, shape, size, and volume of the glomeruli are given in Table I.

Shonyo and Mann (1944) noted that the glomeruli in the cortico-medullary zone were usually larger than those located more peripherally.

The afferent arteriole of the guinea pig kidney was found by Bensley (1929) to be expanded into a sort of reservoir after entering the glomerulus. Primary branches were seen to arise from this expanded sinus. Schloss (1946) observed a similar dilatation in the afferent arteriole of the human kidney and called it "Becher's glomerular sinus."

Dorello (1948) noted that the afferent arteriole in the kidney of the pig was expanded and gave rise to three primary branches, each of which gave origin to three more branches.

Codden (1949) did not find any dilatation in the afferent arteriole of the human kidney after it entered the renal corpuscle. He found a ramification of the afferent arteriole soon after it entered the renal corpuscle.

The glomerular capillary tuft was studied by Wilmer (1941) with the help of celloidin corrosion injection technique. It was

TABLE I

LITERATURE REVIEW ON NUMBER, SIZE, AND VOLUME OF THE GLOMERULUS

Author	Animal	Number of Glomeruli in One Kidney	Diameter of the Glomerulus (μ)	Total Glomerular Volume in One Kidney (cu. mm.)
Vimtrup (1928) . . .	cat	202,813		
	dog	407,155		
	albino rat	33,826		
	man	1,233,360		4-2 c.c.
McGregor (1929) . .	man		200-237	
Kunkel (1930) . .	dog		163	
	pig		166	
	ox		259	
Moore (1931) .	man	800,000 to 1,000,000		
Rytand (1938) . .	cat	214,500	150	227
	dog	408,100	180	1,247
	pig	1,193,000	166	2,859
	ox	3,992,000	244	29,860
	monkey	186,600	166	447
	elephant	7,510,000	338	151,900
Langham et al. . . (1942)	ox	800,000 to 1,700,000		
Greep (1954)	man	1,000,000		

demonstrated that the afferent arteriole of the human kidney gave primary and corresponding secondary branches. It was noted that detailed observations could not be made on approximately the first two-thirds of the afferent arteriolar system. Wilmer did not observe any anastomosis between the capillaries.

Smith (1951) found that the afferent arteriole of the human kidney gave off two to four or more, rarely up to ten, primary branches, which in turn subdivided again, at times into as many as fifty capillary loops. The primary branching gave the tuft a lobulated structure.

Trabucco and Marquez (1952) did not find any evidence that the glomerular tuft had any looping formations between the afferent and efferent arterioles. They noted that the glomerulus was formed from one side of a single vessel bent on itself.

Boyer (1955) demonstrated that the human glomerulus was neither a simple series of loops nor a skein of blind fingerlike sacculations. According to Boyer the glomerular tuft was found to be essentially a dense capillary bed with an afferent and efferent channel. No simple loops were seen. Multiple anastomoses between looping channels were seen to create a complex network which might show short blind sacculations. Hall (1955) observed direct channels in the glomerulus of the rat, cat, dog, rabbit, and man from the

afferent to the efferent end of the lobule. These were thought to function as by-passes for erythrocytes. The large capillaries were seen to give rise medially to numerous small, short branches which joined and divided freely to form a true capillary network; a complex but unified system of communicating, anastomosing capillaries within the lobule.

The efferent arteriole of the guinea pig was found by Bensley (1929) to proceed in a sinuous course toward the renal capsule at first without giving off capillaries. It was found to terminate in a plexus of capillaries around the convoluted tubules of the cortex. The efferent vessels of the middle zone of the cortex, which were usually supposed to be resolved immediately on emergence from the glomeruli into the capillary vessels, were found to continue for some distance as a discrete vessel. The efferent vessels of the juxtamedullary region were much longer and formed the arteriole rectae of the medulla.

Schloss (1946) observed in the human kidney a dilatation in the efferent arteriole where it left the glomerulus. Edwards (1953) demonstrated that in the human kidney 20 to 25 per cent of the efferent arterioles of the glomeruli situated in the cortico-medullary zone were short, thin-walled, and gave rise to a network of capillaries. Such capillaries were found to supply blood to the parts of

all nephrons located in the cortico-medullary zone, whereas the long efferent arterioles which were found to descend into the medulla vascularized only the medullary parenchyma. The long efferent arterioles were found to comprise only 75 to 80 per cent of those arising from the glomeruli in the cortico-medullary zone.

The intercapillary or axial space of the normal glomerulus of man and mammals was found by Bensley and Bensley (1930) to contain a small amount of connective tissue. They observed a layer of reticular fibers surrounding the vessels at their entrance, with sparse and delicate reticular fibers extending into the lobes of the glomerulus.

McManus et al. (1951) made a histochemical study of the human glomerulus and observed the presence of carbohydrate material in the intercapillary space of the normal human glomerulus.

Jones (1953) observed that the normal human glomerulus had an interstitial connective tissue space, which contained connective tissue cells. In childhood these cells were found to be less numerous than either the visceral epithelial layer of Bowman's capsule or the endothelial cells, but by thirty years of age their number was found to increase approximately to that of the endothelial and epithelial cells.

Hall et al. (1953a) found the rat glomerulus to have either exceedingly few interstitial cells and collagenous fibers or none at all. Benedetti and Scapellato (1954) observed argyrophilic fibrils and connective tissue cells in the stroma of the normal renal glomerulus.

The juxtaglomerular apparatus was described by Goormaghtigh (1939) as being composed mainly of smooth muscle cells, devoid of myofibrils, called "afibrillar cells." In the superficial cortical zone of the normal kidney of the rabbit, these cells were found to show a glandular cycle culminating in the formation of acidophil or basophil secretion granules intermingled with minute vacuoles. These afibrillar cells were observed to be in close contact with the lumen of the afferent arteriole or with the glomerular capillaries. In the case of the dog, secretion granules were not found.

Edwards (1940) found in the mammalian kidney a periartiolar pad incompletely surrounding the afferent arteriole and occupying a region between the macula densa and the afferent and efferent arterioles at their junction with the glomerulus. This periarteriolar pad was found to consist of a nestlike group of cells embedded in a delicate, fibrillar network.

McManus (1942) defined the juxtaglomerular apparatus as a group of apparently specialized structures in relation to and including

the afferent and efferent arterioles of the glomerulus. He preferred to use the term "juxtaglomerular complex" instead of Goormaghtigh's "juxtaglomerular apparatus." His "complex" consisted of the juxtaglomerular apparatus and macula densa.

Graef (1943) reported medial hypertrophy and hyperplasia of the arterioles in the case of a pregnant woman, possibly due to a hormonal effect.

Schloss (1946) reported the existence of smooth muscle cells in the area of the "Polkissen" (juxtaglomerular apparatus of Goormaghtigh) in addition to the usual epithelioid cells. These muscle cells contained myofibrils.

McManus (1947b) demonstrated the presence of granules in the juxtaglomerular cells with the help of periodic acid Schiff reagent. Des Prez (1948) used Masson's trichrome stain to demonstrate these granules. These cells appeared large, pale-staining, with large, prominent ovoid nuclei whose chromatin network was arranged in a somewhat radial pattern. They were all afibrillar.

With the help of electron microscopy, Dalton (1951) demonstrated large cytoplasmic granules in the myoepithelial cells of the juxtaglomerular apparatus in the kidney of the rat.

Gomori and Oltvanyi (1951) observed a nerve plexus among the juxtaglomerular cells. Wilson (1952) developed a special staining

technique for demonstrating the granules of the juxtaglomerular cells. The granules were stained deep purple, and nuclei light purple.

Maximow and Bloom (1952) noted the absence of juxtaglomerular cells in lower vertebrates and in children below the age of two years.

The function of the juxtaglomerular apparatus is very controversial. Goormaghtigh (1939, 1940, 1945a, 1945b, 1947, 1949, 1951) believed that the afibrillar cells of the juxtaglomerular apparatus had endocrine function. The endocrine activity of the afibrillar cells was related to the production of the hypertensive substance present in the ischemic kidney. It was suggested that in the normal condition, the afibrillar cells regulated the tonus of the renal arterioles. Kaufmann (1942), Dunihue (1947, 1949), and Hartroft and Hartroft (1952) supported the view of Goormaghtigh that the juxtaglomerular apparatus possessed an endocrine function.

Oberling (1944) did not find any elevation of blood pressure in children and adults whose kidneys possessed abundant granular cells in the juxtaglomerular apparatus. Edwards (1945), Fox and Jones (1945), and Schloss (1948) were unable to find any evidence in support of Goormaghtigh's hypothesis of endocrine function of the juxtaglomerular apparatus.

Graef and Proskauer (1945) and Becher (1949, 1950) thought that the function of the juxtaglomerular apparatus might be to control renal blood flow. Hartroft and Hartroft (1953) suggested that the juxtaglomerular cells were involved in the hormonal regulation of sodium metabolism and blood pressure.

The three primary membranes of the glomerulus were studied by McGregor (1929). McGregor observed the presence of three membranes, epithelial, endothelial, and basement membrane, in the human kidney. Bensley and Bensley (1930) found the glomerular epithelium in human and small mammals to be a continuous layer over the whole extent of the surface of the glomerulus and its lobes. It was composed of separate cells and did not constitute a syncytium. The basement membrane was found to be structureless, supporting the wall of the glomerular capillaries. The endothelium was also found to be continuous.

Bremer (1938) demonstrated a protoplasmic film over the glomerulus which had the property of storing dye granules after vital staining. It did not form a continuous sheet. Only occasional glomerular cells were found to store the vital dyes.

De Renyi (1941), using microdissection techniques, found the epithelial lining noncontinuous. The cells resembled the pericytes of other capillaries. The structure of the endothelium of the

capillary loops was different from the lining of the capillaries of other organs.

McManus (1948a) observed that the basement membrane was derived from Bowman's capsule and was attached to the arterioles at the glomerular root. The capillary loops were also enclosed by the basement membrane. Electron microscopy of the kidney revealed a crenated appearance of the basement membrane which was studded with minute projections (Gautier et al., 1950).

Pease and Baker (1950) found a continuous epithelial layer, a noncontinuous endothelial layer, and a basement membrane whose external surface was covered by a system of interdigitating ridges.

Oberling et al. (1951) and Dalton (1951) found the epithelial layer carrying a system of many-branched villilike processes.

Hall et al. (1953a) observed a continuous and highly porous endothelial layer, a finely porous basement membrane, and an epithelial layer whose cells possessed interdigitating processes.

With the help of histochemical techniques and electron micrographs, Rinehart et al. (1953) found the surface epithelial cells elaborating a cytoplasmic secretion which was in contact with the basement membrane at many points. The basement membrane was considered as being primarily a differentiated cytoplasmic product of the endothelial cells.

Simer et al. (1953) did not find complete visceral epithelial and endothelial layers although every capillary was provided with a fibrillar basement membrane.

Hall (1954) gave the ratio of endothelial to epithelial nuclear count as 3:1. The basement membrane was found to be a complex of three intimately related specialized structures under the electron microscope (rat).

Pease (1955a) made an electron microscopic study of the kidney of the rat and found that the epithelial cells of the glomerular capillaries had long primary and secondary branches that extended over and between the capillary loops and were applied directly to the basement membrane. The basement membrane was found to be continuous and divisible in three layers, the middle layer being of high electron density. The endothelial cytoplasm was extremely attenuated in most parts of the glomerular capillaries.

The secreting area of the glomerulus was found by Book (1936) in a single typical human glomerulus to be 0.3813 square millimeter, while Kirkman and Stowell (1942) found the area of a single albino rat glomerulus to be 0.19 square millimeter.

Bowman's capsule was studied by Oleynik (1952). Oleynik proposed to call Bowman's capsule "Shymlansky's capsule" as he believed that Shymlansky published his results sixty years before Bowman.

Crabtree (1941) found in mice that the parietal layer of Bowman's capsule was partly or completely composed of cuboidal cells. These cuboidal cells were found to be identical with those of the proximal convoluted tubule with respect to the ability to store granules of trypan blue, a vital stain. Indirect evidence indicated that single capsules could be changed from a squamous cell type to a columnar cell type. After puberty the percentage of cuboidal cell capsules began to increase. This occurred earlier in males than in females, suggesting a response to an endocrine factor or factors.

Pease (1955b) made an electron microscopic study of the rat kidney and found that the parietal cells of Bowman's capsule sometimes had cytoplasmic processes suggestive of a rudimentary brush border.

The proximal convoluted tubule. Huber (1932, 1935) found the length of the proximal convoluted tubule in the rabbit to be 9.4 millimeters and the diameter 50μ to 60μ. Grafflin (1939) noticed the average number of turns in the proximal tubules in human kidney to be forty. Huber observed in the rabbit's proximal convoluted tubule a relatively low epithelium with a wide lumen, or a high epithelium with a relatively narrow lumen. He observed that the cells possessed a spherical nucleus, brush border, and mitochondrial granules distributed in a manner to give distinct basal striations.

Grafflin (1942) noted a deposition of yellow to golden-brown iron-containing pigment in the epithelium of the proximal tubule of the rat.

Mayer and Ottolenghi (1947) demonstrated a protrusion of tubular epithelium into the space of Bowman's capsule in the kidneys of dogs and cats. Protruded tubular epithelium was continuous with the proximal tubule and was distinct from the capsular epithelium, being cuboidal in shape.

Harman and Hogan (1949) found multinucleated giant epithelial cells in the proximal convoluted tubules of human kidneys in 15.2 per cent of routine autopsies. Sulkin (1949) observed binucleated cells in the various tubules of the normal kidney of the rat. Unilateral nephrectomy showed a significant increase in the number of binucleated cells.

Lowell et al. (1953) found each nucleus of the cells of the proximal convoluted tubule surrounded by a considerable body of cytoplasm charged with well-preserved rodlets and granules of mitochondrial character. The nuclei were unevenly spaced and occasionally aggregated like the macula densa.

The ultra structure of the proximal convoluted tubules of the mouse kidney as revealed by high resolution electron microscopy was demonstrated by Sjostrand and Rhodin (1953). It was found that

the cell membrane appeared as a thin zone of condensed cytoplasm toward the basement membrane. The mitochondria were found to be rod-shaped. In the intermediate cell zone there were granules and vacuoles.

The brush border was observed by Gautier and Bernhard (1950) as being composed of round or polygonal tubules which originated from the cytoplasm of the proximal tubule and ended in the lumen as pores.

Sjostrand and Rhodin (1953) found the brush border consisted of densely arranged cylindrical ducts closed toward the tubular lumen.

Hall et al. (1953b) noted that the brush border was composed of individual tubular fibers having separate origins from the cell surface.

Pease (1955b) found that the brush border of the proximal tubule was comprised of extensions of the apical cytoplasm. The cytoplasm of the brush border had the same density as that of the remainder of the cell, and similar granules might even be seen within it.

Fat content of the proximal convoluted tubule was studied by several investigators. Modell (1933) and Foote (1936) observed fat in the proximal tubule of the cat. Foote and Grafflin (1938, 1942)

found fat in the proximal tubule of both cat and dog. Dallemagne et al. (1950), Silver (1951), and Platt (1951) demonstrated fat in the proximal tubule of the dog. Foote and Grafflin observed that in the cat the entire pars convoluta and the upper portion of the pars recta of the proximal tubule were normally fat-laden, while the terminal portion of the pars recta was fat-free. In the dog, on the other hand, the reverse was true. The fat was confined solely to the terminal portion of the pars recta.

Segmental differentiation in the proximal convoluted tubule was made by several authors on the basis of the histology and physiology. Foote (1936) and Foote and Grafflin (1938) determined the relative lengths of the two segments (convoluted portion and straight portion) of the proximal tubule in the cat and dog on the basis of fat content. They described them as fat-laden and fat-free segments of the proximal tubule.

Foote and Grafflin (1942) described the cells of the first segment of the proximal tubule of the cat and dog as being highly irregular with a marked degree of interdigitation. The cell contours were more complicated at the lumen. The cell shapes were more irregular in the dog than in the cat. The cell contours of the second segment were essentially rectilinear in both species.

Longley and Fisher (1954) differentiated the two segments of the proximal tubule with the help of staining techniques. Periodic acid Schiff staining differentiated the two segments in the mouse, rat, and cat, and the alkaline phosphatase technique differentiated those segments in mouse, squirrel, cat, dog, and chicken.

The loop of Henle. Huber (1932, 1935) found the diameter of the thin limb of Henle's loop in the rabbit varying from 20μ to 25μ. The thin segment was lined by squamous epithelium. The cells had polygonal forms and relatively large nuclei. The length of the thin segment varied from 1 to 15 millimeters.

Smith (1951) observed that in the human kidney short loops of Henle were about seven times as numerous as long ones, and, in some instances, where the glomeruli were located in the outer cortex, the thin segment might be absent entirely. Where present, the thin segment might occupy only the descending limb of Henle's loop, or it might extend around the loop and for some distance up the ascending limb. Smith noted the presence of the thin segment only in mammals and in a small percentage of the nephron of birds.

The distal convoluted tubule. Huber (1932, 1935) found the length of the distal convoluted tubule in rabbit kidneys varying from 3.6 to 7.8 millimeters. The diameter was found to be between 30μ

and 40μ. The distal tubule was lined by a low columnar or cuboidal epithelium presenting a clear supranuclear zone of cytoplasm. The cells were devoid of a brush border but the basal striations were present, though not quite so distinct as in the case of the proximal tubule.

Grafflin (1939) observed that the distal tubule of the human nephron took a more direct course and in every case passed the glomerulus near the afferent arteriole. The distal tubule was found to make few turns until it arched to join the collecting tubule.

Trautmann and Fiebiger (1952) described the nuclei of the distal tubule in the horse as being especially large.

Pease (1955b) made an extensive study of the tubular cells of the rat kidney with the help of the electron microscope. It was found that the apical ends of the cells of the distal tubule usually had scattered short cytoplasmic processes suggestive of a rudimentary brush border.

The macula densa was demonstrated for the first time by Zimmermann (1933) in the mammalian kidney. Zimmermann gave the name of macula densa because of crowding of the nuclei in the distal convoluted tubule at the area of contact between the distal tubule and the afferent arteriole of the glomerulus.

Edwards (1940) preferred to use the name "epithelial plaque" for macula densa. After an extensive study of the macula densa of the mammalian kidney, he found the epithelial plaque in mammals, birds, and frogs variably elliptical.

It constituted one-half to two-thirds of the wall of the nephron as seen in cross section in the kidney of man, rabbit, and rat, and commonly one-half of this wall in the kidney of the whale, guinea pig, cat, bird, and frog. He found the plaque was composed of staggered rows of columnar cells often markedly taller than those adjacent and so close together that their nuclei were usually in contact not only with others in the same row but also with those of the adjacent row. The cytoplasm of the cells was nongranular and neutrophilic or slightly basophilic and their nuclei were somewhat smaller, contained more chromatin and a more conspicuous nucleolus than those of the adjacent cells.

McManus (1943) and Okkels (1950) observed that the position of the Golgi elements was reversed in the macula densa. The Golgi element in the macula densa was situated towards the basal side of the nucleus, whereas in the rest of the distal tubule it was situated towards the luminal side of the nucleus.

McManus (1947a) reported the absence of a basement membrane in the macula densa. The cytoplasm of the cells of the macula

densa was separated from that of the juxtaglomerular apparatus only by the cell membrane. This absence of the basement membrane was thought to facilitate the exchange of materials between the cells of the macula densa and the juxtaglomerular apparatus. Dina and Martuzzi (1952) found the macular tubular cells to be stratified and the macula densa to be larger than the area of contact with the afferent arteriole.

The function of the macula densa is not yet clear. Schloss (1946) regarded the macula densa as a sensory area, probably a chemo-receptor, influencing the contraction of the vessels. Becher (1949, 1950) thought that the macula densa regulated the flow of blood through the Malpighian bodies of the kidney. Okkels (1950) suggested an angiotrophic role for the macula densa.

