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THE HISTOLOGY OF THE BLADDER AND THE PROXIMAL URETHRA OF THE DOMESTIC ANIMALS

By

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A THESIS

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ABSTRACT

Comparative histological studies of the bladder and proximal urethra were made on forty-eight domestic animals of seven species. The transitional epithelium was highest at the vertex of the bladder. The horse had the highest epithelium, followed in decreasing order by the sheep, pig, cow, goat, cat, and dog; it was lowest in the bladder neck of the cat. The horse had the greatest number of cell layers at the vertex (13), followed by the sheep, cow, and pig (10), the goat (6), and the dog and cat (5). It was impossible to distinguish the species, or any particular region of the bladder, by the shape of the transitional epithelial cells. Lymphocytes occurred in the bladder epithelium, more frequently in the cow and less frequently in the cat. Glands were not observed in any area of the bladder wall of any domestic animal studied. There was a continuous layer of capillaries under the epithelium of some goats. Lymphoid nodules were observed in the tunica propria of most of the cow bladders. The muscularis mucosae was best developed in the horse, very thin in the cow, dog, and pig, represented by only a few muscle cells in the sheep and goat, and not consistently present in the cat. Small ganglia were observed in the submucosa of the horse

and cat bladders only. Fat often appeared in the connective tissue of the muscularis externa of the pig. Ganglia were observed in the muscularis externa of all domestic animals except the sheep and the goat. The serosa of the horse, cow, and dog was thickest; less thick in the sheep, goat, and pig; and thinnest in the cat. The serosa of the cat had the largest amount of elastic tissue, contained ganglia, and fat. Fat was also observed in the serosa of the horse and pig.

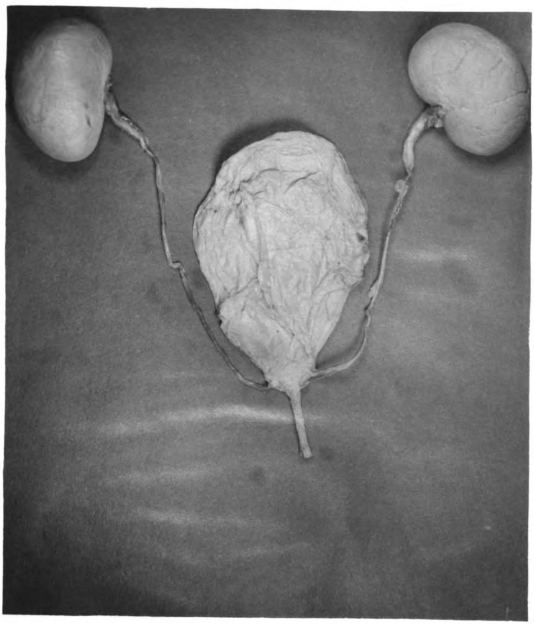
The transitional epithelium of the proximal urethra of all animals was similar in height and structure to that of the bladder neck. The density of the tunica propria appeared greater toward the epithelium in all animals except the cow. Smooth muscle appeared in the tunica propria of all animals except the cat; the horse had the most; in the pig, dog, and sheep it was confined to an area near the muscularis externa; and muscle bundles were absent but individual muscle cells were present in the cow. Glands were present in the tunica propria of the boar and male dog, but not observed in any other animal. The urethra of the sheep and the goat had a single layer of smooth muscle; the cat and dog had two layers of muscle, entirely smooth in the cat and female dog but in the male dog skeletal muscle appeared in both layers; in the cow, horse, and sheep three layers of smooth muscle were present. Skeletal muscle was observed in the bull and the boar. In the boar it was

thick ventrally, thin laterally, and absent dorsally. The connective tissue in the muscularis was scant in the cat and pig, and increased in amount in the dog, sheep, goat, cow, and horse. In addition, elastic fibers appeared in greater numbers in the horse. Fat appeared between the prostate and muscularis externa of the pig bladder. No sex differences were noted in the bladders of domestic animals. No sex differences in the proximal urethra were observed other than those due to basic anatomical differences in the reproductive systems. While it was impossible to differentiate most of the bladders of the domestic animals by a histological examination, the cat bladder might be characterized by a combination of the following observations: an almost complete absence of a muscularis mucosae, a thin serosa with an abundance of elastic tissue in it, and by its relatively thin epithelial layer.

FRONTISPIECE

Urinary system of a male cat. Approximately natural size. Adult.

1. Vertex of the bladder
2. Lateral wall of the bladder
3. Trigone of the bladder
4. Proximal portion of the urethra
5. Ureter
6. Kidney



DEDICATION

This work is dedicated to all of my students--at Olivet College, at Michigan State University, and at Hardin-Simmons University -- without whose inspiration this work would never have been completed.

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Page

Tunica propria 21

Corpus cavernosum 21

Muscularis externa 22

MATERIALS AND METHODS 23

RESULTS AND DISCUSSION 24

Gross Anatomy of the Bladder 24

Histology of the Bladder 26

Epithelium 26

Tunica propria 30

Muscularis mucosae 31

Submucosa 32

Muscularis externa 32

Serosa 34

Gross Anatomy of the Urethra 35

Male 35

Female 35

Histology of the Proximal Urethra 37

Epithelium 37

Tunica propria 37

Corpus cavernosum 38

Muscularis externa 39

TABLE OF CONTENTS

	Page
INTRODUCTION	1
HISTORICAL	3
REVIEW OF LITERATURE	5
Gross Anatomy of the Bladder	5
Description	5
Musculature	5
Blood vessels and lymphatics	6
Innervation	6
Histology of the Bladder	7
Epithelium	7
Tunica propria	11
Muscularis mucosae	12
Submucosa	13
Muscularis externa	14
Serosa	16
Gross Anatomy of the Urethra	16
Histology of the Urethra	19
Epithelium	19

Page

SUMMARY 41

LITERATURE CITED 45

LIST OF TABLES

TABLE Page

I. Average Highest Epithelial Heights in Various Regions of the Bladder and the Number of Cell Layers at the Point Where Measurement Was Taken 28

II. A Comparison of Urethral Epithelial Cell Heights and Cell Layers of This Investigation to Those of Ellenberger 36

LIST OF PLATES

PLATE		Page
I.	Horse bladder showing thick transitional epithelium	52
II.	Bladder of the cow	54
III.	Bladder of the cow	56
IV.	Bladder of the goat	58
V.	Bladder of the pig	60
VI.	Bladder of the horse	62
VII.	Ganglion in the submucosa of the cat bladder	64
VIII.	Bladder of the dog	66
IX.	Bladder of the cat	68
X.	Serosa of the pig bladder	70
XI.	Serosa of the sheep bladder	72
XII.	Bladder of the sheep	74
XIII.	Bladder of the pig	76
XIV.	Duct of prostate gland entering pig urethra	78
XV.	Smooth muscle in the tunica propria of the horse urethra	80
XVI.	Skeletal muscle inserting on the dorsal fibrous connective tissue raphe in the boar urethra	82

PLATE Page

XVII. Elastic connective tissue fibers in the muscularis externa of the horse urethra 84

INTRODUCTION

A study of the comparative histology of the urinary bladder, the vesico-urethral junction, and the proximal part of the urethra was undertaken as part of a continuing problem involving the entire urinary tract of domestic animals. The histology of the human urinary tract has been adequately described by such well-known workers as Mollendorf (1930), Maximow and Bloom (1952), Smith and Copenhaver (1953), and Greep (1954). The histology of the urinary organs of the domestic animals has not received as much attention. Bauch (1911), Ellenberger (1911), and Hiilivirta (1911) did exhaustive studies on the bladder and urethra of domestic animals. English translations of these German works are not available, and developments in histological techniques since that time limit their value. Trautmann and Fiebiger (1952) have very little on the urinary system, and no comparative data on the bladder of domestic animals. Limited areas of certain animals have been described by certain investigators. Paneth (1876) and London (1881) studied the epithelium of the dog bladder. Eggeling (1901) described the bladder epithelium of the cow and guinea pig. Lendorf (1901) investigated the mucous membrane of the bladder of the cat, dog, sheep, pig, and

horse. Rigal (1904) and Graning (1934) described the bladder in some detail, and Graning (1936) studied the bladder musculature of the horse, cow, and pig.

HISTORICAL

Vicary (1490-1561), who gave the first English account of the anatomy of the bladder, stated that the bladder was the first organ to come into view when the pelvis was opened. He observed that "it is compounded by two panniculi, has a cold dry complexion, and holds a pitcher full of urine." Vesalius (1514-1564) stated that the bladder was composed of longitudinal, transverse, and oblique fibers, and he found it to have a varying capacity. Fallopius (1523-1562) was the first to regard the bladder as muscular in nature, and maintained that these muscles were under the control of the will. Spieghel (1578-1625) gave the name "detrusor urinae" to the longitudinal muscles of the bladder because he thought that they expelled the urine. Snape (1644-?) described the horse bladder as a "globose figure shaped like a pear." The neck was longer and narrower in the male than in the female. The sphincter at the neck of the bladder seemed to be nothing more than the middle muscle layer, thicker here than elsewhere. Cowper (1666-1709) proposed that the bladder was nothing more than a dilatation of the ureters. Cheselden (1688-1752) gave the following description: "The bladder of urine is seated in the pelvis of the abdomen and its shape is orbicular.

Its coats are the same as the guts and other organs already described." Lieutaud (1703-1780) was the first to describe the trigone of the bladder. Henle (1809-1885) discovered the external sphincter of the bladder.

The above review was compiled from Griffiths (1891), Snape (1683), and Mettler (1947).

