THE COMPARATIVE MICROSCOPIC ANATOMY OF THE TRACHEAS OF BOS, CAPRA, AND OVIS

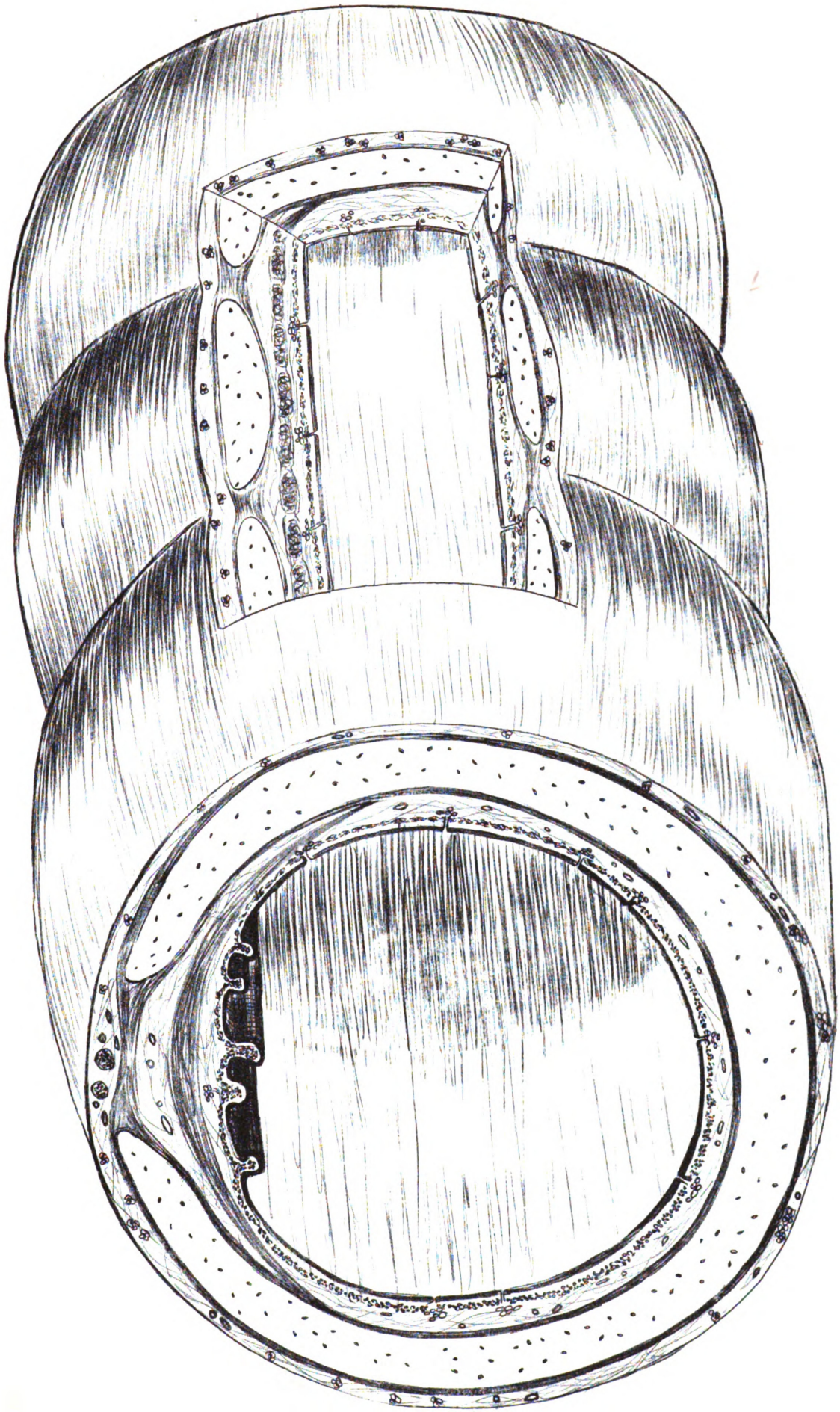
Thesis for the Degree of M. S.
MICHIGAN STATE UNIVERSITY

Cledith A. Miller, Jr.

1963

Frontispiece

A sketch of a typical section from a trachea showing both cross-sectional and longitudinal views.



THE COMPARATIVE MICROSCOPIC ANATOMY OF THE TRACHEAS OF *BOS*, *CAPRA*, AND *OVIS*

By

Cledith A. Miller, Jr.

A THESIS

Submitted to the College of Veterinary Medicine of Michigan
State University of Agriculture and Applied Science
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Anatomy

1963

ACKNOWLEDGMENTS

The author wishes to express his genuine gratitude to his major professor and friend, Dr. M. Lois Calhoun, Chairman and Professor, Department of Anatomy, for her patience and excellent guidance during the course of this investigation. Her contributions to this manuscript have given meaning to the scientist's basic tool--exacting observation and its conveyance to others that they, too, might share in the understanding and appreciation of the organized, living system.

The writer is indebted to Dr. C. W. Titkemeyer, Associate Professor, Department of Anatomy, for his comments and suggestions on the preparation and manner of expression of anatomical concepts contained in this work, and to Dr. Esther M. Smith, Associate Professor, Department of Anatomy, for her skilled assistance in and invaluable contributions to the preparation of the photomicrographs.

Thanks are due to Mr. Richard Witter, Misses Betty Mason, Pauline Ho, and Effie Lou Ball, for they had performed the initial efforts in this study. Their suggestions on technical methods proved beneficial throughout this investigation.

That this manuscript is a reality is in large part the result of the efforts and labors, as well as the constant encouragement of Miss Margaret R. Kuxhaus. The author is deeply grateful to her for having given so many hours to the preparation of this paper.

The writer wishes to express his heartfelt thanks to his parents, who have made this undertaking possible. He is forever grateful to them.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF PLATES

INTRODUCTION

The intent of this paper is to present a study of the normal comparative microscopic anatomy of the tracheas of the bovine, caprine, and ovine species. Because these three species comprise the ruminating domestic animals, they were studied as a single group.

Since diseased conditions can be appreciated most fully in light of the "normal" structural characteristics of a given organ, a demand for the establishment of the normal microscopic anatomy of the tracheas of the bovine, caprine, and ovine species has lead to this particular investigation. It is hoped that a description of this type will serve as a fundamental tool for the pathologist and the anatomist, as well as for other individuals whose work and service entail an understanding of the microscopic anatomy of the trachea.

As the multitude of contributions to veterinary medicine achieves new peaks in medical science, this writer hopes that the results and conclusions of his efforts will serve to add to the information that is of practical value and application to the practitioner.

REVIEW OF LITERATURE

The authors of current histology textbooks have provided adequate descriptions of the minute structures known to exist within the gross confines of the human trachea. Trautmann and Fiebiger (1957) have furnished a brief but inadequate account of the tracheas of domestic animals.

Several notable investigations on various animals appear throughout the available literature, namely: mouse (Andrew and Burns, 1947); dog (Correll and Beattie, 1956, and Niewenhuis, 1961); cat (Macklin, 1929); pig, horse, and cat (Paul, 1913); cattle (Vacirca, 1961); mink (Stowe and Calhoun, 1962); and rat (Schulz, 1959). With the exception of the work done by Stowe and Calhoun, Niewenhuis, Paul, and Vacirca, a majority of the investigators furnishing accounts of the histology of the trachea gathered their data on only a few of the many microscopic structures of the trachea. Many of the past studies on the trachea include detailed reports of their respective subjects; however, with a few noted exceptions, composite descriptions of the trachea of the domestic animals are lacking.

Mucosa

Hayek (1960) stated that the tracheal mucous membrane consists of three layers: 1) an epithelium; 2) a basement membrane; and 3) a membrana propria, referred to by Rhodin and Dalhamn (1955) as the lamina propria. According to Wilson (1859) the mucosa is pale, forms the internal lining of this tubular organ, and exhibits the excretory tubes of numerous glands

opening upon its surface. Vacirca (1961) described the bovine mucosa as having sharp, low folds which have a longitudinal direction. Hayek (1960) maintained these folds are the result of displacement by the loose, underlying submucosa.

The tracheal mucosa contains respiratory epithelium (Edwards, 1956). Lucas (1932), and Miller (1932) both agreed that this type of epithelium, pseudostratified, ciliated, columnar, was composed of four types of cells: 1) basal cells; 2) non-ciliated cells; 3) ciliated cells; and 4) goblet cells. Vacirca (1961) identified the epithelium of bovine trachea as simple columnar with many layers of nuclei and with ciliated and mucous cells. Miller termed the non-ciliated cells as "Ersatzellen" or intermediate cells. The basal cells form the deepest layer and are situated just above the basement membrane. Their nuclei, lying parallel to the basement membrane, are either round or elongated. The basal cells are the only cells of the epithelium not extending through the thickness of the epithelium. The intermediate cells form the second layer of cells. According to Miller, their various forms are due to pressure within their proximity. They are usually spindle-shaped and often extend from the basement membrane to the free surface.

The third type of cell described by various investigators is the ciliated cell. This cell is columnar in shape and has on its outer free end a cuticular border bearing cilia. Lucas (1932) cited Drasch (1879) who found the nuclei situated at a higher level in the ciliated cells than in the intermediate wedge-shaped, non-ciliated cells, due to the greater length of the basal processes in the former. Lucas added that in 1911, Loginoff determined that the length of the ciliated cells was

frequently greater than the height of the epithelium in domestic animals, a fact attributable to the curvature of the basal ends of the cells.

The goblet cell or "chalice" cell is the fourth type of cell found in respiratory epithelium. Attached to the basement membrane, the goblet cell extends throughout the entire thickness of the epithelium. Its lower end may be like a "foot" (Miller, 1932), may terminate in a pointed prolongation, or may end in a number of fine prolongations. The free end of the goblet cell may be widely opened or it may be contracted like the neck of a bottle. The nuclei of goblet cells are usually situated on the same plane as those of the adjoining cells.

Rhodin (1959) reported the occurrence of a fifth cell type in the simple columnar epithelium of the rat trachea. This cell has a dense cytoplasm with small mitochondria scattered throughout the cell. The numerous small extensions on the surface of the cell are similar in appearance to the"brush border extensions"of the intestinal cells. Rhodin maintained that judging from the similarity, one would expect that this particular cell would have resorptive functions and actively participate in regulating the viscosity of the mucous blanket. In cross section the extensions appear to be forming cilia; consequently, the cell would then be a newly formed ciliated cell.

In 1932, Lucas provided an extensive study and review of the literature concerning the ciliated epithelium in man. He noted the findings of Kölliker and von Ebner in the middle and late 19th century, respectively. These two investigators measured cilia in man ranging from 3.3 to 5.7 microns. Stowe and Calhoun (1962) derived an average length of 3.9 microns for cilia in the ranch mink trachea. The average length of the cilia of

dog and cat tracheas measured 5.7 microns and 4.0 microns, respectively (Niewenhuis, 1961). According to Lucas, Valentin and Purkinje, working in the mid-19th century, counted from 10 to 22 cilia on each cell.

Investigators of the late 19th century denied the presence of a cuticular border, but those of the early 20th century claimed it was present in the ciliated tracheal cells of the rat and mouse, and was regarded as a cell product or perhaps a derivative of the ciliary border (Lucas, 1932). Lucas reported basal bodies, about 13 in number (as seen in cross section), lying at the free border of the cell and forming a single layer. Immediately below this layer is a narrow zone in which the cytoplasm, free from granules and mitochondria, displays ciliary rootlets.

Schulz (1959) reported that in the rat trachea the ciliated cells have not only cilia but also filiform processes. He arrived at a figure of 270 cilia per cell. Note the contrast with the report by Lucas (1932) on the number of cilia per cell in man.

A study performed by Chambers and Rényi (1925) on the ciliated cell of the frog's mouth demonstrated excellently the close relationship between the viable state of the cell and the optical appearance of the nucleus. If a ciliated cell be deformed or punctured with a needle without causing any apparent change within the nucleus, the cilia will either beat or can be made to beat upon stimulation. As soon, however, as the nucleus is affected, the cilia stop moving and disintegration of the cell follows.

The most important mechanism of excretion is that of cilia and secretion of mucus, for they extend over most of the respiratory tract

(Barclay, Franklin, and Macbeth, 1938). These investigators noted that ciliated epithelium is distributed throughout the trachea and bronchi down to the very fine bronchioles. In an earlier work, 1937, these same investigators recognized the clockwise spiral direction (as viewed from the oral end) of the ciliary movement in the cat.

The presence of leukocytes in the tracheal epithelium has been reported by several investigators (Paul, 1913; Miller, 1932; Andrew and Burns, 1947; Andrew, 1947; Hayek, 1960; and Vacirca, 1961). Perhaps the most extensive of these reports is that of Andrew and Burns on the large numbers of leukocytes in the tracheal epithelium of the normal adult mouse. Of these leukocytes the predominant type is the lymphocyte, but polymorphonuclear neutrophils are also abundant. Rarely are monocytes and eosinophils seen. The great majority of leukocytes in the trachea are located either below or at the level of the layer of epithelial nuclei. Relatively few appear to be in the process of continuing on through the epithelium to the lumen. Lymphocytes which have reached the apical ends of the epithelial cells generally show a marked pycnosis and decrease in size. The polymorphonuclear leukocytes are more frequently fragmented in this region. Andrew (1947) stated that pycnosis and fragmentation are common in the intestinal epithelium but rare in the trachea. Andrew and Burns (1947) added that while it seems clear that the great majority of leukocytes in the tracheal epithelium lie between the cells, instances have been found in which the leukocytes, particularly the lymphocytes, actually are intracellular, the position which is very common for such cells in the duodenum.

Paul (1913) reported having found leukocytes in the tracheal epithelium of the pig, horse, and cat. In 1961, Vacirca identified lymphocytic invasion in the epithelium of bovine trachea. Miller (1932) and Hayek (1960) asserted that scattered lymphocytes are commonly observed in the human trachea.

Of the literature reviewed only one authority referred to mitotic figures. Dawson (1948) affirmed the infrequent observation of mitotic figures in the tracheal epithelium.

According to Miller (1932), the earliest accounts of stratified squamous epithelium in the human trachea are found in papers published by Griffini and by Baraban in the late 19th century. Baraban found areas of squamous epithelium in the trachea of an executed criminal and thought that the transition of ciliated epithelium into stratified squamous epithelium is due to a low grade of irritation which leads to the loss of the cilia and to the appearance of mucous cells. As was the case with Griffini, all the instances in which Miller found stratified squamous epithelium in the human bronchi were from tuberculous lungs.

Hilding (1932) described squamous epithelium in the upper respiratory tract at the inactive areas (i.e., areas where the impact of air is not so great). He mentioned an additional transitional form of epithelium in proximity to the squamous epithelium. Both of these epithelial types are non-ciliated. At the active areas there is pseudostratified, ciliated, columnar epithelium. Because islands of squamous epithelium are commonly found in the trachea, Hilding suggested that all such changes may be caused by currents or eddies of air.

Hilding proposed that the different forms of epithelium found in the upper part of the respiratory tract are not fixed types, but are more or less interchangeable, according to circumstances. When the flow of air over the columnar epithelium of the nose is sufficiently increased the lining changes to a form much like "squamous" epithelium. Experiments indicate that the islands of similar epithelium found on the turbinates and the patches of stratified squamous epithelium so commonly found in the trachea are caused by eddies in the streams of air which cause more forceful impact in these spots than the columnar epithelium can tolerate.

The observations of Hilding on the replacement of pseudostratified, ciliated, columnar epithelium by a "squamous" epithelium agree with the findings of Koss (1961) that squamous metaplasia, the replacement of one type of epithelium by squamous epithelium that is not normally present in a given location, reflects chronic irritation of the respiratory tracts. Koss stated that squamous metaplasia may be circumscribed or diffuse.

In contrast to the above mentioned reports by Hilding and Koss, Correll and Beattie (1956) through their observations on the destroyed epithelial lining of the trachea of the dog alleged that the epithelium eventually regenerated is of the ciliated columnar type requiring 3-4 weeks to regenerate. Knowlton and McGregor (1928) noted similar circumstances in the maxillary sinuses of dogs.

Ropes (1930) presented evidence of phagocytosis, which is an activity repeatedly denied for tracheal epithelium and which is a function of the ciliated epithelial lining of the trachea and bronchi in rabbits.

He maintained that if particulate matter is suspended in a fluid medium, the ciliated cells do not phagocytize; however, if the particulate matter is inhaled under normal atmospheric conditions, then phagocytosis occurs. Ropes listed the following phagocytic cells: 1) columnar or cuboidal, ciliated cells; and 2) low columnar, cuboidal or rounded cells.

Miller (1932) described the basement membrane as a clear, homogeneous, structureless membrane having been derived from the subepithelial, elastic layer or as made up of elongated cells, placed end to end. In contrast to this Hayek (1960) asserted that the basement membrane is not homogeneous, but rather a network of argyrophilic fibers. According to Vacirca (1961), the basement membrane appears distinct in the bovine trachea. Niewenhuis (1961) found the basement membrane of the cat and dog to be indistinct. Schulz (1959) measured the basement membrane of the cat trachea and found it to be 600Å in thickness.

Rhodin and Dalhamn (1955) included as the main components of the lamina propria of the tracheal mucosa of the rat the fibroblasts, the collagenous and the elastic fibers. The collagenous fibrils, well separated from the fibroblast by its cell membrane, are aggregated in bundles with 1000-2000 fibrils in each. The elastin occurs in dense fibers void of branching, with a diameter of about 1-2 microns. Dawson (1948) reported the presence of reticular fibers in the lamina propria.

According to Hayek (1960), the membrana propria, forming the deep limit of the mucosa, contains a superficial layer with numerous cells and a deeper one which is rich in fibers. The cells are mostly lymphocytes which are found grouped especially about the glandular ducts. He stated

that not only does this layer contain the blood capillaries and lymphatic vascular networks, but also a loose network of collagenous fibers. In the deep layer there are numerous elastic fibers which laterally form a thin layer and dorsally are condensed into thick bundles occupying the longitudinal folds.