The collecting tubules

The collecting tubules are considered by all authors to be comprised of the arched or initial collecting tubule, the straight collecting tubules, and the papillary ducts or ducts of Bellini.

The arched collecting tubules. Huber (1932, 1935) found the primary collecting ducts of the cortex of the rabbit's kidney united in the periphery of the cortex to form collecting tubes which passed

through the cortex without receiving further branches. In the human kidney it was observed that a limited number of primary collecting tubules joined in the periphery of the cortex, and the collecting ducts thus formed received further branches while passing through the cortex. The collecting tubules were found, in general, lined by very regular columnar cells, with clear protoplasm, devoid of specific granules or striations and with relatively large nuclei of spherical or ovoid forms. Trautmann and Fiebiger (1952) described the lining epithelium of the connecting tubule in the domestic animals as composed of polygonal, light-colored cells, distinguishable only by their lesser height from the cells of the collecting tubules.

Greep (1954) stated that the epithelial cells lining the arched tubules of the human kidney were strictly cuboidal.

The straight collecting tubules. Greep (1954) stated that the straight collecting tubules in the human kidney were located in the medullary rays. These tubules were described as making up most of the substance of the pyramids. The straight collecting tubules were stated to fuse with one another in successive fashion in the pyramids to form finally sixteen to twenty large papillary ducts. The diameter of the tubule was 40μ in the medullary ray. The diameter increased as the tubules fused. The epithelium was cuboidal

in the proximal portion, but the cells increased in height as the diameter increased. Trautmann and Fiebiger (1952) described the presence of numerous fat droplets, especially in older domestic animals.

The papillary ducts. Langham et al. (1942) found that while the epithelium of the papillary duct of the bovine kidney acquired a tall columnar form the cells retained the other characteristics of those of the smaller collecting tubules.

Trautmann and Fiebiger (1952) described the epithelium in the papillary ducts as two-layered, changing to transitional near the opening into the pelvis.

Duran-Jorda (1953) doubted the existence of openings of the ducts of Bellini. After examining a few hundred routine sections of the human kidney of all ages, and some serial sections of this organ from different animals, especially the cat, which had only one pyramid, the investigator was skeptical about accepting the existence of openings of the ducts. He was of the opinion that in the normal kidney the urine was dialysed through a papillary epithelium and not excreted directly into the renal pelvis by the ducts of Bellini.

The basement membrane of the uriniferous tubules

Bensley and Bensley (1930) noted the presence of a thin structureless basement membrane interposed between the epithelium of the tubules and the reticular framework. This basement membrane was similar to but thinner than Bowman's capsule.

McManus (1948b) studied the histochemical features of the renal basement membrane, and suggested a passive role for it, closely related to the activity of the tubular epithelium. McManus thought that it was chitinous in nature.

Pease and Baker (1950) and Pease (1955b) found the structure of the basement membrane the same all along the uriniferous tubules. They observed the connective tissue cells so few and far between that they thought the basement membrane must be maintained by the overlying epithelia rather than by fibroblasts. The basement membrane appeared entirely homogeneous even under high resolution.

The Papilla

Langham et al. (1942) observed transitional epithelium covering the surface of the papilla in the bovine kidney. Maximow and Bloom (1952) stated that in the human kidney the simple columnar epithelium of the ducts of Bellini continued on to the surface of the

papilla in the area cribrosa. Trautmann and Fiebiger (1952) stated that, with the exception of the pig and the goat, the transitional epithelium was replaced on the renal papilla by two-layered cuboidal to columnar epithelium.

Vimtrup and Schmidt-Nielsen (1952) observed that the papilla of the kangaroo rat was relatively long and extended into the ureter.

The Interstitial Space

Kirkman (1943) found the presence of fibroblasts and macrophages in the interstitial space of the kidney of the albino rat. The greatest concentration of macrophages and fibroblasts was found at the level of that portion of the thick ascending limb of Henle's loop which was lying in the intermediate zone of the medulla.

Intertubular cell groups or Becher's cells

Schloss (1946) found the intertubular groups of cells in the human kidney at the points where the connective tissue was abundant.

Neumann (1949) reported the lack of intertubular cell groups in the vicinity of the glomeruli of the human kidney.

Becher (1949, 1950) found these cell-islets situated in the human kidney in the immediate neighborhood of the afferent arterioles

and other cortical arterial vessels and called them "paraportal cell-islets."

Regarding the function of these intertubular cell-groups, Schloss (1946) suggested that those Becher cells which were completely isolated and surrounded by connective tissue had an endocrine function. Becher (1949, 1950) thought that those cell-groups might regulate blood flow through the Malpighian bodies of the kidney.

Cell unit of Goormaghtigh or socleplasmodium

Schloss (1946), Neumann (1949), and Becher (1949, 1950) found in the human kidney a cluster of small cells (cells of Goormaghtigh) in the angle between afferent and efferent arterioles of the glomerulus. Becher (1950) regarded this cluster of small cells as an area containing nerve receptors.

Ham (1953) described the presence of a curious little aggregation of small cells with pale nuclei between the macula densa and the glomerulus proper, in the concavity between the afferent and the efferent arterioles. Ham was of the opinion that there was no certainty about their nature, function, or nomenclature.

Blood Vessels

MacCallum (1926) found the arteriolae rectae arising in the dog and cat, exclusively from the vasa efferentia. No arteriolae rectae verae were found in those animals. MacCallum (1939) and Oliver (1939) found a few pathologically changed glomeruli in the normal mammalian kidneys, and the number of such glomeruli was found to increase with age and disease.

Fitzgerald (1940) demonstrated the presence of two main renal arteries supplying each kidney in 10 per cent of the horses and 5 per cent of the dogs examined.

Loomis and Jett-Jackson (1942) and Gouygou (1949) found Ludwig's branches (branches of interlobular arteries that terminate directly in the peritubular capillary plexus without the interposition of a glomerulus) in the human kidney to occur in old age and in conditions of disease.

Grahame (1944a, 1944b) found the arterial tree in the elephant and camel similar to the general plan of the arterial distribution in the kidneys of other mammals.

Cowdry (1950) observed that the individual interlobular arteries supplied definite parts of the kidney and did not anastomose with their neighbors.

These arteries were found to be typical "end-arteries"; when one was occluded the tissue depending on it suffered acutely. These arteries were found to be occasionally anastomosed with branches of the phrenic, adrenal, intercostal, or capsular arteries.

Picard et al. (1950) and Picard and Chambost (1952) observed in the dog and cat a circular thickening situated at the origin of the afferent arterioles of the juxtamedullary glomeruli. It appeared to be valvular in nature.

Ruotolo (1950) described the presence of blocking mechanisms of various types in the tunica intima and tunica media of the arteries of the human kidney.

Montaldo (1951) found a lozenge-shaped lumen of the monopodic branches of the arcuate and low interlobular arteries at their origin in the kidneys of man, dog, and rabbit.

Christensen (1952) described the presence of a few isolated arteriolae rectae verae and Ludwig's arterioles in the dog's kidney. Anastomosis of the afferent and efferent arterioles were also observed in a few instances.

Rotter (1952) considered the cushionlike thickenings of the intima of the arteries of the human kidney as normal. These were regarded as arteriosclerotic changes by many investigators. These thickenings were present in the form of a ring inside the branches

of the arteries and were found to occur even in young children, but increased in size and number with the age of the individual. They were supposed to regulate blood supply and blood pressure in the corresponding vascular territories and to promote an economic distribution of the blood.

Superficial veins of the mammalian kidneys were demonstrated by Kazzaz and Shanklin (1951) with the help of vinylacetate injection and corrosion technique. It was found that the dog's kidney had a system of stellate veins which on the lateral side of the kidney were drained into the interlobular veins and on the medial side directly into the renal vein. The cat was found to have radially arranged veins running along the surface of the kidney and emptying into the renal vein. Numerous tributaries joined each side of the veins and the deep veins connected them to the interlobulars. The human kidney had a system of stellate veins similar to the dog but not so well developed. The veins in the cow and sheep started as spurlike projections and joined the interlobular veins.

Koester et al. (1953) described the presence of cushions of connective tissue which contained many large veins of a sinusoidal nature, protruding into the vein lumina at the arcuate-interlobular junction in the kidney of man and dog.

Circulation through the kidney

Bowman (1842) noted that all the blood of the renal artery (with the exception of a small quantity distributed to the capsule, surrounding fat, and the coats of the large vessels) entered the capillary tufts of the Malpighian bodies. From there, the blood was found to pass into the capillary plexus surrounding the uriniferous tubules, and finally left the organ through the branches of the renal vein.

Morison (1926) studied the renal circulation in man, cat, dog, rabbit, monkey, deer, sheep, and pig with special reference to its finer circulation. It was noted that the parenchyma of the cortex was supplied by the capillaries of the efferent glomerular vessels, and in addition occasional nutrient branches from the interlobular arteries. The interlobular artery might itself terminate by ramifying into a capillary plexus. The nonglomerular sources of nutrient supply were thought to be negligible.

The medulla of the kidney was observed to receive blood supply solely by arteriolae rectae spuriae. No evidence of the presence of the arteriolae rectae verae was found.

White (1939) made observations indicating the absence of intermittance in normal dogs and rabbits as all of the glomeruli

were found open all the time. It was suggested that intermittance might occur in extreme conditions such as severe hemorrhage or sudden increment of circulating epinephrin.

Fox and Jones (1946) and Maegraith and Havard (1946) observed that in the human kidney, during active diuresis, the cortical circulation was fully open, while in anuria the medullary circulation was in action, and the cortical circulation was by-passed.

Heggie (1946, 1947) stated that the redistribution of blood flow within the kidney of the rabbit could be maintained by a circulation via the juxtamedullary glomeruli only. The cortex could remain relatively avascular by vasoconstriction of the peripheral arterial vessels in response to afferent stimuli. Barclay et al. (1946, 1947) supported the view of Heggie that by-passing could be effected, at least in part, via the vasa recta.

Trueta et al. (1946, 1948) made an extensive investigation on circulation in the kidney of the rabbit and came to the conclusion that in the experimental animal a renal circulation could be continued through the medulla via the vasa recta while the cortex was functionally ischemic. Under such conditions the flow of urine in the ureter decreased or was entirely suppressed. Schlegel and Moses (1950) studied circulation in the rabbit's kidney, but were unable to confirm the results of Trueta et al. (1948) indicating a by-pass through the

juxtamedullary glomeruli. More and Duff (1951) confirmed the finding of Trueta et al. (1948) that the only vessels through which blood could circulate in sufficiently large amounts to by-pass the outer cortex were those of the juxtamedullary glomeruli, their efferent arterioles and the corresponding vasa recta of the medulla in sequence.

Moses and Schlegel (1952) found preservation of the juxtamedullary circulation following ligation of the renal artery in the rabbit. They observed that there was ischemia of the outer cortex and the juxtamedullary glomeruli and vasa recta of the medulla contained blood. They also observed direct vascular connections with vessels penetrating the capsule from the perirenal and perihilar tissues. Stripping of the capsule and periureteral tissues resulted in complete renal ischemia.

Arteriovenous anastomoses

Simkin et al. (1948) injected glass spheres 90μ to 440μ in diameter into the renal arteries of normal human kidneys post mortem, and the existence of arteriovenous anastomoses was indicated by recovery from the renal vein of spheres many times greater than the average diameter of a capillary. Similar experiments were made on living anesthetized rabbits and dogs, and recovery of spheres

measuring 50μ to 180μ in diameter was obtained from the venous circulation, indicating the existence of arteriovenous anastomoses in those animals Similar arteriovenous anastomoses were demonstrated in the human kidney by Barrie et al. (1950) and Pompeiano (1951). Christensen (1952) did not find arteriovenous anastomoses in the canine kidney.

Lymphatic Vessels

Peirce (1944) described the lymphatics which accompany the large blood vessels in the kidney of the dog and rabbit. The cortical and perirenal lymphatics were found to connect with each other. Lymph capillary networks were seen in the immediate vincinity of the Bowman's capsule of some glomeruli. Valves were lacking in the renal parenchyma, but were present in the large trunks of the renal sinus.

Rawson (1949) reported the absence of lymphatic channels in the glomeruli, and about the afferent and efferent arterioles, and the intertubular capillaries.

Nerves

Bradford (1889) studied the innervation of the renal blood vessels of the dog and found both vaso-constrictor and vaso-dilator

fibers, the former being well developed. No evidence was obtained of the existence of constrictor fibers in the vagus nerve supplying the kidney.

Gruber (1933) concluded after review of literature that the kidney received fibers from the vagus nerve as well.

Oberling (1944) noted the existence of a highly developed nerve plexus around the preglomerular portion of the afferent arteriole of the human kidney.

Szabo (1948) made an extensive review of literature and concluded that possibly vagal motor nerve endings were present among the epithelial cells of the convoluted tubules.

In the kidney of the cat and rat, Harman and Davies (1948a, 1948b) demonstrated a rich nerve supply occurring in the renal sinus in conjunction with arteries, veins, and epithelium. Throughout the parenchyma, adventitial components were found to penetrate the glomerulus. The perivascular space of the glomerulus was pervaded throughout with a fairly elaborate complex of nerve fibers. Nerve endings were observed in the adventitia of the arteries and veins, in the media of arteriovenous anastomoses, in the epithelium of the convoluted tubules, and in the perivascular tissue of the glomerulus.

Knoche (1950) observed nonmedullated nerve fibers in the various vessels and a terminal reticulum in the convoluted tubules, the glomeruli, the vessels, and the intertubular connective tissue.

Mitchell (1950a, 1950b, 1951) found the kidney of mammals richly innervated. The medulla was found to have a scanty nerve supply from the arcuate nerves accompanying the arteriolae rectae. No nerves were found to enter the medulla directly from the main interlobar nerves. Nerve fibers were found to terminate as free, beaded filaments or as branched or fusiform endings between the epithelial cells or on the basement membrane. Intrarenal ganglia or nerve cells were confirmed.

Malmejac et al. (1951) found the synapses of the vasoconstrictor nerves of the renal vessels, in the ganglia of the solar plexus.

MATERIALS AND METHODS

Source of Animals

For this study the kidneys from sixty-nine animals were used. This group of animals included:

Horses: Ten (five castrated males and five females); all adults; from a slaughterhouse at Grand Rapids, Michigan.

Cattle: Thirteen (nine castrated males and four females); 16 months to 8 years; from the meat laboratory, Animal Husbandry Department, Michigan State University.

Sheep: Eleven (five males and six females); 3 to 24 months; from the meat laboratory.

Goats: Six (four males and two females); 4 to 24 months; from the dissection laboratory of the Department of Anatomy and the autopsy laboratory of the Department of Pathology.

Pigs: Seven (four males and three females); 3 to 7 months; from the meat laboratory.

Dogs: Nine (six males and three females); 2 to 36 months; from the departments of Physiology and Surgery and Medicine.

Cats: Thirteen (two castrated males, three uncastrated males, and eight females); 7 weeks to 5 years; from the departments of Physiology, Parisitology, and Surgery and Medicine.

These animals were in good nutritional condition and appeared to be free from disease.

Techniques

Fixation and Processing of the Tissues

The kidneys were split longitudinally soon after their removal from the freshly killed animals, and were fixed in F.A.A. (Lavdowsky's) mixture for four to six days. Small blocks were cut from the well-fixed tissues for dehydration and further processing. The technique of Barrie (1953) for obtaining blocks from fixed kidney tissues which insured anatomic continuity of the renal tubules in microscopic sections was closely followed. The method took into account the gross anatomy of the medulla so that the tubules and their accompanying vessels could be followed continuously from the papilla to the cortico-medullary junction.

Small blocks (about 1 centimeter wide and 0.5 centimeter thick) were cut in the vertical plane of the straight collecting tubules and the papillary ducts in such a manner as to include a portion of

the pelvis, the papilla, the medulla, the cortex, and the capsule of the kidney. This plane gave a longitudinal section of the uriniferous tubules. Sometimes, in case of large animals, these blocks were divided transversely into two halves at the corticomedullary junction to make them smaller for better sectioning. Blocks were also made to show the cross sections of the cortical and medullary structures. Four blocks were obtained from different parts of both kidneys of each animal.

These blocks of tissues were then dehydrated and infiltrated step by step as follows:

1. Normal butyl alcohol and 95 per cent ethyl alcohol (equal parts)--4 hours.

2. Normal butyl alcohol No. 1--4 hours.

3. Normal butyl alcohol No. 2--16 hours.

4. Normal butyl alcohol and 52°C paraffin (equal parts)--2 hours.

5. 52°C paraffin No. 1--2 hours.

6. 52°C paraffin No. 2--2 hours.

7. 56°C paraffin No. 3--18 hours.

The infiltrated tissues were then embedded in a mixture of two parts of Tissuemat[1] and one part of 56°C paraffin.

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[1] Fisher Scientific Company, Pittsburgh, Pennsylvania.

Sectioning

All sections were cut at seven microns.

Staining and Mounting

Harris' hematoxylin and ethyl eosin were used as routine stains. Weigert and Van Gieson's stains were used for elastic and collagenous tissues and muscle fibers. Gridley's (1951) reticulum stain was employed for the demonstration of reticular fibers.

The stained sections were mounted in gum damar.

Methods of Measuring

Measurements of the diameter of the renal corpuscle, glomerulus, proximal convoluted tubule, thin limb of Henle's loop, straight collecting tubule, and papillary duct were made from random samples of those structures seen under the light microscope. Measurements of the transverse diameter of the longitudinal section of the renal corpuscle and glomerulus were made at their centers, and from only those structures which appeared to be cut through the center in the vertical plane. This was judged by the presence of both vascular and urinary poles in the same section of the renal corpuscle.

Several trials were made with twenty as well as ten measurements of the same structure in the same animal taken at different places in the same as well as in different slides. It was found that the average of ten measurements was as good as that of the twenty measurements, and hence it was decided to take an average of ten measurements of a particular structure from each animal. The mean of the averages of all measurements in different animals of the same species gave the final average measurement of that particular structure in that species.

RESULTS AND DISCUSSION

Gross Anatomy

The mammalian kidneys are described as unilobar (unipyramidal) or multilobar (multipyramidal) according to the number of lobes or pyramids present in one kidney. Some multilobar kidneys present distinct superficial lobation while others do not.

The kidney of the pig is smooth, elongated, bean-shaped, and without any superficial lobation. The length of the kidney is almost twice the width. The hilus is located almost in the middle of the medial border. The longitudinal section of the kidney presents a distinct multipyramidal appearance with the papillae of the pyramids projecting into the calyces minores. Some papillae are narrow and conical while others are wide and flattened. The renal pelvis is funnel-shaped, and divided into calyces majores.

The kidney of the horse is smooth and without external lobation. The left kidney is bean-shaped while the right kidney presents a shape which was described by Chauveau (1873) and Sisson and Grossman (1953) as "the heart on a playing card." The left kidney is longer and narrower than the right one. The location of the hilus is like that of the pig. The kidney in longitudinal section

is found to be unilobar as the organ is not papillated and pyramids were not evident. The inner central part of the medulla forms a concave ridge which projects into the pelvis of the kidney. This projection is described by Sisson and Grossman (1953) as the renal crest. The major and minor calyces are absent.

The kidney of the ox is elongated and presents a well-marked superficial lobation similar to the mammalian fetal lobation. The hilus in the right kidney is an extensive elliptical cavity located on the anterior part of the ventral surface near the medial border. In the left kidney, the hilus presents a deep fissure which is situated on the anterolateral part of the dorsal surface. On section, the renal pyramids are easily made out and the papillae are found to project into the calyces minores. The calyces majores are present but the pelvis is absent.

The kidneys of the sheep and the goat are smooth, bean-shaped, and without external lobation. The situation of the hilus is like that of the pig. The longitudinal section of the kidney presents a unilobar appearance with the renal crest projecting into the pelvis. The major and minor calyces are absent. Elias (1944) observed the multipapillated appearance of the medulla in longitudinal section in a pair of lamb kidneys. Elias assumed that sheep probably had compound kidneys in which the individual lobes were closely united.