REVIEW OF LITERATURE

Gross Anatomy of the Bladder

Description. Chauveau (1873) called the bladder a membranous reservoir, and determined that the average weight of the horse bladder when empty was 16 ounces. M'Fadyean (1884) applied the terms "fundus" and "neck" to the gross parts of the horse bladder. Martin (1915) stated that without overstretching the bladder of the horse could hold from two to three liters of urine. Evans (1936) stated that the bladder of the cat had a long neck. Latimer (1951) found that the bladder made up 0.127 percent of the body weight of the dog. Reighard and Jennings (1935), Hyman (1942), and Leach (1952) described the bladder of the cat as pear-shaped. Van Duzen and Duncan (1953) stated that the human bladder was pear-shaped.

Musculature. Vaughan (1888) maintained that grossly one could distinguish an external longitudinal and an internal circular layer of muscle in the horse bladder. Martin (1915) said of the horse bladder that muscle bundles coursed in all directions so that a regular layering was not apparent. Graning (1934, 1936) gave a detailed account of the gross musculature of the dog, horse, cow,

pig, and man. He dissected the three layers of muscle, and his work contained an elaborate description of the course of each layer. In the dog he commented on other layers as well. Montane et al. (1949) stated that the muscular layer of the horse bladder formed a "matting" which was thinner than in the human. Miller (1952) suggested that it was grossly possible to distinguish an outer longitudinal and an inner circular muscle layer in the dog.

Blood vessels and lymphatics. Hoggan (1881) stated that lymph vessels originated in the trigone, and were large in the horse and sheep bladder. Vaughan (1888) noted that there were many lymphatics in the wall of the horse bladder. Gerota (1896) noted in the cat bladder the lymph vessels of the fundus united with those of the urethra and the vagina. Lendorf (1901) could not demonstrate lymphatic capillaries by a gross technique in the mouse, rat, sheep, cow, or pig. Baum (1912) stated that the mucous membrane of the neck of the bladder of the cow as well as that of the openings of the ureters had more lymph vessels than the mucous membrane of the vertex or the body.

Innervation. Grunstein (1899) noted that in the bladder of the cat, dog, mouse, and rat, ganglia could be observed grossly if well stained. Kleyntjens and Langworthy (1937) found large nerve trunks

at the base of the cat bladder. Langworthy and Kolb (1938) suggested that in the cat bladder the main mass of sympathetic fibers entered medial to the ureter, and the parasympathetic fibers ran lateral to the ureter and made up a larger portion of the long nerves over the surface of the bladder.

Histology of the Bladder

Epithelium. Most workers regarded the epithelial lining of the mammalian bladder as transitional. However, M'Fadyean (1884) called it stratified and transitional. Ellenberger (1911) found it to be "many layered" and Zeitzschmann et al. (1943) stated that it was both stratified squamous and transitional. All investigators agreed that it was distinctive for its distensibility.

The number of cell layers in the epithelium varied depending on the animal and the state of distention of the bladder. London (1881) determined that in the contracted dog bladder there were five cell layers, and in the distended organ there was one. Bauch (1911) stated that the epithelium of the pig bladder was four to five cell layers thick. He found that the epithelium of the horse bladder was six to ten cell layers thick. Gaebler (1921) reported that there were three to four cell layers in the epithelium of the cat bladder. Graning

(1934) stated that there were four to five cell layers in the epithelium of the dog bladder.

Many investigators measured the height of the bladder epithelium of the domestic animals. London (1881) found that the epithelium of the contracted dog bladder was 51 microns thick and four microns in the distended condition. Hey (1895) determined that the epithelium of the cat bladder varied between 2.02 and 4.03 microns. Harvey (1909) noted that the epithelium of the contracted dog bladder was 172 microns and 27.6 microns when it was distended. Bauch (1911) found that the epithelium of the goat, sheep, and cow was higher than that of the pig, and of the ruminants the cow had the highest bladder epithelium, the sheep was next, and the goat was lowest. Bauch also noted that the epithelium of the dog bladder was about the same as that of the pig and sheep. The epithelium of the cat bladder was lower than that of the dog.

The shape of the cells in transitional epithelium has been the subject of many investigations because of the ability of the cells to alter their shapes under various stresses of the bladder. While studying the epithelium of the rat, dog, and rabbit, Paneth (1876) observed that the cells of the surface layer were wider than they were high but not as flat as surface cells of stratified squamous epithelium. The middle layer contained various-shaped columnar cells

which rested on a many-celled basal layer. Paneth found that all three layers flattened upon distention. Doigal (1890) observed three strata of cells in the epithelium of the dog and cat bladders, the surface layer of which was irregular and flat and had a granular and a nongranular portion. These cells contained one, two, or four nuclei, and each nucleus contained up to fifteen nucleoli. Two rows of cells were found under the surface layer, and mitotic figures occurred in the second row. Rigal (1904) and Harvey (1909) studied the bladders of dogs, and both workers described three levels of the epithelium. Rigal found that the basal layer had rounded tips, the cells of the middle layer were spindle-shaped, and the superficial cells had rounded nuclei. However, Harvey considered that the basal layer was composed of cuboidal cells, the middle layer had three rows of polygonal cells, and those of the surface layer were large and ovoid. Upon distention the cell outlines disappeared. Bauch (1911) studied the bladders of the domestic animals and observed arrangements similar to those described by Doigal for the pig except that the cells of the basal layer were small and cuboidal, and in the middle layer the cells were twice the size of those of the basal layer. The surface cells were not seen in all places, but those that were apparent were polyhedral, mostly five-sided.

Bauch described cells peculiar to the pig which had a rod-shaped nucleus directed perpendicularly to the surface. These cells were spindle-shaped and were more numerous in the middle layer. Bauch further noted that it was not as easy to distinguish three strata in the ruminants and observed that the surface cells were not as regular as those of the pig. The basal cells of the horse bladder epithelium were cuboidal to columnar in shape and the cells of the middle layer were generally large. Bauch found that large surface cells characterized the epithelium of the dog bladder and that these cells had large nuclei with one distinct nucleolus. The superficial cells of the cat bladder resembled those of ruminants.

Ellenberger (1911) observed that the superficial cells of the epithelium of the horse bladder were "brick shaped." Graning (1934) reported that the surface cells of dog bladder epithelium were large polygonal cells, and the epithelium was arranged in three strata.

Several authorities agreed that the surface cells of transitional epithelium were sometimes binucleated. These included Dogial (1890), Dawson (1898), Rigal (1904), Gaebler (1921), Fleroff (1936), Bremer and Weatherford (1944), and Smith and Copenhaver (1953).

Dogial (1890), Bauch (1911), Mollendorff (1930), Maximow and Bloom (1952), and Smith and Copenhaver (1953) found lymphocytes in transitional epithelium.

There has been much discussion among investigators regarding the presence of glands in the bladder. Graning (1934), Hill (1937), and Smith and Copenhaver (1953) stated that there were no glands in the bladder. Hey (1895), Ellenberger (1911), Hill (1937), and Maximow and Bloom (1952) agreed that glandlike structures were present. Ebner (1899), Mollendorff (1930), Sobotta (1930), Macalpine (1934), Dawson (1948), Carleton and Leach (1949), Dupreuil and Baudrimont (1950), and Jordan (1952) indicated that true glands were present in mammalian bladders. Lendorf (1901) described glands in the trigone of the dog bladder but not in any other species. Pund et al. (1952) stated that glands were present in the domes of human bladders, while Bremer and Weatherford (1944) noted glands in the fundus of the human bladder.

Tunica propria. All investigators agreed that the tunica propria was composed of loose white fibrous connective tissue. However, the terminology used by the various workers differed. M'Fadyean (1884) called it vascular areolar connective tissue. Vaughan (1888) termed it cellular connective tissue. Rigal found that both loose and dense connective tissue existed in the tunica propria of the dog bladder. Piersol (1910) and Kendall (1947) stated that it was a fibroelastic layer. Bauch (1911) termed the tunica propria of the bladder

of domestic animals "delicate connective tissue." Krasa and Paschkis (1921) and Smith and Copenhaver (1953) observed that it was of loose connective tissue. Langworthy and Kolb (1938) described it as fibrous connective tissue. Mollendorff (1930) suggested that it had a fibrous layer and a capillary layer in the human bladder.

Many workers commented on the amount of elastic tissue present in the tunica propria of the bladder. Ebner (1899), Bauch (1911), Langworthy and Kolb (1938), Patzelt (1945), and Maximow and Bloom (1952) mentioned the presence of elastic tissue but did not discuss the amount. Rigal (1904), Piersol (1910), Graning (1934), Dupreuil and Baudrimont (1950), Policard (1950), and Cowdry (1950) stated that elastic tissue was abundant in the tunica propria of the bladder.

Piersol (1910) and Kendall (1947) referred to lymph nodules in the tunica propria of the mammalian bladder. Gerota (1896) reported lymph vessels in the tunica propria of the dog, cat, and human bladder. Langworthy and Kolb (1938) found numerous capillaries, small arterioles, and venules in the tunica propria of the cat bladder.

Muscularis mucosae. Bauch (1911) reported that a muscularis mucosae was present in the bladder of the horse, cow, pig, sheep,

goat, dog, and cat. Graning (1934) observed that the muscularis mucosae of the dog bladder was not well developed.

Submucosa. Many investigators distinguished a submucosa in addition to the tunica propria of the bladder. Ellenberger (1911), Bauch (1911), Hiilivirta (1911), Krasa and Paschkis (1921), and Zeitzschmann et al. (1943) described a submucosa in all of the domestic animals. M'Fadyean (1884) reported a submucosa in the horse, Graning (1934) in the dog, Langworthy and Kolb (1938) in the cat, and Ebner (1899), Piersol (1910), Mollendorff (1930), Sobotta (1930), Macalpine (1934), Dawson (1948), Policard (1950), Maximow and Bloom (1952), Smith and Copenhaver (1953), and Greep (1954), in the human. All authors agreed that it was diminished or absent in the trigone.