Macklin (1922) conducted an excellent investigation on the elastic membrane, a component of the lamina propria. Macklin described the elastic membrane as a "creamy white," Y-shaped band of elastic tissue, which when stretched snapped back "like a rubber band." He demonstrated the contrast of the sharp recoil before removal from the tracheo-bronchial tree and the sluggish recoil after removal from the tree. A microscopic analysis by Macklin showed the elastic fibers run parallel to the longitudinal axis of the trachea, in agreement with Wilson (1859) and Sauser (1957), the latter adding that this is the basic functional structure. Each fiber follows a gently undulating course and branches frequently; thus, a meshwork of elastic fibers, elongated longitudinally, is formed. Macklin noted a tendency for the fibers to assemble into fasciculi, which themselves interbranch. The elastic membrane forms a complete, extensible sheath for the epithelium of the trachea.

Miller (1947) presented a correlation by Zuckerkandl between the longitudinal folds of tracheal mucosa and the bundles of elastic fibers. The elastic fibers appear in the form of bundles because of the folds having been formed by the contraction of the trachealis muscle and the inherent elasticity of the cartilages, and not by the bundles of elastic fibers.

Stowe and Calhoun (1962) determined the thickness of the elastic membrane of the ranch mink trachea to be 7-10 microns. Niewenhuis (1961)

gave average values of 94.3 microns for the dog and 29 microns for the cat.

Paul (1913) reported that in the trachea of the horse, cat, and pig the elastic fibers may be interspersed among the lobes of the glands, which are frequently present in the lamina propria.

Dawson (1948), Trautmann and Fiebiger (1957), and Vacirca (1961) reported the presence of lymphatic nodules in the lamina propria. Trautmann and Fiebiger pointed out their frequent presence in sheep tracheas. Vacirca recognized their common occurrence around the ducts of glands.

Submucosa

According to Hayek (1960), Schaffer maintained the differentiation of a submucosa as a true layer is justifiable--contrary to von Schuhmacher and Petersen, who did not recognize this layer--at least in the region of the membranous wall, since the mucous membrane there can be displaced and can lie in folds, a circumstance permitted by the loose submucosa. Particularly in the region of the cartilage, the submucosa is lamellar in structure and passes without sharp demarcation into the perichondrium of the cartilage.

Stowe and Calhoun (1962) reported the secretory portions of the serous and mixed, sero-mucous glands and loose connective tissue comprise the major portion of the submucosa in the ranch mink trachea. Greep (1954) and Jordan (1952) noted loose fatty and areolar connective tissue, small tubuloacinar mucous glands with mucous cells and serous crescents, large blood vessels, and nerves in the submucosa of the

human trachea. The submucosa of domestic animals is rich in elastic fibers (Trautmann and Fiebiger, 1957).

Glands

The glands of the trachea are found in the submucosa (Florey, Carleton, and Wells, 1932), in the lamina propria (Ham and Leeson, 1961), external to the annular ligament, between the annular ligament and the trachealis muscle, and in the substance of the annular ligament between the cartilage rings (Wilson, 1859), and external to the cartilaginous rings (Trautmann and Fiebiger, 1957).

Florey, Carleton, and Wells (1932) found acini of gland cells lying in the submucosa of the cat trachea. These cell groups are serous, mucous or mixed in type. Stowe and Calhoun (1962) reported similar findings in the ranch mink trachea. Quain (1882) and Stirling (1883) had described purely mucous glands. Bremer and Weatherford (1946) reported the glands consisted of mucous cells with serous crescents. According to Florey, Carleton, and Wells, gland cells which on a morphological basis would be termed "serous" often appear to be capable of elaborating mucus, as evidenced by their histological reactions.

Paul (1913) reported the presence of glands in the whole course of the trachea as well as the complete circumference. Although their main site is in the submucosa, they are abundant, as well, in the lamina propria (in agreement with Ham and Leeson, 1961). Paul described predominantly complex tubular, particularly tubuloalveolar, glands in the pig. He also reported that in the pig they are mucous in type and serous in the horse and cat; mixed types are rarely present in any of these species.

Vacirca (1961) found tubuloacinous glands of a mixed type in the submucosa of the trachea of cattle.

Miller (1947) described glands of a tubuloacinar type situated in the submucosa. They are more abundant in the anterior wall than in the lateral wall of the human trachea. In the posterior membranous wall, they are situated not only in the submucosa but also within and posterior to the trachealis muscle with their ducts passing through the muscular layer in order to reach the surface of the mucosa. Frequently the ducts open on the surface of the mucosa by a funnel-shaped enlargement.

Cartilage

The cartilaginous rings, which serve as the framework for the trachea, are generally considered to be C-shaped (Bloom and Fawcett, 1962, and Copenhaver and Johnson, 1958). Sauser (1957) described the rings as horse-shoe-shaped. Straus (1931) cited variations of cartilage form among the primates, ranging from complete to incomplete enclosure with the presence or absence of overlapping rings.

In their review, Stowe and Calhoun (1962) presented the variations in certain species regarding the number of rings and ring types. Among those having incomplete rings are man, pig, dog, cow, cat, and horse. Complete rings are found in the lemur and fowl. Of those species reviewed, the number of rings varied from 18-20 (man) to 110-120 (turkey).

These same investigators found the margin of the tracheal rings in the ranch mink to vary greatly from ventral to dorsal, if viewed in cross section. They established an increase in ovoid elongation from ventral to dorsal (i.e., the ventral cross sectional view may be considered oval,

whereas the dorsal cross sectional view may be considered spatulate). In a longitudinal section through the trachea, the cross sections of the individual rings show a flat, outside margin and a convex, inside margin (Hayek, 1960).

With one exception, authorities (Bloom and Fawcett, 1962; Ham and Leeson, 1961; and Copenhaver and Johnson, 1958) agree that the tracheal rings are comprised of hyaline cartilage. Paul (1913) found, in some cases, cartilage of an elastic character present in the trachea of the horse and cat. In old age, the hyaline cartilages show fibrous degenerative changes, and may become partly calcified (Bremer and Weatherford, 1946). Niewenhuis (1961) reported no significant amount of calcification in the tracheal rings of either the dog or the cat.

Hayek (1960) asserted the perichondrium, thicker externally than internally, consists principally of collagenous fibers which encircle the trachea, and among which are inter-mingled a few elastic fibers.

Vacirca (1961) called attention to a ridge, extending the length of the bovine trachea, formed by the opposition of the cartilage tips in the dorsal region.

The site of bifurcation of the trachea is marked by the "carina tracheae" (Miller, 1904). From a study of 150 cat tracheas, Miller concluded the carina is rarely membranous and the bronchial cartilages either alone or in combination with the tracheal cartilage form the great majority of the carinae.

In a later study (1947), Miller maintained if cartilage were present, then it is classified accordingly: "When the cartilage was derived from a bronchial crescent it might be either 'bronchial right' or 'bronchial left,'

or when, as in some cases, both bronchial cartilages entered into the carina, 'double bronchial.' Occasionally a fused tracheal and bronchial crescent entered the carina; then called 'tracheo-bronchial' and like the simple 'bronchial,' it could be either 'right' or 'left'."

Annular Ligament

The cartilaginous, tracheal rings are held together by a strong fibrous membrane, which is elastic and yielding to a certain extent, and not only occupies the intervals between them, but is prolonged over their outer and inner surfaces, so that they are, as it were, imbedded in the membrane (Quain, 1882). Wilson (1859) had claimed this membrane to cover only the outer surface of the rings as well as extending from one cartilage tip to its opposing tip.

Stowe and Calhoun (1962) reported the presence of white fibrous connective tissue and the absence of elastic fibers in the annular ligament of the ranch mink trachea. Paul (1913) found elastic fibers in this membrane in the pig and horse. Niewenhuis (1961) identified small amounts of elastic fibers in the annular ligaments of the dog and the cat. If elastic fibers are present, they have a longitudinal course (Hayek, 1960).

Trachealis Muscle

The mammalian trachealis muscle is located in the posterior membranous portion of the trachea (Towers, 1953). Chauveau (1873) cited Leyh as having described longitudinal fibers in the anterior wall of the human trachea, between the mucous membrane and the cartilaginous rings.

Paul (1913) identified the circularly directed fibers in the horse, pig, and cat. Stirling (1883) claimed to have observed longitudinally

directed fibers arranged in several bundles located outside the transversely disposed fibers. Chauveau (1873) reported Kölliker had found some longitudinal fibers passing across the transverse ones at the posterior part of the trachea. Macklin (1929) identified a few longitudinal fibers, scattered mainly in the region of the carina.

According to Miller (1920), Cuvier was the first to point out that the musculature of the trachea in some animals is inserted on the outer surface of the cartilages, in others on the inner surface. In agreement with Meckel and Luschka, Miller (1913) found an external attachment in all the examined carnivora. In monotremes and insectivora the attachment is internal. As a rule, the attachment is internal in herbivora, e.g., ox. The rabbit is an exception to this rule. In man, an omnivore, it is internal.

The trachealis muscle is inserted into the perichondrium by attachments of elastic connective tissue (Paul, 1913). Hayek (1960) referred to these elastic components as "elastic tendons." According to Miller (1913), Guieysse stated that in the smaller animals the insertion is directly into the perichondrium, but in the larger animals an elastic tendon is interposed between the muscle and the perichondrium. Niewenhuis (1961) reported having observed transverse elastic fibers serving as attachments for the trachealis muscle onto the outer perichondrium of the trachea of both the dog and the cat.

According to Macklin (1929), the trachealis muscle exhibits a peristaltic wave resembling that of the digestive tract. Its length may reach to 10 cm. Macklin claimed the speed of masses so propelled too rapid to be accounted for by ciliary action. Bullowa and Gottlieb described the

peristaltic mechanism as "bellows-like," and Reinberg found it so marked in the trachea as to suggest the designation "tracheal vomiting." (Macklin, 1929).

Adventitia

In the cervical region of Equus, Bos, Ovis, Sus, and Canis, the adventitia of the trachea blends with the superficial layer of deep fascia. A more intimate fascia propria forms a tubular sheath around the trachea (Sisson and Grossman, 1959). In man, the adventitia is continuous with the loose connective tissue of the mediastinum and contains abundant blood and lymphatic vessels and both medullated and non-medullated nerves.(Greep, 1954).

Blood and Lymphatic Vessels

Blood and lymphatic vessels are found in both the lamina propria (Hayek, 1960) and submucosa (Vacirca, 1961). According to Cover (1953), the lamina propria of the turkey trachea is highly vascular. Jordan (1952) maintained the submucosa was occupied by the larger blood vessels. Trautmann and Fiebiger (1957) noted a submucous, a periglandular, and a subepithelial plexus of blood vessels, as well as a deep and superficial network of lymphatics in the tracheas of domestic animals.

Nerves

Nerves, located in the adventitia of the tracheas of domestic animals, possess microscopic ganglia and consist of both myelinated fibers and unmyelinated fibers, the latter ending on the smooth muscle cells (Trautmann and Fiebiger, 1957). A large number of small ganglia

are found in the dorsal wall of the trachea of the mouse from the caudal portion of the cricoid cartilage of the larynx to the bifurcation of the trachea (Honjin, 1954). These ganglia form a chain and are connected serially by nerves.

Elftman (1943) found two types of afferent nerve endings in the tracheal wall of a four-day old puppy. One of these types terminated in swellings or reticulations among the smooth muscle cells. The other type of afferent ending in the trachea showed subepithelial branches with swellings at their intersections and a ring termination. In addition, some of the branches continued up between the epithelial cells. Lucas and Douglas (1935) found no motor innervation of the tracheal epithelium.

MATERIALS AND METHODS

The data obtained for this study came from the tracheas of thirty-six animals--twelve each of cattle, sheep, and goat. All of the specimens exhibited no pathological disorders with the following exceptions: one 6-month old cow with mastitis, a second 2-year old cow with peritonitis, and one sheep with a mild inflammatory response in the respiratory passages.

Upon obtaining each of the thirty-six tracheas, sections from three levels of each trachea were procured for further study. The levels resected were the following: first, tissue approximately three rings below the cricoid cartilage; second, tissue approximately three rings above the first bifurcating bronchus; and third, tissue at a level approximately midway between the anterior and posterior ends of the trachea. The tissue of freshly killed or embalmed animals was placed in F.A.A. (Lavdowsky's mixture, Guyer, 1949).

In order to dehydrate and infiltrate the tissue, the author used the butyl alcohol method as prescribed by Johnson, et al., 1943. Bioloid* served as the medium for imbedding the tissues.

Ten specimens of each of the three species were utilized for cross-sections, while two specimens of each species were used for longitudinal sections.

A routine hematoxylin and eosin stain was performed to enable studying, in general, the mucosa and submucosa. This stain also allowed detailed observation of the epithelium. A Weigert-Van Gieson connective

* Will Corporation, Rochester, New York

tissue stain provided for the differentiation of collagenous and elastic components of the mucosa and submucosa, as well as demonstration of the nature of the cartilaginous tissue. A third stain, toluidine blue, (Lillie, 1954), made possible the distinction between mucous and serous cells of the glands, the enhancement of the outline of the goblet cells of the epithelium, and the demonstration of the metachromatic nature of mast cells.

As a result of these methods slides prepared from each of the thirty-six tracheas represented the dorsal, lateral, and ventral regions at each of the three levels.

With the aid of a calibrated ocular micrometer, measurements of various structures were determined in microns and recorded. In order that a range of numerical values might be derived, the author attempted to evaluate the greatest and least magnitude, as well as intermediate, representative magnitudes.

A list of the structures and characteristics that were measured follows:

Epithelium - height

Cilia - length

Elastic membrane - thickness

Elastic fibers - diameter

Submucosa - depth

Cartilage - thickness

Perichondrium (inside) - thickness

Perichondrium (outside) - thickness

Trachealis muscle - thickness

RESULTS AND DISCUSSION

The tracheas of Bos, Capra, and Ovis, both male and female, display three major layers, namely, 1) a mucosa containing an epithelium, a basement membrane, and a lamina propria; 2) a submucosa; and 3) a fibroelastic-cartilaginous layer (Plate I).

MUCOSA

Epithelium

The mucous membrane of the tracheas of Bos, Capra, and Ovis is lined predominantly by a pseudostratified, ciliated, columnar epithelium (Plates I and II) containing goblet cells. This type of epithelium is present at each of the three tracheal levels examined, as well as the dorsal, ventral, and lateral regions.

In several cases of each species patches of a non-keratinized, metaplastic, stratified squamous epithelium appears dorsally. The presence of this type of epithelium in the trachea has been recognized by other investigators, has been considered relatively common, and has been attributed to an increase in attrition during both inhalation and exhalation.

Four cell types exist in the tracheal epithelium (Plate II) and are readily identifiable in each specimen examined. The first of these cell types, the goblet cell, is most abundant ventrally, less laterally, and least dorsally. The base of the goblet cell rests on the basement membrane while the apex of this cell reaches the lumen of the trachea. The nuclei of the goblet cells, the product of which is a mucous secretion,

are situated within the vicinity of the adjacent intermediate and ciliated cells. The size of the goblet cells appears to vary in proportion to the degree of mucous content. In instances of abundant mucus, cells adjacent to the goblet cells appear laterally compressed.

The basal cells, perhaps the most readily identifiable of the four cell types, are situated in a conspicuous row immediately above the basement membrane. These cells do not extend to the lumen of the trachea, and consequently possess no free border. The oval nuclei of the cuboidal basal cells occupy most of the cellular cytoplasm.

The intermediate and ciliated cells of the epithelial lining present a narrow and elongated profile. The former extend throughout most of the thickness of the epithelium; frequently reaching the free surface of the epithelium; whereas the latter extend from the basement membrane to the lumen, their cilia obviously exposed to the overlying mucous blanket.

The cilia (Tables 1, 2, and 3) appear as hair-like projections, the fixed ends of which are in contact with a distinct striated border (Plate III). The striated border is continuous throughout the circumference (as seen in cross section) of the mucous membrane and is interrupted only by the apex of the goblet cells.

The fifth cell type (dense cytoplasm with scattered mitochondria and small extensions on the surface) of the simple columnar epithelium of the rat trachea described by Rhodin (1959) was not discerned.

Observation of mitotic figures is rare in the trachea of Bos, Capra, and Ovis. Those identified were situated in the basal region of the epithelium (Plate IV).

Leukocytic invasions of the epithelium are frequently seen in the tracheas of Bos, Capra, and Ovis. Lymphocytes are the outstandingly predominant type of leukocyte; however, in a few isolated specimens of each species, polymorphonuclear neutrophils can be identified. The leukocytic invasions exhibited two architectural patterns. In one of these patterns the leukocytes are aggregated into patches which extend completely through the epithelium to reach the mucous blanket (Plate VI) or to lower limits of the epithelium. The second pattern of leukocytic invasions is one of a scattered or dispersed nature.

Bos. The epithelium displays slight undulations with a general uniformity in height (Table 1).

Capra. Pronounced undulations of the epithelium are apparent. As in Bos the epithelium maintains a uniform thickness (Table 2) throughout its course. Crypts are usually absent.

Ovis. The intraepithelial crypts render a denticulate appearance to the epithelium. The epithelium at the base of these crypts is of considerably less height than the epithelium between any two crypts, as evidenced by the range in height recorded in Table 3. (Plate X).

Basement Membrane

Bos, Capra, and Ovis. The methods employed in this investigation did not provide for a critical examination of the basement membrane. However, in each of the animals examined, a faint but discernible line can be observed immediately adjacent to the lower limits of the cytoplasm of cells in contact with this line, which appears somewhat more refractile than the cellular membrane (Plate IV).

