

COMPARATIVE HISTOLOGY OF THE TRACHEA
OF THE DOG AND CAT

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By

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INTRODUCTION

Although the microscopic anatomy of the trachea of man, or at least certain features of it, has been thoroughly investigated and recorded in medical literature, relatively little can be found concerning the detailed histology of the trachea of domestic animals. The few English sources which are available treat the subject very superficially. Several German works (Oppel 1905, Sussdorf 1911, Loginoff 1911, and Paul 1913) are excellent concerning the microscopic anatomy of the trachea of domestic animals, however, they are not complete in all details.

This study is an attempt to supplement existing information by comparing the histology of the dog and cat trachea with the hope that it may be useful in the fields of Anatomy, Cytology, and Pathology.

REVIEW OF LITERATURE

Present day information regarding the histology of the trachea stems from the collective work of many investigators who have studied the trachea as part of a general histological study, have concentrated on some particular feature of it, or have considered it in a study of the respiratory system. These studies included a variety of animals, the majority of them have been done on man. Therefore, in reviewing the literature it is advantageous to consider in detail, the work done on the trachea in general before concentrating specifically on the limited amount of comparative work done on the dog and cat.

ANATOMY OF THE TRACHEA IN GENERAL

Many authors (Dawson 1948, Nonidez and Windle 1949, Cowdry 1950, Maximow and Bloom 1957, Copenhaver and Johnson 1958, and Ham 1957) recognized the following layers in the tracheal wall: (a) mucosa, (b) submucosa, (c) fibroelastic membrane which contains the cartilagenous rings, (d) adventitia, and (e) muscularis found only dorsally. Bremer and Weatherford (1946) and Jordan (1952) combined the fibroelastic membrane, adventitia and muscularis into one layer. Trautmann and Fiebiger (1952) did not recognize the submucosa

as a separate layer. Von Hayek (1960) mentioned that such a layer is justifiable because the mucosa is displacable and subject to folding especially in the dorsal region; a feature permitted by the loose submucosa underneath.

Mucosa

The trachea in man and domestic animals is lined with pseudostratified ciliated columnar epithelium and contains goblet cells which are often numerous. The epithelium rests on a basement membrane which varies greatly in thickness among different species. Lucas (1932) and Miller (1932) divided the epithelium into four layers of cells: (a) basal cells, (b) intermediate or non-ciliated, (c) ciliated, and (d) goblet. Garvin (1957) described the basal cells as rounded or polygonal cells with large nuclei which do not reach the surface but lie between the feet of the taller cells. These cells, according to Miller (1932), develop into intermediate cells which become elongated and often reach the surface. Intermediate cells do not bear cilia and usually taper to a point at their outer surface. They in turn give rise to the ciliated columnar cells, which are normally the most numerous and goblet cells, which may represent a mucous degeneration of ciliated cells. Miller also mentioned that

regeneration of tracheal epithelium is very slow under normal conditions. Mitotic figures are rarely seen.

Chambers and Renyi (1925) found ciliated cells structurally related and held together at their ciliated surface by a cuticular border which bears the cilia. This is not an organic relationship as they believed was true of the cells in stratified squamous epithelium. Rhodin (1959) by means of electron microscope studies showed that the surface of the epithelium consists of microvilli and is striated in nature similar to the striated border in the intestinal tract.

Florey et al. (1932) studying mucous secretion in the trachea of cats, noticed that goblet cells are not affected in any way by nerve stimulation but instead are discharged by contact or direct stimulation. Chronic irritations caused by constant injections of formalin or dust inhalation resulted in a great increase in the number of goblet cells. Lucas and Douglas (1935) studying ciliary activity noticed that the normal mucous layer covering the tracheal epithelium consists of two layers of fluid; an inner one of thin watery fluid and an outer layer composed of more viscous mucoid material. They concluded the rate of mucus removal is more likely due to changes in the composition and proportion of these layers than to changes in the rate of ciliary beat.