Ebner (1899), Mollendorff (1930), and Sobotta (1930) noted fat in the submucosa of the human bladder. Bauch (1911) found fat in the submucosa of all domestic animals, and Rigal (1904) described fat in this area of the dog bladder.

Bauch (1911) stated that the submucosa of the bladder of all domestic animals was quite vascular. Graning (1934) observed large arteries in the submucosa of the dog bladder.

Muscularis externa. The arrangement and thickness of the muscle layers in the bladder are most difficult to describe because of their complex nature. Harvey (1909) found that when the dog bladder was contracted the muscularis was 4762.8 microns thick; when distended it was 382.8 microns thick. Bauch (1911) stated that in pig and cat bladders the muscle fibers were not arranged in definite layers, and that in the ruminants the muscle layers were more distinct where the bladder wall was thickest. The layers were most regular in the horse and dog bladders, and in general the outer and inner layers coursed longitudinally while the circular fibers were directed transversely. There were exceptions to these general statements. Ellenberger (1911) also mentioned inner and outer longitudinal layers and a middle circular layer in the bladder of domestic animals, but made no reference to differences between species. Krasa and Paschkis (1921) found that in the cow the innermost muscle bundles formed a network but were mostly oriented longitudinally. According to Graning (1934), it was difficult to get a clear concept of the course of the muscle fibers in the dog bladder, but three definite layers were demonstrated on the dorsal and ventral walls. Graning (1936) found that in the cow bladder the external longitudinal layer was thickest at the vertex and became thinner caudally, that the transverse layer was thickest on the dorsal and ventral surfaces, and that an oblique

layer was thickest on the lateral surfaces. The inner longitudinal layer was thinnest, and it was better developed ventrally than dorsally. Graning found that the longitudinal muscle was better developed over the body of the pig bladder and that it was thickest at the vertex. Only oblique fibers were present on the lateral surface of the pig bladder.

Bauch (1911) described connective tissue septa that contained no muscle cells in the muscularis of the pig, sheep, goat, and dog bladder. These septa contained elastic tissue, and fat was present specifically in the muscularis externa of the pig, sheep, and horse. The muscle of the goat bladder had fat only in a few areas. Krasa and Paschkis (1921) noted "concentrically layered bodies" which resembled Pacinian corpuscles in the muscularis of the cat bladder, and that the well-developed fibers of the dog bladder were intertwined with loose connective tissue. Kleyntjens and Langworthy (1937) reported aggregates of "elastic tissue cells" between the muscle fibers. Langworthy and Kolb (1938) observed blood vessels penetrating the cat bladder muscularis from the outside.

Bauch (1911) noted nerves and groups of ganglion cells in the intermuscular septa of the pig bladder. Ellenberger (1911) indicated that ganglia were especially numerous in the muscularis externa of the pig and cat bladder Schabadasch (1928) reported that

nerve trunks formed a closed network and that there were a large number of ganglia in the bladder wall of the dog. Graning (1934) noted a closed nerve plexus and numerous ganglia of various sizes in the muscularis of the dog. Langworthy and Kolb (1938) saw nerve trunks penetrating the muscle of the cat bladder.

Serosa. Little detailed information is available on the serosal coverings of the domestic animals. Bauch (1911) found a serosa on the bladders of all the domestic animals and that it was rich in elastic fibers. Graning (1934) stated that numerous elastic fibers accompanied the collagenous fibers of the dog serosa, and that blood and lymph vessels as well as nerve plexuses and ganglia were found in the subserosa. Fat was present in the caudal part of the lateral folds of the serosa. Langworthy and Kolb (1938) described the serosa of the cat bladder as a narrow band of connective tissue upon which rested the single-celled layer of the serous peritoneal coat. Kendall (1947) stated that the adventitia of the mammalian bladders was of fibro-elastic tissue and that it merged with a peritoneal coat.

Gross Anatomy of the Urethra

Chauveau (1873) stated that the urethra of the horse had long folds. M'Fadyean (1884) reported that the first few inches of the

horse urethra, the prostatic and membranous portions, were contained within the pelvis, the first inch or two was surrounded by the prostate gland. The female urethra was much shorter but wider than the corresponding portions of the male urethra. Vaughan (1888) noted that the prostatic portion of the male urethra was very short, was the most dilatable portion of the canal, and it passed through the prostate gland below the middle lobe. Griffiths (1891) observed that the membranous urethra was very short in man, longer in the dog, and about two inches long in the cat. Ellenberger (1911) stated that there were small longitudinal folds in the urethra of the horse, ruminants, boar, and tom cat and added that they were lacking in the dog urethra. The female urethra was equal to the pelvic portion of the male urethra. Hiilivirta (1911) suggested that the mucous membrane of all the domestic animals had low folds. Graning (1936) noted that the pelvic portion of the stallion urethra was 10 to 15 centimeters long and three to four centimeters wide, that the pectoral portion of the bull urethra was 15 to 18 centimeters long and 3.5 centimeters thick, and that the urethra of the cow was 10 to 13 centimeters long. The pelvic portion of the boar urethra was about 20 centimeters in length, and that of the sow was about 8 to 10 centimeters. Kendall (1947) noted that the mammalian female urethra presented longitudinal folds. Leach (1952) stated that the

female cat urethra was relatively short and undifferentiated. Sisson and Grossman (1953) gave the following lengths for the intrapelvic portions of the male urethrae: horse, 10 to 12 centimeters; bull, 12 centimeters; boar, 15 to 20 centimers; and the dog, "relatively short," and gave the following lengths for the female urethrae: horse, 5 to 7.5 centimeters; cow, 10 to 12 centimeters; and pig, 7 to 8 centimeters.

Chauveau (1873) stated that the mucous membrane of the horse urethra was covered by Wilson's muscle, a single muscle composed of a superior and an inferior part, consisting of a fleshy layer of circular fibers behind the prostate. M'Fadyean (1884) noted that the muscular coat of the horse urethra was composed of circularly disposed smooth muscle. Griffiths (1891) found the external longitudinal muscle bundles to be especially abundant on the exterior of the dog and the cat urethra. Kalischer (1900) said that the muscle tissue of the dog and cat ureters, trigone, and urethrae were continuous. Ellenberger (1911) noted that urethral muscle replaced the capsule of the prostate in ruminants and the boar, that on the border of the urethral muscle there was smooth muscle mixed with skeletal muscle fibers in the sheep, horse, and cat, and that generally the urethral muscle was well developed. Graning (1936) observed muscle fibers of the trigone which terminated in the dorsal wall of the horse

urethra, and that in ruminants, which had a disseminate prostate, the urethra and the prostate were surrounded by the urethral muscle. Kendall (1947) observed that the mammalian urethra was surrounded by inner longitudinal and outer circular muscle coats. Miller (1952) found the urethral muscle in the dog to be almost completely confined to the pelvis, and that cranially it overlapped the caudal portion of the prostate. Sisson and Grossman (1953) reported that the pelvic portion of the horse urethra was surrounded by the urethral muscle, that it consisted of longitudinal and transverse fibers, and that it functioned to ejaculate the seminal fluid and evacuate the last of the urine in micturition.

Histology of the Urethra

Epithelium. Chauveau (1873) called the epithelium of the horse urethra stratified and cylindrical, while M'Fadyean (1884) termed it simple and columnar beyond the neck of the bladder. Strickland-Goodall (1902) found that the cat and sheep urethrae were lined with stratified squamous epithelium. Ellenberger (1911) termed the urethral lining of the male domestic animals simply as a "layered" epithelium, and that of the females a stratified epithelium. Langworthy and Kolb (1938) wrote that the epithelium of the cat urethra was transitional. Kendall (1947) indicated that the mammalian

urethra was lined with transitional epithelium near the neck of the bladder.

Strickland-Goodall (1902) noted that the epithelium of the cat urethra was thick, and that of the sheep was six to twelve cell layers high. Ellenberger (1911) studied the epithelial heights and the number of cell layers in the urethra of the domestic animals. The height of the epithelium of the horse was 20 to 30 microns with four to seven cell layers, that of the cow was 85 to 100 microns with five to six cell layers, the sheep and goat had five cell layers, that of the pig 30 to 40 microns high with no more than three cell layers, the dog had a three-layered epithelium, and that of the cat was two to three layers high. Langworthy and Kolb (1938) found that in the cat the urethral epithelium was six to ten layers high.

Strickland-Goodall (1902) stated that few glands were present in the urethra of the cat and the sheep. Ellenberger (1911) described four series of glands in the stallion urethra, that the bull, ram, goat, and boar had a glandular stratum, and that the urethra of the tom cat and the dog was poor in glands. Ellenberger also reported a glandular layer in the females of these species. Lesbouyries (1949) observed no glands in the tunica propria of the mammalian urethra. Kendall (1947) observed that in the mammalian

female urethra there were glandular pockets with mucous cells, and deeper sinuses with muco-serous glands.

Tunica propria. Ellenberger (1911) found fairly compact connective tissue in the tunica propria of the stallion urethra, it was thin and loose in the bull, and that a gland-free tunica propria was present in the boar. A wide tunica propria existed in the tom cat, and in female animals the tunica propria consisted of compact connective tissue permeated by elastic fibers.