Lamina Propria

The deepest zone of the mucosa, the lamina propria, consists of white fibrous connective tissue, containing elastic and collagenous fibers, acini of glands and their ducts, blood and lymphatic vessels of a small caliber, connective tissue cells, lymphoid tissue, including nodules, and mast cells.

The elastic fibers (Tables 1, 2, and 3) are organized into a clearly delineated structure, commonly referred to as an "elastic membrane" (Plate XVII). In a cross-sectional view of the trachea, the elastic fibers manifest a longitudinally oblique deposition. Two of the ovine tracheas examined contain a few scattered elastic fibers coursing circularly in the ventral region at the middle level.

Interspersed throughout the lamina propria are collagenous fibers (Plate I), which are more densely distributed among the elastic fibers of the elastic membrane. Their random deposition and irregular direction provide a dense meshwork of white fibrous connective tissue. In Capra and Ovis their concentration is greatest in the lower limits of the elastic membrane. However, in Bos the collagenous fibers are equally concentrated throughout the zone of the elastic membrane (Plate I).

In longitudinal view the elastic and the collagenous fibers are seen deviating from their usual direction in order to circumvent the ducts and acini of the glands. The collagenous fibers, but not the elastic fibers, establish contact with the epithelial cells of the glands and ducts. A few collagenous fibers traverse between acini of the glands producing an entwined character for the glands.

Cross-sectional views of the trachea of each species (Bos, Capra, and Ovis) reveal fasciculated aggregations of the elastic fibers. These bundles are least conspicuous in Bos and Capra, but are quite evident in the trachea of Ovis (Plate I). The fasciculi of elastic fibers tend to correspond with the mucosal undulations. In the dorsal region of the trachea the relationship, as seen in cross section, is most apparent (Plate V). The morphology of this elastic membrane-mucosal undulation relationship leads one to deduce that the "wavy" surface of the epithelium may be attributable to the fasciculation of the elastic membrane during the exhalation phase of mechanical respiration or during a phase when distention of the trachea is at a minimum.

Lymphoid tissue is commonly seen in the lamina propria of the bovine, caprine, and ovine tracheas. In addition to the presence of a mild concentration of lymphocytes immediately below the epithelium of the ventral, lateral, and dorsal regions at all levels, lymph nodules occur frequently and may protrude into the submucosa (Plate VI). Although the nodules are invested by collagenous fibers, lymphocytes are often situated in the nearby connective tissue substance.

Connective tissue cells are scattered in moderate abundance throughout the area of the lamina propria. Mast cells, the metachromatic nature of which is demonstrated by the toluidine blue stain (Plate XII), are frequently observed in the lamina propria and are usually within the vicinity of or immediately adjacent to the small blood vessels.

SUBMUCOSA

White fibrous connective tissue and glands comprise the greater part of the submucosa (Plate XIX). The depth of the respective submucosae in Bos, Capra, and Ovis decreases from the ventral to the lateral region and is, in many cases, absent or shallow in the dorsal region at all the levels. The white fibrous connective tissue, accompanied by varying amounts of adipose tissue confer a loose nature upon the submucosa (Plate I). The collagenous fibers of the submucosa, as in the lamina propria, exhibit a random deposition with the exception of those circularly directed fibers which blend with the perichondrium of the inner surface of the cartilaginous ring. Circularly directed elastic fibers are frequently intermingled with the collagenous fibers which blend with the inner perichondrium (Plate XVIII).

Lymph nodules are seen less frequently in the submucosa than in the lamina propria. When present they have the same characteristics as those found in the lamina propria. As previously stated, lymph nodules may be so large as to occupy both the lamina propria and the submucosa. Lymphocytes, which presumably have migrated from these nodules, are usually clustered at the peripheral margins of the ducts of glands as the ducts proceed through the submucosa and mucosa to reach the lumen of the trachea.

Bos. The depths of the submucosae of Bos and Ovis are nearly equal (Table 6). Relative to the thickness of the cartilage, the submucosa of the bovine trachea is markedly more shallow than the submucosa of Ovis.

Capra. The submucosa is approximately half as deep as those of Bos and Ovis (Table 5).

Ovis. The depth of the submucosa is nearly equal in both the lateral and ventral regions (Table 4).

GLANDS

The glands of the tracheas of Bos, Capra, and Ovis are of the branched, tubuloacinar type whose acini are most frequently mixed in character (i.e., sero-mucous) (Plates VIII, X, XI, XIV). A few isolated acini of a purely serous or purely mucous nature are observed (Plates XII and XIII). In each of the three species, the glands are most numerous ventrally, less abundant laterally, and least numerous dorsally. No discernible gradation of quantity from the cranial level through the middle level to the caudal level was established.

The glands are present in both the lamina propria and the submucosa, a majority of them situated in the latter. When located in the lamina propria the acini of the glands tend to occupy the deeper zone of this layer, while in the submucosa the acini are inclined to reside in the upper limits of that layer (Plate XI).

The tracheal glands of Bos, Capra, and Ovis are, as a rule, located in the lateral and ventral regions; however, in many cases the glands are situated in the membranous area external to the dorsally fixed trachealis muscle or within the muscle tissue (Plates IX, XII, and XIII). In either case, the ducts of these glands pass through the trachealis muscle in order to reach the surface of the mucosa.

In Capra, the glands are commonly implanted in the ventral or lateral regions of the adventitia between the cartilaginous rings (as seen in a longitudinal view) and may be enveloped, in part, by the annular ligament (Plate XVII). In a cross-sectional view of the ventral or lateral region of the caprine trachea, tubuloacinar glands can be seen external to the cartilaginous rings (compare Plates XIV and XV).

In both Capra and Ovis the tracheal glands (as seen in cross section) appear as clusters or like a bunch of grapes. In Bos the acini of the tracheal glands (as seen in cross section) appear to be arranged like a string of beads (compare Plates X and XI).

In one ovine specimen, in the ventral region at the cranial level, the glands are situated between three overlapping cartilaginous rings (Plate XVIII). Such a location of tracheal glands is apparently uncommon.

The epithelial cells of the gland acini vary from low columnar to cuboidal in all three species of domestic ruminants (Plate IX). No pattern of distribution of the serous and mucous cells is discernible with the exception that a single acinus may contain all serous or all mucous cells or varying quantities of both cell types. Each of the two cell types is either serous or mucous in character and displays no serous or mucous crescents.

The nuclei of the serous cells possess an oval or round margin, while those of the mucous cells are compressed toward the base of each cell, depending on the amount of mucous content.

Epithelial cells of the ducts exhibit a gradation from low columnar or cuboidal to tall columnar at the outlet on the surface of the

mucosa. Mucous cells frequently line the ducts.

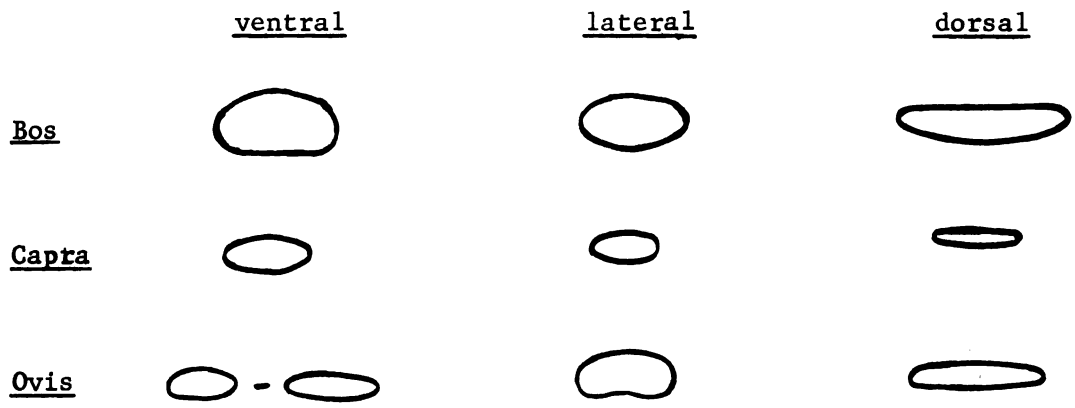
Tall, ciliated, columnar cells are present in the ducts of glands in Bos, Capra, and Ovis as the ducts course through the pseudostratified epithelium. The cilia of these columnar cells are directed toward the outlet of the duct.

As previously stated, collagenous fibers and connective tissue cells comprise the interstitial elements of the glands.

CARTILAGE

The dorsally incomplete cartilaginous rings, present in the tracheas of Bos, Capra, and Ovis, are composed of hyaline cartilage, (Plates XXI, XVI, XVII, XVIII and XX), incased by a thin inside and thick outside perichondrium. The rings have a C-shaped form in sheep, goats, and young cattle. However, in older cattle the tips of the rings oppose each other to lie parallel, thus forming a dorsally located ridge, macroscopically visible in an excised trachea. The cartilaginous rings of the tracheas of Bos, Capra, and Ovis are thickest ventrally, thinner laterally, and least thick dorsally (Table 4). Considered as a whole, the rings are thickest in Bos, thinner in Ovis, and still thinner in Capra (Table 6). Apparently the thickness of the tracheal rings of these three species decreases consistently from the cranial level to the caudal level..

In a longitudinal view of the tracheas of Bos, Capra, and Ovis, the cross sections of the cartilaginous rings can be observed. A description of the margin of the rings is best served by the diagrams on the following page.



Note: For orientation purposes the internal surface is at the top of the diagram and the external at the bottom.

The perichondria, both internal and external, are composed of dense white fibrous connective tissue containing collagenous fibers and cells of an intermediate form between chondrocytes and ordinary fibroblasts. The perichondria are present throughout the circumference of the cartilaginous rings, decreasing in thickness from the ventral to the dorsal region of the ring. In all regions the thickness of the perichondria appears enhanced by the adjacent collagenous fibers of the annular ligament.

ANNULAR LIGAMENT

The annular ligament, composed of collagenous and elastic fibers (Plate I), completely encompasses the cartilaginous rings of the tracheas of Bos, Capra, and Ovis. The annular ligament is best described as a membranous, tubular structure extending the entire length of the trachea. As seen in cross section, the annular ligament consists of two concentric, white fibrous connective tissue sheaths condensed into a single layer

dorsally between the ring tips, as well as throughout the perimeter of the cylinder between two adjacent cartilaginous rings, as seen in a longitudinal section. The cartilaginous rings are actually contained within the annular ligament; consequently, the architectural relationship of these two structures renders an externally corrugated appearance to the trachea. Circularly directed collagenous fibers predominate throughout the ligament, while circularly and longitudinally directed elastic fibers are plentiful only in the condensed area between the ring tips. The transversely directed elastic fibers extend for a short distance along the internal and external surfaces of the cartilage. Throughout the remainder of the annular ligament are isolated elastic fibers having a random direction (Plate XX).

TRACHEALIS MUSCLE

The trachealis muscle, composed of smooth muscle tissue, occupies a dorsal position in the tracheas of Bos, Capra, and Ovis (Plates IX, XII, XIII and XX). The smooth muscle fibers are circularly disposed and attached to the inner perichondrium a short distance from the cartilaginous ring tips. Several transversely arranged elastic fibers are interposed between the smooth muscle fibers and the inner perichondrium of the cartilage (Plate XX). The trachealis muscle is most expansive at the dorsal mid-line of the trachea and tapers to narrower proportions laterad. In Bos the magnitude of the trachealis muscle increases from the cranial to the caudal level; in Ovis, as in Capra, the magnitude remains constant, but in the former the thickness increases slightly from the anterior to the posterior end; in Capra the thickness of the trachealis muscle is nearly equal at all levels (Table 5).

The trachealis muscle is frequently occupied by tracheal glands and pierced by the ducts of these glands (Plates IX and XII).

No longitudinally disposed smooth muscle fibers were observed.

BLOOD AND LYMPHATIC VESSELS

The smallest blood vessels are found in large quantities throughout the lamina propria. Numerous larger blood vessels are present in the submucosa in the ventral and lateral regions; however, in the submucosa of the dorsal region, few blood vessels are present, and those which exist are of a small caliber. Blood vessels of a diameter between those of the lamina propria and the larger ones of the submucosa are located within the vicinity of the tracheal glands.

The adventitia contains large blood vessels whose walls are the thickest of any of the blood vessels seen in the trachea.

The membranous region external to the trachealis muscle is usually well populated by blood vessels.

Lymphatic vessels are difficult to distinguish, but careful examination reveals small numbers of these collapsed vessels in the lower depths of the lamina propria.

NERVES

Large nerve trunks are usually seen in the dorsal region in either the adventitia or in the membranous area external to the trachealis muscle. In older cattle possessing a ridge formed by the extended opposing ring types, one and frequently two nerve trunks are seen in the adventitia whose medial margin is marked by the ring tip having the greater curvature. An extreme variation of this relationship is depicted in Plate XXII.

Smaller nerve trunks are, in many instances, situated laterally in the adventitia. No nerve trunks are seen in the ventral adventitia.

ADVENTITIA

Peripheral to and completely investing the tracheas of Bos, Capra, and Ovis is a layer of loosely arranged collagenous fibers and adipose connective tissue, the latter decidedly the most abundant component of the adventitia (Plate XVI). Connective tissue cells are sparsely distributed throughout this investment. As previously stated, the adventitia contains blood vessels, as well as nerve trunks.

COMPARATIVE HISTOLOGY

The aim of the veterinary histologist is to establish the general histological criteria by which he can diagnose a given organ or its counterpart peculiar to several species. The results of this investigation, as well as those of Niewenhuis (1961), appear in a chart (page 34), which is a condensed presentation of those histological characteristics considered the distinguishing features of the tracheas of Bos, Canis, Capra, Felis, and Ovis.

A Comparison of the Tracheas of Bos, Canis, Capra, Felis, and Ovis

	Mucosa					Trachealis muscle
	Pseudostratified ciliated columnar epithelium with goblet cells	Crypts	Patches of transitional-like or stratified squamous epithelium	Basement membrane	Elastic membrane	(smooth muscle)
Felis	Present	Present	Transitional-like	Indistinct	Thin; non-fasciculated; compact band of longitudinal fibers	Circularly directed fibers; external attachment
Canis	Present	Present	Less amount of transitional than Felis	Indistinct	Like Felis with loosely arranged longitudinal fibers	As above
Bos	Present	Absent	Moderate patches of stratified squamous	Distinct	Thick; fasciculated; diffuse near epithelium, dense near submucosa; longitudinal fibers	Circularly directed fibers; internal attachment
Capra	Present	Usually absent	Occasionally stratified squamous	Distinct	Compact; relatively thick; fasciculated; dense throughout; longitudinal fibers	As above
Ovis	Present	Present	Occasionally stratified squamous	Distinct	Moderately compact; similar to Capra, but diffuse	As above

Note: Similarities for all species exist in the following: a submucosa of connective tissue with lymph nodules, glands, and blood and lymphatic vessels; mixed, tubuloacinar glands in lamina propria and submucosa; C-shaped, hyaline cartilage rings with a thin internal and a thicker external perichondrium; an annular ligament of white fibrous connective tissue and scattered elastic fibers completely incasing the rings and extending throughout the length of the trachea. (Specifications for Canis and Felis were derived from work of Niewenhuis, 1961.)

Table 1

Table 1

Measurements (in microns) of Microscopic Structures of Trachea of Bos

Structure	Region*	Level** a		b		c	
		Range	Mean	Range	Mean	Range	Mean
Epithelium (height)	D	22 - 76	45	20 - 72	50	40 - 72	56
	L	32 - 65	53	31 - 74	56	41 - 68	55
	V	45 - 88	61	36 - 81	58	43 - 74	58
Cilia (length)	D	6.4 - 7.2	6.9	6.4 - 7.2	6.9	6.4 - 7.2	6.9
	L	6.4 - 7.2	6.7	6.4 - 7.2	6.8	6.4 - 7.2	6.8
	V	5.6 - 7.2	6.8	6.4 - 7.2	6.8	5.6 - 7.2	6.6
Elastic Membrane (thickness)	D	161 - 657	190	89 - 928	329	72 - 757	312
	L	177 - 483	305	89 - 650	306	97 - 419	235
	V	242 - 483	322	225 - 812	357	161 - 386	238
Elastic Fibers (diameter)	D	1.6 - 2.4	2.2	1.6 - 2.4	2.1	1.6 - 2.4	1.8
	L	1.6 - 2.4	2.1	1.6 - 2.4	2.1	1.6 - 2.4	1.7
	V	1.6 - 2.4	2.1	1.6 - 2.8	2.1	1.6 - 2.4	1.7

* D - dorsal
L - lateral
V - ventral

** a - cranial
b - middle
c - caudal

Table 1 (continued)

Structure	Region*	Level** a Range	a Mean	b Range	b Mean	c Range	c Mean
Submucosa (depth)	D	0 - 266	93	0 - 928	203	0 - 290	107
	L	0 - 692	278	97 - 626	284	177 - 636	306
	V	113 - 1485	607	64 - 928	400	161 - 928	285
Cartilage (thickness)	D	201 - 1067	382	129 - 1067	469	116 - 905	397
	L	881 - 2807	1783	660 - 2506	1614	603 - 3480	1752
	V	1694 - 5359	2984	1531 - 3573	2754	1021 - 2529	1698
Perichondrium (outside) (thickness)	D	40 - 81	48	32 - 81	55	32 - 81	50
	L	24 - 121	78	40 - 177	66	33 - 185	84
	V	40 - 177	113	48 - 169	105	32 - 185	116
Perichondrium (inside) (thickness)	D	16 - 56	37	16 - 64	32	16 - 48	29
	L	24 - 97	62	24 - 97	74	32 - 73	45
	V	24 - 105	44	16 - 72	41	24 - 72	49
Muscle (thickness)	D	306 - 882	432	113 - 1322	622	225 - 1926	727