The kidneys of the dog are smooth and bean-shaped. The hilus has the same location as that of the pig. The longitudinal section of the kidney presents a unilobar appearance with the renal crest projecting into the pelvis. The renal crest presents curved ridges. The major and minor calyces are absent. In the German shepherd dog Elias (1944) observed multipapillated kidneys resembling that of the pig.

The kidneys of the cat are smooth and bean-shaped. The hilus is situated in the middle of the medial border. The section of the kidney gives a very distinct unilobar appearance with a single elongated papilla projecting into the pelvis. The major and minor calyces are absent.

Blood Vessels

The renal artery enters the kidney at the hilum and splits into a number of large branches, the interlobar arteries. These ascend the renal columns to a position level with the base of the pyramids over which they send arching branches, the arcuate arteries. These arteries do not anastomose with one another. From the arcuate arteries numerous smaller branches, interlobular arteries, arising at regular intervals and at almost right angles to the main vessels, extend radially between the medullary rays. These

arborize near the surface of the kidney and send some small branches into the capsule. As the interlobular arteries pass through the cortical labyrinth, numerous side stems arise, each of which is an afferent arteriole to a glomerulus. As the afferent arteriole enters the renal corpuscle, it divides and subdivides to form the capillary loops of the glomerulus. The loops recombine to form the efferent arteriole. The efferent vessels from cortical glomeruli branch to form a network that supplies the neighboring tubules and the kidney capsule. The efferent vessels emerging from the juxtamedullary glomeruli divide repeatedly, forming a tassel of long straight vessels of near capillary size, the arteriolae rectae spuriae, which descend into the medulla, supplying the tubular components of the pyramids. Efferent vessels arising in the central zone of the cortex contribute mainly to the blood supply of the convoluted tubules and also send some branches into the medullary rays.

Small venules draining the capsule and the outer margin of the cortex unite to form the stellate veins. These combine to form the interlobular veins, which return along the path of the corresponding arteries and receive numerous tributaries from anastomotic nets around the cortical tubules. At the cortico medullary border the interlobular veins join to form the arcuate veins, which extend across the base of the pyramids. Venae rectae, which return blood from the

medulla, open into the arcuate veins. Through confluence of arcuate veins the interlobar veins are formed which course between pyramids, in company with the corresponding arteries, to the hilum of the kidney where they join to form a main channel, the renal vein.

Lymphatic Vessels

There is an elaborate network of lymphatic vessels in the cortex, but apparently none in the medulla. Large lymphatic channels accompany the interlobar, arcuate, and interlobular vessels, surrounding them in an irregular anastomotic network, particularly rich around the arteries. A second plexus underlies the capsule, and a third penetrates the perinephric fat, the last two communicating freely with each other. The lymphatics do not enter the glomeruli. All lymphatics drain into renal lymphatic vessels which leave the kidney at the hilum and end in the lateral aortic lymph nodes. Valves are lacking in the lymph vessels of the renal parenchyma, but are present in the large trunks of the renal sinus.

Nerves

The nerves of the kidney are derived from the renal plexus of the sympathetic division of autonomic nervous sytem. The nerve fibers, which are mostly unmyelinated, enter the kidney with the

renal vessels and terminate among the afferent and efferent arterioles. Nerve fibers penetrate the basement membrane to end adjacent to the tubular cells, especially in the proximal segment. Others terminate among the juxtaglomerular cells, in the parietal layers of Bowman's capsule, and in the perivascular spaces of the glomerular tuft. The vagus nerve is also generally considered to supply the kidney.

The above description of the gross anatomy of the kidney of the domestic animals has been made short as the scope of this study is confined to the microscopic structures only. Hence for a detailed gross description of the organ, the work of Chauveau (1873), Reighard and Jennings (1923), Zietzschmann et al. (1943), and Sisson and Grossman (1953) may be referred to.

Microscopic Anatomy

The Capsule

The outer surface of the kidney is covered with a delicate fibrous capsule (tunica fibrosa) composed of collagenous and elastic fibers. The capsule is easily lifted from the kidney when normal. Any unusual adherence in this regard is indicative of a fibrous hyperplasia throughout the kidney substance. Outside the tunica fibrosa there is a fatty layer, the capsula adiposa. From the inner surface

of the capsule fine strands of loose connective tissue extend into the kidney, forming the interstitial tissue.

The tunica fibrosa of the capsule of the kidney of the pig was found to be thick and composed of two distinct layers. The outer thick layer consisted of dense collagenous fibers and a few elastic fibers. The inner thin layer was composed of loose collagenous and reticular fibers. A few smooth muscle cells were also observed in the inner layer of the tunica fibrosa. The reticular fibers from the inner layers were found to penetrate the parenchyma of the kidney. The internal surface of the inner layer presented a corrugated appearance due to the impression left by the underlying uriniferous tubules. The capsula adiposa was lying just outside the tunica fibrosa and was found to contain blood vessels and nerves.

The capsule of the kidney of the horse, ox, sheep, goat, dog, and cat was similar to that of the pig in general. The following exceptions were noted:

Of the outer and inner layers of the tunica fibrosa, the inner layer was better developed in the horse, both layers equally developed and well demarcated in the sheep and goat, and the inner layer absent in the cat.

In comparison with the pig all other domestic animals except the dog and cat had more smooth muscle in the inner layer of the

tunica fibrosa. The ox, sheep, and goat contained so much smooth muscle that it formed almost a distinct muscular layer in the deeper portion of the capsule (Plate I). The dog had less than the pig, and the cat had none.

Tereg (1911) and Trautmann and Fiebiger (1952) described smooth muscle in the deeper portions of the capsule of the kidney of the sheep and ox but did not mention amounts or refer to any other species. Of the current authors of histology texts, Greep (1954) was the only one to mention smooth muscle in the capsule of the human kidney.

While all specimens observed presented some elastic fibers in the outer layer, those of the sheep seemed to have the most.

Reticular fibers seemed to be least developed in the capsule of the kidney of the cat.

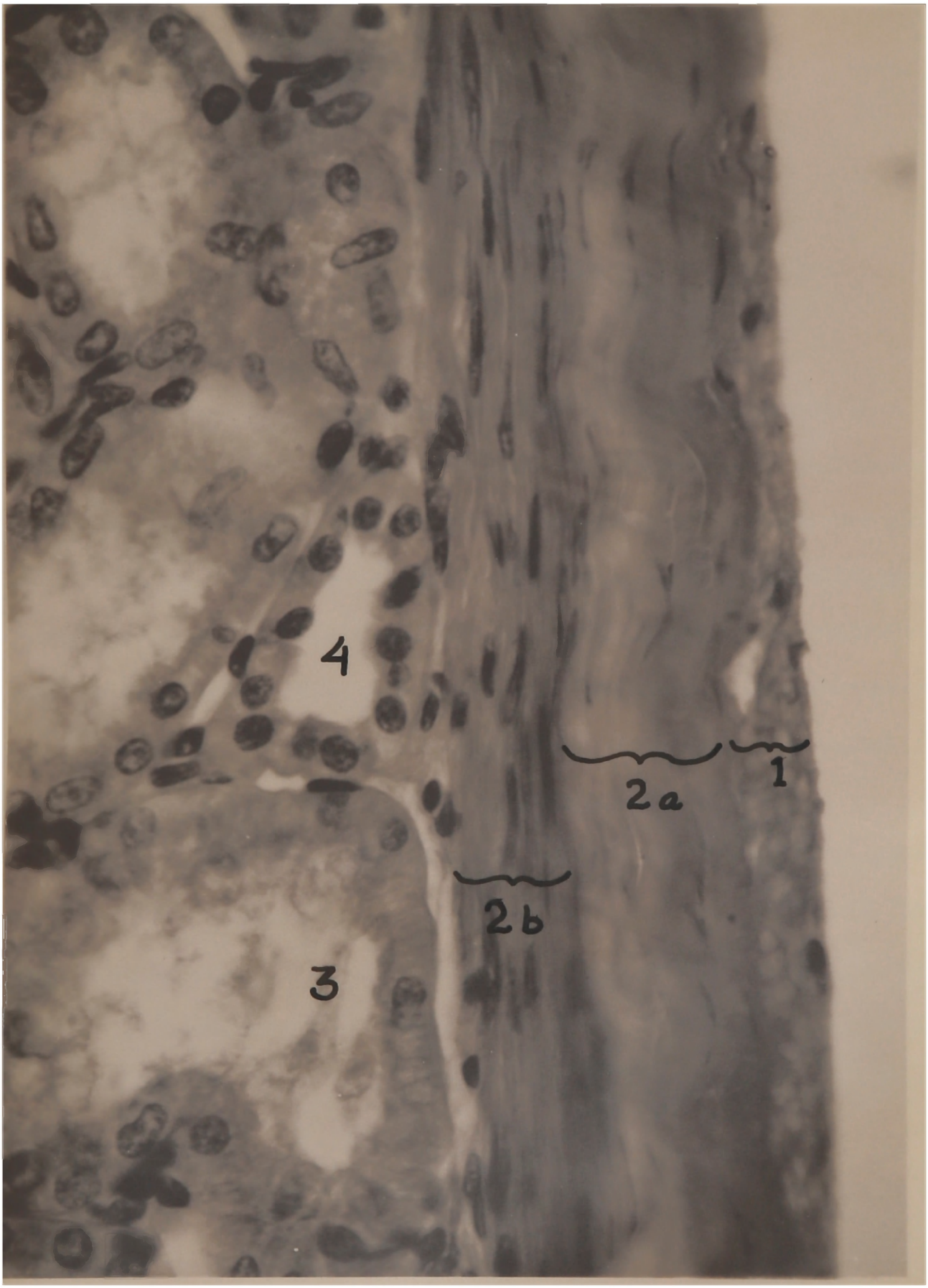
The Uriniferous Tubules

The kidney is a compound tubular gland made up of a large number of uriniferous tubules. Each uriniferous tubule is composed of two segments, a secretory tubule, or nephron, and a collecting tubule.

PLATE I

Capsule of the kidney of the goat, showing the capsula fibrosa and capsula adiposa. Note the muscle cells in the inner layer of the capsula fibrosa. H. and E. 1237x. Nine months old.

1. Capsula adiposa
2. Capsula fibrosa: (a) outer layer; (b) inner layer
3. Proximal convoluted tubule
4. Distal convoluted tubule



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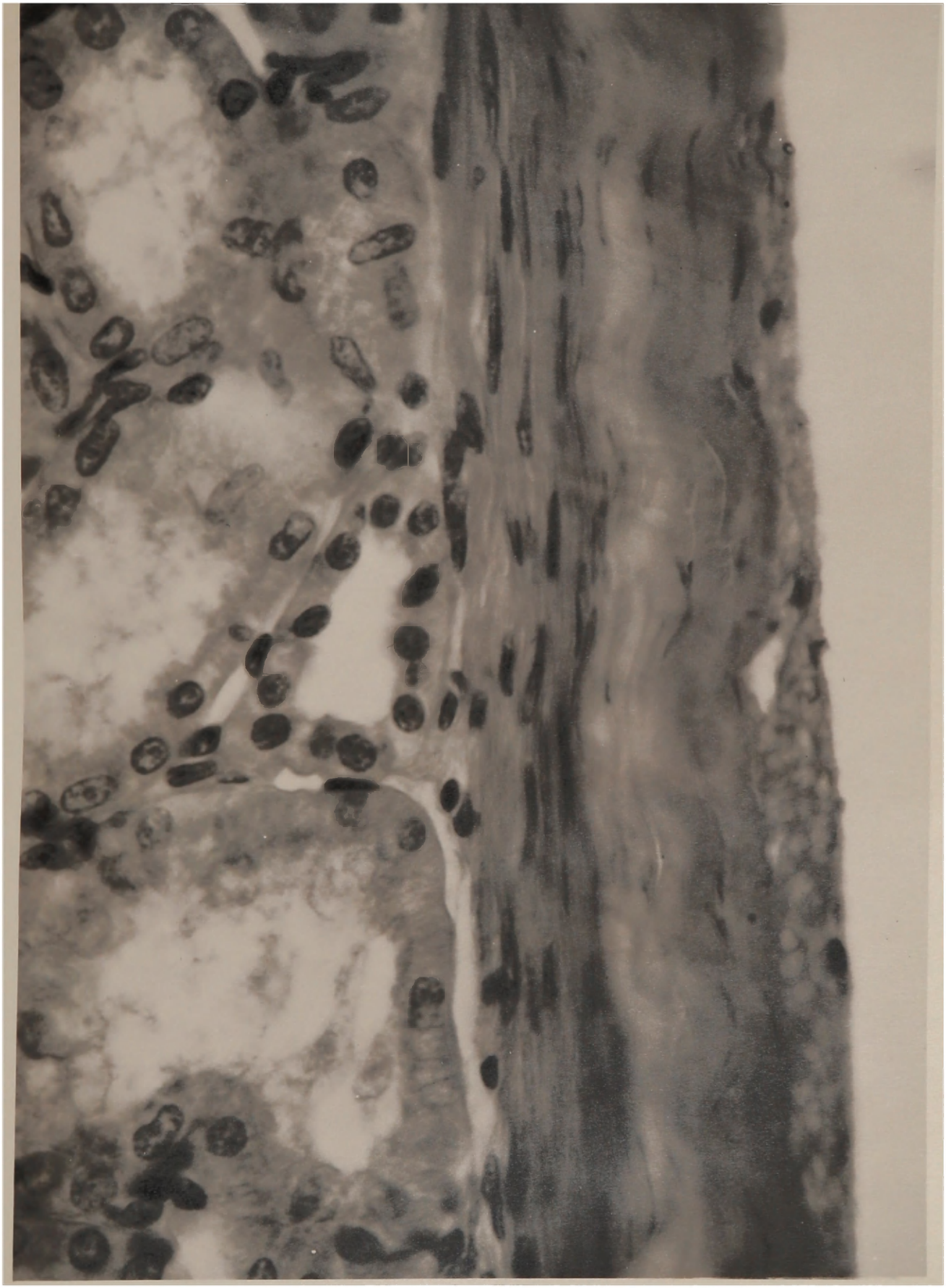

PLATE I

The nephron

The nephron is the structural and functional unit of the kidney and is the secretory portion of the uriniferous tubule. It consists of the renal corpuscle, the proximal convoluted tubule, the loop of Henle, and the distal convoluted tubule.

The renal corpuscle. Each uriniferous tubule begins in a spherical expansion, known as Bowman's capsule, which encloses a tuft of capillaries, the glomerulus. Bowman's capsule and the glomerulus together form the Malpighian or renal corpuscle. Each renal corpuscle has a vascular pole, marked by the point where glomerular vessels enter and leave, and nearly opposite to this is the urinary pole, where the dilated uriniferous tubule invests the glomerulus to form Bowman's capsule.

The renal corpuscle of the pig kidney was found to be pear-shaped. The average transverse diameters of the cortical and juxtamedullary renal corpuscles were 137μ and 156μ, respectively, as shown in Table II. The size of the renal corpuscle was observed to increase with the advancement of age, reaching maximum at the adult stage.

In the horse, the shape of the renal corpuscle was similar to that of the pig. The transverse diameter of the cortical

TABLE II

DIAMETER OF THE URINIFEROUS TUBULE, WITH EPITHELIAL HEIGHT
(in microns; average based on ten counts per animal)

Species	No.	Renal Corpuscle		Glomerulus	
		Cortical Di.[1]	Juxtamedullary Di.	Cortical Di.	Juxtamedullary Di.
Horse	10	178	191	159	166
Ox	13	181	173	150	141
Sheep	11	153	147	123	123
Goat	6	158	157	127	126
Pig	7	137	156	114	130
Dog	9	122	124	98	100
Cat	13	96	106	82	87

[1] Diameter.

[2] Epithelial height.

TABLE II (Continued)

Proximal Convoluted Tubule		Thin Segment of Henle's Loop		Distal Convoluted Tubule		Straight Collecting Tubule		Papillary Duct	
Di.	E.H.[2]	Di.	E.H.	Di.	E.H.	Di.	E.H.	Di.	E.H.
56	15	30	6	50	9	66	14	138	55
50	13	26	5	45	8	53	12	91	33
45	11	22	4	36	7	39	10	59	18
48	11	24	5	38	8	42	12	57	22
45	14	23	5	36	8	50	14	96	21
39	11	22	5	33	7	37	9	54	13
41	14	21	4	30	7	37	5	60	14

renal corpuscle was 178μ and that of the juxtamedullary was 191μ.

The renal corpuscle of the ox was also pear-shaped and had a diameter of 181μ in the cortical region and 173μ in the juxtamedullary region of the kidney.

In the sheep, the shape of the renal corpuscle was similar to that of the pig. The diameter of the cortical renal corpuscle was 153μ and that of the juxtamedullary was 147μ. In the goat, the renal corpuscle was pear-shaped and the diameter in the cortical region was 158μ and in the juxtamedullary region was 157μ.

In the dog and cat, the shape of the renal corpuscle was more or less spherical. The diameter of the cortical and juxtamedullary renal corpuscles of the dog were 122μ and 124μ, respectively. In the cat, the diameter of the cortical renal corpuscle was 96μ and that of the juxtamedullary was 106μ.

Ham (1953) stated that the juxtamedullary corpuscle of the human kidney was generally larger than those nearer the capsule, probably because the juxtamedullary corpuscles were the first to form during development and hence were the oldest. In this investigation it was observed that the above statement of Ham was also true for the horse, pig, dog, and cat. In the case of the ox, sheep, and goat it was found that the reverse was true. The juxtamedullary

renal corpuscles of the ox, sheep, and goat were smaller than the cortical corpuscles.

The glomerulus consists of a tuft of capillaries supplied by an afferent arteriole and drained by an efferent arteriole. This capillary tuft is formed by the abrupt division of the afferent arteriole which in turn subdivides again. The primary branching of the capillaries near the arteriole tends to give the tuft a lobulated structure. The visceral layer of Bowman's capsule is closely applied to the capillary tuft.

Hall (1955) observed anastomoses between the capillaries of the glomerulus of the cat, dog, and man. In this investigation, no attempts were made to demonstrate such anastomoses between the capillaries of the glomerulus of the animals under investigation.

The intercapillary or axial space of the glomerulus of the pig kidney was observed to contain a small amount of connective tissue. Collagenous and reticular fibers were found to surround the capillary tuft of the glomerulus. Fibroblasts and histiocytes were also observed in the axial space of the glomerulus.

Similar structures were also observed in the axial space of the glomerulus of the horse, ox, sheep, goat, dog, and cat.

The three primary membranes of the glomerulus consists of the visceral layer of Bowman's capsule covering the glomerulus,

the endothelial layer lining the glomerular capillaries, and the basement membrane lying between the above two structures.

These three primary membranes of the glomerulus were found to be present in the pig and other animals of this investigation. The finer details of these three membranes could not be observed with the ordinary light microscope (Plate II).

Bowman's capsule is formed by the deep invagination of the expanded end of the proximal tubule. It is double layered. The outer or parietal layer forms the wall of the capsule and the inner or visceral layer envelops the loops of the capillaries of the glomerulus. The capsular space situated between the two layers is continuous with the proximal convoluted tubule.

Both the parietal and the visceral layers of Bowman's capsule in the kidney of the pig and other animals under investigation were observed to have a flattened squamous epithelium. The capsular space was found to be larger in the goat, ox, and sheep; smaller in the horse and cat; and almost equal in the dog, as compared to that of the pig.

The juxtaglomerular apparatus consists of the modified cells of the media of the afferent arterioles of the glomerulus. Near the entrance into the glomerulus, the smooth muscle cells of the afferent arterioles become large, and pale-staining. Their nuclei, instead

PLATE II

Kidney of the goat. Note a single-layered macula densa and juxtaglomerular cells. H and E. 612x. Five months old.