Corpus cavernosum. Strickland-Goodall (1902) reported cavernous tissue ventrally in the cat urethra, and large venous sinuses in the mucous membrane of the sheep urethra. Ellenberger (1911) found that in the bull and stallion the stratum cavernosum surrounded the entire urethra and was equally thick in all places, that in the boar it was broken up as it approached the urethral bulb, and that in the dog it was abundant in the bulb but extended through the entire urethra. Ellenberger observed the cavernosum to be lacking between the bladder and the prostate but abundant in the bulb of the tom cat, in the ram and goat it was extensive and filled with wide spaces, and a cavernous mucosa was noted in females. Langworthy and Kolb (1938) noted numerous capillaries, arterioles, and venules in the mucous membrane of the cat.

Muscularis externa. Strickland-Goodall (1902) noted well-marked circular muscle in the cat urethra, and much circular muscle in the sheep urethra. Ellenberger (1911) found smooth and skeletal muscle throughout the length of the pelvic portion of the horse urethra. The skeletal muscle was the urethral muscle, and it coursed longitudinally. The urethral muscle formed the bulk of the tissue. Ellenberger noted mostly circular fibers in the bull. In the sheep there was an inner smooth muscle layer absent dorsally in the region of the seminal colliculus, and an outer skeletal muscle layer which was the urethral muscle. The goat was similar to the sheep except that the smooth muscle was complete dorsally. In the dog urethra the smooth muscle appeared in bundles which had many "stray" skeletal muscle fibers. Ellenberger added that smooth muscle was entirely lacking under the skeletal muscle in the tom cat, and that in the females of these animals both smooth and skeletal muscle was present in the urethra.

MATERIALS AND METHODS

A total of forty-eight animals was used for this investigation and their distribution was as follows: nine male and six female pigs; three male and four female cats; four male and four female horses; four male and four female dogs; one male and two female sheep, one sheep that the sex was not recorded; two male and two female cows; and five male and one female goat. These animals were obtained from the departments of Anatomy, Animal Pathology, Bacteriology, and Animal Husbandry at Michigan State University, and from slaughter houses near Lansing and Grand Rapids, Michigan. The urinary systems of these animals were normal as far as it was known. In addition, two pathological dog bladders were obtained from the Department of Surgery and Medicine, Michigan State University.

Sections were taken from the vertex, lateral wall, and bladder neck of each animal (Frontispiece). In small animals it was possible to secure a section around the entire bladder neck, and in large animals an attempt was made to get a section through the dorsal bladder neck. Sections were obtained along varying lengths of the proximal urethra of every animal.

The tissues were fixed in Lavdowsky's mixture (Guyer, 1943). After fixation the tissues were dehydrated and infiltrated according to the butyl alcohol-paraffin mush method of Johnson et al. (1943). Hematoxylin-eosin, and Weigert-Van Gieson's stain for connective tissue were used routinely.

Measurements of epithelial heights were made with a calibrated ocular micrometer. The lowest and the highest typical area of the epithelium was measured. Depths and heights of the folds, as well as sections where the epithelium had obviously been cut obliquely, were avoided. The epithelial measurements were the only ones taken because of the questionable validity of any others which could have been made.

RESULTS AND DISCUSSION

Gross Anatomy of the Bladder

The bladders of all domestic animals are similar. The vertex, or dome, is directed cranially and slightly ventrally, while the neck is directed caudally. The main portion of the bladder is termed the fundus or body (Frontispiece).

The bladder is supported by paired lateral ligaments, the remains of the umbilical arteries, and the median ligament, the remnant of the allantoic canal, which is termed the urachus.

The ureters enter the bladder obliquely from a dorsal and lateral direction, and the urethra leaves the organ caudally. On the inside of the bladder is a triangular area between the openings of the ureters and the urethra, termed the trigone (Frontispiece).

The reflections of the peritoneum over the surface of the bladder vary among the domestic animals. The bladder of the pig, dog, and cat is almost completely covered by peritoneum. The entire dorsal surface of the horse bladder is covered by peritoneum which recedes over the lateral surface to invest only half of the ventral surface. The peritoneum of the cow and sheep extends further caudally than does the horse.

The bladder receives its blood supply from the cranial and caudal vesical arteries which are branches of the internal pudendal, and from the obturator and umbilical arteries. The venous drainage of the bladder is by way of the internal pudendal vein, and the lymphatic drainage is into the internal iliac and lumbar lymph nodes.

The bladder receives sympathetic nerve fibers from the lower ganglia of the sympathetic chain, and parasympathetic fibers from the third and fourth sacral segments of the spinal cord.

When contracted the mucous membrane of the bladder lies in irregular folds (Plate VIII). These folds disappear when the bladder is distended.

Histology of the Bladder

Epithelium. The bladders were lined by transitional epithelium. The name "transitional" was given to this epithelium by Henle in 1841 (Bremer and Weatherford, 1944) because he believed it to be a form intermediate between stratified squamous and simple columnar epithelium. Maximow and Bloom (1952) preferred to use the word in quotations but in this investigation there was little to indicate that it could not be used as a specific type of epithelium.

The transitional epithelium was highest at the vertex of the bladder. The horse had the highest epithelium in this region (Plate I),

followed in decreasing order by the sheep, pig, cow, goat, cat, and dog (Plates I-VI, VIII, IX, XII). The epithelium decreased in height on the bladder neck, and except for the horse, dog, and cat where it was higher, it decreased slightly on the lateral wall. The epithelium of the goat bladder, however, seemed to show a more marked decrease on the lateral wall. The epithelium of the bladder neck of the cat was the lowest of any animal (Plate IX).

The horse exhibited the greatest number of cell layers of the domestic animals, the average highest epithelium being thirteen at the vertex. The pig, cow, and sheep were next with ten, the goat had six layers, and the dog and cat each had five layers. The cell layers on the lateral wall and the bladder neck were about equal, and fewer than on the vertex. In general the height of the epithelium varied directly with the number of cell layers.

Paneth (1876), Doigal (1890), Rigal (1904), and Bauch (1911) observed three strata of cells in the epithelial layer of animal bladders. No sound morphological basis for doing this was apparent; however, the basal, intermediate, and surface layers did show slight changes in form.

Stiles (1950, 1956) believed that the surface layer of cells were desquamated and were replaced by the cells immediately below them. Stiles stated that the cells of the surface layer were cuboidal

TABLE I

AVERAGE HIGHEST EPITHELIAL HEIGHTS[a] IN VARIOUS REGIONS OF THE BLADDER AND THE NUMBER OF CELL LAYERS AT THE POINT WHERE MEASUREMENT WAS TAKEN

Animal	Bladder Vertex		Lateral Wall		Bladder Neck	
	Height (microns)	No. of Cell Layers	Height (microns)	No. of Cell Layers	Height (microns)	No. of Cell Layers
Horse . .	171	13	86	9	74	8
Cow . . .	85	10	67	7	76	7
Pig	99	10	50	6	52	6
Sheep . .	111	10	68	7	94	5
Goat . . .	69	6	33	4	70	5
Dog	49	5	53	6	52	6
Cat	65	5	40	4	23	3

[a]This figure represents an average of the highest typical epithelial height in the section. It was believed that this figure represented a more reliable interpretation of typical transitional epithelial height since measurements taken where the epithelium was very low were apt to be at an area where the cells were displaced. These low areas represented a very small percentage of the entire surface.

and pear-shaped in the human bladder. This study revealed that the cells which lined the surface of the bladder epithelium showed much variation (Plate I), but in general were the shape of elongated cubes or rounded, and in the distended bladder spindle-shaped. Bauch (1911) and Graning (1934) found the surface cells of the dog bladder epithelium to be enlarged. Rigal (1904) also studied the dog bladder and did not verify this finding, and enlarged cells were not found in this study (Plate VIII). The nuclei of the surface cells were rounded or oval and directed parallel to the surface (Plates I, II, and VIII). The karyoplasm was slightly granular and contained one or two nucleoli. Bauch noted that the cells under the surface layer were polyhedral, spherical, oval, spindle-shaped, columnar, pear-shaped, spiral-shaped, and star-shaped. All of these shapes could be recognized in the bladder epithelium of the domestic animals. The nuclei of these cells were oval or round and sometimes appeared to be very fragile and folded similar to the nucleus of a monocyte. They had one or two prominent nucleoli and their karyoplasm was granular. The cells of the basal layer were cuboidal or columnar with oval nuclei in the center of the cell which were oriented perpendicular to the surface. In many places the cells were so crowded that the cell outlines were not apparent. The basal layer of cells showed

the most regularity. Binucleated cells were frequently observed in all sections studied (Plates I and II).

It was impossible to characterize the bladder, or the region of the bladder, of any animal by the shape of its epithelial cells.

Lymphocytes were found in the bladder epithelium of all domestic animals (Plate XII). They were most frequent in the cow and least frequent in the cat.

Bremer and Weatherford (1944) stated that capillaries often appeared to lie within the basal layer of the epithelium of the human bladder. No capillaries were observed in the bladder epithelium of the domestic animals.

Hey (1895), Ellenberger (1911), and Kendall (1947) reported that glands were present in animal bladders, and Lendorf (1901) agreed with this in his work on the dog bladder. Graning (1934) indicated that no glands were present in the dog bladder. No glands were observed in the areas investigated in this work; viz., vertex, lateral wall, and bladder neck of any domestic animal.

Tunica propria. The tunica propria of the bladders of all domestic animals was composed of elastic and collagenous fibers, the latter oriented parallel to the surface. The elastic fibers were more numerous toward the submucosa. Bauch (1911) observed the

tunica propria to be rich in cells. This investigation revealed the presence of fibroblasts and histiocytes with an occasional lymphocyte. The connective tissue was not papillated, and there was no basement membrane beneath the epithelium. The tunica propria contained numerous capillaries, small nerve trunks, and fine nerve plexuses. Capillaries could sometimes be seen to form a continuous layer under the epithelium of the goat bladder (Plate IV). Lymphoid nodules were found consistently only in the cow bladder (Plate III). There were no differences in the tunica propria of the different areas of the bladders examined (Plates I-IX).