* D - dorsal
L - lateral
V - ventral

** a - cranial
b - middle
c - caudal

Table 2

Measurements (in microns) of Microscopic Structures of Trachea of *Capra*

Structure	Region*	Level** a		b		c	
		Range	Mean	Range	Mean	Range	Mean
Epithelium (height)	D	18 - 61	37	22 - 65	35	18 - 65	39
	L	22 - 72	44	25 - 68	49	32 - 76	51
	V	41 - 94	48	34 - 74	46	29 - 63	50
Cilia (length)	D	5.6 - 7.2	6.3	5.6 - 7.2	6.7	5.6 - 7.2	6.8
	L	5.6 - 7.2	6.6	5.6 - 7.2	6.5	5.6 - 7.2	6.6
	V	5.6 - 7.2	6.5	5.6 - 7.2	6.6	5.6 - 7.2	6.6
Elastic Membrane (thickness)	D	72 - 330	163	48 - 386	156	48 - 684	171
	L	72 - 266	125	56 - 306	135	40 - 233	114
	V	56 - 475	139	32 - 765	99	56 - 225	97
Elastic Fibers (diameter)	D	0.8 - 1.6	1.1	0.8 - 1.6	1.2	0.8 - 1.6	1.2
	L	0.8 - 1.6	1.1	0.8 - 1.6	1.0	0.8 - 1.6	1.2
	V	0.8 - 1.6	1.1	0.8 - 1.6	1.1	0.8 - 1.6	1.0

* D - dorsal
L - lateral
V - ventral

** a - cranial
b - middle
c - caudal

Table 2 (continued)

Structure	Region*	Level** a Range	a Mean	b Range	b Mean	c Range	c Mean
Submucosa (depth)	D	0 - 233	57	0 - 411	77	0 - 242	40
	L	56 - 483	180	72 - 394	198	89 - 499	168
	V	0 - 773	206	0 - 660	241	113 - 773	260
Cartilage (thickness)	D	89 - 467	260	121 - 459	216	81 - 904	291
	L	385 - 1137	726	394 - 1531	670	302 - 974	621
	V	603 - 1276	943	789 - 1624	973	418 - 1021	720
Perichondrium (outside) (thickness)	D	8 - 48	28	8 - 48	23	8 - 48	20
	L	24 - 89	49	24 - 145	51	16 - 81	35
	V	32 - 97	61	40 - 145	68	40 - 81	56
Perichondrium (inside) (thickness)	D	8 - 89	16	8 - 32	12	8-- 32	11
	L	16 - 64	33	16 - 48	26	8 - 40	20
	V	8 - 48	21	8 - 40	18	8 - 32	15
Muscle (thickness)	D	81 - 378	159	72 - 322	168	32 - 346	131

* D - dorsal
L - lateral
V - ventral

** a - cranial
b - middle
c - caudal

Table 3

Measurements (in microns) of Microscopic Structures of Trachea of Ovis

Structure	Region*	Level** a Range	a Mean	b Range	b Mean	c Range	c Mean
Epithelium (height)	D	7 - 101	51	9 - 90	48	24 - 138	49
	L	34 - 103	61	34 - 101	53	41 - 115	61
	V	31 - 104	61	32 - 83	51	38 - 85	57
Cilia (length)	D	3.2 - 7.2	5.8	2.4 - 7.2	5.4	3.2 - 7.2	5.8
	L	3.2 - 7.2	5.5	3.2 - 7.2	5.9	3.2 - 7.2	6.0
	V	3.2 - 7.2	5.9	3.2 - 7.2	5.8	3.2 - 7.2	6.2
Elastic Membrane (thickness)	D	48 - 394	153	32 - 338	133	40 - 354	116
	L	48 - 225	129	24 - 169	106	32 - 177	87
	V	24 - 242	111	48 - 193	101	48 - 113	75
Elastic Fibers (diameter)	D	0.8 - 2.4	1.2	0.4 - 3.2	1.2	0.8 - 1.6	1.1
	L	0.8 - 3.2	1.3	0.8 - 2.4	1.2	0.8 - 2.4	1.1
	V	0.8 - 2.4	1.2	0.8 - 1.6	1.1	0.8 - 1.6	1.0

* D - dorsal
L - lateral
V - ventral

** a - cranial
b - middle
c - caudal

Table 3 (continued)

Structure	Region*	Level** a Range	a Mean	b Range	b Mean	c Range	c Mean
Submucosa (depth)	D	0 - 346	114	0 - 242	75	0 - 225	86
	L	97 - 773	483	73 - 764	410	72 - 781	289
	V	161 - 620	376	121 - 789	456	121 - 660	341
Cartilage (thickness)	D	137 - 660	382	81 - 626	392	139 - 580	366
	L	464 - 1624	1071	620 - 1422	937	534 - 1422	844
	V	603 - 1508	1216	812 - 1647	1188	719 - 1160	1102
Perichondrium (outside) (thickness)	D	13 - 97	43	18 - 72	40	16 - 72	38
	L	22 - 97	71	16 - 129	75	18 - 97	64
	V	25 - 121	77	32 - 169	96	22 - 121	73
Perichondrium (inside) (thickness)	D	3.6 - 48	23	8 - 48	21	3.6 - 40	15
	L	3.6 - 110	34	9 - 48	25	7 - 40	19
	V	3.6 - 56	20	7 - 70	22	8 - 32	13
Muscle (thickness)	D	89 - 644	265	97 - 668	297	86 - 1021	307

* D - dorsal
L - lateral
V - ventral

** a - cranial
b - middle
c - caudal

Table 4

Comparison of the mean values (in microns) of the structural dimensions of the tracheas of Bos, Capra, and Ovis at the dorsal, lateral, and ventral regions

Structure	Region*	Bos	Capra	Ovis
Epithelium (height)	D	50	37	50
	L	55	48	58
	V	59	48	56
Cilia (length)	D	6.9	6.6	5.7
	L	6.8	6.6	5.8
	V	6.8	6.6	5.9
Elastic Membrane (thickness)	D	281	164	134
	L	282	126	107
	V	295	112	95
Elastic Fibers (diameter)	D	2.0	1.1	1.1
	L	2.0	1.1	1.2
	V	2.0	1.0	1.1
Submucosa (depth)	D	134	58	92
	L	306	180	394
	V	431	236	391
Cartilage (thickness)	D	416	253	380
	L	1716	672	951
	V	2479	879	1169
Perichondrium (outside) (thickness)	D	50	24	40
	L	76	45	70
	V	112	62	82
Perichondrium (inside) (thickness)	D	33	13	20
	L	61	26	26
	V	44	18	18
Muscle (thickness)	D	594	153	290

* D - dorsal
L - lateral
V - ventral

Table 5

Comparison of the mean values (in microns) of the structural dimensions of the tracheas of *Bos*, *Capra*, and *Ovis* at the cranial, middle, and caudal levels

Structure \ Level*	*Bos* a	*Bos* b	*Bos* c	*Capra* a	*Capra* b	*Capra* c	*Ovis* a	*Ovis* b	*Ovis* c
Epithelium (height)	53	55	56	43	43	47	58	51	56
Cilia (length)	6.8	6.8	6.7	6.5	6.6	6.7	5.7	5.7	6.0
Elastic Membrane (thickness)	272	331	261	142	130	127	131	113	93
Elastic Fibers (diameter)	2.1	2.1	1.7	1.1	1.1	1.1	1.2	1.2	1.1
Submucosa (depth)	326	296	233	148	172	156	324	314	239
Cartilage (thickness)	1716	1612	1282	643	620	544	889	839	771
Perichondrium (outside) (thickness)	80	75	83	46	47	37	64	70	58
Perichondrium (inside) (thickness)	48	49	41	23	19	15	26	23	16
Muscle (thickness)	432	622	727	159	168	131	265	297	307

*a - cranial
b - middle
c - caudal

Table 6

Comparison of the total mean values (in microns) of microscopic structures of the tracheas of Bos, Capra, and Ovis

Structure	Bos	Capra	Ovis
Epithelium (height)	55	44	55
Cilia (length)	6.8	6.6	5.8
Elastic Membrane (thickness)	286	133	112.2
Elastic Fibers (diameter)	1.9	1.1	1.1
Submucosa (depth)	290	158	292
Cartilage (thickness)	1537	591	833
Perichondrium (outside) (thickness)	79	44	64
Perichondrium (inside) (thickness)	46	19	22
Muscle (thickness)	594	153	290

SUMMARY AND CONCLUSIONS

Routine histological staining methods were used to study the tracheas of thirty-six animals--twelve each of Bos, Capra, and Ovis--including both male and female specimens. A range and mean value (in microns) were established for each structure measured.

The tracheas of Bos, Capra, and Ovis display three major layers, namely, 1) a mucosa containing an epithelium, a basement membrane, and a lamina propria; 2) a submucosa; and 3) a fibroelastic-cartilaginous layer.

The mucous membrane of the tracheas of Bos, Capra, and Ovis is lined predominantly by a pseudostratified, ciliated, columnar epithelium containing goblet cells. This type of epithelium is present at each of the three levels examined, as well as the dorsal, ventral, and lateral regions. Four cell types exist in the tracheal epithelium and are readily identifiable in each specimen examined. The goblet cell, most abundant ventrally, less laterally, and least dorsally, rests on a basement membrane and extends through the epithelial layer to reach the lumen of the trachea. The basal cells are situated in a conspicuous row immediately above the basement membrane. The intermediate cells may or may not extend through the mucous membrane. The bases of the ciliated cells lay fixed on the basement membrane, while the apices are covered by the mucous blanket of the lumen.

In Bos the epithelium displays slight undulations with a general uniformity in height. The epithelium of Capra exhibits pronounced undulations with uniform thickness. In Ovis, intraepithelial crypts are evident and the height of epithelium is not uniform.

Leukocytic invasions of the epithelium are frequently seen in the tracheas of Bos, Capra, and Ovis. Lymphocytes are the outstandingly predominant type of leukocyte.

The longitudinally directed elastic fibers of the lamina propria are organized into a fasciculated elastic membrane. The fasciculi are least conspicuous in Bos and Capra, but evident in Ovis.

Lymphoid tissue is commonly present in the lamina propria of the bovine, caprine, and ovine tracheas. In addition to the presence of a mild concentration of lymphocytes immediately below the epithelium, lymph nodules occur frequently in the lamina propria and the submucosa. Lymphocytes are often situated in the nearby connective tissue substance.

White fibrous connective tissue and glands comprise the greater part of the submucosa. The depths of the respective submucosae in Bos, Capra, and Ovis decrease from the ventral to the lateral region and are, in many cases, absent or shallow in the dorsal region at all levels. The depths of the submucosae of Bos and Ovis are nearly equal. The submucosa of the trachea of Capra is approximately half as deep as those of Bos and Ovis.

The glands, present in both the lamina propria and submucosa of the tracheas of Bos, Capra, and Ovis, are of the branched, tubuloacinar type, the acini of which are most frequently mixed in character. In each of the three species, the glands are most numerous ventrally, less abundant laterally, and least numerous dorsally. The glands may or may not be situated posterior to the trachealis muscle. In Capra, the glands are commonly implanted in the ventral and lateral regions of the adventitia between the cartilaginous rings and are enveloped, in part, by the annular ligament.

The epithelial cells of the gland acini vary from low columnar to cuboidal. A single acinus may contain all serous or all mucous cells or varying quantities of both cell types.

The dorsally incomplete, cartilaginous rings, present in Bos, Capra, and Ovis, are composed of hyaline cartilage. The rings have a C-shaped form in the sheep, goats, and young cattle; however, in older cattle the tips of the rings oppose each other to lie parallel for a short distance. The cartilaginous rings of each species are thickest ventrally, thinner laterally, and least thick dorsally. The thickness of the tracheal rings decreases from the cranial to the caudal level. The internal and external perichondria are composed of white fibrous connective tissue. The latter is thinner than the former.

The annular ligament, composed of white fibrous connective tissue with interspersed elastic fibers, completely encompasses the cartilaginous rings of the tracheas of Bos, Capra, and Ovis. The cartilaginous rings, therefore, are actually contained within the annular ligament.

The trachealis muscle, composed of circularly directed smooth muscle fibers, occupies a dorsal position and attaches to the internal face of the cartilaginous rings by means of elastic tendons. The thickness of the muscle is greatest at the dorsal mid-line, tapering to smaller dimensions laterad. Glands frequently occupy the trachealis muscle.

The smallest blood vessels are found in large quantities throughout the lamina propria. Numerous larger blood vessels are present in the submucosa. The adventitia contains blood vessels, the walls of which are the thickest of any of the blood vessels seen in the tracheas. Blood vessels are numerous in the dorsal, membranous region of all the tracheas.

Nerve trunks are present in the dorsal region in either the adventitia or in the membranous area external to the trachealis muscle. Small nerve trunks are situated in the lateral adventitia.

Peripheral to and completely investing the tracheas of Bos, Capra, and Ovis is a layer of loosely arranged collagenous fibers and adipose connective tissue comprising an adventitia. The adipose tissue is the most abundant component of the adventitia.

Differences between male and female specimens of each species are not observed in the trachea.

LITERATURE CITED

Andrew, W. 1947. Leucocyte migration into and through the epithelium of the trachea in the mouse. Anat. Rec. 97:411.

Andrew, W. and M. R. Burns. 1947. Leucocytes in the tracheal epithelium of the mouse. J. Morph. 81:317-341.

Barclay, A. E., K. J. Franklin and R. G. Macbeth. 1937. Contribution to study of ciliary movement. J. Physiol. 90:347-348.

Barclay, A. E., K. J. Franklin and R. G. Macbeth. 1938. Roentgenographic studies of the excretion of dusts from the lungs. Am. J. Roentgenol. 39:673-686.

Bloom, W. and D. Fawcett. 1962. A Textbook of Histology. W. B. Saunders Co., Philadelphia.

Bremer, J. L. and H. L. Weatherford. 1946. A Textbook of Histology. The Blakiston Co., Philadelphia.

Chambers, R. and G. S. Rényi. 1925. The structure of the cells in tissues as revealed by microdissection. 1. The physical relationships of the cells in epithelia. Am. J. Anat. 35:385-402.

Chauveau, A. 1873. Comparative Anatomy of the Domesticated Animals. W. R. Jenkins, New York.

Copenhaver, W. M. and D. D. Johnson. 1958. Bailey's Textbook of Histology. 14th ed. The Williams & Wilkins Co., Baltimore.

Correll, N. O., Jr. and E. J. Beattie, Jr. 1956. The characteristics of regeneration of respiratory epithelium. Surg. Gynecol. Obstet. 103:209-211.

Cover, M. S. 1953. Gross and microscopic anatomy of the respiratory system of the turkey. II. The larynx, trachea, syrinx, bronchi, and lungs. Am. J. Vet. Res. 14:230-238.

Dawson, H. L. 1948. Lambert's Histology. The Blakiston Co., Philadelphia.

Edwards, L. F. 1956. Concise Anatomy. McGraw-Hill Book Co. Inc., New York.

Elftman, A. G. 1943. The afferent and parasympathetic innervation of the lungs and trachea of the dog. Am. J. Anat. 72:1-27.

Florey, H., H. M. Carleton and A. Q. Wells. 1932. Mucus secretion in the trachea. Brit. J. Exp. Path. 13:269-284.

Greep, R. O. 1954. Histology. The Blakiston Co. Inc., New York.

Guyer, M. F. 1949. Animal Micrology. Univ. of Chicago Press, Chicago.

Ham, A. W. and T. S. Leeson. 1961. Histology. J. B. Lippincott Co., Philadelphia.

Hayek, H. von. 1960. The Human Lung. Trans. by Vernon E. Krahl. Hafner Pub. Co., New York.

Hilding, A. 1932. Experimental surgery of the nose and sinuses. Arch. Otolaryngol. 16:9-18.

Honjin, R. 1954. On the ganglia and nerves of the lower respiratory tract of the mouse. J. Morph. 95:263-287.

Johnson, E., F. N. Andrews and C. L. Shrewsbury. 1943. The preparation of the muscular tissue for histological study. J. Anim. Sc. 2:244-250.

Jordan, H. E. 1952. A Textbook of Histology. Appleton-Century-Crofts, Inc., New York.

Knowlton, C. D. and G. W. McGregor. 1928. How and when the mucous membrane of the maxillary sinus regenerates; an experimental study in the dog. Arch. Otolaryngol. 8:647-656.

Koss, L. G. 1961. Diagnostic Cytology and its Histopathologic Bases. J. B. Lippincott Co., Philadelphia.

Lillie, R. D. 1954. Histopathologic Technic and Practical Histochemistry. The Blakiston Co., New York.

Lucas, A. M. 1932. Ciliated epithelium. Cowdry's Special Cytology. Paul B. Hoeber, New York.

Lucas, A. M. and A. C. Douglas. 1935. Principles underlying ciliary activity in the respiratory tract. Arch. Otolaryngol. 21:285-296.

Macklin, C. C. 1922. A note on the elastic membrane of the bronchial tree of mammals, with an interpretation of its functional significance. Anat. Rec. 24:119-135.

Macklin, C. C. 1929. The musculature of the bronchi and lungs. Physiol. Rev. 9:1-60.

Miller, W. S. 1904. The carina trachea of the domestic cat. Anat. Anz. 25:377-382.

Miller, W. S. 1913. The trachealis muscle. Its arrangement at the carina tracheae and its probable influence on the lodgement of foreign bodies in the right bronchus and lung. Anat. Rec. 7:373-385.

Miller, W. S. 1920. A morphological study of the tracheal and bronchial cartilages. Cont. to Embryol., Carnegie Inst. Publ. No. 272. 9:285-298.

Miller, W. S. 1932. The epithelium of the lower respiratory tract. Cowdry's Special Cytology. Paul B. Hoeber, New York.

Miller, W. S. 1947. The Lung. Charles C. Thomas, Springfield, Illinois.

Niewenhuis, R. 1961. Comparative Histology of the Trachea of the Dog and Cat. Thesis. Michigan State University.

Paul, O. 1913. Beiträge zur vergleichenden Histologie der Trachea von Pferd, Schwein und Katze. Inaug. Diss. Leipzig.