Rhodin (1959) referred to a second type of secretory cell which he identified in the tracheal epithelium of man and believed it to be responsible for a serous secretion. The cell is columnar but does not assume a goblet appearance.

Barclay et al. (1938) noticed that insufflated dusts are excreted rapidly from the lower respiratory tract of the cat due to ciliary activity and rapid propulsion of mucus. Fluids, however, are not arrested by the cilia but pass into the lungs.

Replacement of tracheal epithelium by stratified squamous epithelium (metaplasia) has been reported. Miller (1932) referred to the work of Griffini in 1875 and Baraban in 1890 who first described the presence of stratified squamous epithelium in the trachea of man. Baraban believed that this transition resulted from a low grade irritation which led to loss of cilia and appearance of mucus in the cells. Miller himself often found stratified squamous epithelium in the bronchi of patients suffering from tuberculosis and assumed that constant coughing played the key role in the transition. Florey et al. (1932) found that constant and intense irritation of the tracheal epithelium of cats resulted in a change of pseudostratified into transitional epithelium similar to that found in the urinary bladder. Sussdorf (1911)

reported spots of stratified squamous epithelium in the upper trachea of old cats.

Leucocytes are frequently seen in tracheal epithelium. Andrew and Burns (1947) studied this feature in detail in mouse tracheae. They stated that lymphocytes are the most numerous but polymorphonuclear leucocytes are found frequently. Monocytes and eosinophils are rarely seen. Occasionally leucocytes are found intracellularly. Age has no affect upon leucocyte infiltration and migration. Most of the leucocytes are found at or below the level of the epithelial nuclei; those found near the surface of the epithelium show marked pycnosis. They also mentioned that Flemming found leucocytes in nearly every mammalian trachea as early as 1885. Von Hayek (1960) referred to their presence in human tracheal epithelium.

Ropes (1930), using rabbits, found ciliated tracheal epithelial cells capable of exhibiting phagocytic activity. He divided these phagocytic cells into two major groups; a columnar slightly phagocytic group and a cuboidal or low columnar, highly phagocytic group with many transitional stages between the two. These cells increase in number after exposure to carbon.

According to Ham (1957) the basement membrane is a condensation of the lamina propria. Trautmann and Fiebiger (1952) stated that many animals have only a rudimentary basement membrane. The basement membrane in man is about 10 μ thick and is not a homogeneous membrane but a network of argyrophilic fibers (Von Hayek 1960). All the cell types in the epithelium are firmly fastened to it. Goblet and ciliated cells may be attached to it by a foot, a single pointed prolongation or a number of fine prolongations (Miller, 1947). Rhodin (1959) recently found, with electron microscopy, that some ciliated and goblet cells in the tracheal epithelium of man do not reach the basement membrane. This contradicts the commonly held idea that all cells in pseudostratified epithelium reach or rest on the basement membrane. He also noted that the basement membrane in the rat trachea is a homogeneous continuous structure, while in man there is a layer of densely packed collagen fibers in random orientation on the subepithelial surface of the membrane. Stirling (1890) mentioned that the basement membrane is not as distinct in the cat as it is in man.

The lamina propria was described by Trautmann and Fiebiger (1952) as the area between the basement membrane and the elastic membrane. It consists of fine fibers and often

many lymphocytes and lymph nodules. Von Hayek (1960) called this area the membrana propria and included the elastic layer or membrane as a deeper layer of the same area. The cells in the superficial layer of the membrana propria consist mostly of lymphocytes which are clustered around the gland ducts. Blood capillaries, lymphatic vascular networks and a loose network of collagenous and elastic fibers are found in this area.

The elastic membrane, generally considered to take the place of the muscularis mucosa found in the gastrointestinal tract, was described by Macklin (1922). He dissected out this membrane from a pig and demonstrated that it is the most important recoil mechanism of the respiratory tract. The elastic fibers vary in thickness, the smaller ones are scattered through the lamina propria near the basement membrane. The fibers form a dense thick meshwork which is thicker in the trachea than other parts of the respiratory tract. Lateral branches are given off which connect to the perichondrium of the cartilages, the muscle, and some even mingle with fibers of the adventitia.