Muscularis mucosae. The muscularis mucosae of the bladder of domestic animals differed extensively. It was best developed in the horse where the muscle bundles were widely separated with little connective tissue between them (Plate VI). The cow, dog, and pig had a very thin muscularis mucosae which was very close to the muscularis externa (Plate V). In some places that of the cow seemed to be two-layered. The muscularis mucosae of the sheep and goat was represented by a few sparsely scattered smooth muscle cells or bundles (Plate IV). In most areas of all regions of the cat bladder no muscularis mucosae existed. An occasional section contained a few scattered muscle bundles which might be interpreted as a muscularis

mucosae. In all animals the muscularis mucosae diminished considerably at the bladder neck.

Submucosa. A submucosa was present in the bladders of all domestic animals (Plates II, IV-VII). It was generally looser than the tunica propria, more vascular, and contained more elastic fibers. Fat cells were not observed in the submucosa of any animal, contrary to the findings of Bauch (1911). Ellenberger (1911) described small ganglia in the mucosa of the cat bladder. In this study ganglia were found in the submucosa of the cat (Plate VII) and the horse. The submucosa decreased considerably or was absent as the bladder joined the urethra.

Muscularis externa. Bauch (1911) observed that the musculature of the bladder was not arranged as simply as in the other hollow organs. This was readily apparent in this investigation. The muscle had the most orderly arrangement at the vertex and on the lateral wall. In some cases it was possible to distinguish three muscle layers at these points, the outer and inner layers were parallel, and perpendicular to the middle layer. Unless the orientation of the section in the block was known it was impossible to state whether the bundles of muscle took a longitudinal or a transverse course through the wall of the bladder. All layers interdigitated

(Plate IX). At the bladder neck the muscle mass thickened and the bundles became very diffuse. Layers in this area were exceedingly difficult to make out; most of the muscle was cut in cross section or obliquely. Graning (1934, 1936) worked out the layering of the bladder muscle wall of the dog, horse, cow, and pig, and this work should be consulted for detailed accounts. It was not possible to differentiate the species of domestic animal by the arrangement of the bladder musculature.

It was impossible to find any degree of uniformity relative to the thickness of the muscle layers in any of the domestic animals. In many cases the musculature increased toward the bladder neck. Bremer and Weatherford (1944) stated that the circular muscle was strengthened to form a sphincter in the human bladder neck.

The connective tissue of the muscularis externa of the animal bladders was composed of loose collagenous tissue with elastic fibers (Plate XI). This increased toward the neck of the bladder. Fat often appeared between the muscle bundles of the pig bladder (Plate XIII). Ganglia were found in the muscularis externa of all the animals except the sheep and the goat. The ganglia varied in size and contained large ganglion cells which were presumed to be originations of postganglionic parasympathetic fibers. These ganglia were not orderly arranged between the muscle layers, as in the intestine.

The muscle layer had numerous blood vessels of various sizes coursing through it.

Serosa. A true serosa existed on the lateral wall and the vertex of the bladder of all domestic animals, and it exhibited wide variations. (See the gross anatomy section for the peritoneal reflections.) It was composed of mesothelium and a submesothelial layer consisting of bundles of collagenous fibers oriented parallel to the outer surface. Near the muscle these layers were very compact and followed the muscle fascicles a short distance into the muscularis externa. They were best developed in the dog, moderately developed in the cow, horse, pig (Plate X), and cat, poorly developed in the goat, and absent in the sheep (Plate XI). Small to moderate amounts of elastic tissue were present in all the animals; the cat had a large quantity. The serosa of the horse, cow, and dog was relatively thick, the sheep, goat, and pig moderately thick; that of the cat was the thinnest. The serosa of the cat was tightly adherent at the vertex and looser at the lateral and ventral surfaces. Fat was found under the mesothelium of the horse, pig, and cat bladders. Ganglia were found in the cat serosa. There were blood vessels and nerves of varying sizes, some rather large, in all areas of the subserous layer of all domestic animal bladders. At the bladder neck the serosa

was replaced by an adventitia which contained blood vessels and nerves.

Gross Anatomy of the Urethra

Male. The intrapelvic portion of the male urethra is a long tube leading from the neck of the bladder to the arch of the ischium. Near the bladder it is surrounded by the prostate gland whose ducts open into it. On the dorsal wall, medially, is a rounded prominence, the seminal colliculus, upon which the ejaculatory ducts open. In the horse, dog, cat, and goat a skeletal muscle, the urethral muscle (of Wilson) surrounds the urethra. In the cow, sheep, and pig this muscle is present ventrally and laterally but is lacking dorsally. The pelvic portion of the male urethra receives its blood supply by way of the middle haemorrhoidal artery, a branch of the internal pedundal artery. It is drained by branches of the internal pudendal vein.

Female. The female urethra is much shorter than that of the male, and is homologous to that portion of the male urethra between the bladder neck and the seminal colliculis. It lies ventral to the vagina and opens into the anterior end of the vestibule. Its blood supply is the same as that of the pelvic portion of the male.

TABLE II

A COMPARISON OF URETHRAL EPITHELIAL CELL HEIGHTS AND CELL LAYERS OF THIS INVESTIGATION TO THOSE OF ELLENBERGER (1911)

Animal	Ellenberger		This Study	
	Range of Heights (microns)	No. of Cell Layers	Average Height (microns)	No. of Cell Layers
Horse	20-30	4-7	76	2-8
Cow	85-100	5-6	50	3-7
Pig	30-40	3 or under	27	2-4
Goat	-	-	32	3-5
Sheep	-	5	-	-
Dog	-	3-4	24	2-7
Cat	-	4-5	25	3-4

Histology of the Proximal Urethra

Epithelium. The urethra in its proximal portion was lined with transitional epithelium, very similar in height and structure to that found in the bladder neck. Because of the anterior extention of the disseminate prostate the epithelium of the male pig urethra was often pierced with ducts from the prostate gland (Plate XIV). Maximow and Bloom (1952) reported mucous goblet cells frequently present in the surface epithelium of the human male urethra. No such cells were apparent in the epithelium of the proximal urethra of any domestic animal studied in this investigation.

Tunica propria. The tunica propria of all of the domestic animals was comprised of fibrous connective tissue. The fibers were oriented transversely. The density of the fibers varied, being greatest toward the epithelium except the cow where the reverse was true in some areas. Elastic tissue appeared sparse toward the epithelium but increased slightly toward the muscularis in all animals. The amount of smooth muscle also varied among the animals. The horse had the most, with quite large bundles scattered throughout the tunica propria (Plate XV). In the pig, dog, and sheep these bundles were confined to areas near the muscularis. In the cow very few smooth muscle bundles appeared, but there seemed to be some individual

muscle cells which were oriented longitudinally. No smooth muscle appeared in the tunica propria of the cat. Glands were present in the tunica propria of the male pig and in one instance in a male dog. The glands in the pig were the tubules of the disseminate prostate (Plate XIV). In the pig the collagenous fibers of the tunica propria continued into the prostate gland forming septa. In one male dog there was a group of mucous cells near the muscularis. No glands were noted in the tunica propria of the cow, cat, sheep, goat, or horse. Ellenberger (1911) stated that the cow had a disseminate prostate, and that it was impossible to describe the urethra without considering the prostate. In the two bulls considered in this study no prostatic tissue was observed. Large nerve trunks were seen in the tunica propria of the cow. In other animals there were fine nerve fibers and plexuses in the tunica propria.

Corpus cavernosum. All male animals had large and small arteries in the tunica propria. Large, thin-walled sinuses appeared throughout the tunica propria of all male domestic animals. Sometimes these were very flattened with the two sides approximated, appearing as slitlike structures in the tunica propria. The tunica propria of the urethra of the female domestic animals also contained many arteries and sinuslike structures, but they were not as

numerous or as large as in the male. According to Ellenberger (1911), these vessels in the female should not be called corpora cavernosa.

Muscularis externa. The course of the muscle bundles of the muscularis externa varied considerably among the domestic animals, and like the bladder, was not orderly in many cases. In the sheep and goat urethra only one layer of smooth muscle, which coursed longitudinally, could be recognized. In the cat two layers of smooth muscle, an inner circular and an outer longitudinal appeared. In the dog the same arrangement was present but both smooth and skeletal muscle were intermingled. In the cow, horse, and female pig three layers of smooth muscle became evident. These were not as clearly marked in the female pig. The outer and inner layers were thick and directed longitudinally, while the middle layer was thin and coursed in a circular direction. Ellenberger (1911) described only a single longitudinal layer in the horse but stated that transverse fibers appeared in it.

Skeletal muscle appeared in the proximal urethra of the male dog, the bull, and the boar. It had a unique arrangement in the boar where it formed a thick mass over the ventral portion of the prostate, becoming thin laterally, and disappearing completely dorsally. There

was a dense white fibrous connective tissue raphe over the dorsal portion of the urethra into which the skeletal muscle inserted (Plate XVI).

The connective tissue between the muscle bundles also differed. It was small in amount and composed of white fibrous connective tissue with few elastic fibers in the cat and the pig. The amount of white fibrous connective tissue increased in the dog, cow, sheep, and goat. Elastic fibers as well as white fibrous connective tissue increased in the horse (Plate XVII). Fat appeared between the muscularis externa and the prostate gland in the boar.

Surrounding the muscularis externa of many animals was an adventitia-like covering containing large blood vessels, nerve trunks, and fat.

SUMMARY

Comparative histological studies of the bladder and proximal urethra, using hematoxylin-eosin and Weigert-Van Gieson's stains, were made on forty-eight domestic animals of seven species.