Quain's Elements of Anatomy. 1882. ed. by A. Thomson, A. E. Schäfer and G. D. Thane. 9th ed. Longman's Green, and Co., London.

Rhodin, J. 1959. Ultrastructure of the tracheal ciliated mucosa in rat and man. Ann. of Otol. Rhinol. and Laryngol. 68:964-974.

Rhodin, J. and T. Dalhamn. 1955. Electron microscopy of collagen and elastin in the lamina propria of the tracheal mucosa of rat. Exptl. Cell Res. 9:371-375.

Ropes, M. W. 1930. Phagocytic activity and morphological variations of the ciliated epithelial cells of the trachea and bronchi in rabbits. Cont. to Embryol. Carnegie Inst. Publ. No. 414. 22:77-90.

Sauser, G. 1957. Paries elastico-muscularis tracheae. Acta Anat. 30:705-712.

Schulz, H. 1959. Die Submikroskopische Anatomie und Pathologie der Lunge. Springer-Verlag, Berlin.

Sisson, S. and J. D. Grossman. 1953. The Anatomy of the Domestic Animals. W. B. Saunders Co., Philadelphia.

Stirling, W. 1883. The trachealis muscle of man and animals. J. Anat. Physiol. 17:204-206.

Stowe, H. D. and M. L. Calhoun. 1962. Gross and microscopic anatomy of the trachea of the ranch mink. Am. J. Vet. Res. 23:649-656.

Straus, W. L. 1931. The form of the tracheal cartilages of primates with remarks on the supposed taxonomic importances. J. Mammal. 12:281-285.

Towers, B. 1953. The muscle-cartilage relationship in the extrapulmonary bronchi. J. Anat. 87:337-344.

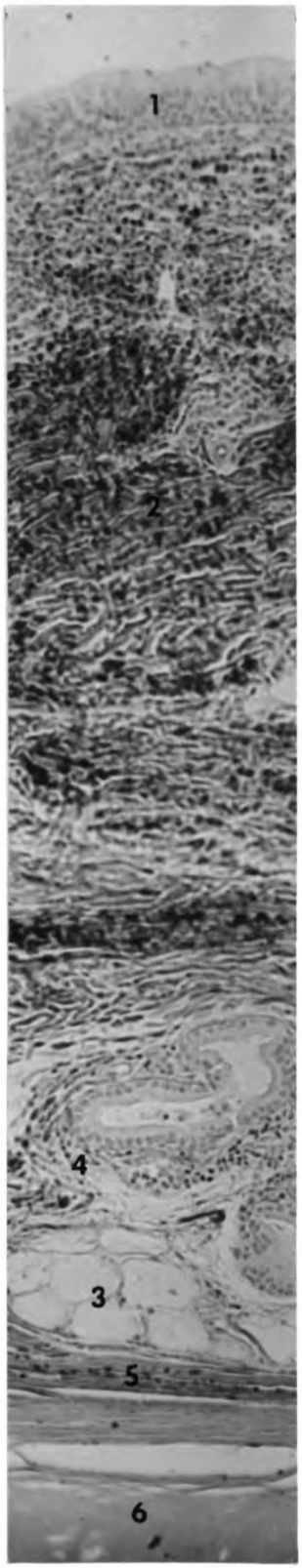
Trautmann, A. and J. Fiebiger. 1957. Fundamentals of the Histology of Domestic Animals. Trans. by R. E. Habel and E. L. Biberstein. Comstock Publishing Assoc., Ithaca, New York.

Vacirca, G. 1961. Diagnostica e terapia delle malattie dell'apparato respiratorio dei bovini. Veterinaria, Milan. 10:360-364.

Wilson, E. 1859. A System of Human Anatomy. ed. by. W. H. Gobrecht. Blanchard & Lea., Philadelphia.

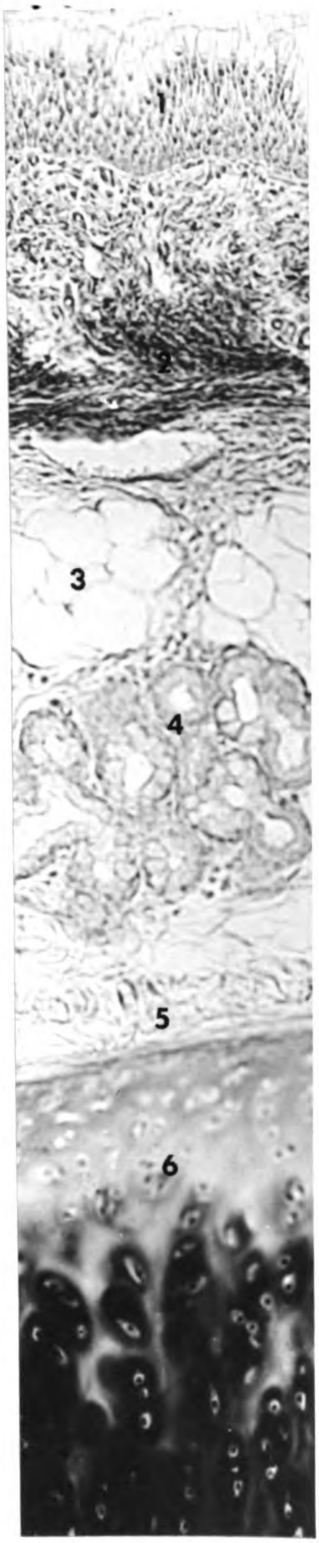
Plate I. A comparison of cross-sectional views of the bovine, caprine, and ovine tracheas; ventral region, caudal level. Note the relative thicknesses of each layer. Hematoxylin and eosin stain; x 140.

1. epithelium
2. elastic membrane
3. adipose tissue
4. submucosa
5. collagenous fibers
6. cartilage



Bos

Capra



Ovis

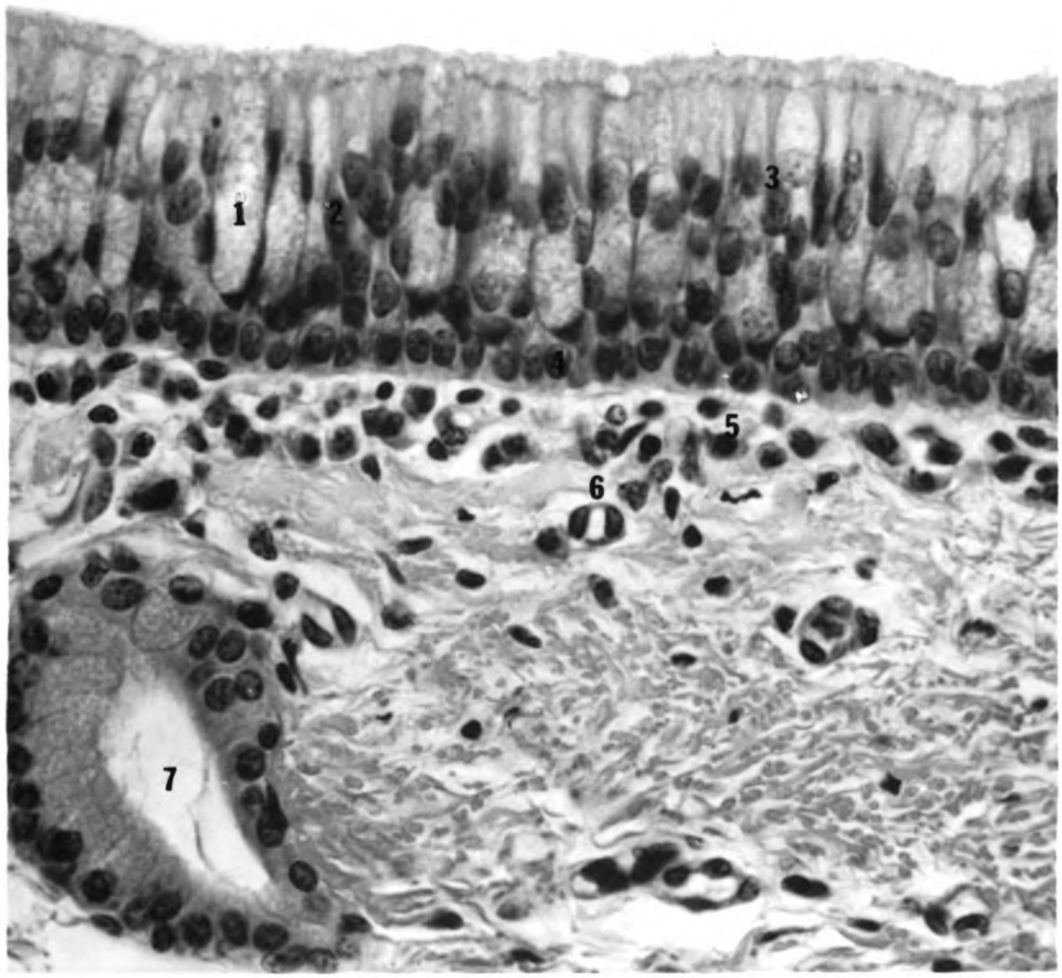


Plate II. Cross-sectional view of ovine tracheal epithelium and its four cell types; ventral region, cranial level. 1, goblet cell; 2, intermediate cell; 3, ciliated cell; 4, basal cell; 5, lymphocyte; 6, blood capillary; 7, gland duct. Hematoxylin and eosin stain; x 364.

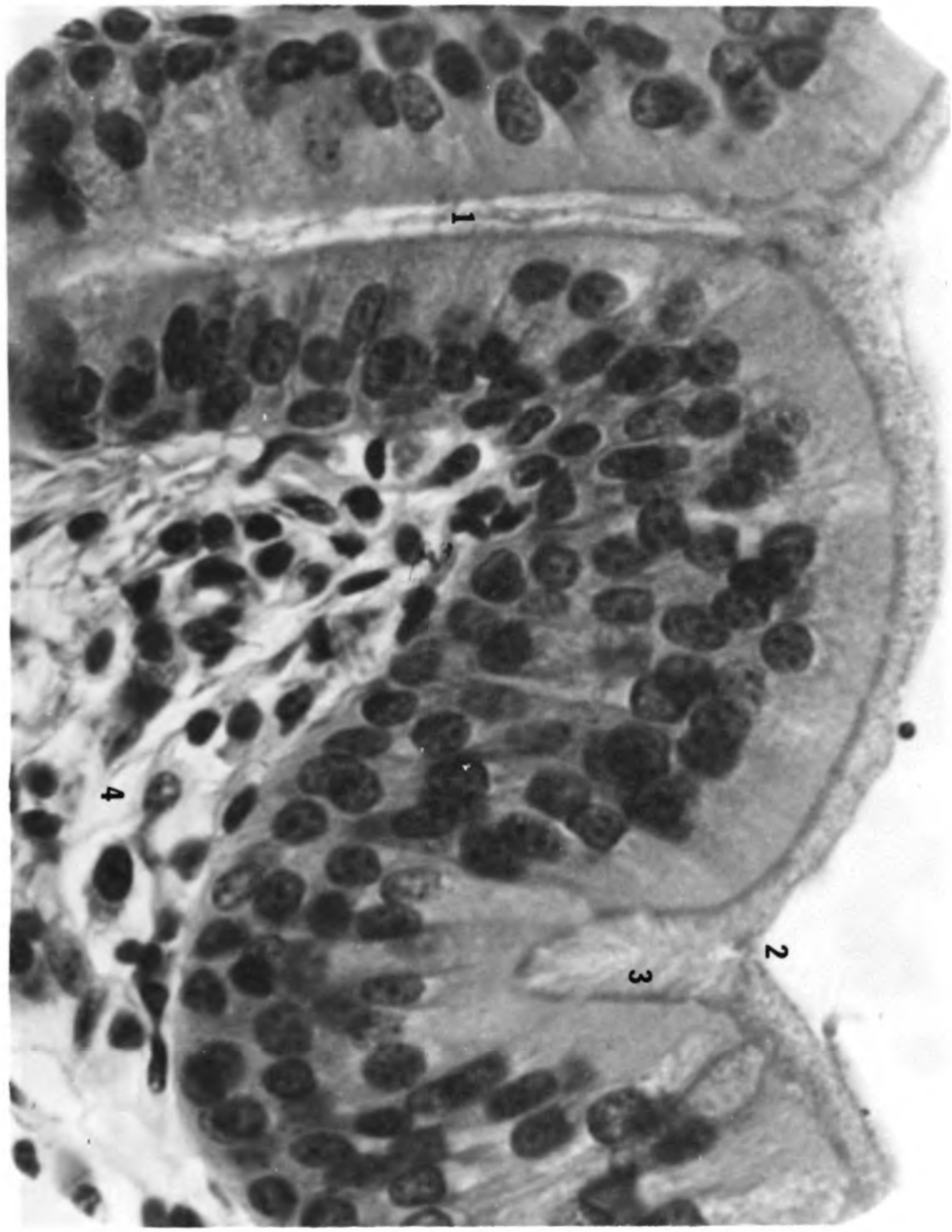


Plate III. Cross-sectional view of ovine tracheal mucous membrane; lateral region, middle level. Note the difference in cell alignment at bottom of crypt and at corresponding level of duct. 1, duct; 2, crypt; 3, cilia; 4, lamina propria. Hematoxylin and eosin stain; x 813.

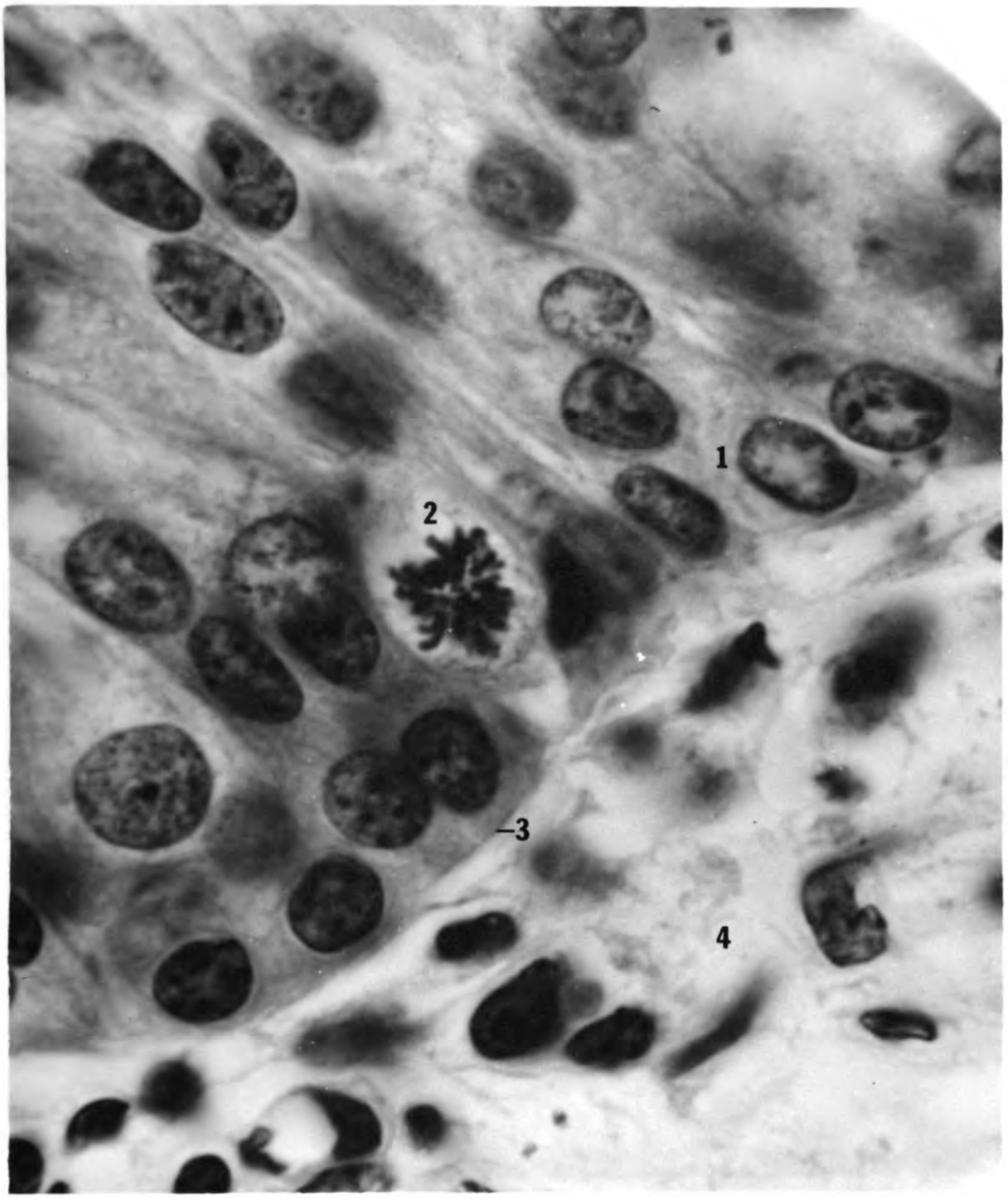


Plate IV. Polar view of basal cell during metaphase of mitotic division; lateral region, middle level of ovine trachea. 1, basal cell; 2, mitotic figure; 3, basement membrane; 4, lamina propria. Hematoxylin and eosin stain; x 2067.