1. Juxtaglomerular apparatus
2. Macula densa
3. Glomerulus
4. Parietal layer of Bowman's capsule
5. Visceral layer of Bowman's capsule
6. Endothelial cell of the glomerulus
7. Basement membrane of the glomerulus

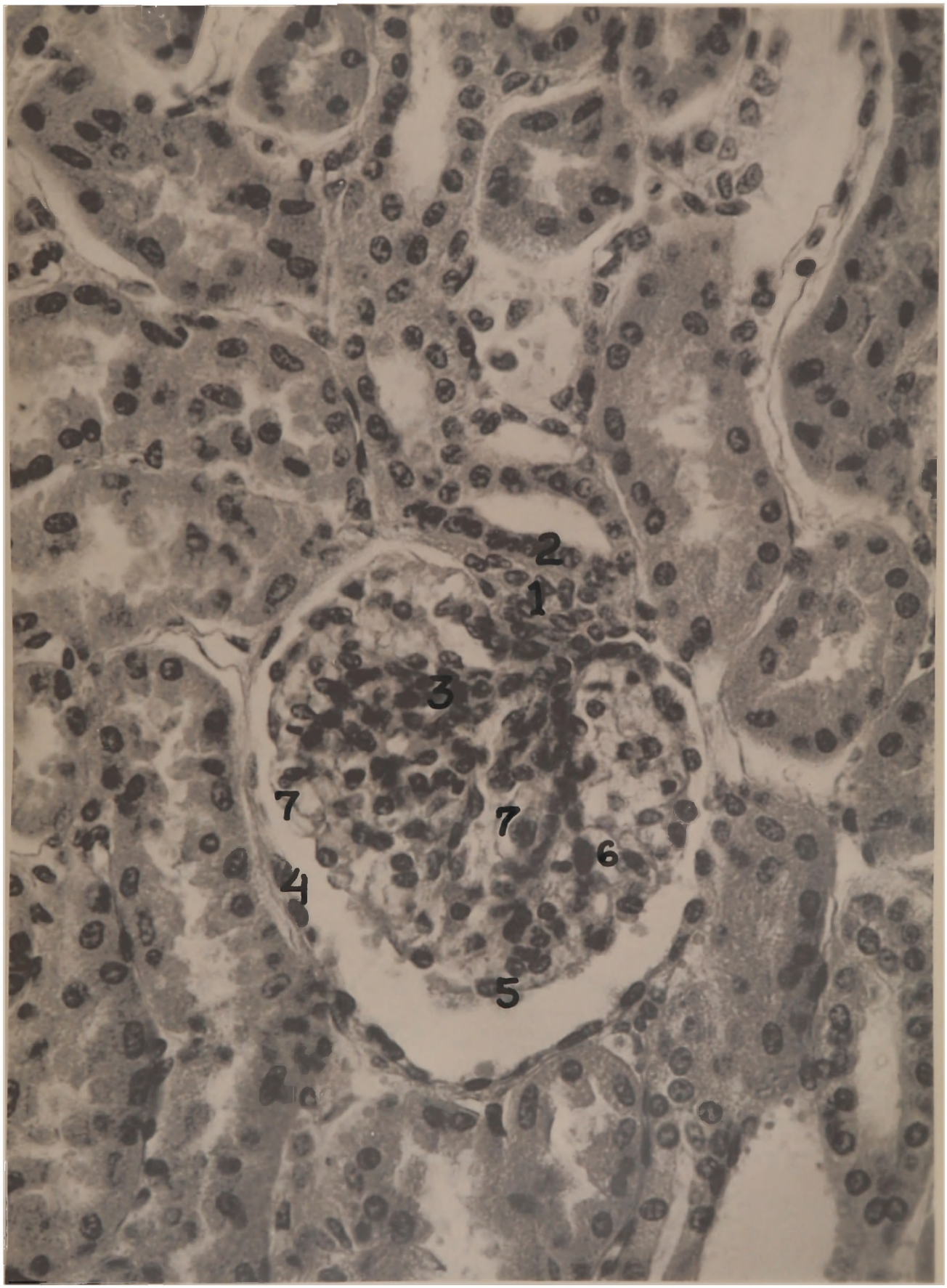

PLATE II

PLATE II

Kidney of the goat. Note a single-layered macula densa and juxtaglomerular cells. H. and E. 612x. Five months old.

1. Juxtaglomerular apparatus
2. Macula densa
3. Glomerulus
4. Parietal layer of Bowman's capsule
5. Visceral layer of Bowman's capsule
6. Endothelial cell of the glomerulus
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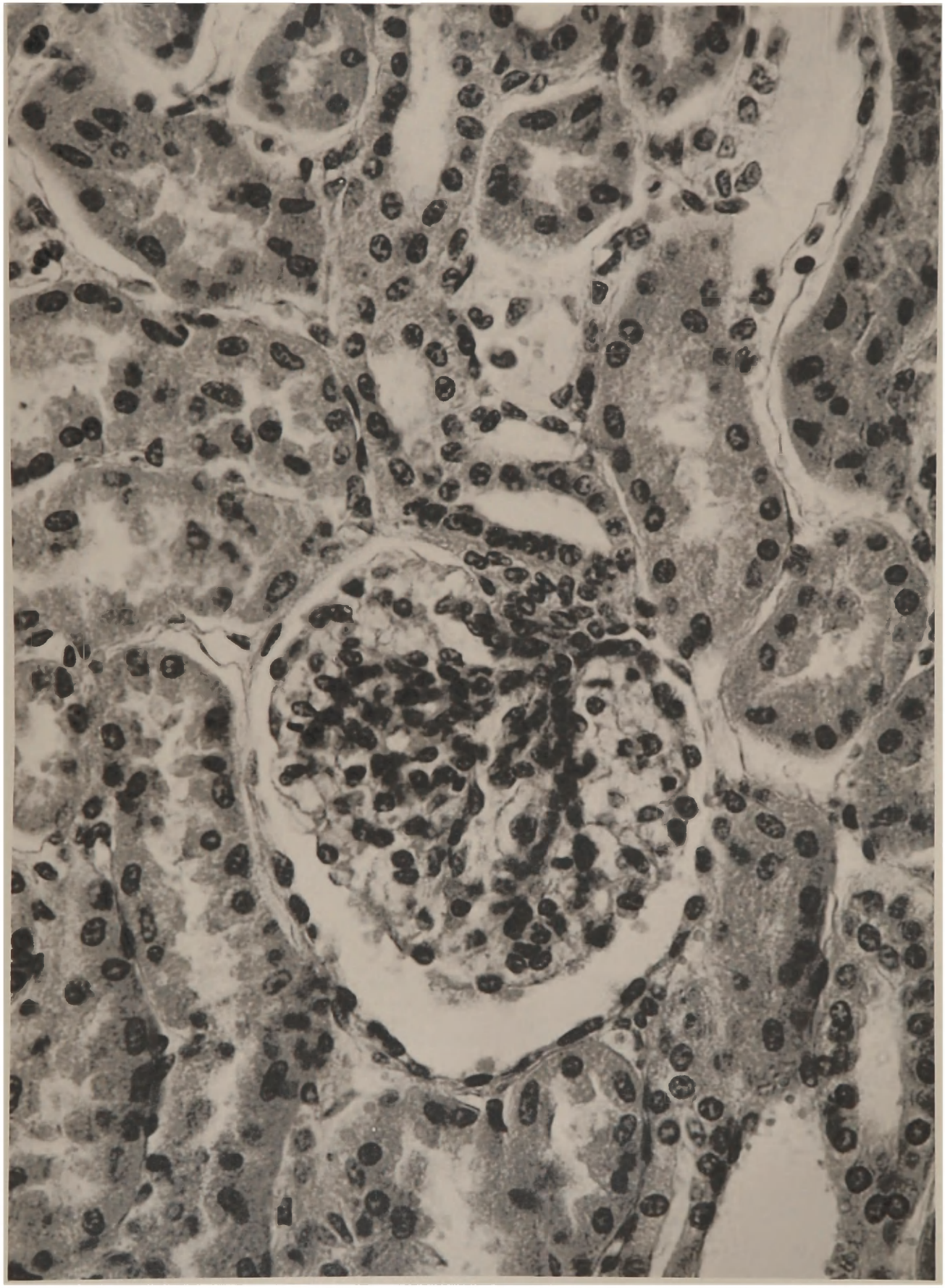

PLATE II

of being elongated, are rounded, and their cytoplasm, instead of containing myobibrils, usually contain granules. Moreover, the shape of these cells is such that they resemble epithelial cells. These myoepithelioid cells are called juxtaglomerular cells. These cells thicken the arteriolar wall and tend to form an asymmetrical cap on one side of the glomerulus.

The nuclei of the juxtaglomerular cells in the pig kidney were found to be round and somewhat deeply stained with hematoxylin and eosin stains. They were found to be closely associated with the macula densa. Along with these modified cells of the media some of the spindle-shaped smooth muscle cells were also observed.

The structure of the juxtaglomerular apparatus of the horse, ox, sheep, and cat were similar to that of the pig. In the case of the goat and dog, the cells of the juxtaglomerular apparatus were more numerous than those of the pig (Plate II).

Goormaghtigh (1951) stated that granules were absent in the juxtaglomerular cells of the kidneys of the dog and man. According to Maximow and Bloom (1952) the juxtaglomerular cells are absent in children below the age of two years. In this investigation, juxtaglomerular cells were demonstrated in a two-month-old cat. Observations were not made on young animals of the other species, so no conclusions can be drawn regarding this point.

The proximal convoluted tubule. The proximal convoluted tubule has the widest diameter of any portion of the nephron, and is lined by simple cuboidal or truncated pyramidal cells having abundant protoplasm and large basally placed spherical nuclei. It is characterized by the presence of a brush border, basal striations, and the absence of clear cell boundaries. The brush border is the cuticular covering of the free end of the cell lining the proximal tubule. The basal striations are either the mitochondria or the spaces between the mitochondria of the cells of the proximal tubule. The proximal convoluted tubule pursues a looped and tortuous course in the immediate vicinity of the renal corpuscle from which it originates. This convoluted portion of the proximal tubule is called the pars convoluta. The pars convoluta then enters the medullary ray, becomes straight, and continues as the descending limb of the loop of Henle. This straight portion of the proximal tubule is called the pars recta, and constitutes the descending thick limb of Henle. The structure of the pars recta is the same as that of the pars convoluta of the proximal tubule.

The proximal tubule of the pig was found to have an average diameter of 45μ. It was lined by simple truncated pyramidal cells whose average height was found to be 14μ. The cytoplasm of the cell was somewhat coarsely granular. These granules were more

or less evenly distributed and hence basal striations were not distinct. These granules masked the cell boundaries, and therefore they were not clear. The nuclei were usually basal, but in some cells they were found to be situated in the middle or even towards the apex of the cells. These nuclei were circular, and deeply stained with hematoxylin and eosin stains. Each nucleus contained a prominent nucleolus and some deeply stained chromatin granules. The contour of the lumen of the proximal tubule was found to be very irregular. The brush border was prominent and formed a separate cluster for each cell. These clusters were found to be separated from one another (Plate III).

The general structures of the proximal tubule of the rest of the animals under investigation were similar to those of the pig.

The diameter of the proximal tubule was greater in the horse, ox, and goat; equal in the sheep; and smaller in the dog and cat, in comparison to that of the pig (Table II). The height of the cells lining the tubule was greater in the horse; equal in the cat; and smaller in the ox, sheep, and dog, as compared to that of the pig. The lumen of the proximal tubule was larger in the horse, goat, ox, and sheep; almost equal in the dog; and smaller in the cat. The contour of the lumen in the rest of the animals of this investigation was more regular than that of the pig. Some of the

PLATE III

Kidney of the pig. Note the brush border forming a cluster on each cell of the proximal tubule. H. and E. 2460x. Seven months old.

1. Proximal tubule
2. Brush border
3. Distal tubule
4. Interstitial connective tissue cells

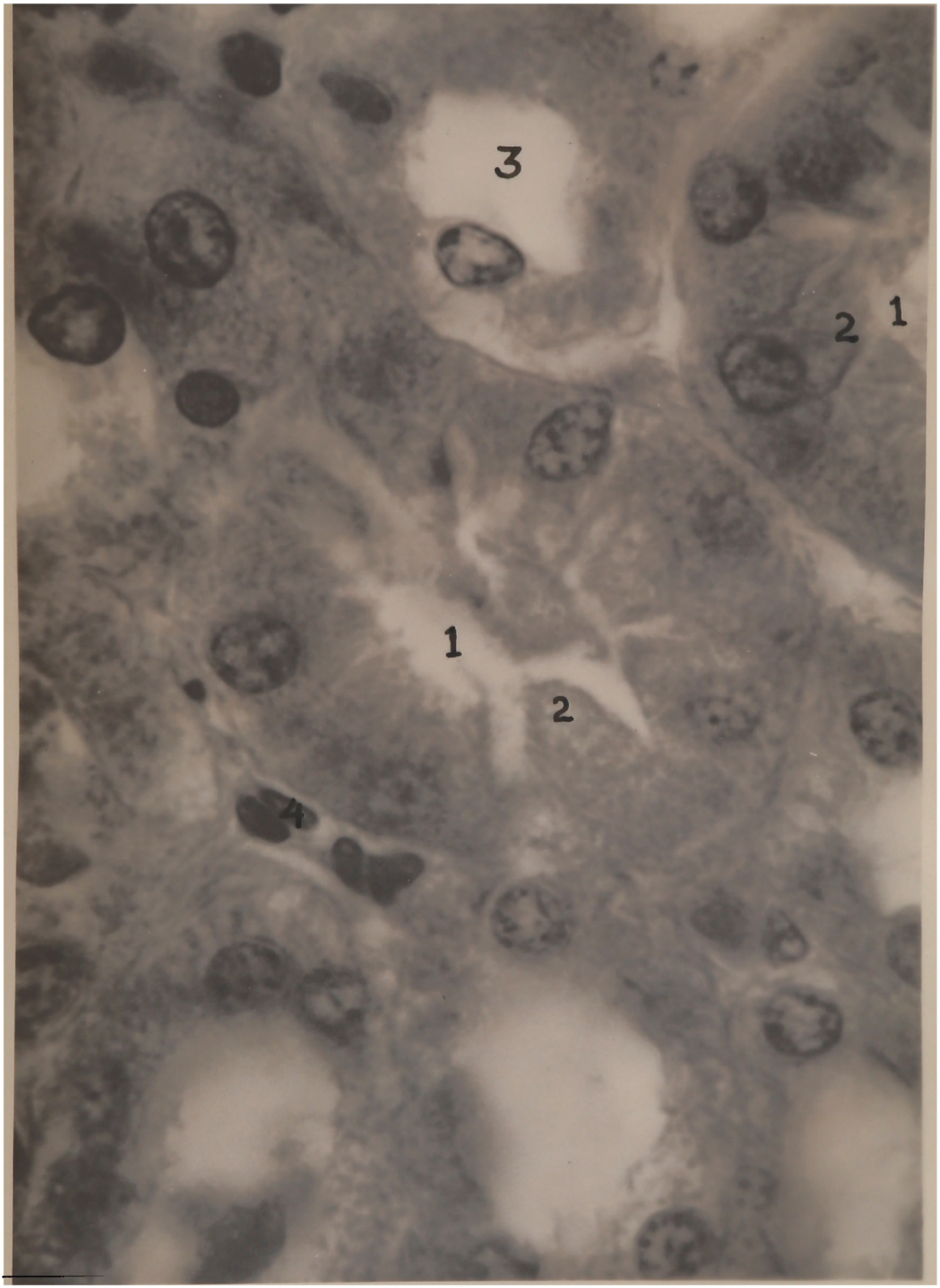

PLATE III

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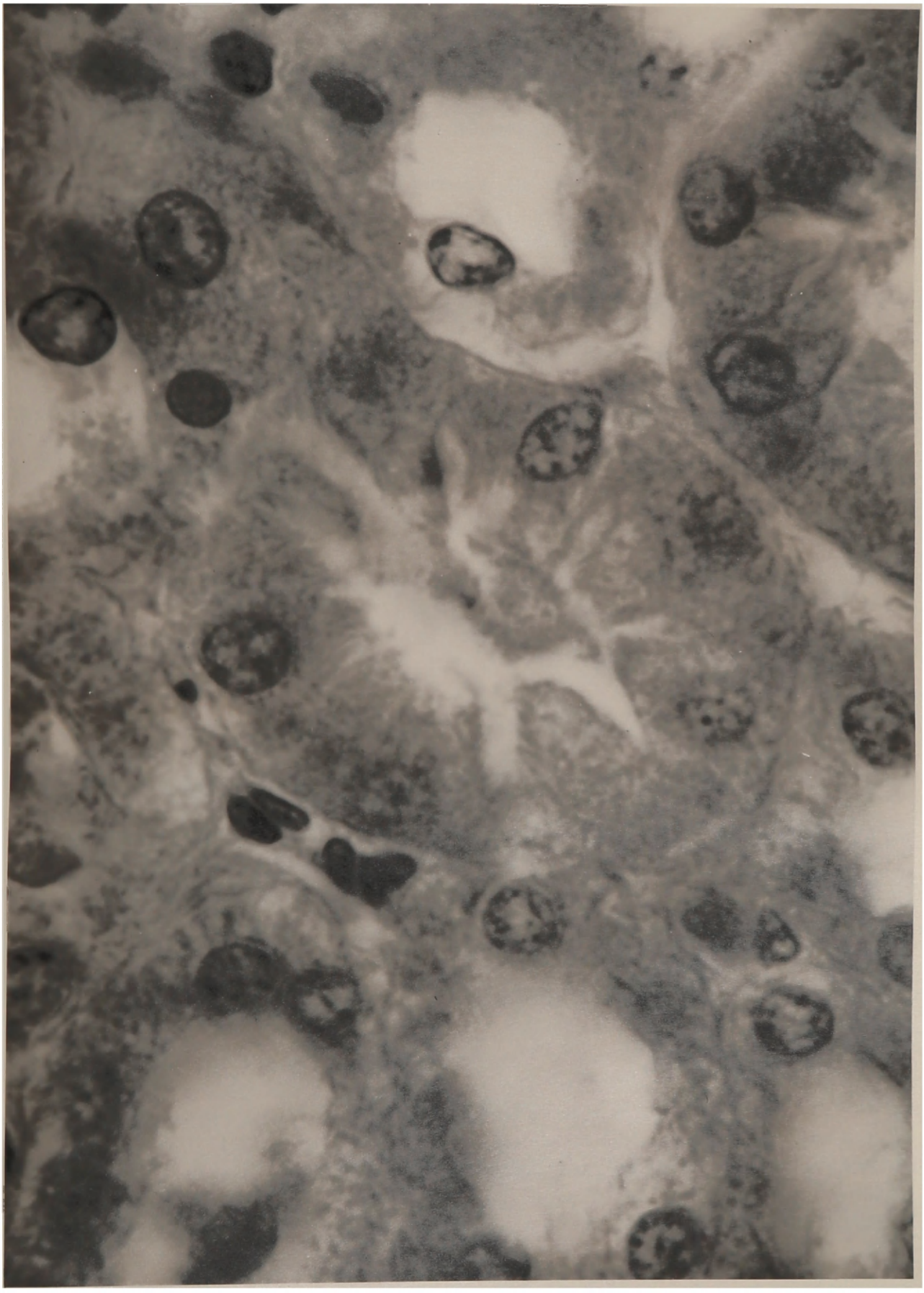


PLATE III

nuclei of the cells of the proximal tubule were oval in the ox and goat. The brush border was uniformly arranged along the apices of the cells of the proximal tubule in the case of the rest of the animals under investigation. They did not form clusters as was observed in the pig. Basal striations were more distinct in the dog than in the pig. Fat globules were observed in the cells of the proximal tubules of the cat and dog (Plate IV).

Grafflin (1942) noted a deposition of yellow to golden-brown iron-containing pigment in the epithelium of the proximal tubule of the rat. No such pigment was observed in any of the animals under investigation.