All areas of the bladder of all domestic animals were lined with transitional epithelium. The epithelium was highest at the vertex of the bladder and decreased in height on the bladder neck and lateral wall. The horse had the highest epithelium, followed in decreasing order by the sheep, pig, cow, goat, cat, and dog. The epithelium of the bladder neck of the cat was lowest of any animal. The horse also had the greatest number of cell layers in the epithelium (13), followed by the sheep, cow, and pig (10), the goat (6), and the dog and cat (5). It was impossible to distinguish the species or any particular region of the bladder of any domestic animal by the shape of the transitional epithelial cells. Lymphocytes were found in the bladder epithelium of all domestic animals; more frequently in the cow, and less frequently in the cat. No capillaries were observed in the bladder epithelium of any animal studied. Glands were not observed in the vertex, lateral wall, or bladder neck of any domestic animal.

Capillaries were sometimes seen to form a continuous layer under the epithelium of the goat bladder. Lymphoid nodules were found in the tunica propria of most of the cow bladders. No differences existed in the tunica propria of the various regions of the bladders studied.

The muscularis mucosae was best developed in the horse, very thin in the cow, dog, and pig, represented by only a few muscle cells in the sheep and goat, and not consistently present in the cat. Small ganglia were observed in the submucosa in the horse and cat only.

It was not possible to differentiate the species of domestic animal by the arrangement of the bladder musculature. Fat often appeared in the connective tissue between the muscle bundles of the pig bladder. Ganglia were observed in the muscularis externa of all animals except the sheep and goat.

Compact collagenous bundles from the subserosa invested the muscle bundles of the muscularis externa in most of the domestic animals. They were most complete in the dog, moderately developed in the cow, horse, and pig, not as apparent in the goat, and absent in the sheep. The serosa of the horse, cow, and dog was relatively thick, that of the sheep, goat, and pig moderately thick, and thin in the cat. The cat had the largest amount of elastic tissue in the

serosa, and ganglia were present. Fat was observed under the mesothelium of the horse, pig, and cat bladder only.

No goblet cells were observed in the epithelium of the proximal male urethra of the domestic animals as reported by Maximow and Bloom (1952) for the human species.

The density of the tunica propria of the proximal urethra was greater toward the epithelium except in the cow. Smooth muscle appeared in the tunica propria of all animals except the cat. The horse had the most; it was confined to an area near the muscularis externa in the pig, dog, and sheep, and muscle bundles were absent but individual cells were present in the cow. Glands were present in the tunica propria of the boar and male dog, but were not seen in any other animal.

The urethra of the sheep and the goat had a single layer of smooth muscle; the cat and dog had two layers of muscle, entirely smooth in the cat but in the dog skeletal muscle appeared in both layers; in the cow, horse, and female pig three layers of smooth muscle were present. Skeletal muscle also appeared in the bull and the boar. In the boar it was thick ventrally, thin laterally, and absent dorsally where it was replaced by a dense white fibrous connective tissue raphe. The connective tissue between the muscle bundles was scant in the cat and pig; it increased in amount in the dog,

sheep, goat, cow, and horse. In addition, elastic fibers occurred in greater numbers in the horse. Fat appeared between the prostate and the muscularis externa in the pig urethra.

No sex differences were noted in the bladders of domestic animals. No sex differences in the proximal urethra were observed other than those due to basic anatomical differences in the reproductive systems.

While it was impossible to differentiate most of the bladders of the domestic animals by a histological examination, the cat bladder might be characterized by a combination of observations; an almost complete absence of a muscularis mucosae, a thin serosa with an abundance of elastic tissue in it, and by its relatively thin epithelium.

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PLATE I

Bladder of the horse showing the thickest transitional epithelium. Lateral wall. H. and E. 155 ×. Adult.

1. Binucleated transitional epithelial cell.
2. Tunica propria.

epithe-

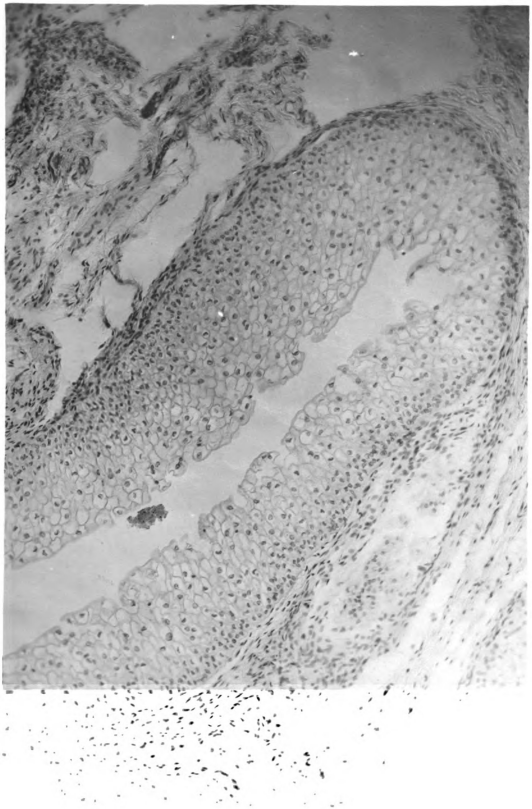

PLATE II

Bladder of the cow. Lateral wall. H. and E. 248 ×. Adult.

1. Flattened surface epithelial cells.
2. Dense tunica propria under the epithelium.
3. Loose tunica propria.
4. Submucosa (muscularis mucosae not apparent at this point).
5. Muscularis externa.
6. Binucleated surface cell.

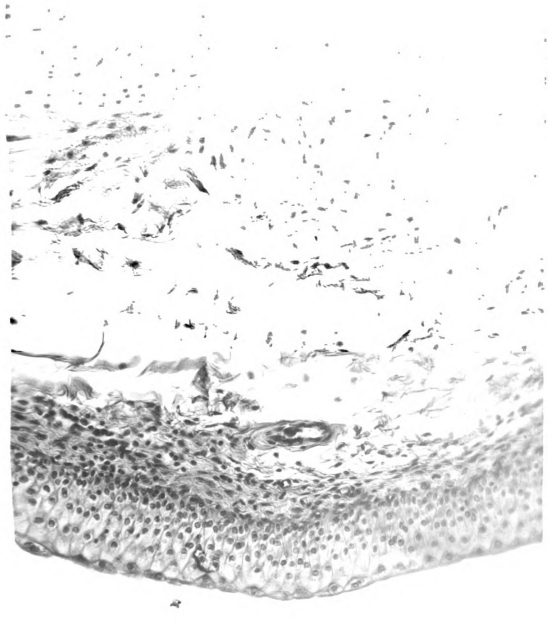

PLATE III

Bladder of the cow. Vertex. H. and E. 182 ×. Age unknown.

1. Transitional epithelium.

2. Tunica propria--note fine, orderly arranged fibers near the epithelium and the coarse, irregularly arranged fibers nearer the muscularis mucosa.

3. Lymph nodule.

4. Bundles of the muscularis mucosae.

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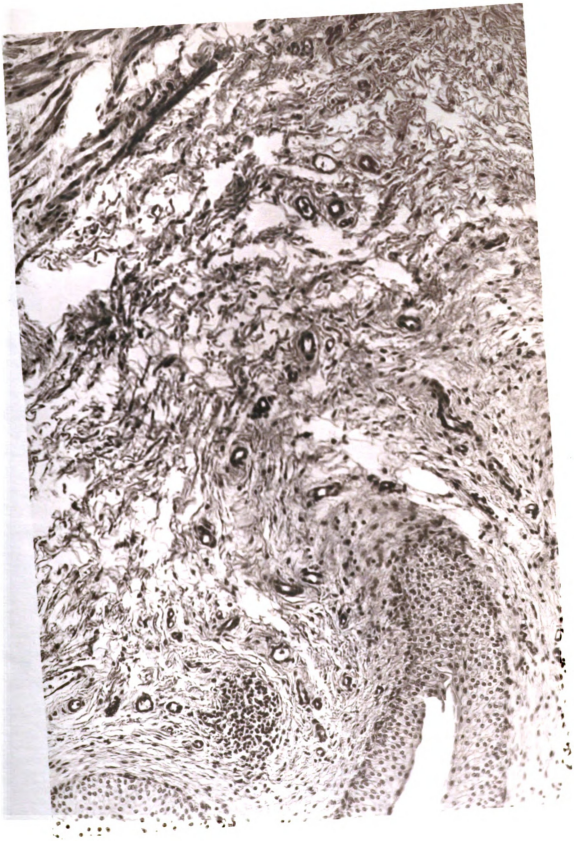

PLATE IV

Bladder of the goat. Vertex. Note the extensive vascularity, especially the capillary plexus beneath the epithelial layer. H. and E. 152 ×. Adult.

1. Transitional epithelium.
2. Tunica propria.
3. Two bundles of muscularis mucosae.
4. Submucosa.
5. Muscularis externa.