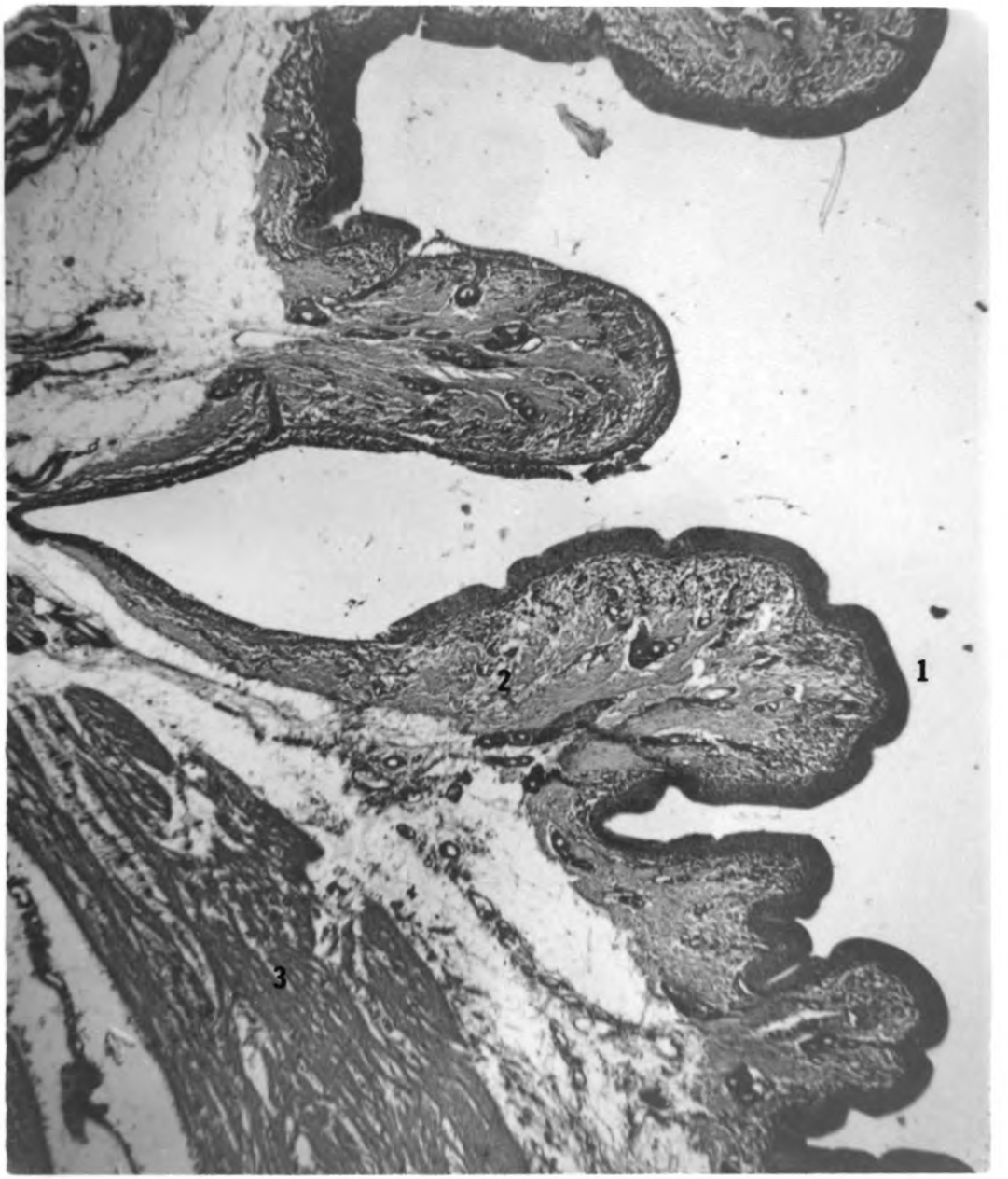


Plate V. Cross-sectional view of pronounced mucosal folds in dorsal region of middle level of bovine trachea. 1, mucosal fold; 2, lamina propria; 3, trachealis muscle. Toluidine blue stain; x 57.

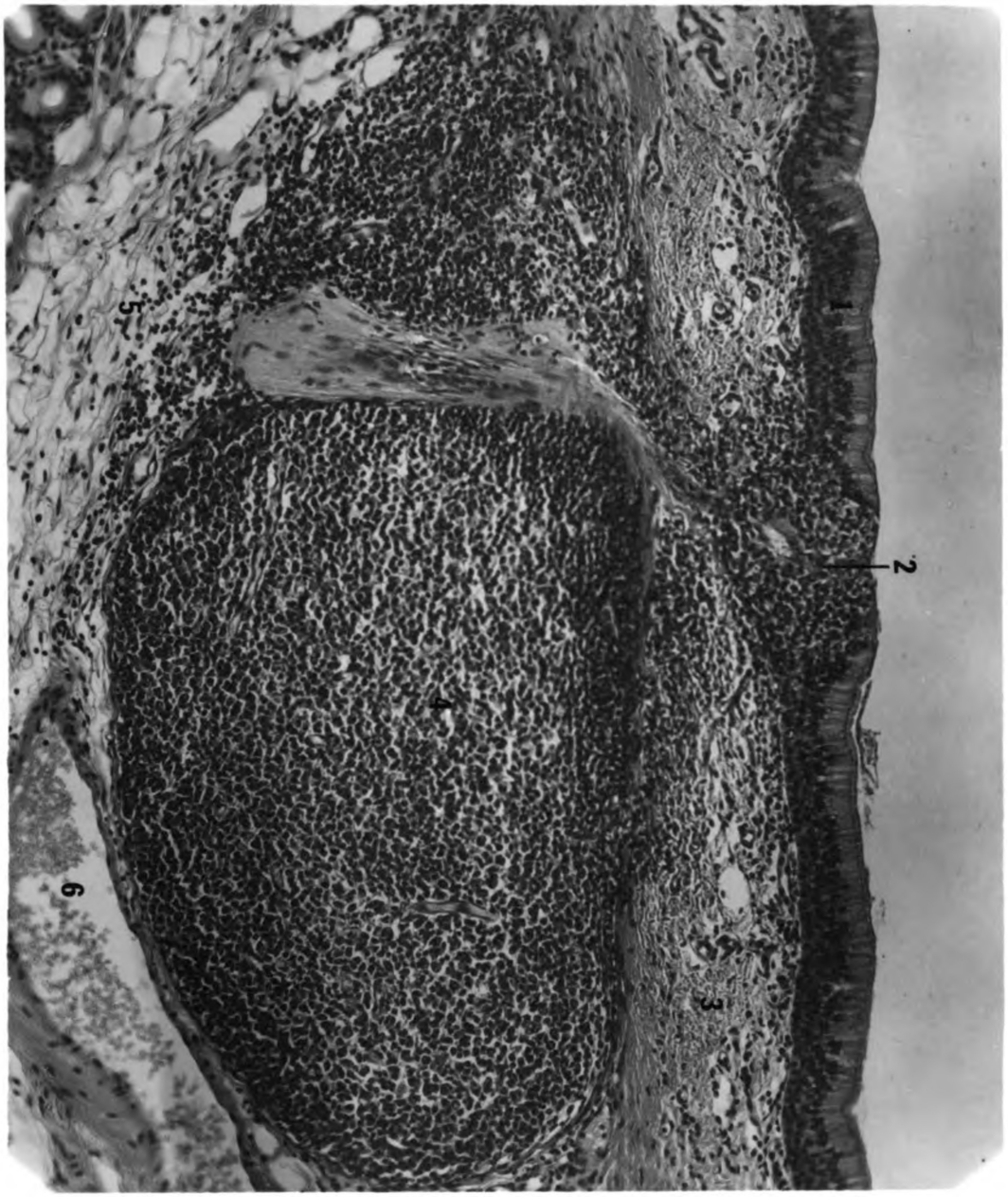


Plate VI. Cross-sectional view of ovine trachea showing lymph nodule in submucosa and lymphocytic invasion of epithelium; ventral region, middle level. 1, epithelium; 2, lymphocytic invasion; 3, lamina propria; 4, lymph nodule; 5, scattered lymphocytes; 6, blood vessel. Hematoxylin and eosin stain; x 126.

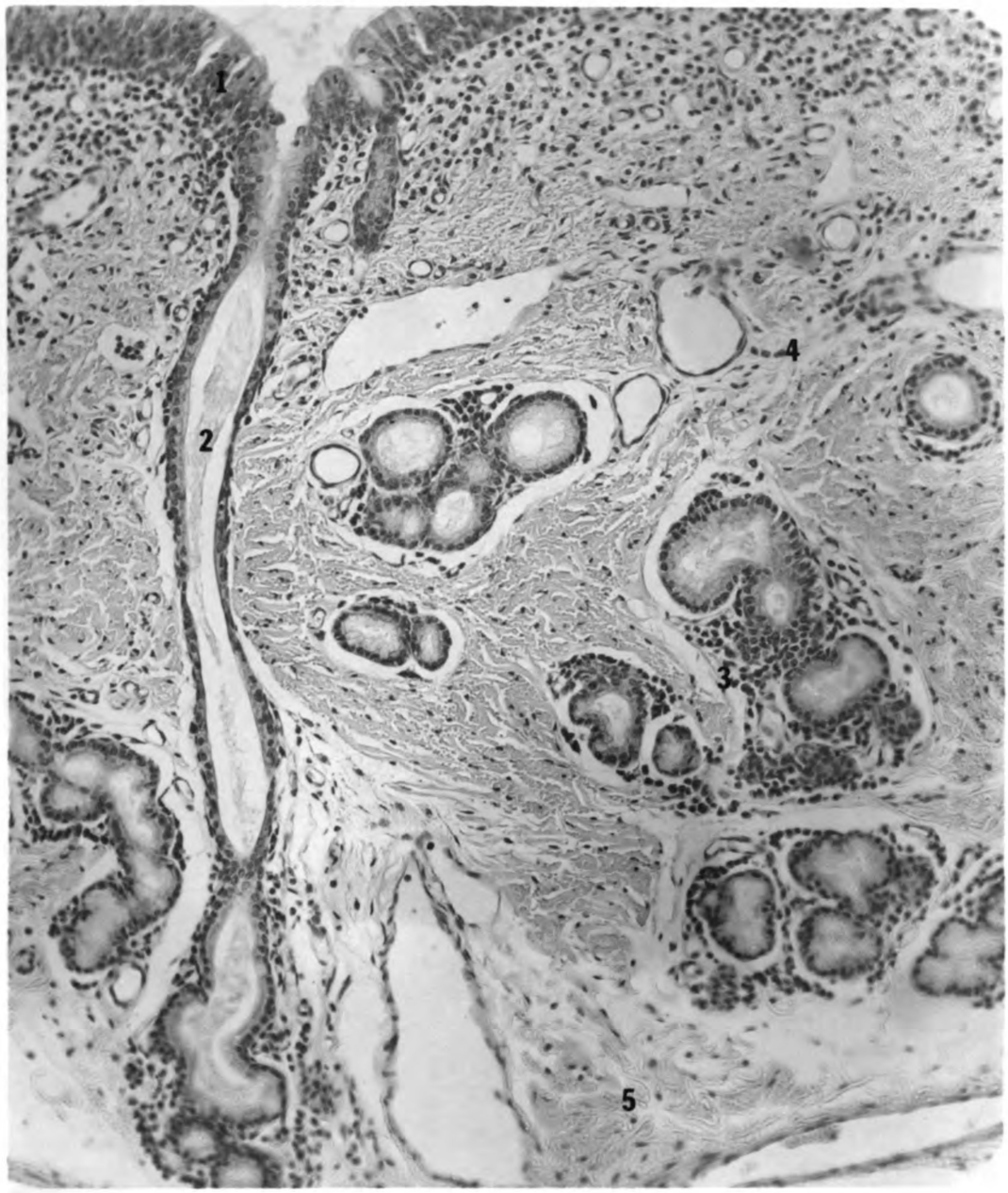


Plate VII. Cross-sectional view of bovine trachea showing long, patent duct of mixed, sero-mucous gland; lateral region, cranial level. 1, epithelium; 2, duct containing glandular secretion; 3, gland acini; 4, lamina propria; 5, submucosa. Hematoxylin and eosin stain; x 156.

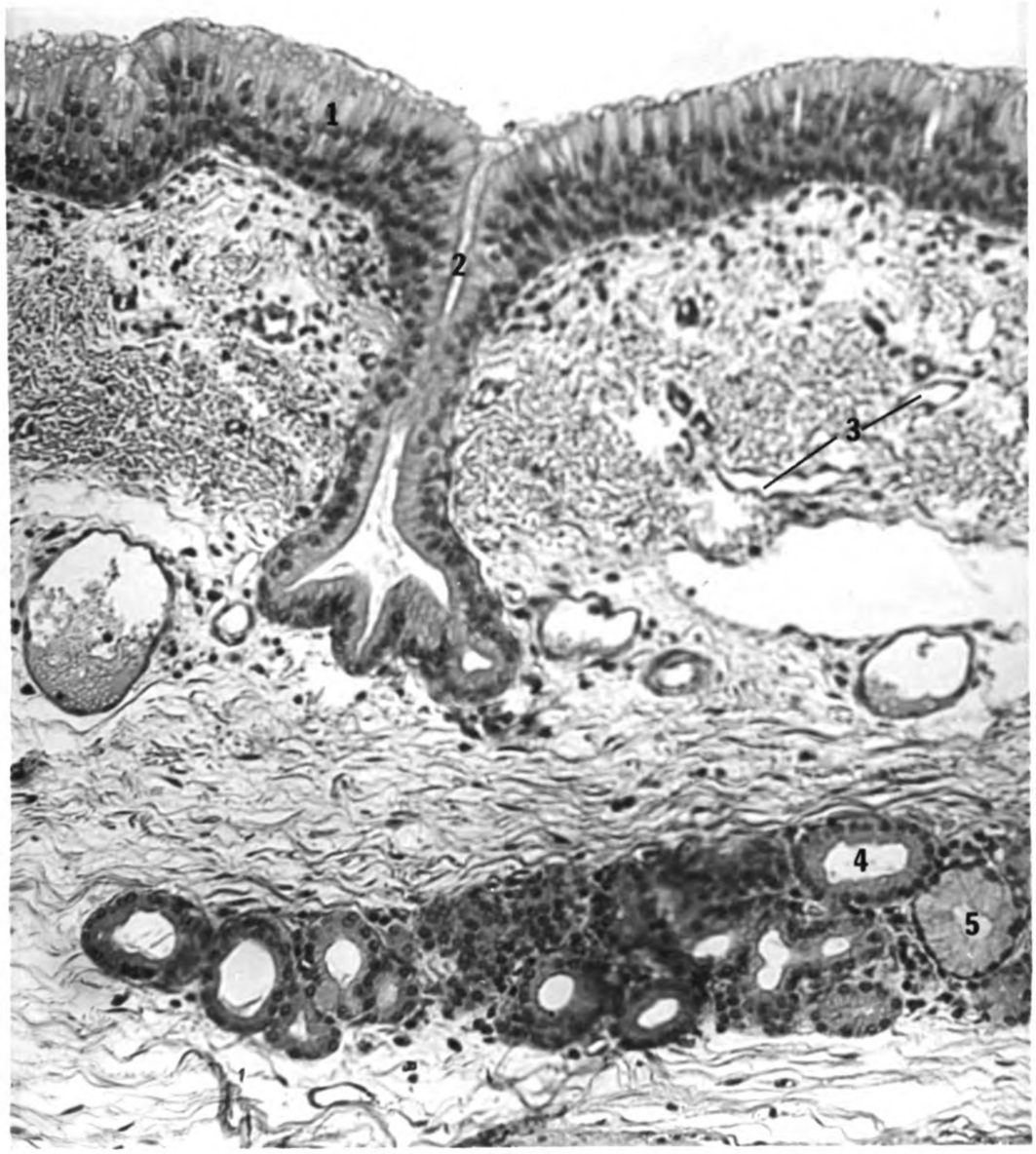


Plate VIII. Cross-sectional view of ovine trachea showing short, patent, branched duct of mixed, sero-mucous gland; ventral region, middle level. 1, epithelium; 2, patent duct of branched tubular gland; 3, lymphatic vessels in lamina propria; 4, serous cells; 5, mucous cells. Hematoxylin and eosin stain; x 220.

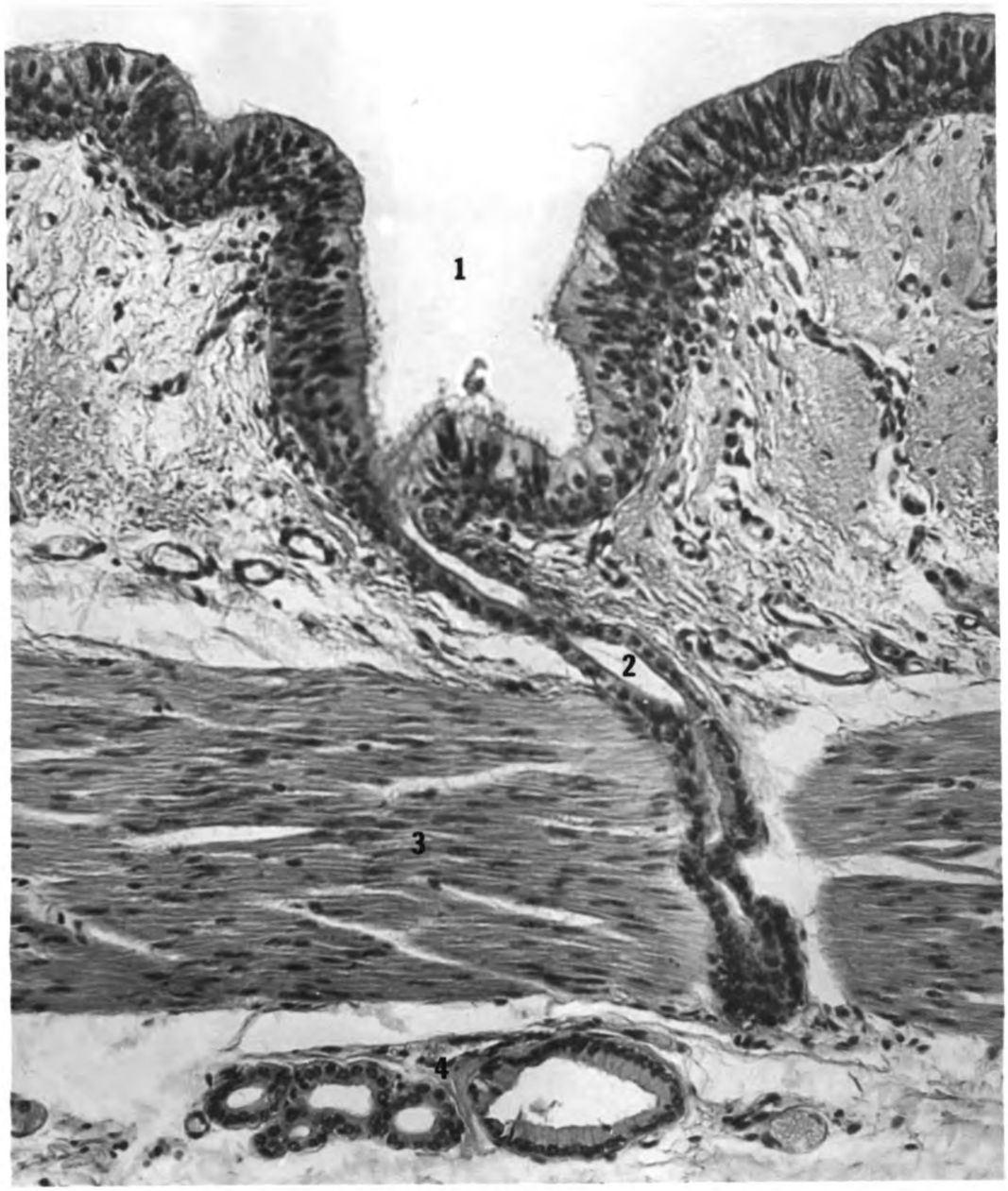


Plate IX. Cross-sectional view of ovine trachea showing gland duct piercing the trachealis muscle; dorsal region, caudal level. 1, lumen; 2, duct; 3, trachealis muscle; 4, gland acini. Hematoxylin and eosin stain; x.68.