Von Hayek (1960) reported that this elastic layer in man is wider and the fibers thicker in the region of the muscle than they are in the area of the cartilage rings. He also mentioned that Schaffer described bundles of

smooth muscle in this elastic membrane. Miller (1947) observed that the elastic fibers appear in bundles in the dorsal part of the tube but this is solely the result of the folds of the mucosa. Rhodin and Dalhamn (1955) mentioned that the elastic fibers are 1 - 2 μ in diameter in the rat and are in turn composed of longitudinally arranged fibrils of the magnitude of about 70 $\overset{\circ}{\text{A}}$. In contrast to the report of Macklin they did not notice any branching of elastic fibers in their studies on the rat.

Submucosa

This layer lies between the elastic membrane and cartilage rings. It is composed of loose connective tissue, is rich in elastic fibers and fat and blends with the perichondrium of the cartilage rings. The glands of the trachea are found mainly in this area.

According to Krölling and Grau (1960) these glands are mostly mixed tubular and are most abundant ventrally and laterally.. Smooth muscle fibers are usually associated with the ducts. Miller (1947) and Von Hayek (1960) reported mixed glands in man (both mucous acini capped with serous demilunes and pure serous acini). They are embedded in the submucosa between tracts of elastic fibers which connect the elastic membrane with the perichondrium and annular ligaments. In

longitudinal section the glands are seen grouped between the cartilages, except in the dorsal region where they lie largely outside of the trachealis muscle. The ducts often open on the surface of the mucosa by a funnel-shaped enlargement. The larger ducts are frequently lined for some distance with ciliated epithelium.

Florey et al. (1932) found that glands of the trachea are activated by stimulation of the recurrent laryngeal nerves and administration of pilocarpine. Ham (1957) noted that in man some glands may occasionally be found in the lamina propria, in between bundles of smooth muscle or in the adventitia. Garvin (1957) mentioned that the glands are more numerous in some animals, such as the cat, than they are in the human species.

Fibroelastic cartilagenous layer

Von Hayek (1960) referred to this layer of the tracheal wall as the tunica fibrosa or tunica cartilagineo-fibrosa because it includes the hyaline cartilage rings plus the fibroelastic membrane covering and connecting them. In a longitudinal section of the trachea from the ventral area, he observed that the rings are flattened on their external surface but convex internally. The perichondrium is thicker externally than internally. The periphery of the cartilage

itself is also copiously supplied with collagenous fibers which extend inward from the perichondrium. Stirling (1883) noticed that the cartilage rings in the dog, cat and man become thinner in the dorsal region and overlap adjacent rings. Chauveau (1873) also mentioned this as a characteristic of domestic animal tracheae. The rings are sometimes bifurcated and fused with each other although all are incomplete dorsally. Straus (1931) found differences in the structure and shape of the cartilage rings in many primates.

Miller (1920) described the marked irregularities in the shape of the cartilage rings in man. He also studied the carina tracheae in the cat (1904) and described it as a "...prominent ridge running anteroposteriorly across the bottom of the trachea between the origin of the two bronchi." The carina tracheae may be derived from a tracheal or bronchial cartilage ring or a combination of these; occasionally it is absent altogether. He stated later (1947) that the same is true in man.

The cross-sectional shape of the cartilage rings in mink was described by Stowe and Calhoun (1961) as oval ventrally, elliptical laterally and spatulate in the dorsal region where they overlap.

Sussdorf (1911) and Trautmann and Fiebiger (1952) stated that the hyaline cartilage rings often calcify and ossify in old animals. According to Maximow and Bloom (1957) and Bremer and Weatherford (1946) the cartilages in man become fibrous or partly calcified in old age. Stowe and Calhoun (1961) found that calcification in the tracheal cartilages of mink has already started in the 49-day-old and is complete in about 68 days.