The loop of Henle. The loop of Henle consists of a descending and an ascending arm connected by a sharp bend or curve. It is divided into a thick and a thin segment. The thick descending arm of the loop of Henle is formed by the pars recta of the proximal tubule; the thick ascending arm is formed by the pars recta of the distal convoluted tubule. The loop of Henle of those tubules arising from the outer cortical renal corpuscles passes only a relatively short distance into the medulla, the thin segment of this loop being very short. On the other hand, the loop of Henle of the tubules of the juxtamedullary renal corpuscle descends deeply into the medulla

PLATE IV

Kidney of the cat. Note the fat globules in the pars recta of the proximal tubule. H. and E. 700x. Four months old.

1. Fat globule
2. Pars recta of the proximal convoluted tubule
3. Pars convoluta of the proximal convoluted tubule
4. Brush border of the proximal convoluted tubule
5. Basal striations of the proximal convoluted tubule

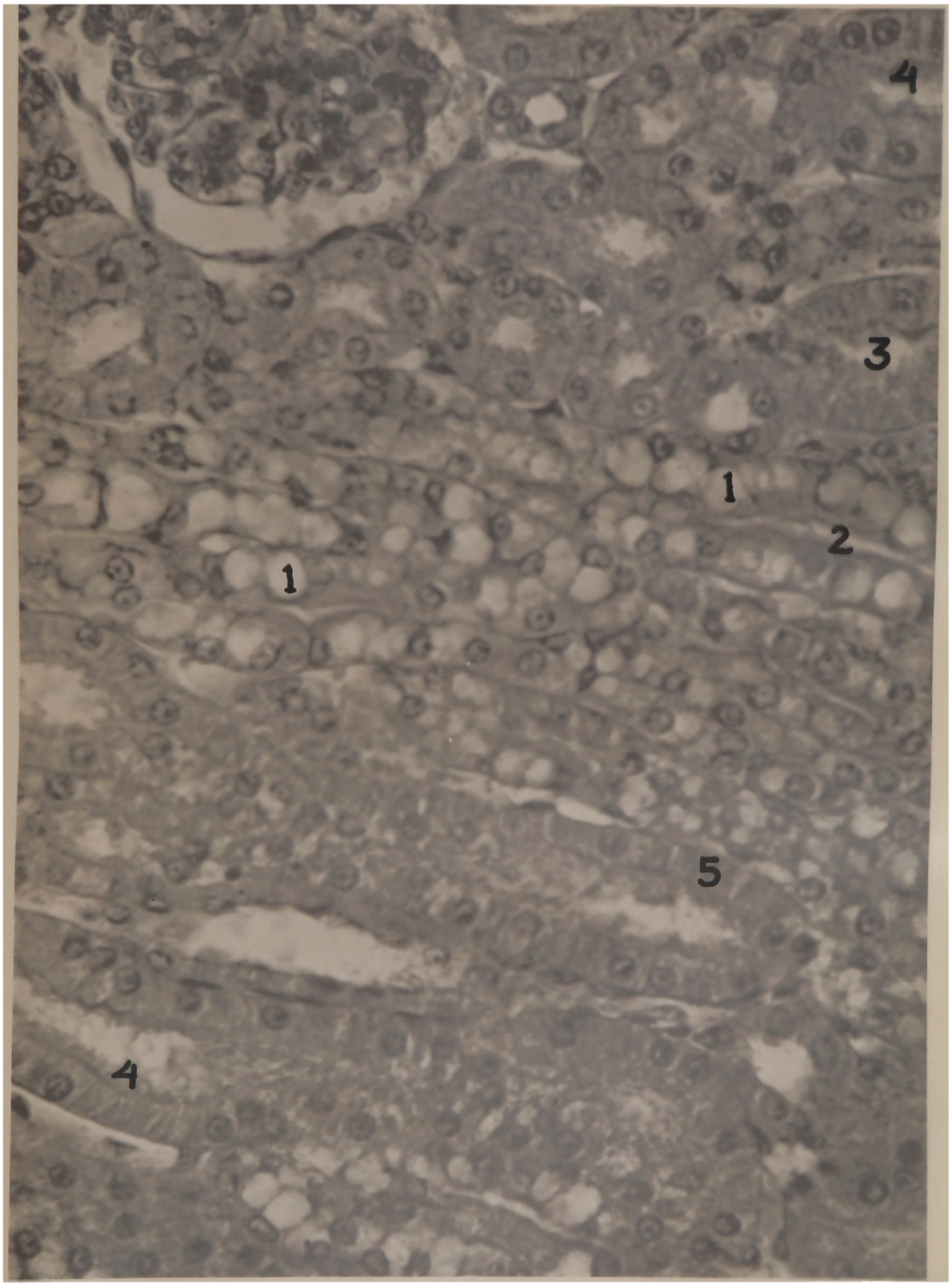


PLATE IV

PLATE IV

Kidney of the cat. Note the fat globules in the pars recta of the proximal tubule. H. and E. 700x. Four months old.

1. Fat globule
2. Pars recta of the proximal convoluted tubule
3. Pars convoluta of the proximal convoluted tubule
4. Brush border of the proximal convoluted tubule
5. Basal striations of the proximal convoluted tubule

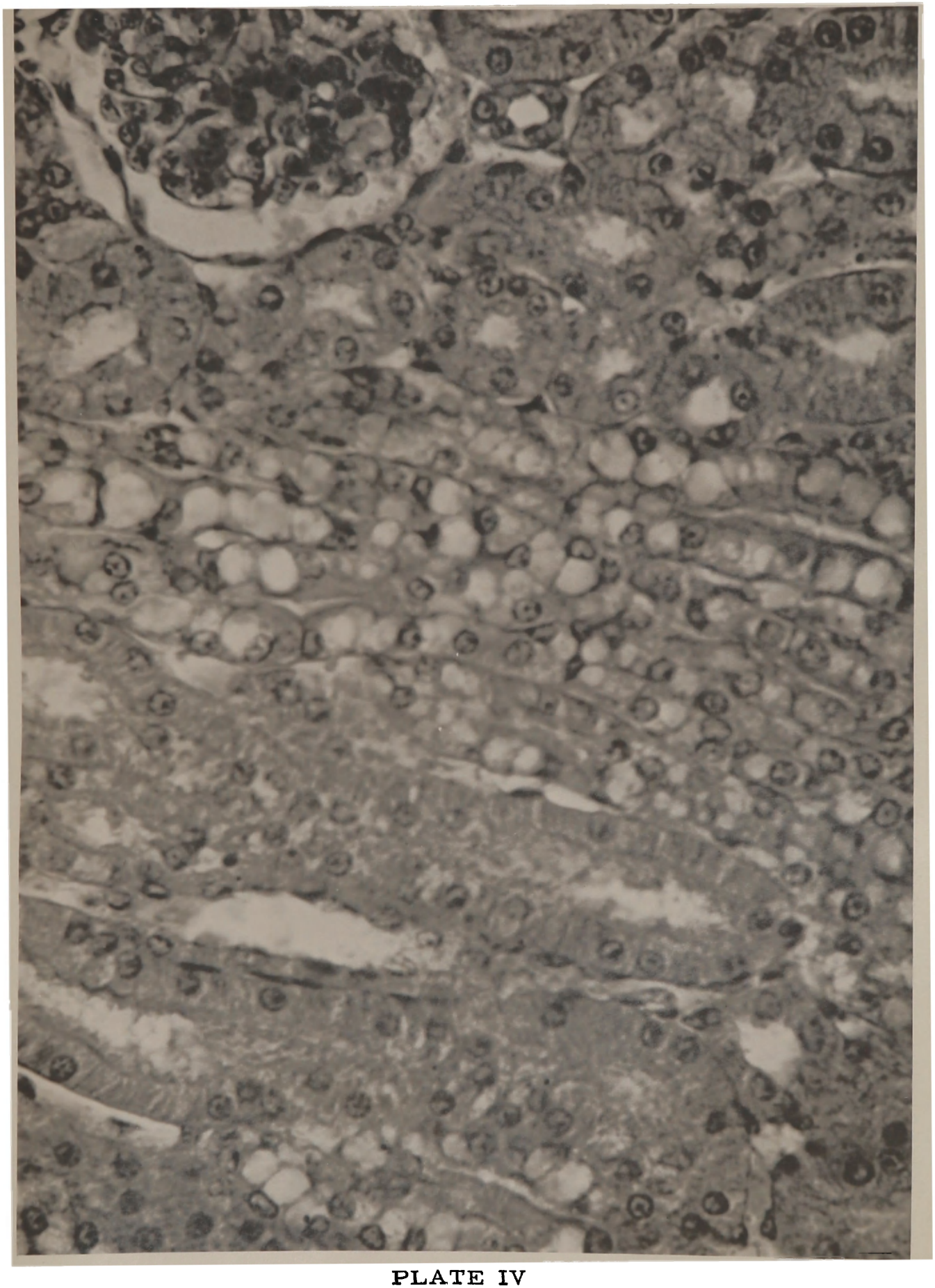


PLATE IV

often as far as the papilla. The greater part of the loop within the medulla is made up of the thin segment. The epithelial lining of the descending thick segment of Henle's loop resembles that of the proximal tubule; the epithelial lining of the ascending tubule resembles that of the distal tubule. The thin segment is smaller in diameter than either the proximal or distal tubules and is made up of a flattened epithelium with nuclei which bulge into the lumen. The protoplasm is less granular and therefore stains less eosinophilic than either proximal or distal tubule. The transition from the thick to thin segment of Henle's loop is abrupt.

The diameter of the thin segment of Henle's loop in the pig kidney was found to be 23μ. It was lined by flattened epithelium having an average height of 5μ. The cells were markedly less eosinophilic than those of the proximal tubule. The cytoplasm was more or less clear with a spherical nucleus bulging into the lumen of Henle's loop. This bulging of the nucleus gave a wavy contour to the lumen of the tubule. A brush border was absent and the basal striations indistinct.

The general structure of the thin limb of Henle's loop of all animals under investigation was similar to that of the pig. The following few exceptions were noted:

The diameter of the thin limb of Henle's loop was greater in the horse, ox, and goat; and smaller in the sheep, dog, and cat, as compared to that of the pig (Table II). The cell height was slightly greater in the horse, and somewhat smaller in the sheep and cat, the other animals having cells of equal height to those of the pig. The lumen of the loop of Henle was wider than that of the pig, in the horse, ox, sheep, and goat, and narrower in the dog, the cat being equal.

The distal convoluted tubule. The distal convoluted tubule is composed of two segments, the pars recta and the pars convoluta. The pars recta forms the thick ascending limb of Henle's loop. The thick segment of the ascending loop of Henle leaves the medullary ray, becomes convoluted (pars convoluta), and returns to the glomerulus from which the nephron has its origin. The distal tubule, returning to the neighborhood of the glomerulus, makes tangential contact over an extensive region with the afferent arteriole. In this region of contact the nuclei of the distal convoluted tubule become densely crowded and constitute the macula densa. There are fewer convolutions in the distal than in the proximal tubule. The cells in the distal tubule are cuboidal with spherical or ovoid nuclei. The cells in the distal tubule are much less broad than those that line

the proximal tubule and hence the nuclei appear more closely spaced in the distal tubule. Cytoplasm is not nearly so acidophilic as the proximal tubule. Faint basal striations are present although a brush border is lacking in the distal tubule.

The diameter of the distal tubule in the pig kidney was found to be 36μ. The tubule was lined by cuboidal epithelium 8μ in height. The lumen was larger and its contour less irregular than that of the proximal convoluted tubule. The cytoplasm was granular and less eosinophilic; the granules were finer than those of the proximal tubule. The nuclei were spherical and basally placed although a few oval nuclei were also noticed. These nuclei were closer to each other than those of the proximal tubule. The nucleus presented one or two prominent nucleoli and darkly stained coarse chromatin granules. The cell boundaries were not clear. The brush border was absent and the basal striations were not very distinct.

Except for a few differences, the distal tubule of all animals under investigation was similar to that of the pig. Compared with it, the diameter of the distal tubule was larger in the horse, ox, and goat; equal in the sheep; and smaller in the dog and cat. By a similar comparison the epithelial height was greater in the horse; equal in the ox and goat; and smaller in the sheep, dog, and cat.

The lumen of the distal tubule was greater in the horse, ox, sheep, and goat; and smaller in the dog and cat.

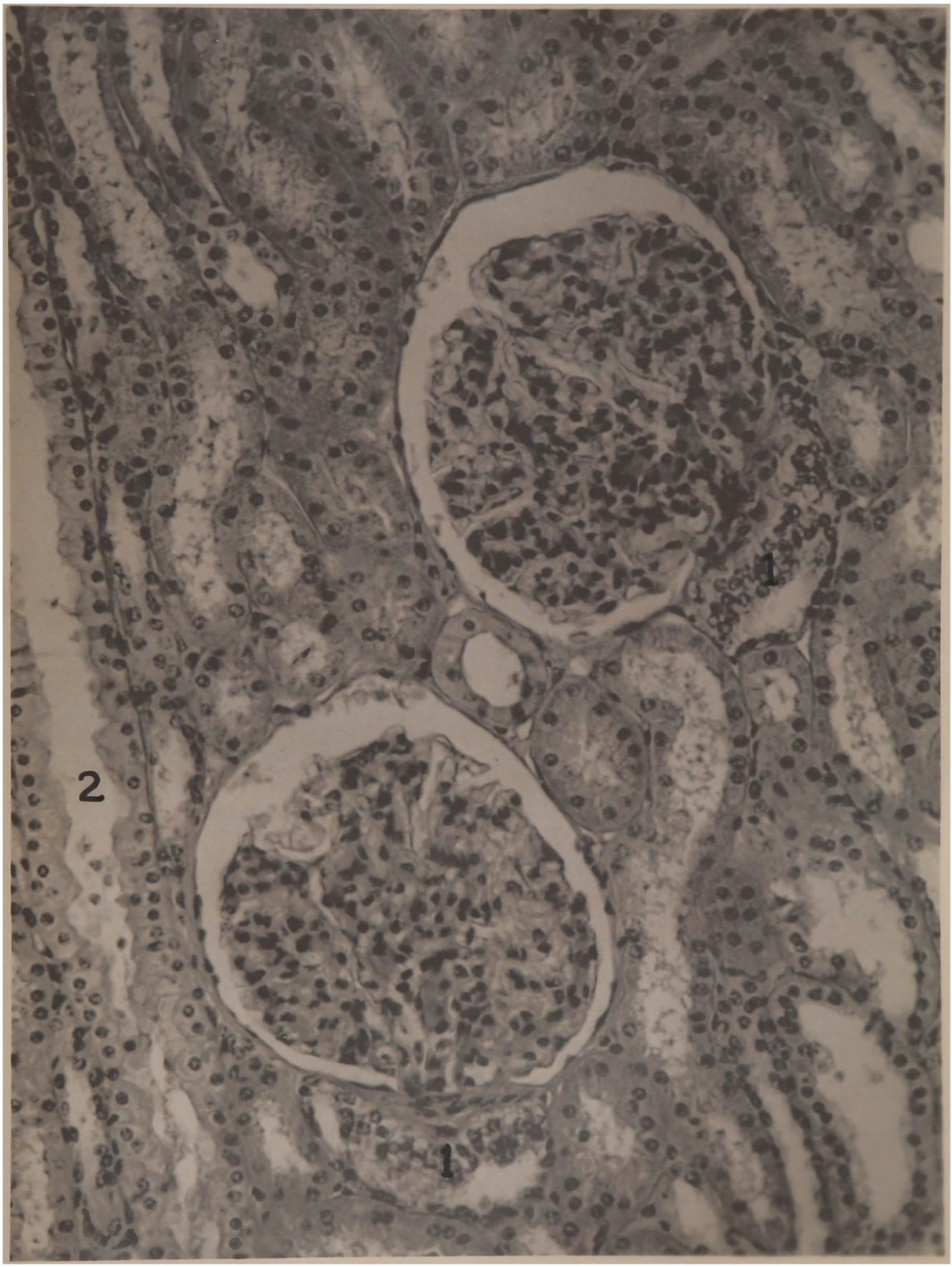
The macula densa in the pig constituted about half of the wall of the distal convoluted tubule as seen in cross section. The cells forming the macula densa were single-layered and appeared to be slightly taller than the rest of the cells of the distal tubule. The cytoplasm was faintly stained around the nucleus. The cells of the macula densa were closely associated with the juxtaglomerular cells. The cytoplasm of the cells contained very few fine granules. The nucleus was spherical and contained a dark stained nucleolus and coarse chromatin granules.

The macula densa in all animals under investigation was similar to that of the pig except in the horse, which presented some special features. The macula densa in the horse kidney was stratified although the stratifications were not distinct, as the nuclei were very irregularly crowded (Plate V). The height of the stratified epithelium of the macula densa appeared to be more than double that of the other cells lining the same tubule. The cells of the macula densa were almost nongranular and did not take the stain, especially towards the base. The change from simple to stratified epithelium of the macula densa of the horse was abrupt.

PLATE V

Kidney of the horse. Note the stratified macula densa. H. and E. 400x. Adult.

1. Macula densa
2. Straight collecting tubule



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2. Straight collecting tubule

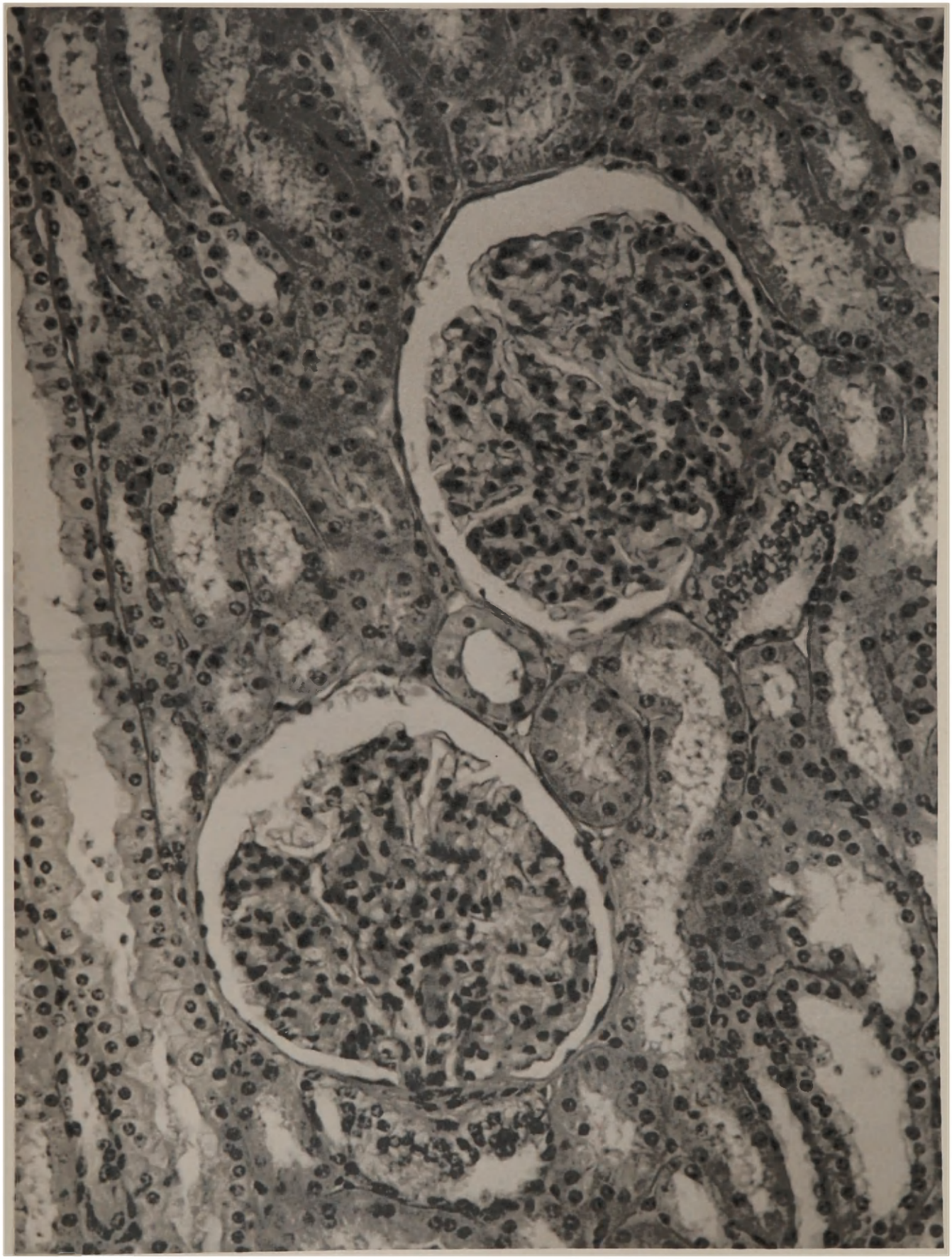

PLATE V

McManus (1943) and Okkels (1950) demonstrated the reversed position of the Golgi element in the macula densa of the cat and man. Golgi elements were not studied in this work.