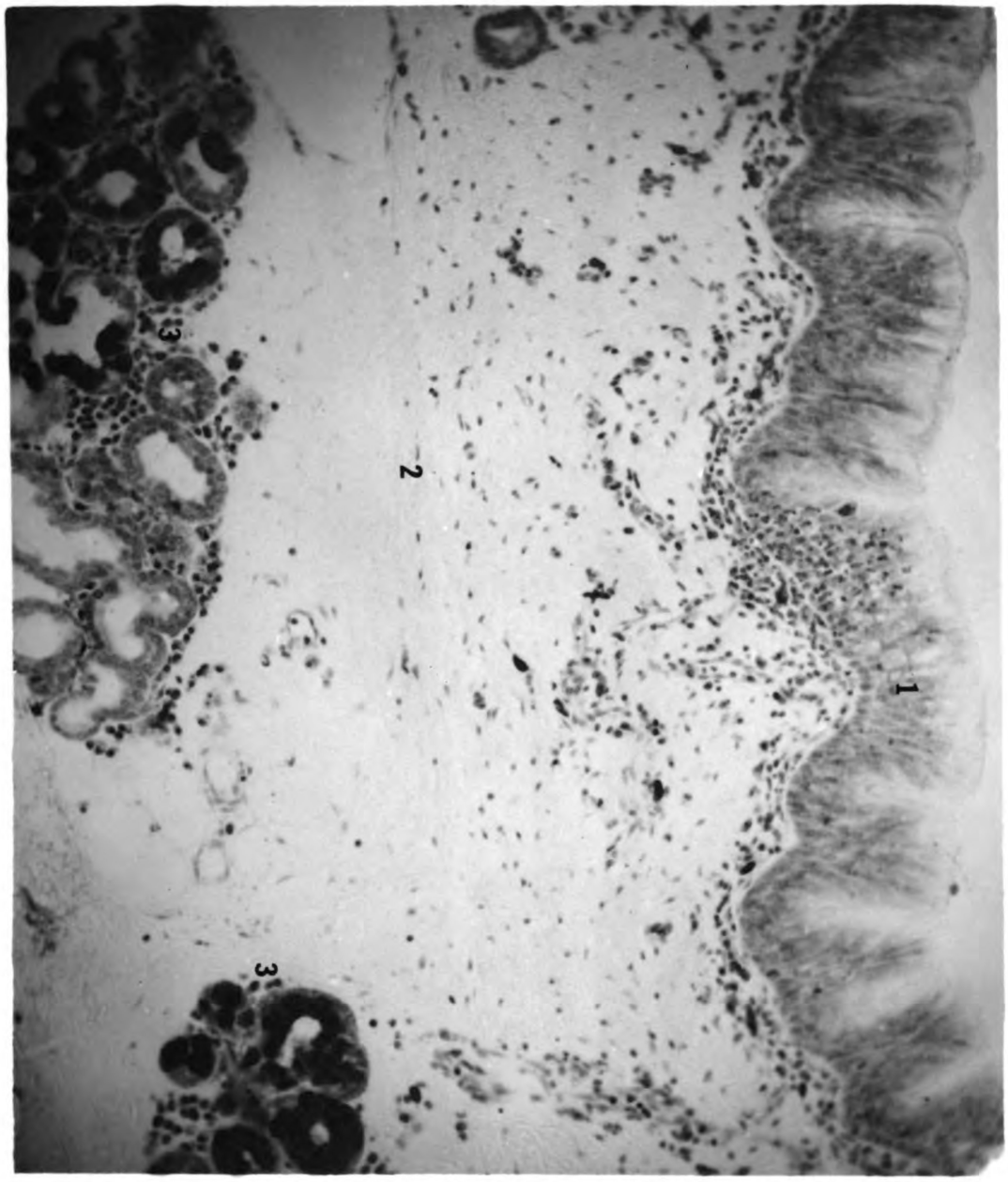


Plate X. Mixed, sero-mucous glands in submucosa as seen in a cross-sectional view of ovine trachea; ventral region, cranial level. 1, epithelium; 2, lower limit of mucosa; 3, branched; tubuloacinar, mixed, sero-mucous glands. Toluidine blue stain; x 136.

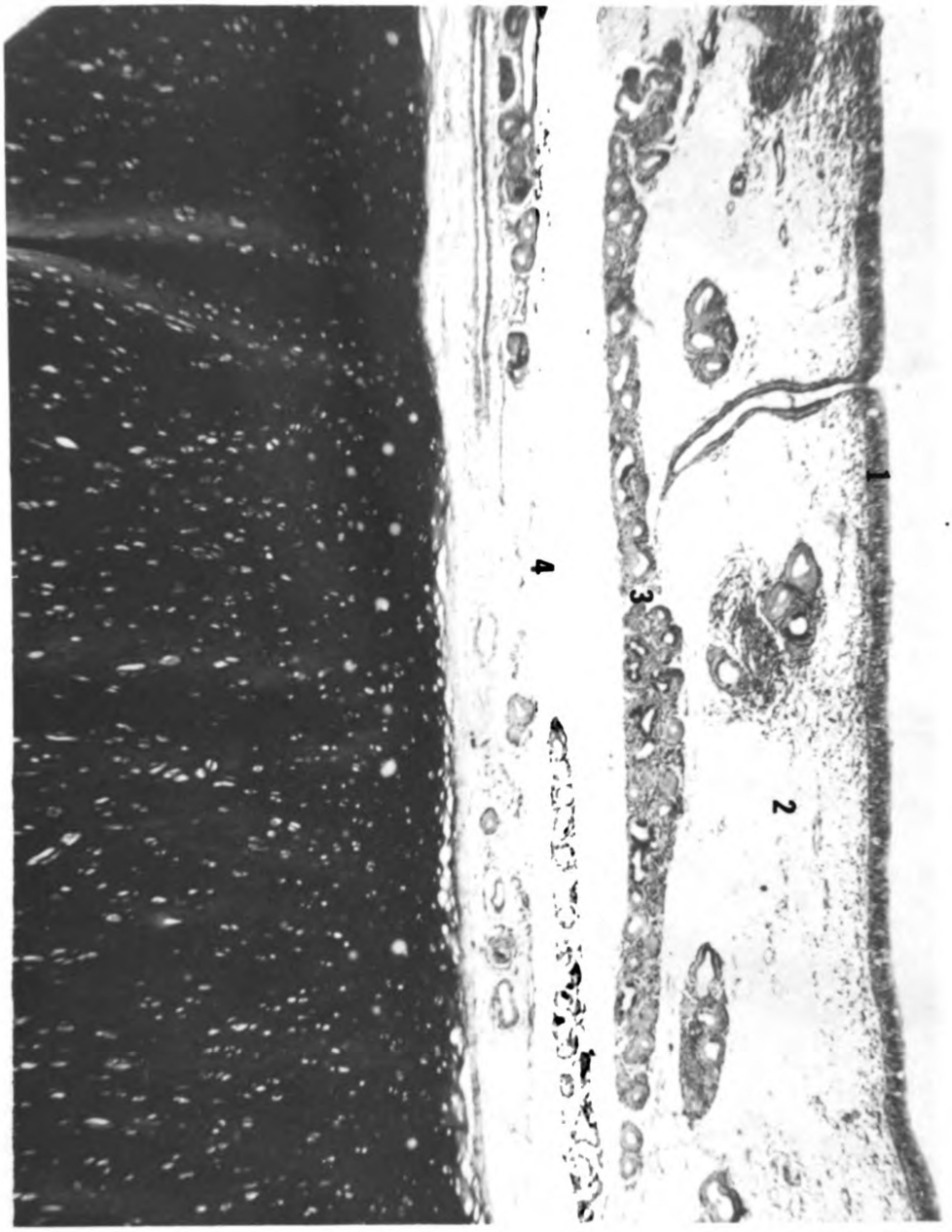


Plate XI. Cross-sectional view of bovine tracheal glands; ventral region, caudal level. 1, epithelium; 2, lamina propria; 3, branched, tubuloacinar, mixed, sero-mucous gland; 4, submucosa. Toluidine blue; x 64.

Plate XII. A field of mucous acini situated within the trachealis muscle as seen in a cross-sectional view of ovine trachea; dorsal region, cranial level. 1, goblet cells; 2, mast cell; 3, trachealis muscle; 4, mucous acini of tubuloacinar gland. Toluidine blue stain; x 186.

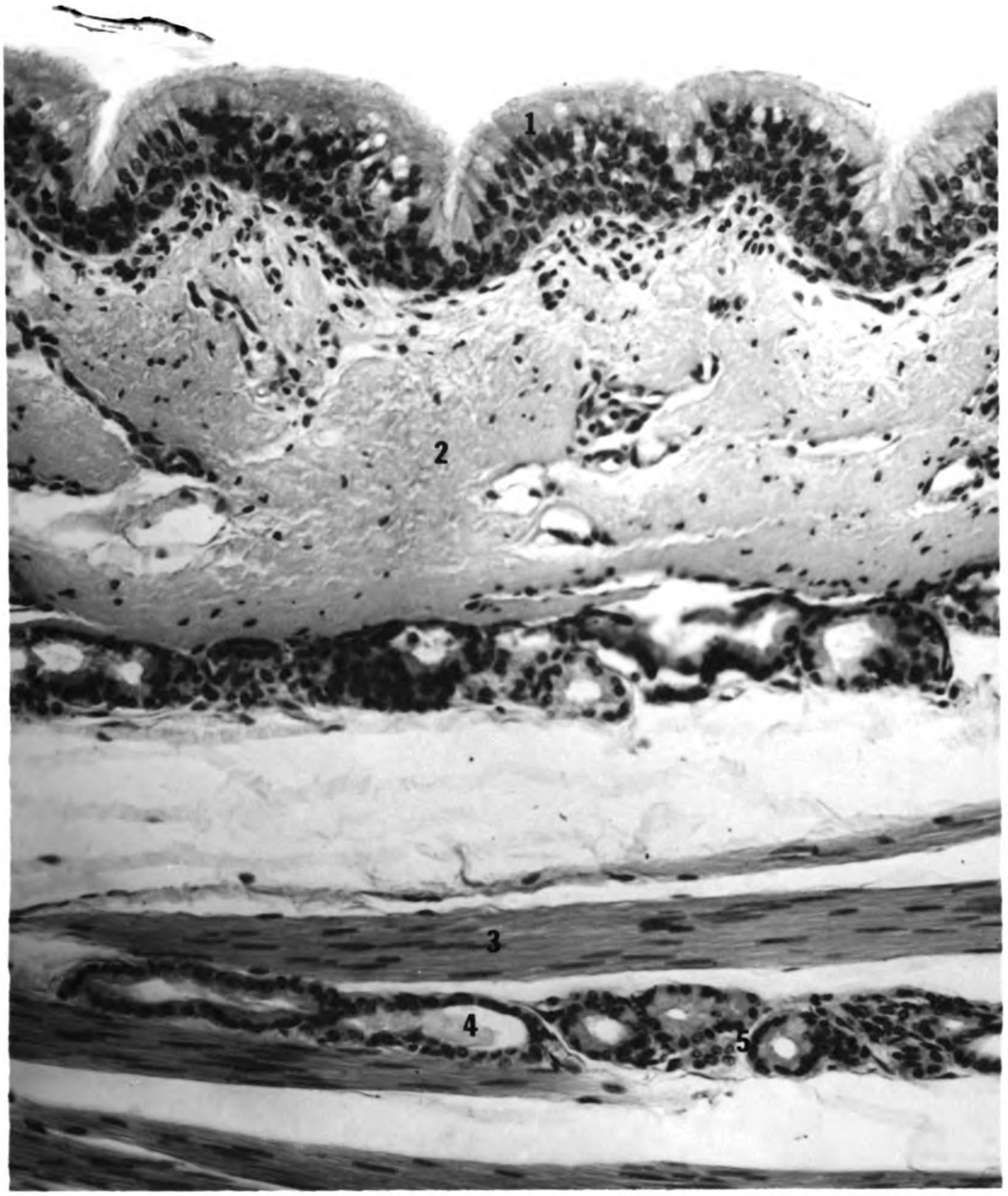


Plate XIII. A field of serous acini situated within the trachealis muscle as seen in a cross-sectional view of ovine trachea; dorsal region, cranial level. 1, epithelium; 2, lamina propria; 3, trachealis muscle; 4, gland duct; 5, gland acini. Hematoxylin and eosin stain; x 220.

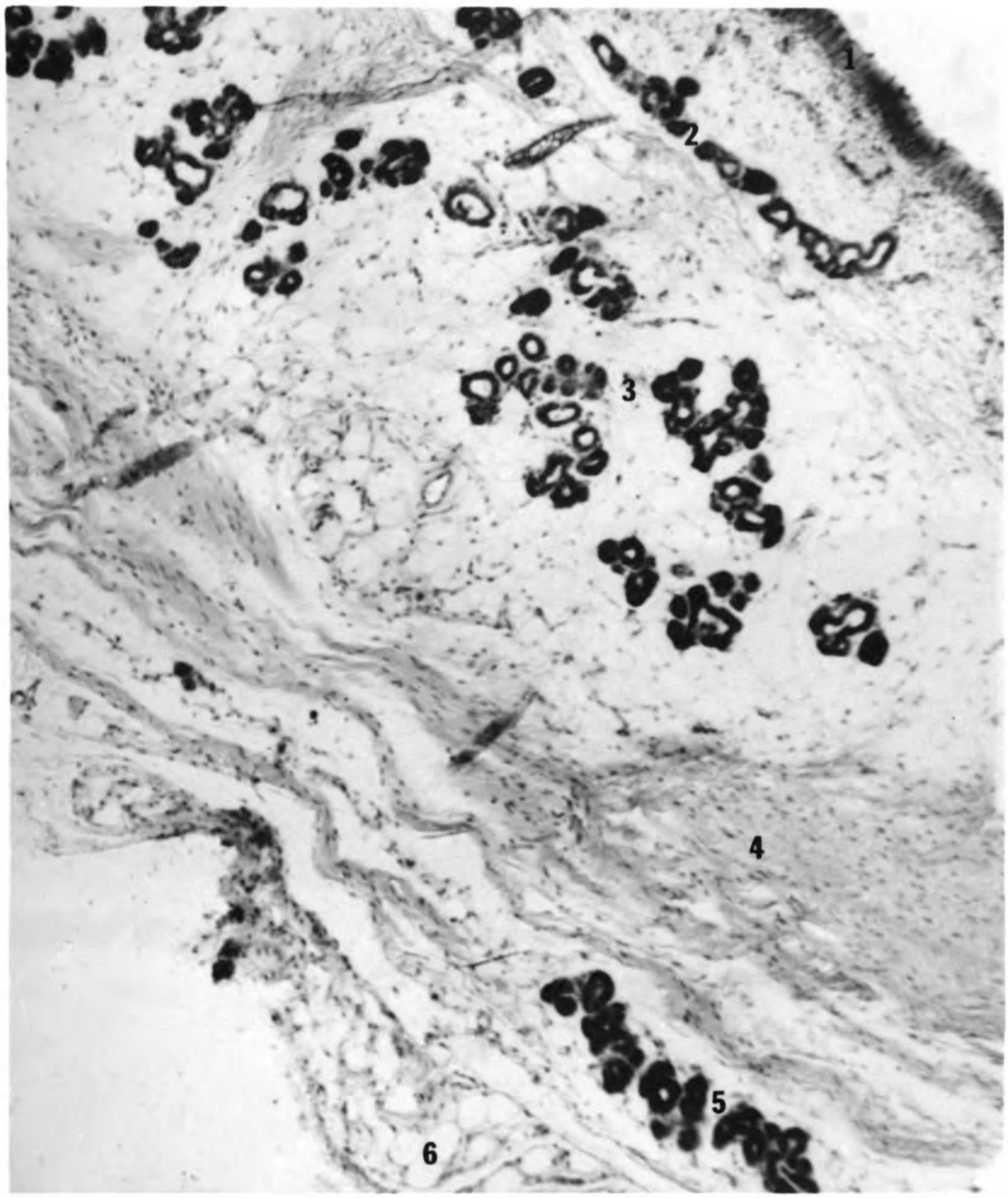


Plate XIV. Cross-sectional view of intercartilaginous area of caprine trachea; ventral region, middle level. 1, epithelium; 2, gland acini in lamina propria; 3, gland acini in submucosa; 4, annular ligament; 5, gland acini in adventitia; 6, adipose tissue. Toluidine blue stain; x 96.