Wolf-Heidegger (1947) stated that the annular ligaments, the sheets of fibrous tissue between the cartilagenous rings, consist of three layers in man; (a) a strong outer layer attached to the outer perichondrium, (b) a middle layer which connects the edges of the rings, and (c) a weaker inner layer attached to the inner perichondrium. Fat cells and glands are frequently found between these layers of collagenous and elastic fibers which are oriented somewhat obliquely so as to form a crisscrossing, distensible latticework. A strong longitudinal band consisting predominantly of elastic fibers and continuous with the fibroelastic membrane spans the dorsal ends of the tracheal rings. These layers of fibroelastic tissue blend with the perichondrium but can be distinguished from it because they contain a greater percentage of elastic fibers. Edwards (1956) described it as one continuous sheet

or membrane of fibroelastic tissue from top to bottom. Nonidez and Windle (1949) also made reference to a fairly dense fibroelastic membrane which lies outside or dorsal to the trachealis muscle and spans the area between the ends of the cartilage rings. This forms a unified structure with the rest of the fibroelastic layer. According to Copenhaver and Johnson (1958) the trachealis muscle is embedded in this fibroelastic membrane.

Trachealis Muscle

Miller (1947) mentioned that Cuvier was the first to describe the different trachealis muscle attachments in man and various animals. The general rule is that in carnivores the attachment is external to the cartilage rings, in herbivores the attachment is internal. Man who lives on a mixed diet has a muscle attachment which is internal but relatively close to the ends of the rings. There are various exceptions to these rules and Miller admitted that he has found no good reason for this variation.

Von Hayek (1960) described the trachealis muscle as a unified layer of thick bundles of smooth muscle transversely oriented which insert by means of elastic tendons into the perichondrium and annular ligaments. Occasionally isolated bundles of longitudinal muscle are found external to the main body of muscle. These insert into the tunica fibrosa

and infrequently into the ventral wall of the esophagus. Borelli (1949) observed that the muscle in man is heavier in proportion to the rings at the top of the trachea than at the bifurcation. Towers (1953) described the transition of the trachealis muscle into the bronchial muscle. Greep (1954) mentioned that there are many elastic fibers scattered among the muscle cells. Krölling and Grau (1960) observed that contraction of the trachealis muscle causes longitudinal folds in the mucosa of the dorsal part of the tube.

Lymphatics

Sbernini and Bozzana (1953) reported two highly developed anastomosing lymphatic networks in the trachea, one in the mucosa and the other in the submucosa. The one in the mucosa may be reduced with increasing age while the one in the submucosa shows no reduction during lifetime. Miller (1947) stated that in the area of the cartilage rings the principle lymph vessels run parallel to the rings while in the membranous portion of the trachea the vessels run primarily in a longitudinal direction.

Blood vessels

Schaeffer (1953) and Edwards (1956) stated that branches of the inferior and superior thyroid, bronchial and mammary

arteries furnish the arterial blood to the human trachea. Venous radicles come together in the annular ligaments and join lateral veins on each side of the trachea which in turn empty into a plexus of neighboring thyroid veins. Trautmann and Fiebiger (1952) referred to a submucous, periglandular and subepithelial plexus of vessels which supply blood to all parts of the trachea in the domestic animals.

Nerves

One of the most thorough studies of the innervation of the trachea was done by Honjin (1954) in the mouse. He found all the ganglia concentrated in the adventitia of the dorsal wall of the trachea. They are connected by nerves to form a "...gangliated nerve meshwork..." called the tracheal plexus. The trachea is supplied from the recurrent laryngeal nerves or directly from the vagus. Branches from the right and left cervical sympathetic cords join with the vagal branches and innervate the trachea in company with the parasympathetics. A few small sympathetic twigs innervate the trachea directly. Elftman (1943) described various types of nerve endings in the muscle, lamina propria, epithelium and perichondrium in the dog. Larsell and Burget (1924) found that double vagotomy of rabbits and dogs abolishes the cough reflex. Sampaolo (1950) observed Ruffini's corpuscles among the smooth muscle

fibers of the trachea. Trautmann and Fiebiger (1952) mentioned the presence of both myelinated and non-myelinated nerve fibers in the trachea.