The collecting tubule

The collecting tubule consists of the arched or initial collecting tubule, the straight collecting tubule, and the papillary duct or duct of Bellini.

The distal convoluted tubule is joined directly to an arched collecting tubule, into which it discharges. These arched tubules are short stems that branch from the sides of the straight collecting tubules located in the medullary ray. The arched tubules are situated in the cortical labyrinth.

The straight collecting tubules lie side by side and make up most of the substance of the pyramids. The straight tubules join with one another in successive fashion in the pyramids to form finally the large papillary ducts. The diameter increases as the tubules join and it reaches a maximum in the papillary ducts. The collecting tubules are nearly always very regular in outline when viewed in cross section. The epithelial cells lining the arched tubules and the proximal portion of the straight tubule are strictly

cuboidal. The cells increase in height as the tubules increase in diameter.

The papillary ducts empty into the minor calyces through the foramina situated on the surface of the papilla.

The arched collecting tubule. The arched collecting tubule in the pig kidney was observed to have a greater diameter than the distal tubule. It was lined by a simple cuboidal epithelium with quite distinct cell boundaries. The lumen of the arched tubule was more regular and wider than that of the distal tubule. The cytoplasm of the cells lining the arched tubule was faintly stained and devoid of characteristic granules of the nephron. The nuclei were either spherical or oval, and basally placed. Each nucleus contained a nucleolus and some deeply stained chromatin granules.

Except for the diameter and cell height, other structures of the arched collecting tubules of the horse, ox, sheep, goat, dog, and cat resembled that of the pig. The diameter was greater in the horse and ox, and smaller in the sheep, goat, dog, and cat. The cell height was greater in the horse and smaller in the rest of the animals.

The straight collecting tubule. The general structure of the straight collecting tubule of the pig kidney was similar to that of

the arched collecting tubule. The diameter of the straight collecting tubule was 50μ and the cell height was 14μ. The lumen had a regular contour and was wider than the arched collecting tubule. The straight collecting tubule was lined by a simple cuboidal epithelium which became somewhat wider and taller towards the papillary duct. The cytoplasm was clear, faintly stained, and free from granules. The nuclei were larger than the arched collecting tubule and each contained a deeply stained nucleolus and a few coarse chromatin granules. The cell boundaries were distinct.

The general structure of the straight collecting tubule in all animals under investigation was similar to that of the pig. The following differences were noted:

The diameter of the straight collecting tubule was greater in the horse and ox; and smaller in the sheep, goat, dog, and cat (Table II). The cell height was greater in the horse; and smaller in the ox, sheep, goat, dog, and cat. The lumen of the tubule was greater in the horse, ox, and cat; and smaller in the sheep, goat, and dog. The cell boundaries were more distinct in the horse, ox, goat, and dog; and less distinct in the sheep and cat.

Trautmann and Fiebiger (1952) noted the presence of numerous fat droplets in the straight collecting tubules especially that of

the older domestic animals. No such fat droplets were observed in the straight collecting tubules of the animals under investigation.

The papillary duct. The general structure of the papillary duct of the pig kidney resembled that of the straight collecting tubule. The diameter and epithelial height of the papillary duct were greater than those of the straight collecting tubule. The papillary duct was lined by a simple tall columnar epithelium which became transitional near the opening of the duct on the papilla. This transitional epithelium of the papillary duct continued as the epithelium of the papilla. The change from simple to transitional type of epithelium in the papillary duct was found to be abrupt. The diameter and the epithelial height of the papillary duct were found to be 96μ and 21μ, respectively (Table II). The tall columnar cells of the papillary duct were faintly stained and nongranular. The nuclei were large, spherical, and situated almost in the center of the cell. A dark-staining nucleolus and chromatin granules were observed in each nucleus. The cell boundaries were distinct and the contour of the lumen was regular.

The general structure of the papillary duct in all animals in this investigation resembled that of the pig. The following exceptions were noted:

The diameter of the papillary duct was greater in the horse and smaller in the rest of the animals under investigation. The epithelial height was greater in the horse, ox, and goat, and smaller in the sheep, dog, and cat. In the horse, ox, goat, and sheep the papillary duct was lined by a transitional epithelium for a greater distance from its opening on the papilla than that of the pig. The papillary duct of the dog kidney was lined by a simple columnar epithelium throughout its course. At the junction of the simple columnar epithelium of the papillary duct and the transitional epithelium of the papilla, a beaklike process of the transitional epithelium was found in longitudinal section (Plate VI). The extension of the transitional epithelium in the papillary duct of the cat kidney was found to be almost equal to that of the pig.

Langham and Hallman (1939) considered the transitional epithelium of the papillary duct in the bovine kidney as pathological. This investigation has revealed that the transitional epithelium of the papillary duct in bovine kidney is a normal one (Plate VII). Langham et al. (1942) found that only tall columnar cells lined the papillary duct of the bovine kidney. From this study it has been determined that transitional epithelium lines the papillary duct of the bovine kidney for a distance of about 1500μ from the opening of

PLATE VI

Papillary ducts in the dog kidney. H. and E. 320x. One year old.

1. Simple columnar epithelium lining papillary ducts
2. Beaklike process at opening of the papillary duct
3. Oblique section of the papillary duct opening
4. Pelvis

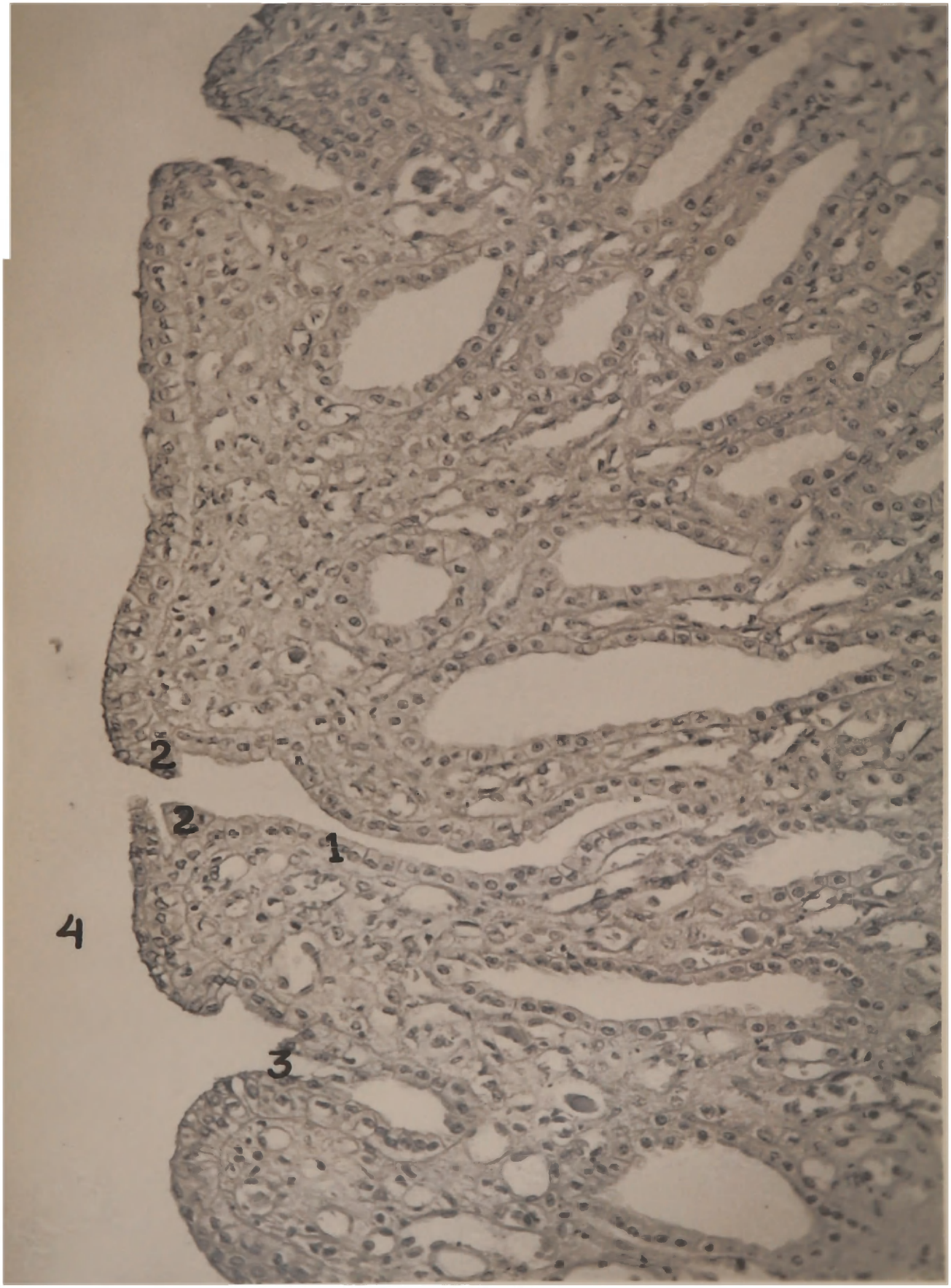

PLATE VI

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Papillary ducts in the dog kidney. H. and E. 320x. One year old.

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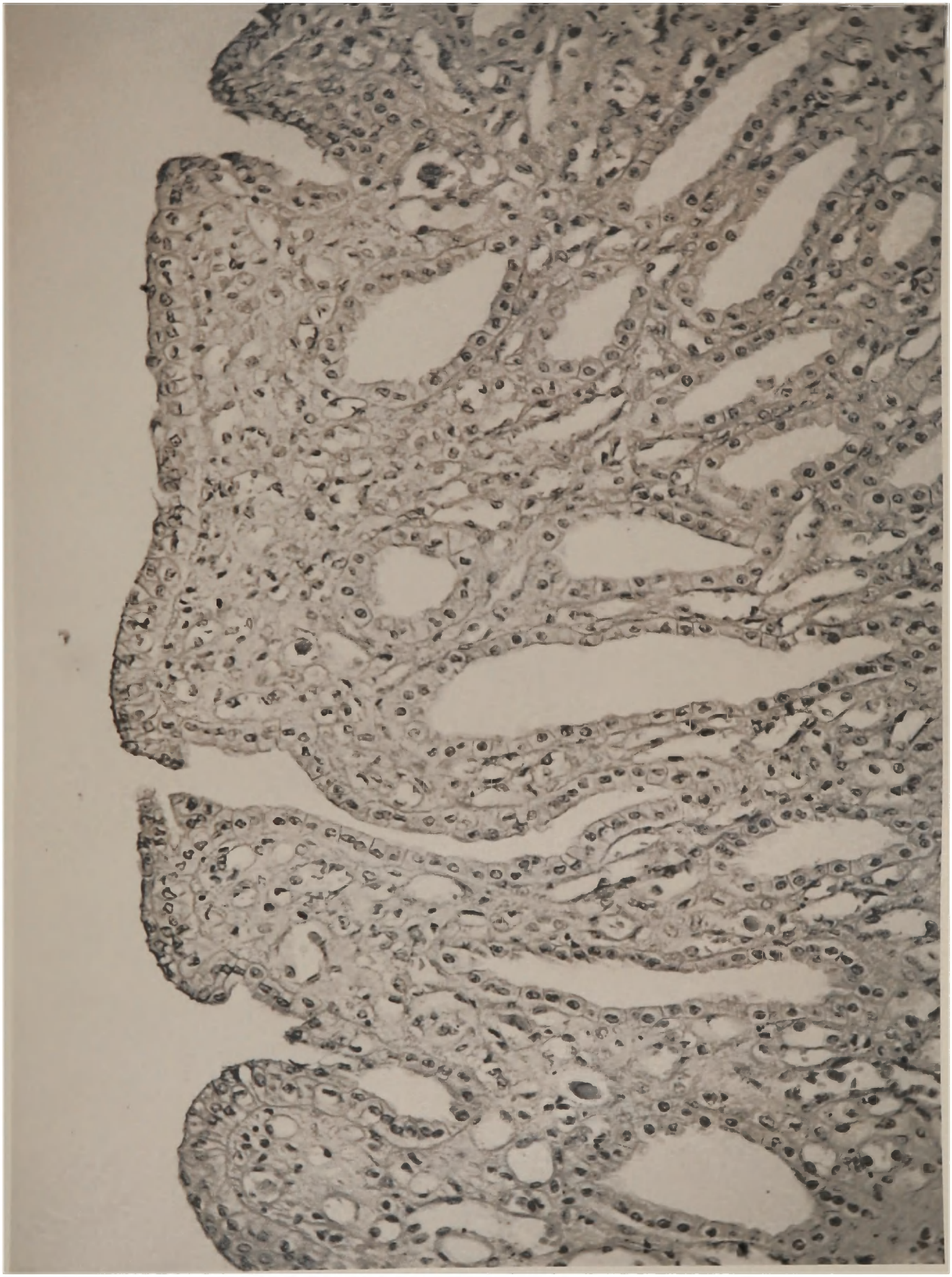

PLATE VI

PLATE VII

The papillary ducts in the ox kidney. H. and E. 320x. Nineteen months old.

1. Transitional epithelium
2. Opening of papillary duct on the papilla

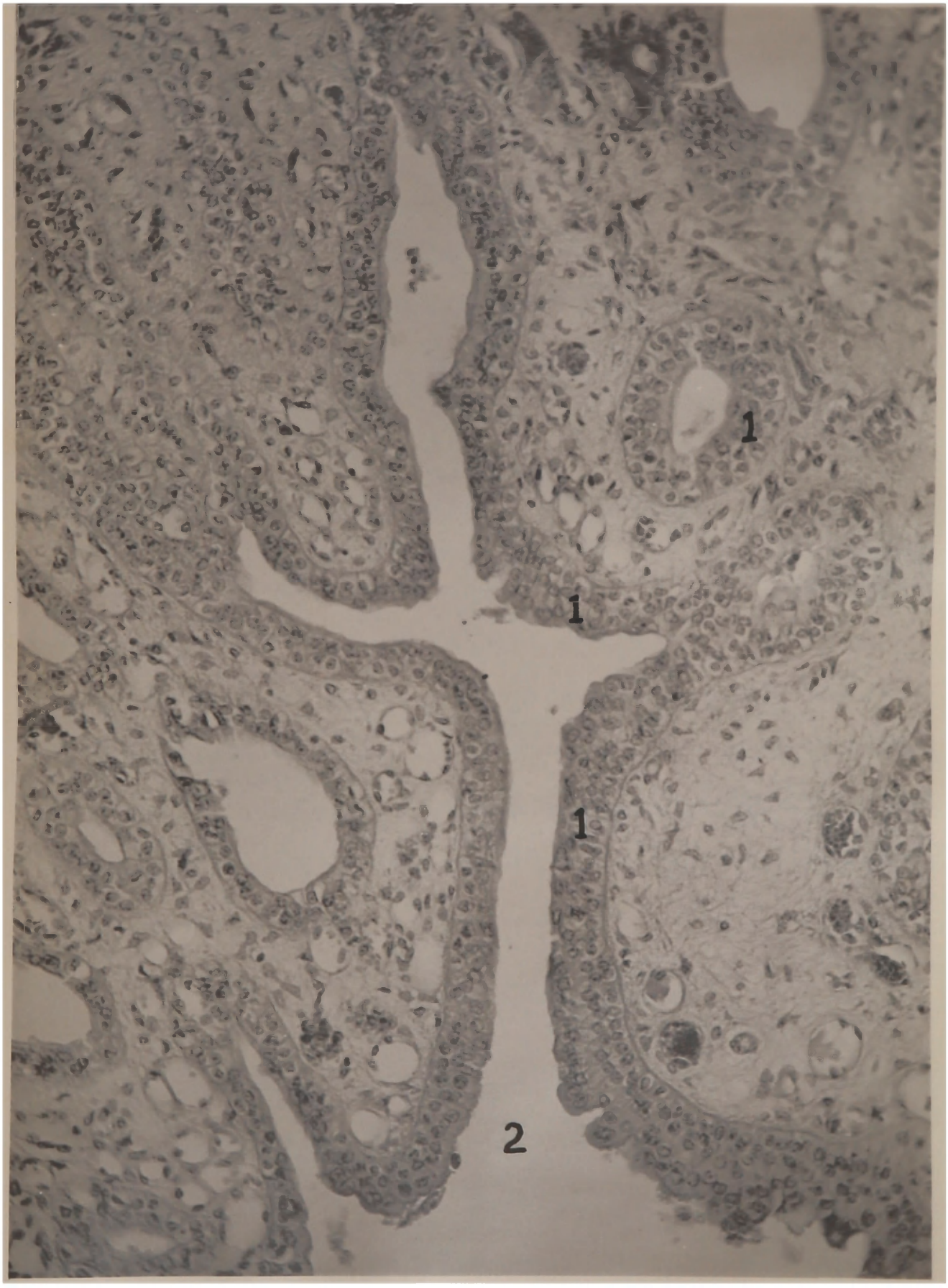

PLATE VII

PLATE VII

The papillary ducts in the ox kidney. H. and E. 320x. Nineteen months old.