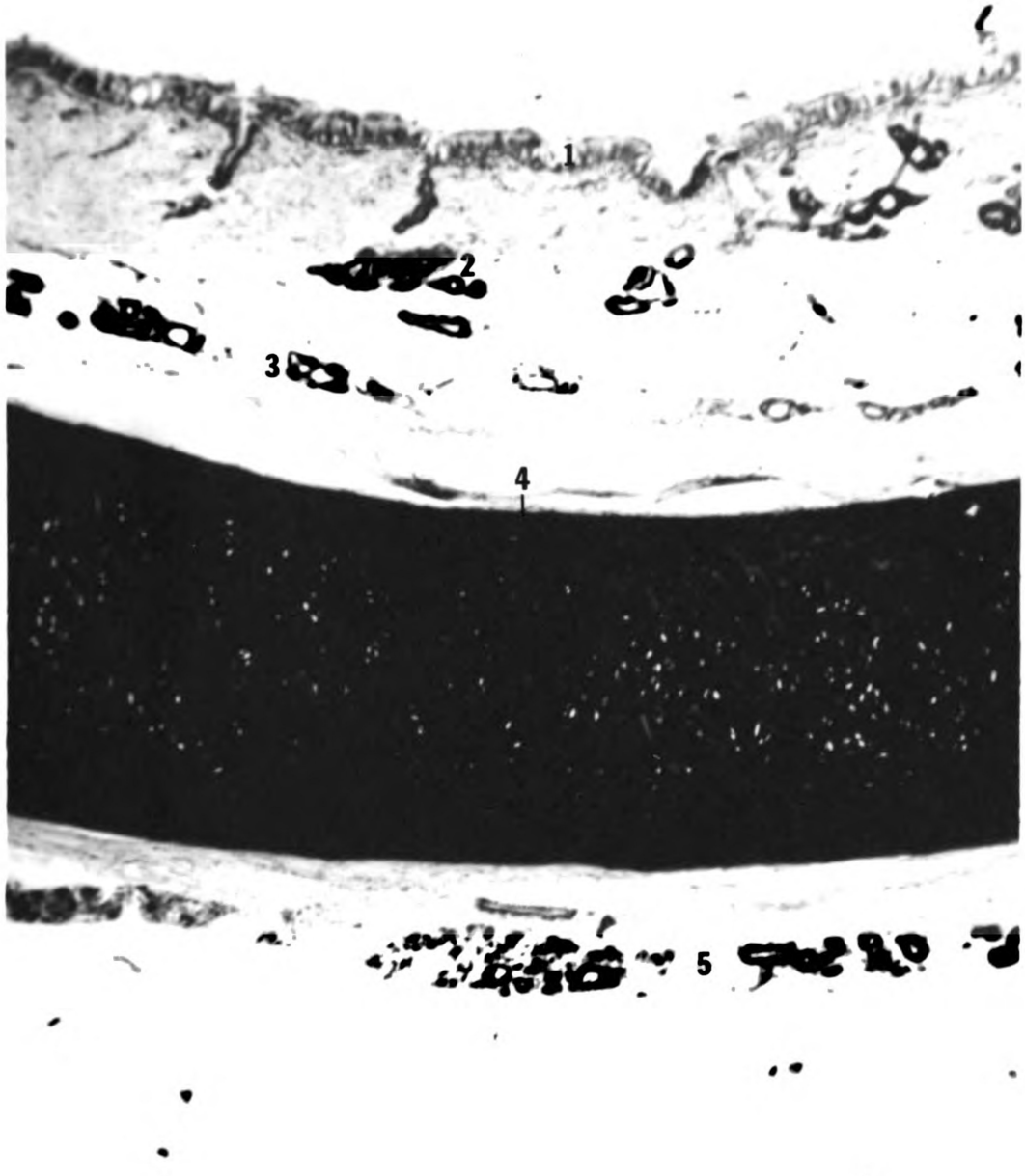


Plate XV. Cross-sectional view of caprine trachea depicting glands both internal and external to cartilaginous ring; ventral region, cranial level. 1, epithelium with goblet cells; 2, gland acini in lamina propria; 3, gland acini in submucosa; 4, cartilaginous ring; 5, gland acini in adventitia. Toluidine blue stain; x 74.

Plate XVI. Longitudinal view of intercartilaginous area of caprine trachea; lateral region, caudal level. 1, epithelium; 2, gland duct; 3, glands in submucosa; 4, hyaline cartilage; 5, glands in adventitia; 6, adipose tissue. Toluidine blue stain; x 101.

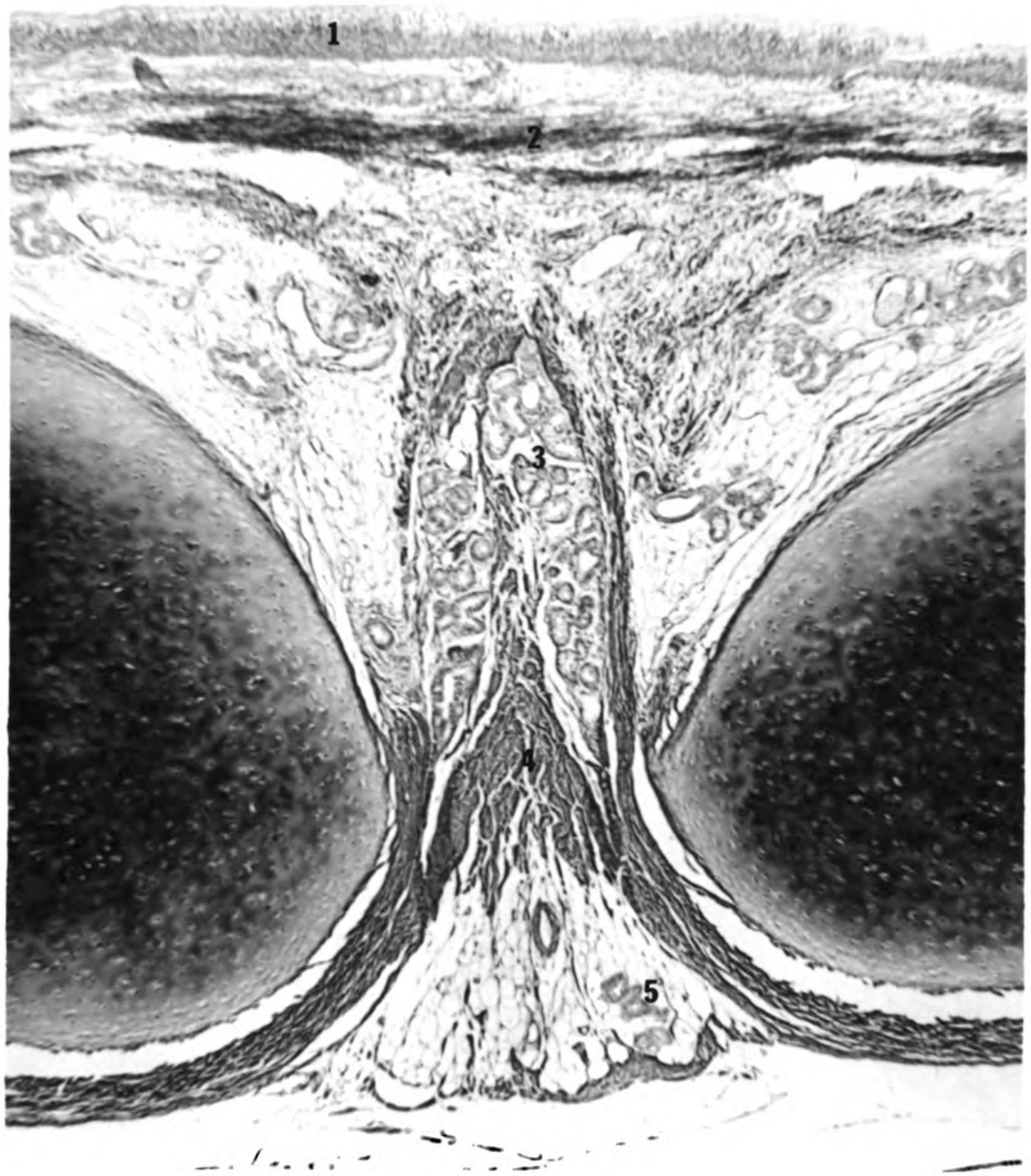


Plate XVII. Glands of the intercartilaginous area enveloped by annular ligament as seen in a longitudinal view of caprine trachea; ventral region, caudal level. 1, epithelium; 2, elastic membrane (note longitudinal direction of fibers); 3, gland acini enveloped by annular ligament; 4, annular ligament; 5, gland acini in adventitia. Weigert-Van Gieson stain; x 111.

Plate XVIII. Longitudinal view of three overlapping rings with intervening glands in ovine trachea; ventral region, cranial level. 1, epithelium; 2, hyaline cartilage; 3, gland acini; 4, elastic fibers. Weigert-Van Gieson stain; x 74.

Plate XIX. Cross-sectional view of bovine trachea showing typical arrangement of layers; ventral region, cranial level. 1, epithelium; 2, lower limit of lamina propria; 3, submucosa containing glands. Hematoxylin and eosin stain; x 158.

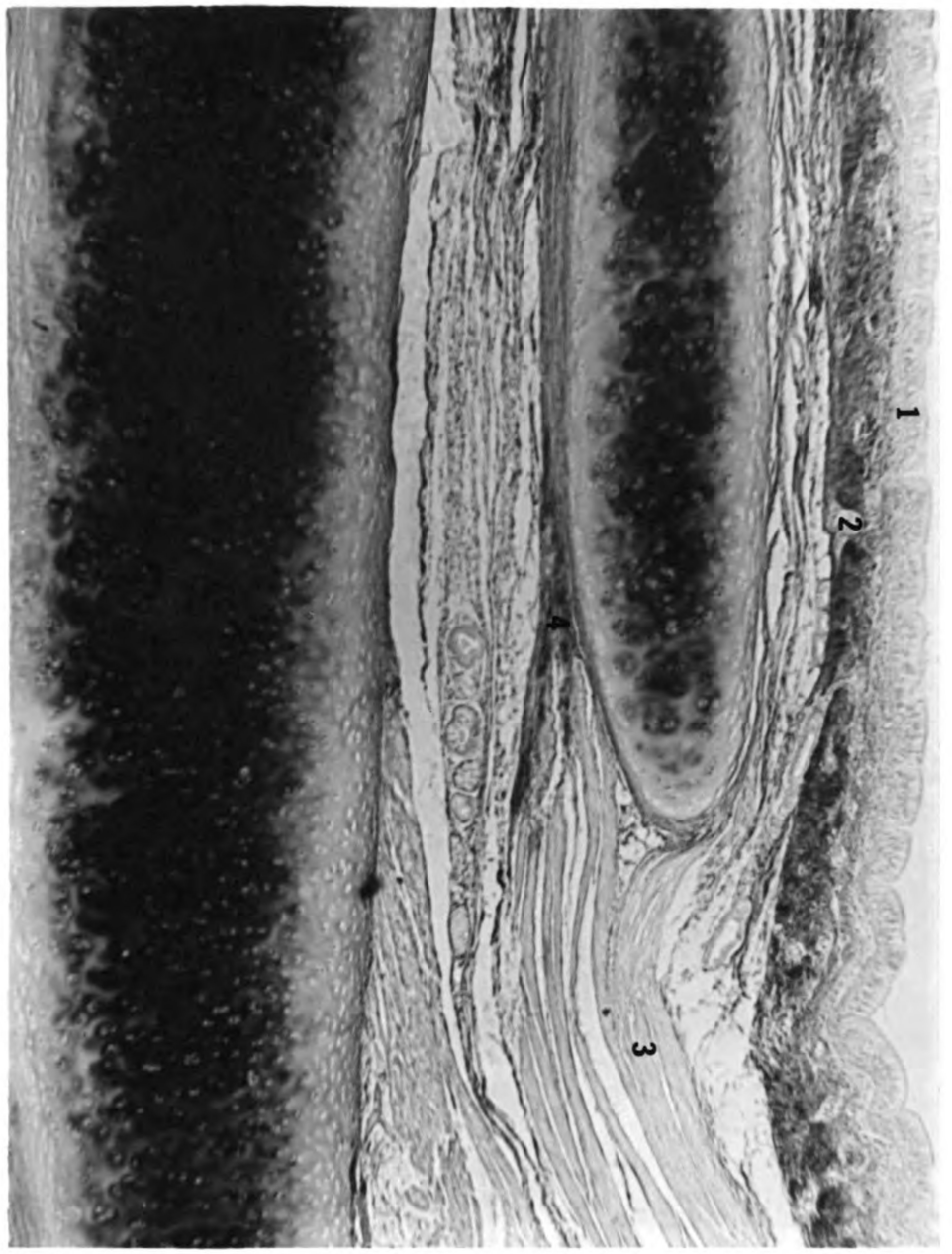


Plate XX. Cross-sectional view of ovine trachea showing insertion of trachealis muscle and "elastic tendons"; dorsal region, middle level. 1, epithelium; 2, elastic membrane; 3, trachealis muscle (note its insertion on outer face of the inner of two overlapping rings); 4, elastic tendon. Weigert-Van Gieson stain; x 63.

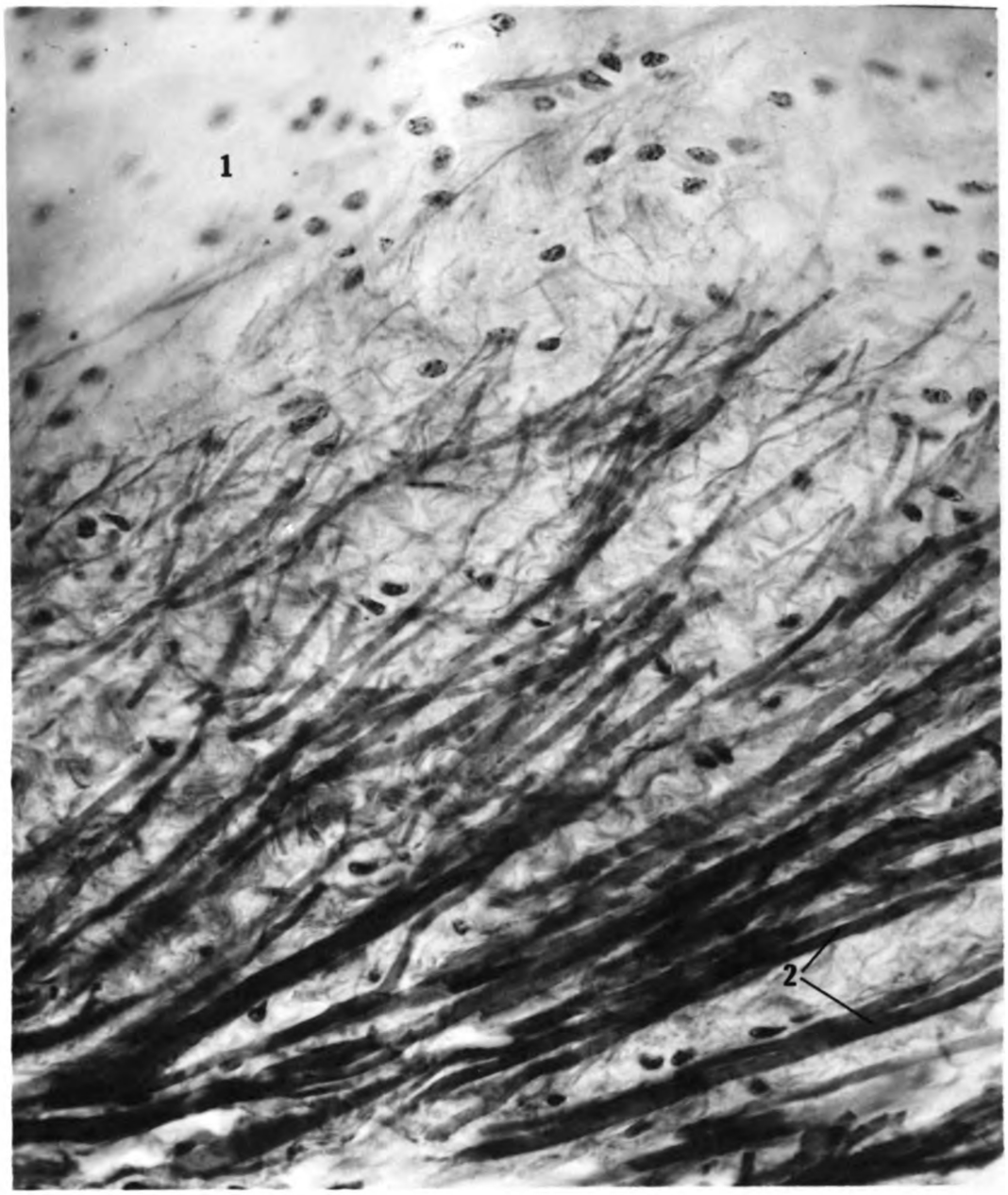


Plate XXI. Longitudinal view of bovine trachea showing elastic character of hyaline cartilage; dorsal region, middle level. 1, hyaline cartilage; 2, elastic fibers. Weigert-Van Gieson stain; x 394.

Plate XXII. Cross-sectional view of bovine trachea showing atypical location of two nerve trunks; dorsal region, middle level. 1, cartilage ring tip; 2, nerve trunks; 3, adventitia. Hematoxylin and eosin stain. x 85.

[redacted]

NOV 28 [illegible]