Tracheal movements and structural exceptions

Macklin (1925), Cowdry (1950), Bruckner (1952), and Von Hayek (1960) discussed passive changes in the trachea during inspiration, expiration, swallowing, head movements, coughing and changes in body positions. They showed that the trachea is not a rigid stationary tube but continually undergoes changes in length and diameter. Sauser (1957) correlated movements in the respiratory system with differences of rigidity in various parts of the respiratory tract and noted increased flexibility from top (nasal portion) to bottom (bronchioles).

Atwood (1947), Zeek (1951), and Cover (1953) noted interesting exceptions to the general tracheal structure discussed above in whales, penguins, aquatic and domestic birds.

ANATOMY OF THE TRACHEA OF THE DOG AND CAT

Although the microscopic structure of the dog and cat trachea are basically the same as that discussed previously, some differences and special features have been reported.

Lucas (1932) referred to the work of Haycroft and Carlier who, in 1890, observed that pseudostratified epithelium of the trachea in both the cat and the dog is gradually replaced by stratified epithelium in the region where the cartilages overlap. They believed that this results from friction. Florey et al. (1932) found in their experiments with cats that there are no goblet cells present in the epithelium over the posterior tracheal fold. However, they made no mention of a change in the epithelium in this area. Loginoff (1911) also mentioned that the cells of the epithelium in the dorsal or membranous part of the cat trachea have a tendency to lose their cilia and become flattened. Comparatively he noted that the epithelial cells of the dog are usually somewhat higher but smaller than those of the cat. In the dog the cells in the epithelium over the membranous portion are shorter than cells elsewhere in the trachea.

Oppel (1905) found goblet cells to be more numerous in the dog than in man. The tracheal glands are described as less numerous in the dog than in the pig and all acini lie medial to the muscle. The basement membrane in the dog is very thin and indistinct and even more so in the cat. The glands in the submucosa of the cat are more numerous in the ventral portion than in the lateral and dorsal areas and are

concentrated in front of the annular ligaments. The gland ducts are narrowed in the area of the elastic layer and are enlarged where they open on the epithelial surface. Elastic fibers penetrate the entire thickness of the hyaline cartilage rings in both the dog and cat.

Stirling (1883) described the external muscle attachment in the dog and cat and the overlapping of cartilage rings in the dorsal area. He also mentioned that many nerve ganglia are found in the dorsal area and that they seem to be supplied by the recurrent laryngeal nerves. The mucous glands of the cat are more numerous and granular than they are in the dog. The muscle does not seem to be as thick in the dog and in both animals longitudinal muscle fibers exist outside of the transverse ones. No gland acini occur outside the tracheal muscle as they do in man.

Sussdorf (1911) stated that of all the domestic animals, tracheal glands are most abundant in the cat and least abundant in the dog. Isolated glands are occasionally found in the adventitia outside of the cartilage rings and muscularis in the dog and cat. The acini are both mucous and serous and the submucosa is small and loosely built in both animals. Patches of stratified squamous epithelium are occasionally seen in the upper trachea of old cats.

According to Paul (1913) the tracheal epithelium in the cat is thinner than in the horse and pig. He concluded that the thickness of the epithelium increases with an increase in the size of the animal. In the cat, goblet cells are more numerous ventrally and laterally than they are dorsally. Leucocytes migrate from the submucosa through the lamina propria into the epithelium. Lymph nodules are more frequently found in the ventral and lateral regions. He reported the presence of flattened epithelium in the dorsal wall in the trachea of the cat and the pig. The basement membrane in the cat trachea is a fine structureless border frequently covered with numerous leucocytes. The glands are limited to the submucosa, are seldom found outside of the cartilage rings and never found outside of the muscle.

Paul (1913) described the perichondrium in the cat as rich in elastic fibers which penetrate the cartilages. The internal perichondrium is thinner than the external one. The annular ligaments are also composed of elastic fibers and the cartilage is not entirely hyaline but more or less elastic in character. The trachealis muscle is heavier at the distal end than at the proximal end of the tube. No longitudinal muscle fibers were found and no glands were seen between the muscle bundles. The muscle in the cat is thinner and smaller than in the pig and horse.