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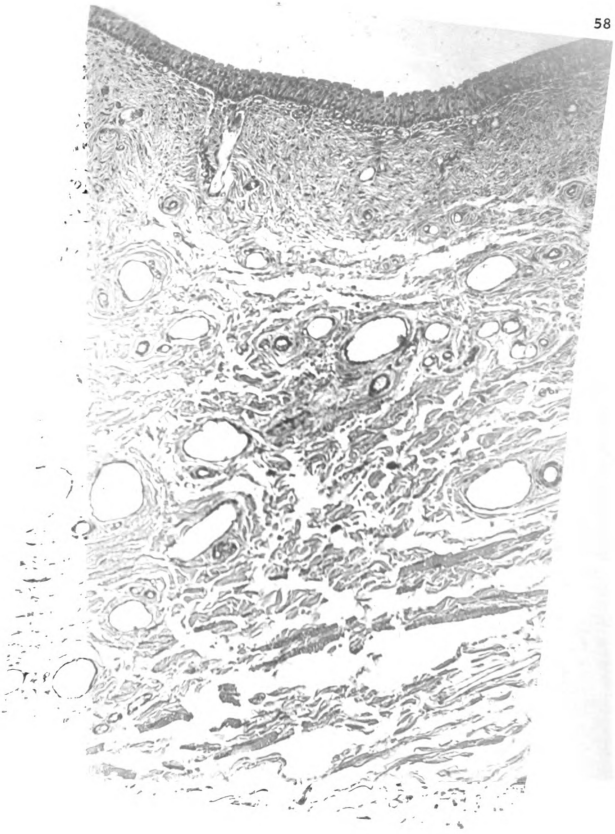

PLATE V

Bladder of the pig. Vertex. H. and E. 162 ×. Adult.

1. Transitional epithelium.
2. Tunica propria.
3. Lymph nodule.
4. Muscularis mucosae.
5. Thin submucosa.
6. Bundles of muscularis externa.

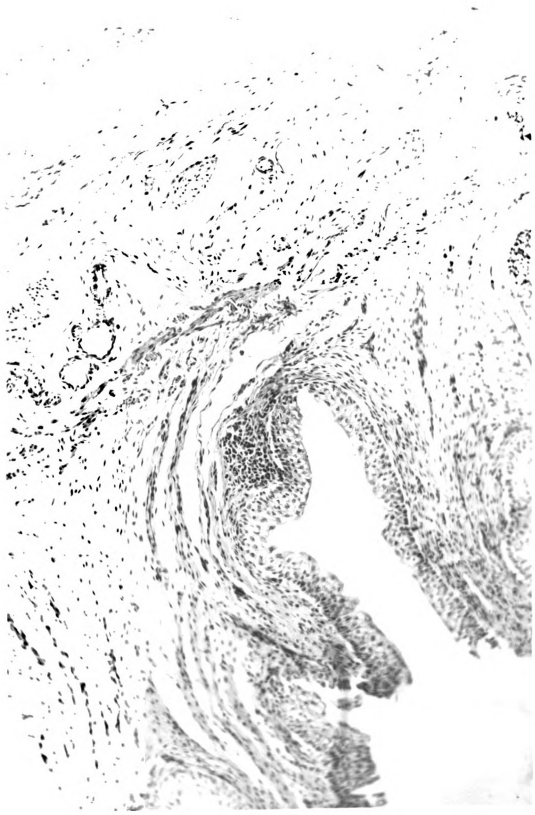

PLATE VI

Bladder of the horse. Lateral wall. H. and E. 383 ×. Adult.

1. Transitional epithelium.
2. Tunica propria.
3. Diffuse single-layered muscularis mucosae.
4. Submucosa.
5. Bundles of muscularis externa.

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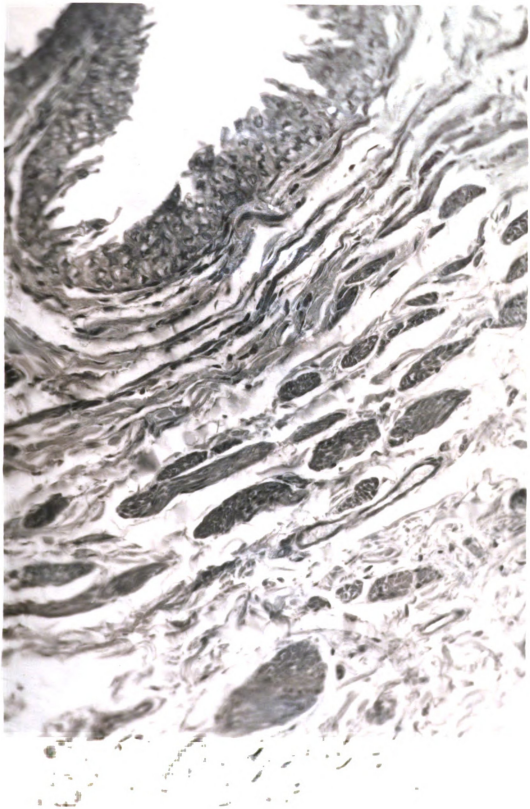

PLATE VII

Ganglion in the submucosa of the cat bladder. Bladder neck. H. and E. 870 ×. Three months old.

PLATE VIII

Bladder of the dog. Vertex. H. and E. 220 ×. Age unknown.

1. Folds in a contracted bladder.
2. Transitional epithelium showing flattened surface cells.
3. Tunica propria.

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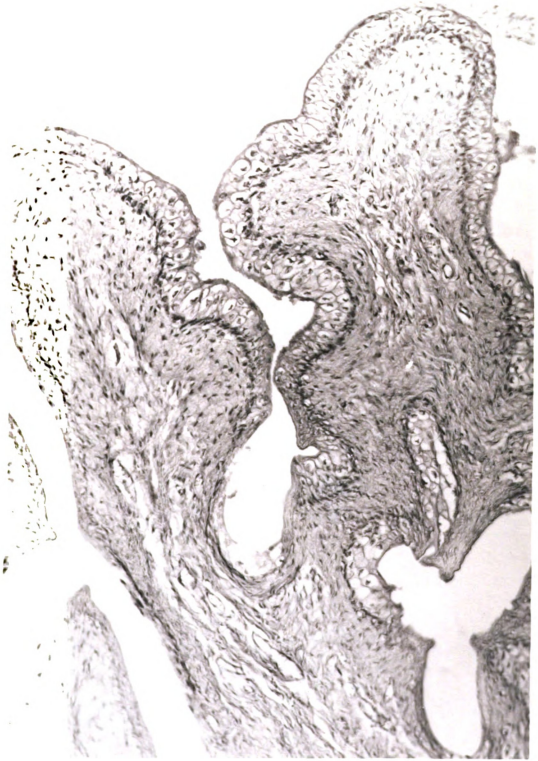

PLATE IX

Bladder of the cat. Bladder neck. H. and E. 148 ×. Three months old.

1. Transitional epithelium.
2. Tunica propria and submucosa (?).
3. Muscularis externa--note the irregular arrangement.
4. Adventitia.

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PLATE X

Serosa of the pig bladder. Dorsal wall. H. and E. 306 ×.

Age not recorded.

1. Serosa.
2. Mesothelium.
3. Submesothelial collagenous layer of serosa.
4. Septum from the serosa investing a bundle of muscularis externa.
5. Muscularis externa.

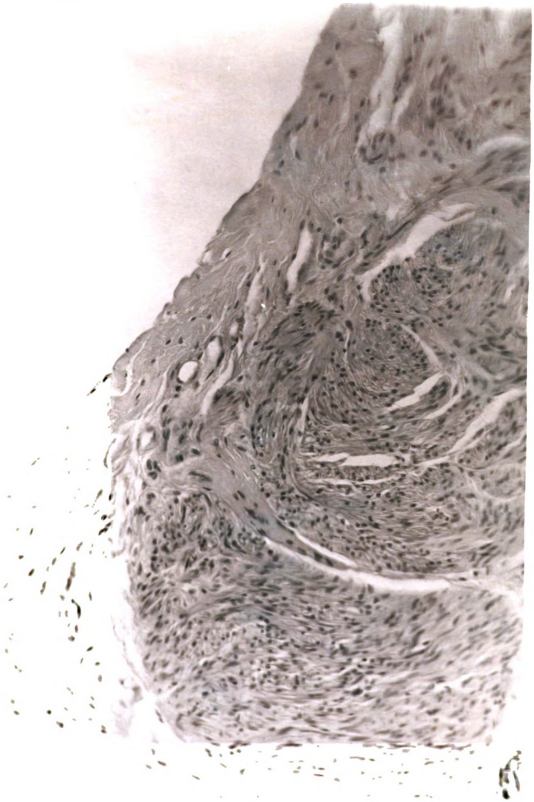


PLATE XI

Serosa of the sheep bladder. Vertex. H. and E. 345 ×. Age not determined.

1. Serosa.
2. Mesothelium.
3. Dense collagenous submesothelial layer--note the absence of connective tissue investments.
4. Muscularis externa.
5. Connective tissue in the muscularis externa.

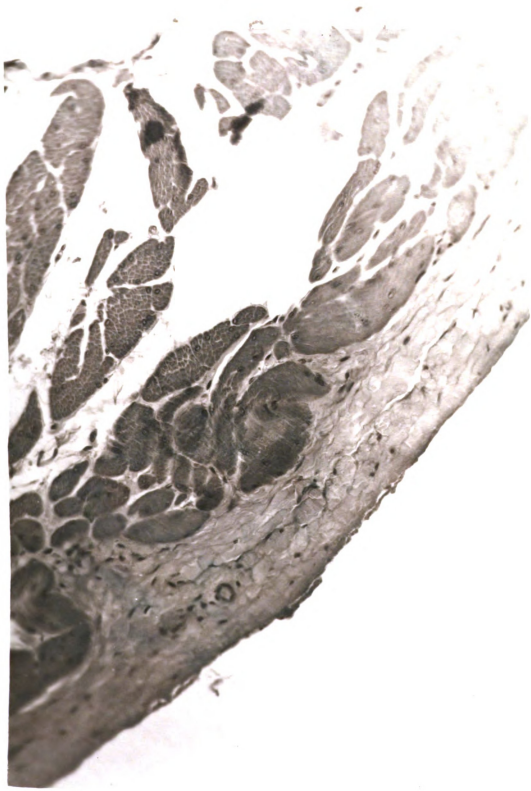
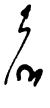


PLATE XII

Bladder of the sheep. Vertex. H. and E. 330 ×. Adult.