1. Transitional epithelium
2. Opening of papillary duct on the papilla

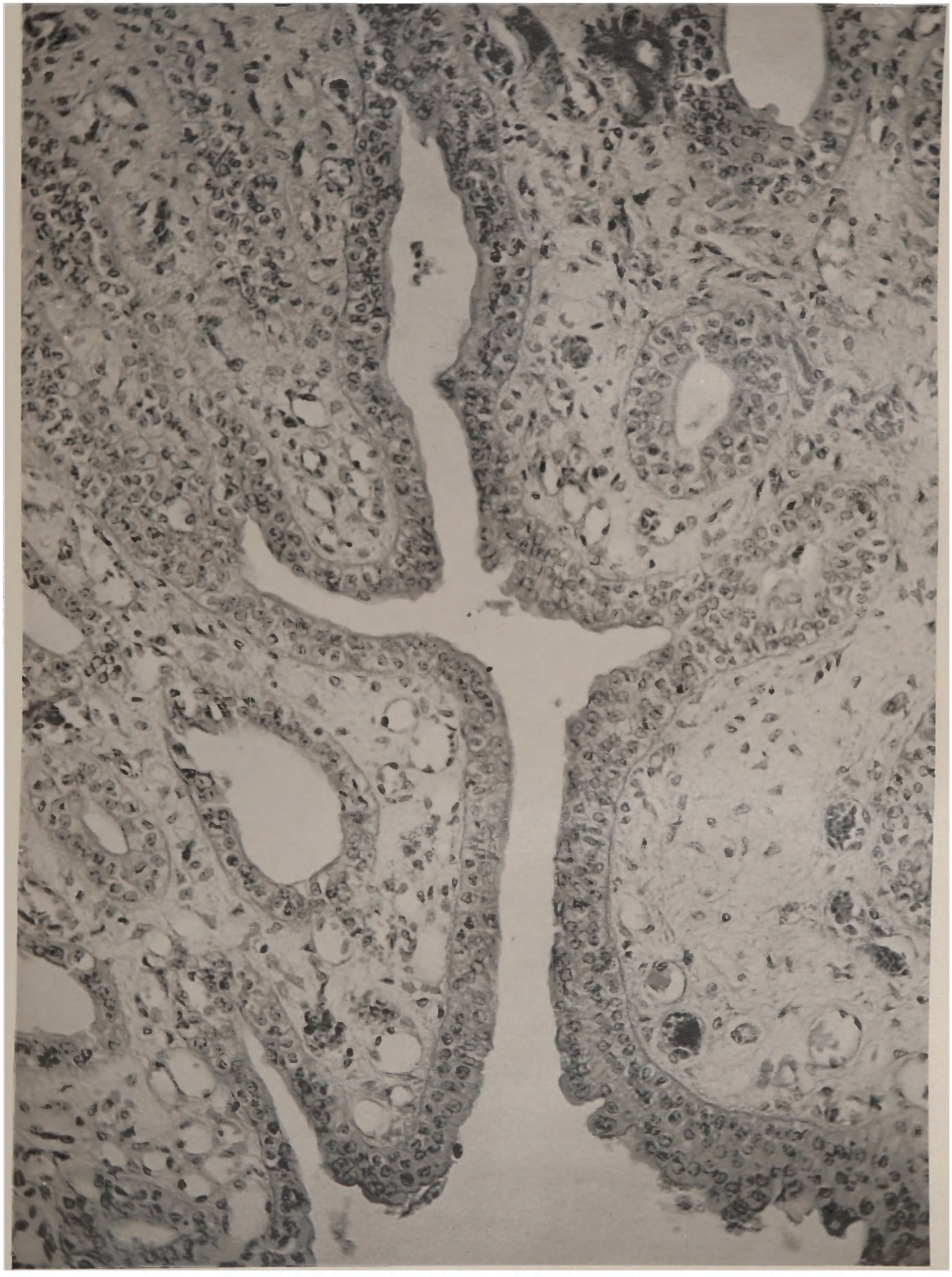

PLATE VII

the papillary duct at which point it changes to simple columnar epithelium.

Duran-Jorda (1953) could not observe the openings of the papillary ducts in the cat kidney and hence came to the conclusion that urine was dialysed through the papillary epithelium. The openings of the papillary duct in the cat kidney were observed in this investigation (Plate VIII).

The basement membrane of the uriniferous tubule

The renal tubules and the excretory ducts are enveloped externally by a well-developed and distinct basement membrane.

The presence of the basement membrane of the uriniferous tubule was observed in the pig kidney although details of its finer structures could not be studied with the ordinary light microscope. No difference was noted in the basement membrane of the uriniferous tubules of other animals of this investigation.

The Papilla

The papilla is the apex of the renal pyramid, the base of which is located at the corticomedullary junction of the kidney. The surface of the papilla is perforated by foramina which are the openings of the papillary ducts. This perforated area of the papilla is

PLATE VIII

The papillary ducts in the cat kidney. H. and E. 220x. Seven weeks old.

1. Opening of papillary ducts
2. Papilla
3. Junction of transitional with simple columnar epithelium

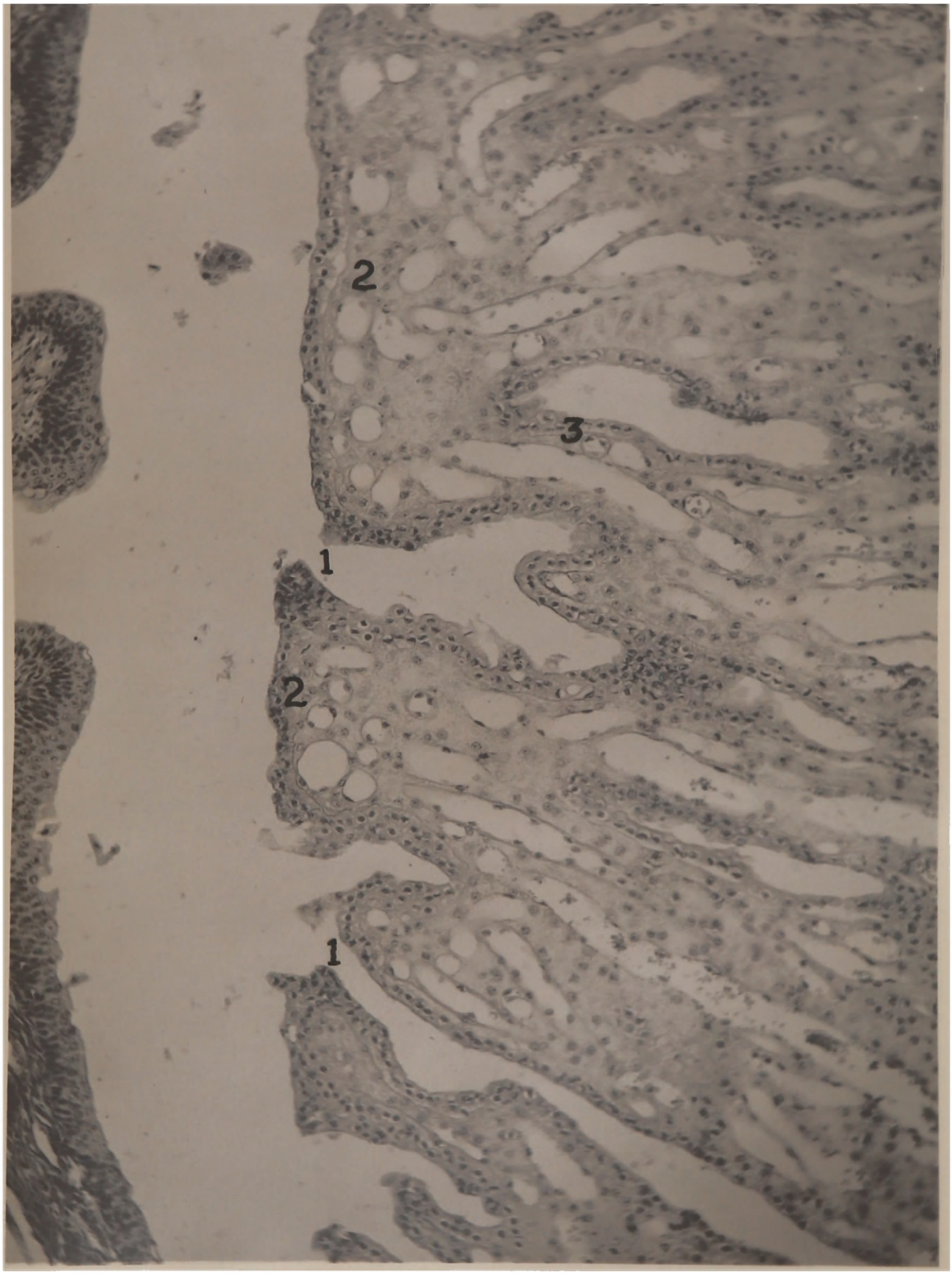

PLATE VIII

PLATE VIII

The papillary ducts in the cat kidney. H. and E. 220x. Seven weeks old.

1. Opening of papillary ducts
2. Papilla
3. Junction of transitional with simple columnar epithelium

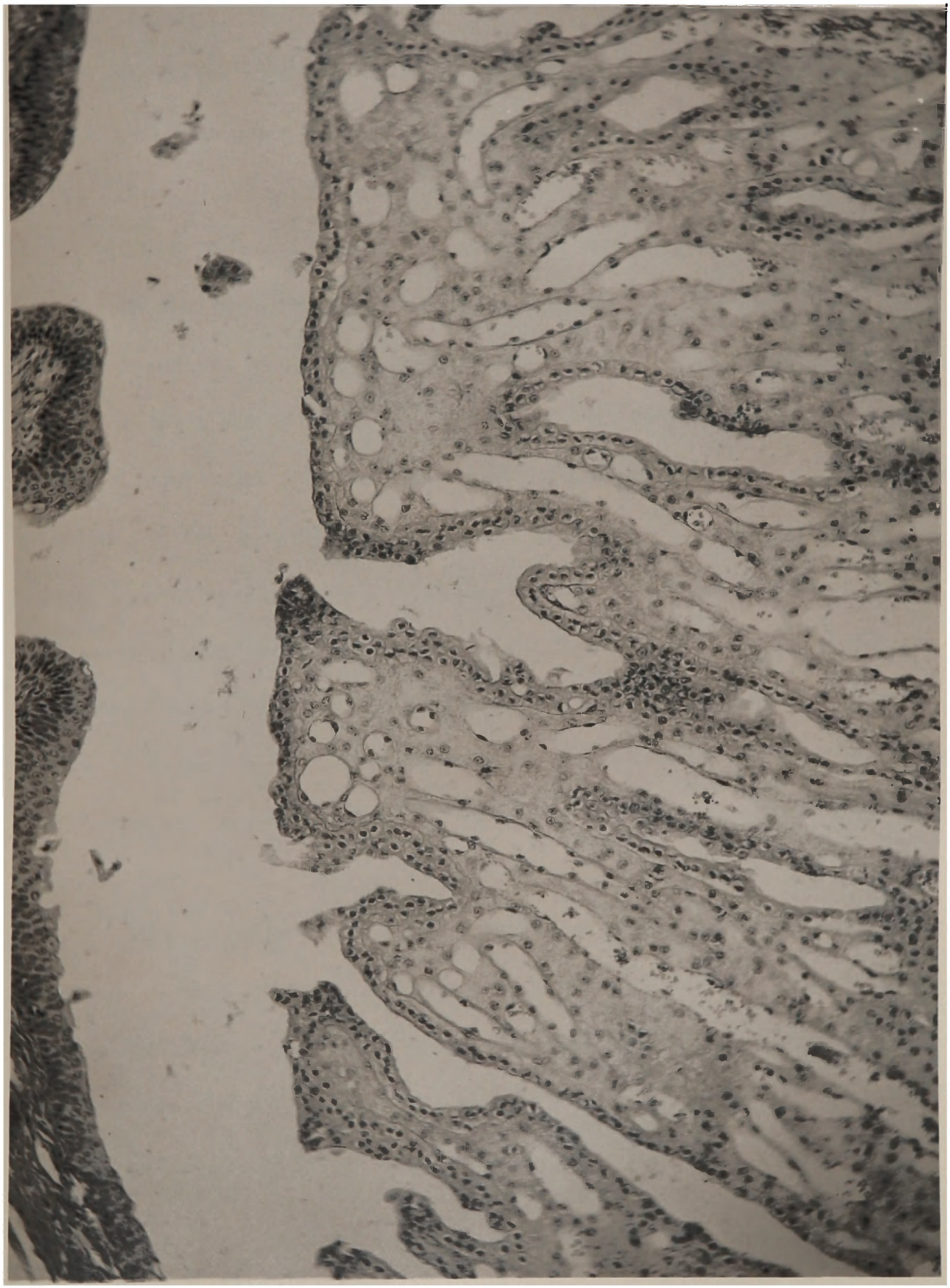

PLATE VIII

called the area cribrosa. The transitional epithelium of the calyx minor reflects over the surface of the papilla and forms the papillary epithelium. This papillary epithelium blends with the epithelium of the papillary ducts at their openings on the papilla.

In the pig, the transitional epithelium of the calyx minor was found to reflect over the sides of the papilla. In the angle of reflection, the high transitional epithelium of the calyx minor became very low and continued as such for some distance along the sides of the papilla. After a short distance this low transitional epithelium became higher and covered the sides and apex of the papilla. The papillary transitional epithelium maintained almost uniform height over the entire surface of the papilla except on the sides near the angle of reflection. The height of the transitional epithelium of the papilla never acquired the original height which lined the calyx minor.

The papillae of the other animals under investigation were similar to that of the pig except that the transitional epithelium of the papilla was higher in the horse; almost equal in the ox; and lower in the sheep, goat, dog, and cat.

The Interstitial Connective Tissue

The interstitial connective tissue is very scanty in the normal mammalian kidney and consists of delicate reticular tissue which forms a fine network between the tubules. The tissue is more abundant in the papillary portion of the medulla. Collagenous and elastic fibers are found only in the walls of the larger blood vessels. Some loose connective tissue is present between the papillary ducts. A few strands of connective tissue enter the glomerulus along the blood vessels. Fibroblasts and histiocytes are also found in the interstitial space of the mammalian kidney. Proliferation of this connective tissue throughout the kidney may play an important part in disease.

The interstitial space of the pig kidney was mainly occupied by reticular fibers which extended from the capsule to the apex of the papilla (Plate IX). Reticular fibers were found to be more numerous near the blood vessels and in the interstitial spaces of the medulla. Collagenous fibers were also found to surround the large blood vessels especially at the corticomedullary junction. A few very fine collagenous fibers were observed to invest the uriniferous tubules and the Bowman's capsule of the kidney. Fibroblasts, histiocytes, and mast cells were also noted in the interstitial space of the pig kidney.

PLATE IX

Kidney of the pig stained for reticular connective tissue. Note the distribution of reticular fibers in the interstitial spaces of the parenchyma and the glomerulus. Silver Stain (Gridley modification). 460x. Seven months old.

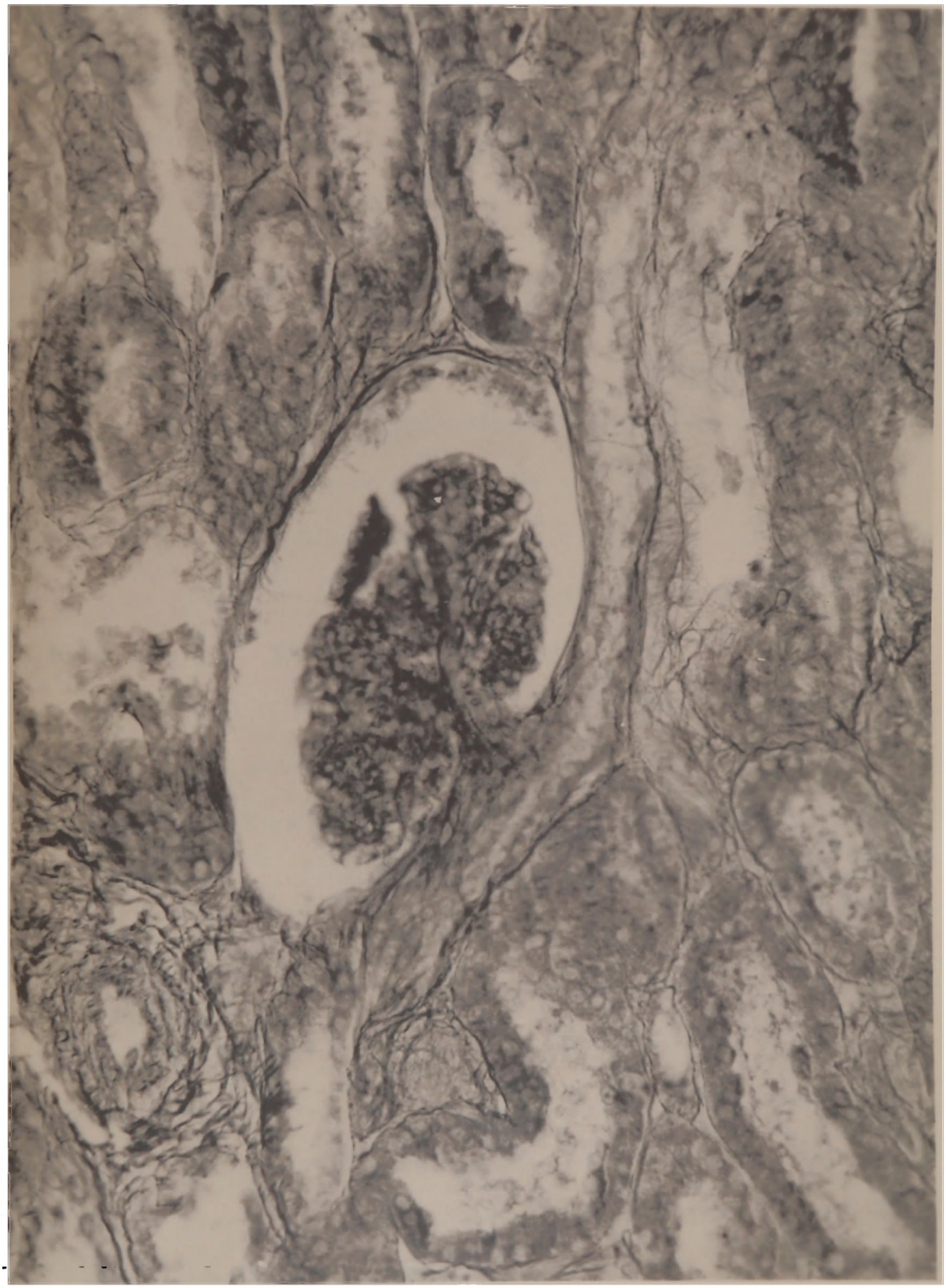

PLATE IX

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Kidney of the pig stained for reticular connective tissue. Note the distribution of reticular fibers in the interstitial spaces of the parenchyma and the glomerulus. Silver Stain (Gridley modification). 460x. Seven months old.

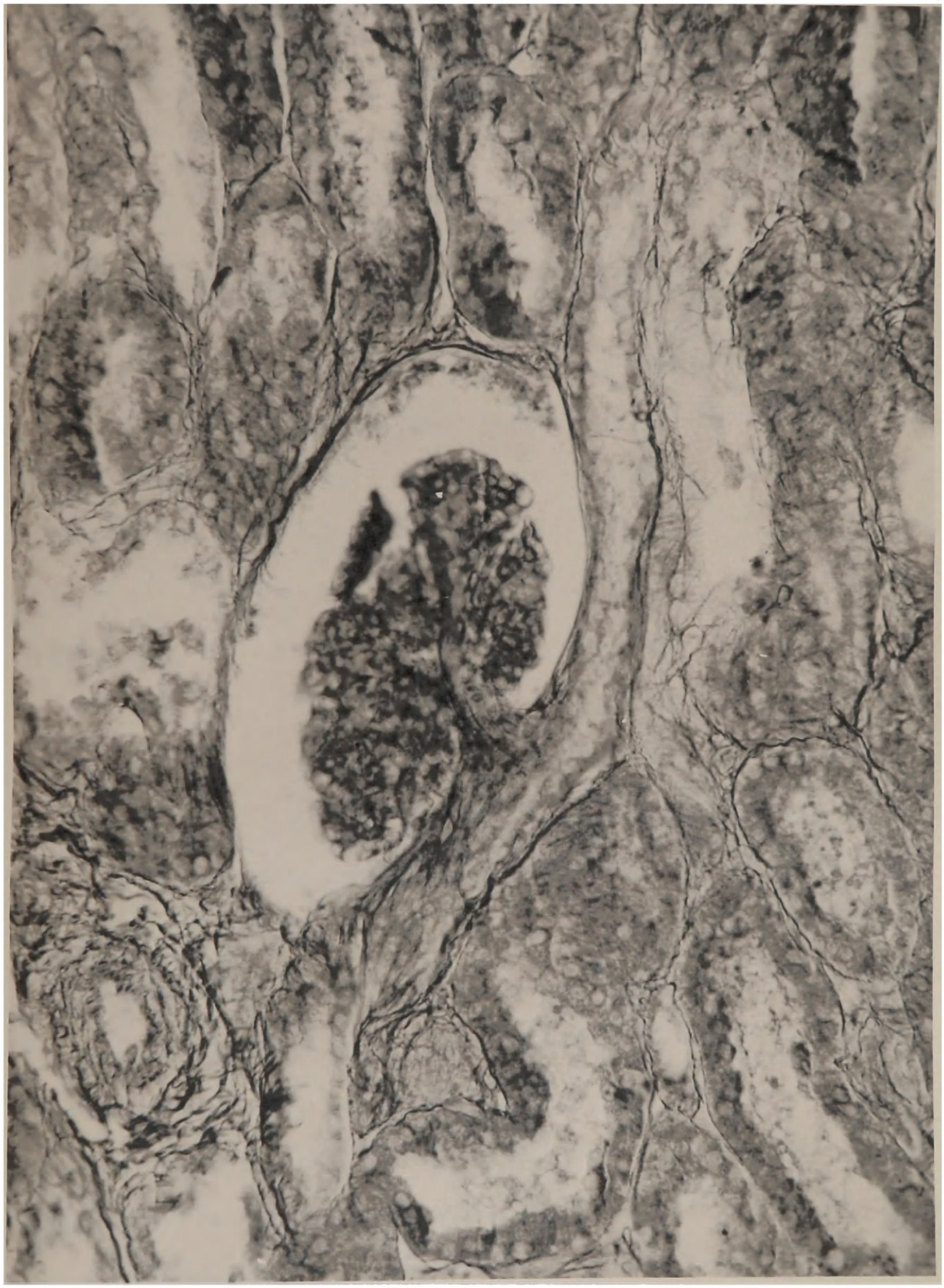

PLATE IX

The interstitial connective tissue of the other animals under investigation was similar to that of the pig except that the mast cells were absent in the dog and cat.