1. Transitional epithelium.
2. Tunica propria.
3. Lymphocytes in the epithelium.

1



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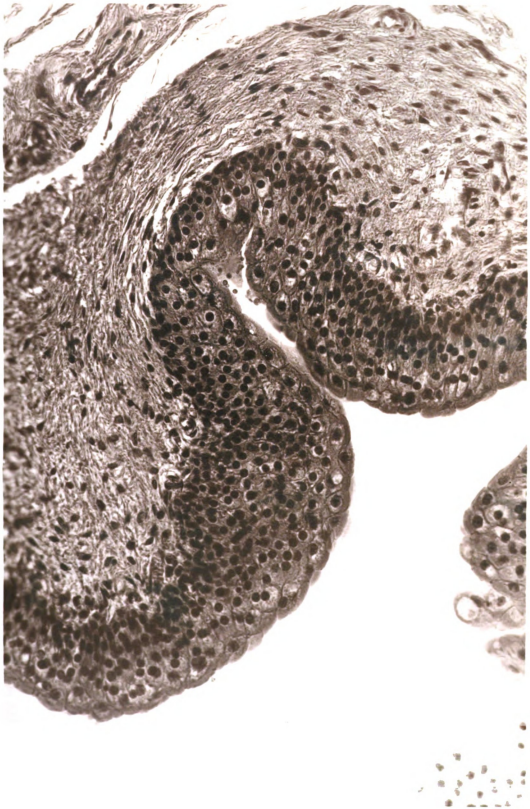

PLATE XIII

Bladder of the pig. Dorsal wall. H. and E. 152 ×. Two months old.

1. Adipose connective tissue between the bundles of the muscularis externa.
2. Muscularis externa.
3. Serosa.
4. Nerve trunks.

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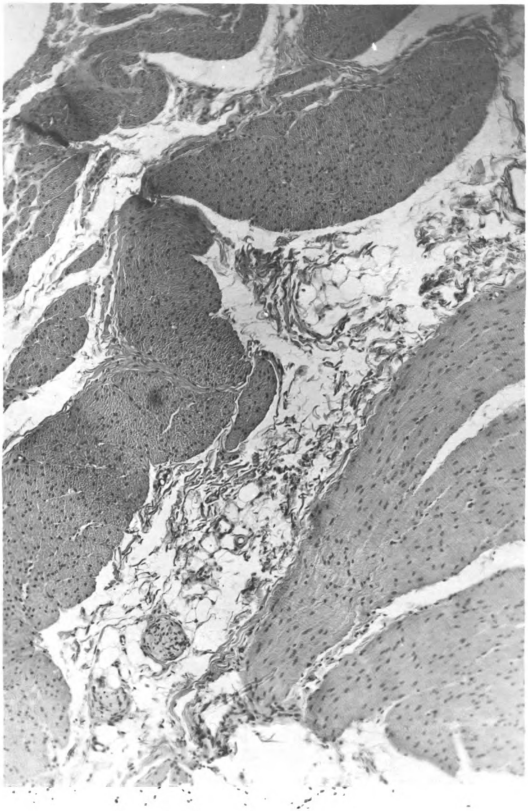

PLATE XIV

Duct of the prostate gland entering the pig urethra. H. and E. 460 ×. Age not recorded.

1. Low transitional epithelium.
2. Tunica propria.
3. Prostatic duct.
4. Prostatic alveolus.

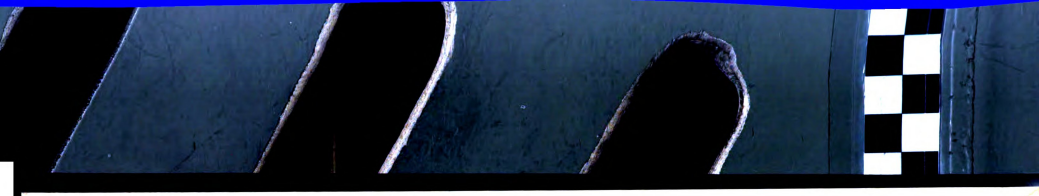

PLATE XV

Smooth muscle in the tunica propria of the horse urethra. H. and E. 158 ×. Adult.

1. Transitional epithelium.
2. Smooth muscle bundles in the tunica propria.
3. Edge of the muscularis externa.

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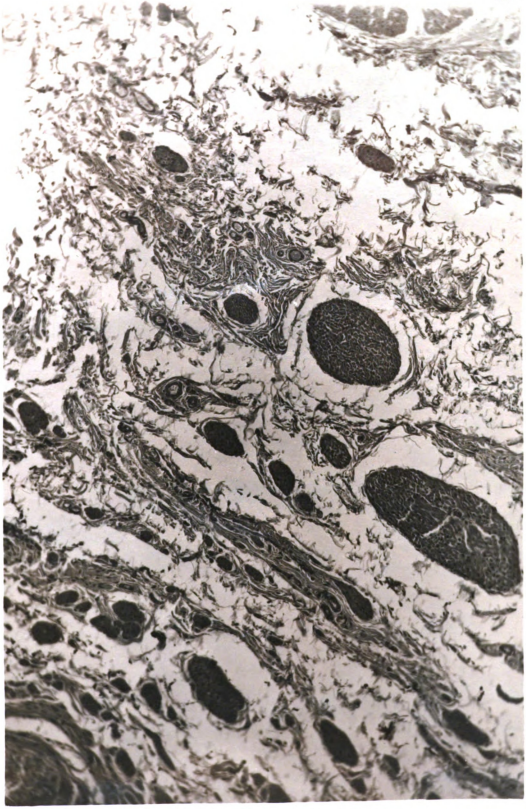
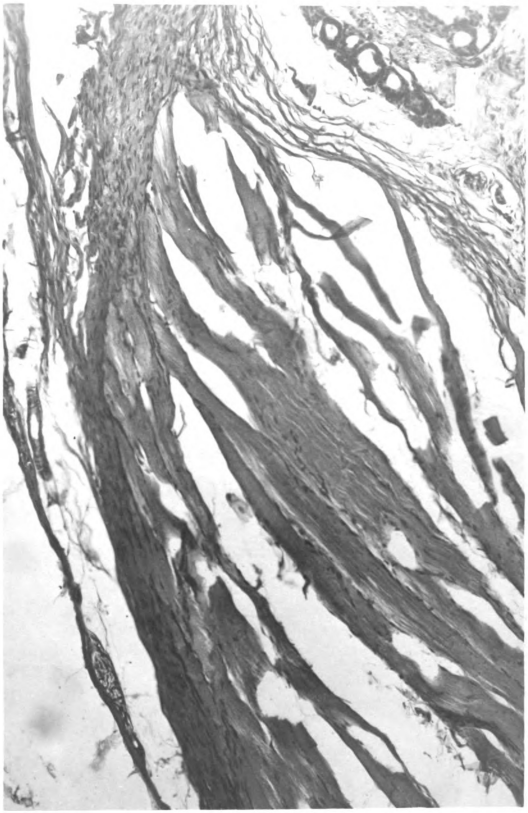


PLATE XVI

Skeletal muscle inserting on the dorsal fibrous connective tissue raphe in the boar urethra. H. and E. 220 ×. Six months old.

1. Skeletal muscle (urethral muscle of Wilson).
2. Fibrous raphe.
3. Prostate gland.
4. Adventitia containing fat, blood vessels, and nerve trunks.



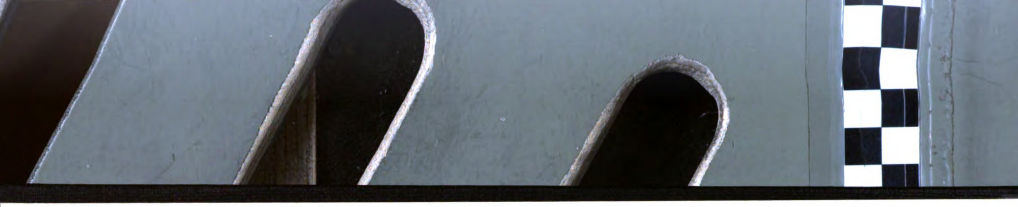
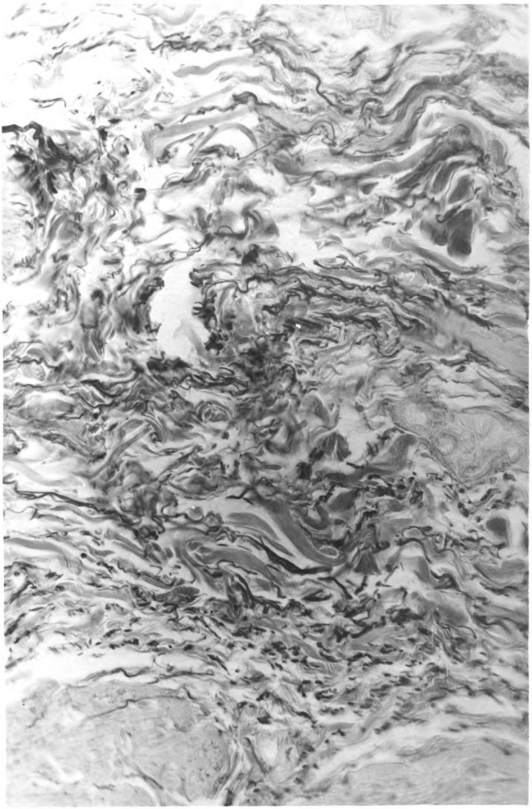


PLATE XVII

Elastic connective tissue fibers in the horse urethra. Weigert and VanGieson. 402 ×. Adult.

1. Elastic fibers.
2. Collagenous bundles.
3. Smooth muscle bundles.



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