The intertubular cell groups or Becher's cells (Plate X)

The presence of intertubular cell groups in the human kidney was reported by Schloss (1946), Neumann (1949), and Becher (1949, 1950). These intertubular cell groups are situated in the human kidney at the points where the connective tissue is abundant, in the immediate neighborhood of the afferent arterioles, and other cortical arterial vessels. These intertubular cell groups are also called "paraportal cell islets" by Becher. The presence of intertubular cell groups has not yet been reported in the domestic animals.

In the kidney of the pig, these intertubular cell groups were observed in the interstitial spaces of the cortical region between the uriniferous tubules. They were also found in the close vicinity of Bowman's capsule and around the cortical arteries. Those surrounding the arteries usually were found to be larger. Some of the smaller groups were found to be encapsulated. The cells did not present a regular shape. Most of the cells were polygonal except a few which were found to be oval. The cytoplasm was faintly eosinophilic and nongranular. The nucleus was smaller and darker than

PLATE X

Kidney of the ox. H. and E. 634x. Six years old.

1. Intertubular cell group or Becher's cells
2. Interlobar artery
3. Proximal convoluted tubule
4. Distal convoluted tubule
5. Thin limb of Henle's loop

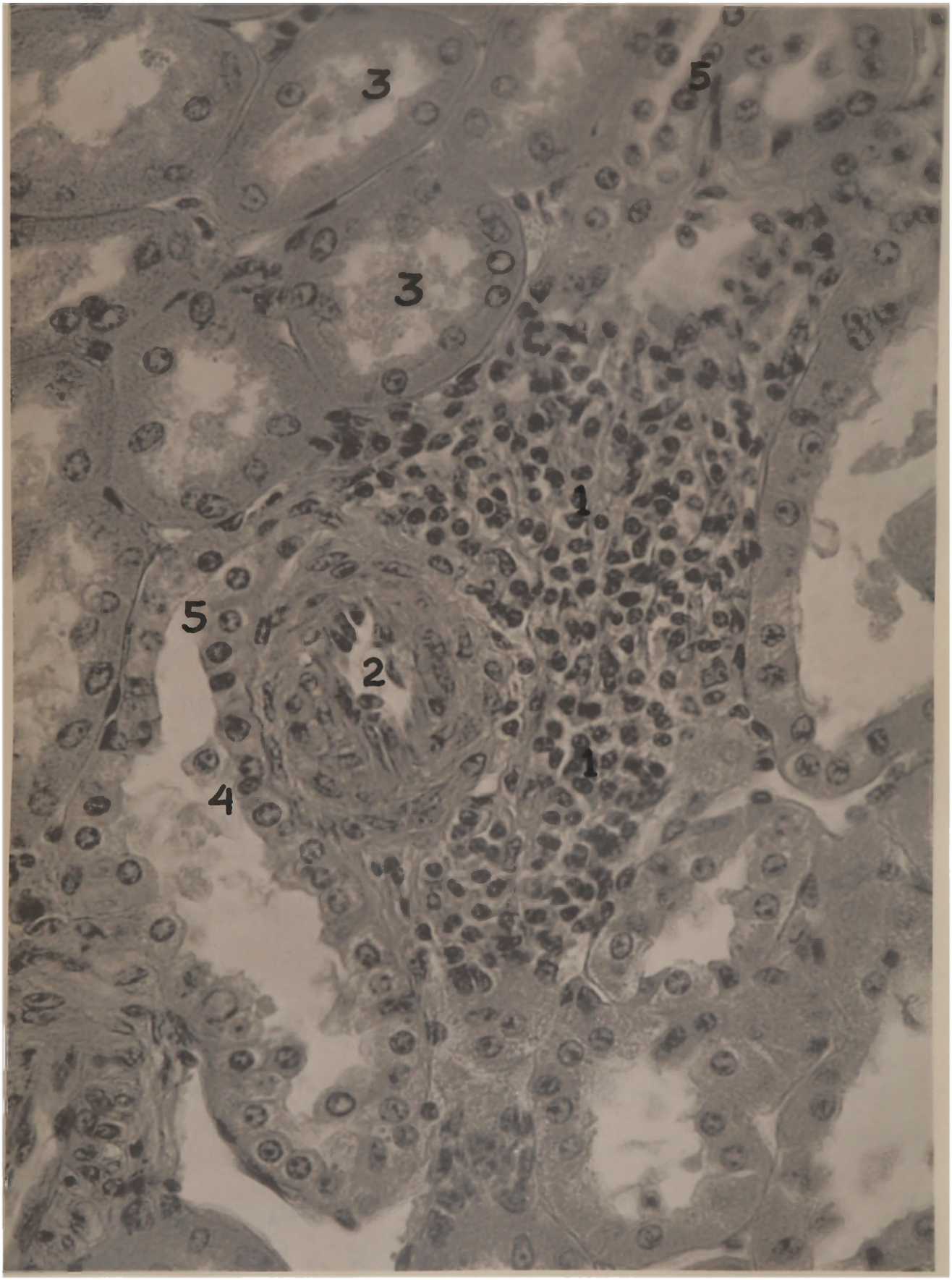

PLATE X

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Kidney of the ox. H. and E. 634x. Six years old.

1. Intertubular cell group or Becher's cells
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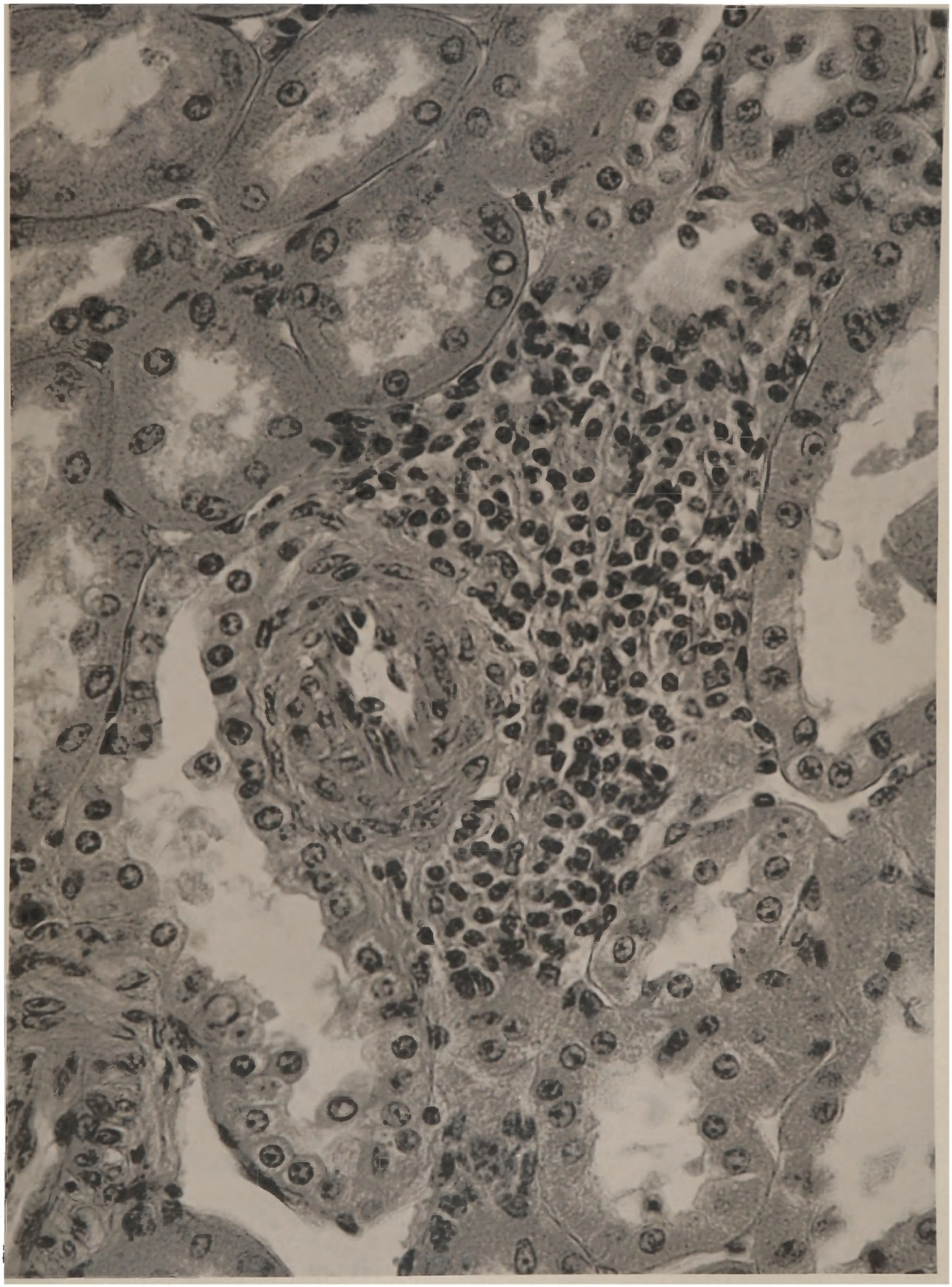

PLATE X

that of the surrounding tubules. The nuclei of these cells were generally spherical, although a few oval nuclei were also noticed. They were located either in the center or towards one corner of the cell. The nucleus presented a characteristic appearance. Four or five crescent-shaped dark nucleoli were found to be present along the periphery of the nucleus in close approximation to each other and the nuclear membrane. A large deeply stained nucleolus was situated at the center of the nucleus. The space between these nucleoli was found to be unstained and free from chromatin granules.

These cell groups were found to be more numerous and better developed in the ox and horse than those of the pig. In the ox, the cells were more eosinophilic and contained more cytoplasm than that of the pig (Plate X). These cell groups were less developed in the sheep, goat, and dog, and absent in the cat.

Cell unit of Goormaghtigh or socleplasmodium (Frontispiece)

A cluster of small cells with pale nuclei between the macula densa and the glomerulus proper, in the concavity between the afferent and the efferent arterioles of the mammalian kidneys can be seen in microscopic sections. This cluster of small cells is called the cell unit of Goormaghtigh, or Goormaghtigh's cells.

In the pig kidney these cells were found to be closely associated with the juxtaglomerular cells and the cells of the macula densa. Goormaghtigh cells of other animals of this investigation were found to be similar to that of the pig.

SUMMARY AND CONCLUSIONS

1. Comparative microscopic studies were made on the kidneys of sixty-nine domestic animals of seven different species, the pig being chosen as a type. Tissues were routinely fixed in F.A.A., sectioned at seven microns, and stained with hematoxylin and eosin stains. Additional stains were used to demonstrate special structures.

2. The tunica fibrosa of the capsule of the kidney of the domestic animals in this investigation was found to consist of two layers, an outer and an inner, with the exception of the cat, where the kidney capsule had only one layer, the inner layer being absent. The outer layer of the tunica fibrosa consisted of dense collagenous and a few elastic fibers, and the inner layer was formed by loose collagenous and reticular fibers, with smooth muscle fibers present in all animals except the cat. In the sheep and goat, and to a lesser extent in the ox, the muscle fibers were very numerous, and appeared to form a distinct muscular layer. No reports have been found which mention the presence of smooth muscle cells in the capsule of horse, goat, pig, and dog.

3. The juxtamedullary renal corpuscles in the horse (191μ), pig (156μ), dog (124μ), and cat (106μ) were larger than the cortical ones; the cortical renal corpuscles in the horse, pig, dog, and cat were 178μ, 137μ, 122μ, and 96μ, respectively. The reverse was true in the ox, sheep, and goat, where the juxtamedullary renal corpuscles were 173μ, 147μ, and 157μ, respectively, and the cortical ones were 181μ, 153μ, and 158μ, respectively. Juxtamedullary renal corpuscles ranged between 106μ and 191μ in different species, being larger in the horse, ox, and goat; and smaller in the sheep, dog, and cat, as compared to those of the pig. The cortical renal corpuscles were larger in the horse (178μ), ox (181μ), sheep (153μ), and goat (158μ), and smaller in the dog (122μ) and cat (96μ) than that of the pig (137μ). No reports have been found for any species which stated that cortical renal corpuscles were larger than those of the juxtamedullary ones as seen in the ox, sheep, and goat in this investigation.

4. The juxtamedullary glomeruli were larger than the cortical ones in the pig (130μ), horse (166μ), dog (100μ), and cat (87μ); the cortical glomeruli in the pig, horse, dog, and cat were 114μ, 159μ, 98μ, and 82μ, respectively. In the ox the cortical glomeruli (150μ) were larger than the juxtamedullary ones (141μ). The cortical and juxtamedullary glomeruli in the sheep were equal (123μ), and in

the goat they were 127μ and 126μ, respectively. The juxtamedullary glomeruli of the horse (166μ) and ox (141μ) were larger than those of the pig (130μ), while in the sheep (123μ), goat (126μ), dog (100μ), and cat (87μ) they were smaller. The cortical glomeruli of the horse (159μ), ox (150μ), sheep (123μ), and goat (127μ) were larger than those of the pig (114μ), while in the dog (98μ) and cat (82μ) they were smaller.

5. The intercapillary space of the glomerulus of all animals under investigation contained small amounts of collagenous and reticular fibers along with fibroblasts and histiocytes.

6. The capsular space of Bowman's capsule was larger in the goat, ox, and sheep; smaller in the horse and cat; and almost equal in the dog, as compared to that of the pig.

7. The juxtaglomerular apparatus in all animals in this investigation contained some spindle-shaped smooth muscle cells of the media of the afferent arteriole along with the usual myoepithelioid cells. The juxtaglomerular apparatus of the horse, ox, sheep, and cat was similar to that of the pig. In the goat and dog, the juxtaglomerular cells were more numerous and better developed.

8. In comparison with the pig (45μ), the diameter of the proximal convoluted tubule was greater in the horse (56μ), ox (50μ), and goat (48μ); equal in the sheep (45μ); and smaller in the dog (39μ)

and cat (41μ). The height of the cells lining the tubule (pig, 14μ) was greater in the horse (15μ); equal in the cat (14μ); and smaller in the ox (13μ), sheep (11μ), goat (11μ), and dog (11μ). The brush border was found to form a cluster from each individual cell in the proximal tubule of the pig kidney, whereas in other animals of this investigation they were uniformly arranged along the luminal border of the cells. The basal striations were more distinct in the dog. Fat globules were observed in the proximal tubule of the cat and dog.

9. The diameter of the thin segment of the loop of Henle ranged between 21μ and 30μ in different species, being greater than the pig in the horse, ox, and goat; and smaller than the pig in the sheep, dog, and cat. The lumen was wider than the pig in the horse, ox, sheep, and goat; equal to it in the cat; and narrower in the dog.

10. The diameter of the distal tubule ranged between 30μ and 50μ in different species, being larger in the horse, ox, and goat; equal to the pig in the sheep; and smaller in the dog and cat. Compared to that of the pig (8μ), the epithelial height was greater in the horse (9μ); equal in the ox (8μ) and goat (8μ); and smaller in the sheep (7μ), dog (7μ), and cat (7μ). The lumen of the distal tubule was greater in the horse, ox, sheep, and goat; and smaller in the dog and cat.

11. The macula densa in all animals in this investigation was single-layered except in the horse, in which it was found to be stratified and contained more faintly stained cells. No reports were found regarding the stratified nature of the macula densa of the horse.

12. Compared with the pig (50μ), the diameter of the straight collecting tubule was greater in the horse (66μ) and ox (53μ); and smaller in the sheep (39μ), goat (42μ), dog (37μ), and cat (37μ). The cell height was equal in the horse (14μ); and smaller in the ox (12μ), sheep (10μ), goat (12μ), dog (9μ), and cat (5μ) than that of the pig (14μ). The lumen of the tubule was greater in the horse, ox, and cat; smaller in the sheep, goat, and dog. The cell boundaries were more distinct than the pig in the horse, ox, goat, and dog; and less distinct in the sheep and cat.

13. The papillary duct was lined by a faintly stained simple tall columnar epithelium which became transitional toward the opening of the duct on the papilla in all animals of this investigation except the dog. The diameter of the papillary duct ranged from 54μ (dog) to 138μ (horse), the other species measuring as follows: pig, 96μ; ox, 91μ; cat, 60μ; sheep, 59μ; goat, 57μ. As compared with that of the pig (21μ), the epithelial height was greater in the horse (55μ), ox (33μ), and goat (22μ); and smaller in the sheep (18μ), dog (13μ),

and cat (14μ). In the horse, ox, goat, and sheep, the transitional epithelium extended for a greater distance in the papillary ducts from their openings on the papilla than in the pig. The papillary duct of the dog kidney was lined only by a simple columnar epithelium throughout its course. The openings of the papillary ducts on the papilla were found to be present in all animals of this investigation. Langham et al. (1942) found only simple columnar epithelium lining the papillary ducts of the bovine kidney. In the present study transitional epithelium extended about 1500μ into the papillary duct in the specimens examined. Duran-Jorda (1953) doubted the existence of the openings of the papillary ducts in the cat kidney and thought that urine was dialysed through the papillary epithelium into the pelvis. These openings of the papillary ducts of the cat kidney were found to be present in this investigation.

14. The epithelium covering the papilla was found to be transitional in all domestic animals in this study.

15. The interstitial spaces were found to contain reticular fibers; a few collagenous fibers around the tubules, Bowman's capsule, and blood vessels; fibroblasts, histiocytes, and mast cells in all animals in this investigation except in the dog and cat where mast cells were absent. No reports were found regarding the presence of mast cells in the kidney of any species including man and laboratory animals

16. The intertubular cell groups or Becher's cells were found to be present in the interstitial spaces in the cortical region, especially in the close neighborhood of Bowman's capsule, the cortical arteries, and arterioles. The cell groups near the arteries were larger than cell groups elsewhere. Some of the smaller groups were found to be encapsulated. The cells were mostly polygonal with faintly eosinophilic cytoplasm and darkly stained nuclei. In comparison with the pig, these cell groups were found to be more numerous in the ox and horse; less numerous in the sheep, goat, and dog; and absent in the cat. In the ox the cells were larger and more eosinophilic than that of the pig. This is thought to be the first report regarding the presence of these cell groups in the kidney of domestic animals.

17. The cell unit of Goormaghtigh was found in all animals under study to be present in close association with the juxtaglomerular cells and the cells of the macula densa in the triangular space formed by the afferent and efferent arterioles and the macula densa. No species differences were observed. No reports were found concerning the presence of these cells in the kidney of large domestic animals. Ham (1953) stated that there was as yet no certainty about their nature, function, or nomenclature in the human kidney.

From the results of this investigation it is concluded that the general plan of the structure of the kidney of all domestic animals is the same except a few species variations.

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