No references to any differences existing in the histology of the male and female trachea were found.

MATERIALS AND METHODS

The tracheae from twenty-five animals, fourteen dogs and eleven cats, were used in this study. Eight dogs and six cats were males, six dogs and five cats were females. The animals were obtained from the departments of Anatomy and Physiology at Michigan State University. The tracheae were removed from the freshly killed animals and immediately placed in F. A. A. (Lavdowsky's mixture, Guyer 1949) for fixation. Those of two dogs were obtained from specimens embalmed upon death and appeared in good condition.

Sections of each trachea, four or more cartilage rings in length, were taken from three areas: an upper one immediately below the larynx, a middle area, and a lower one directly above the bifurcation. Both ventral and dorsal longitudinal sections were taken from an upper and lower area in four dogs and four cats.

After fixation the dehydrating and infiltrating method of Johnson et al. (1943) was followed using "Tissuemat"* as the embedding medium. Sections were cut at 7 microns and stained with Harris' hematoxylin and eosin, Weigert's and Van Gieson's connective tissue stain to identify elastic

*Fisher Scientific Company, Pittsburgh, Pennsylvania

and collagenous tissue, toluidine blue (Lillie, 1954) for determination of mucous acini and goblet cells, and von Kossa's stain (Lillie, 1954) to aid in the identification of calcium salts in the cartilage.

Using slides of both longitudinal and cross sections, the following observations and measurements were made:

Epithelial thickness

Length of cilia

Goblet cell distribution

Elastic layer thickness

Elastic fiber diameter

Submucosal thickness

Distribution of gland acini

Cartilage thickness

Muscle thickness - measurements were taken across the widest area of the muscle bundle.

Presence and location of nerve trunks and ganglia.

The measurements were made in microns with the aid of an ocular micrometer and are recorded in Tables I and II. Goblet cells and gland acini were recorded as (1), (2), or (3) depending on the quantity present.

RESULTS AND DISCUSSION

I. THE TRACHEA OF THE CAT

The measurements of the various structural elements of the cat trachea referred to below, are found in Table I.

Epithelium

The trachea of the cat is lined with pseudostratified ciliated columnar epithelium containing goblet cells. Basal cells and intermediate or non-ciliated cells are also present, thus the four types of cells described in man, by Lucas (1932) and Miller (1932) can be identified here. Ciliated cells are much more numerous than goblet cells. The distal surface of the cells is covered by microvilli which appear as a thin dark membrane under the microscope. The cilia average $4.0\ \mu$ in length and appear to arise from the striated border. As a rule they are longer and appear more numerous over the ventral part of the trachea than the dorsal area. Goblet cells are more numerous in the ventral and lateral than the dorsal epithelium (this was reported by Paul 1913), however, no trend appears in the number of goblet cells between the proximal and distal areas. Intermediate or developing columnar cells are infrequently seen and are difficult

to identify while basal cells are more numerous rounded cells whose nuclei lie nearest the basement membrane.

In agreement with Oppel (1905) and Paul (1913) the basement membrane in the cat trachea is indistinct and difficult to see with ordinary stains. In many areas, however, it can be distinguished as a very thin, light seam or border between the epithelium and the lamina propria. It is frequently covered by leucocytes.

The epithelium is often folded especially in the dorsal region. For this reason an oblique section through a fold can result in what appears to be an intraepithelial pocket lined with cilia and containing cellular debris as illustrated in Plate III.

In the dorsal area of the trachea the epithelium differs from the usual pseudostratified type to one similar in appearance to transitional epithelium found in the urinary tract (Plate IV). This epithelial transition in the cat has been described by Haycroft and Carlier (Lucas 1932), Loginoff (1911) and Paul (1913) who refer to the epithelium in the dorsal area as a flattened stratified type. This epithelium was found to a greater or lesser extent in all the cats used in the study and varied in height from 2 - 8 layers of cells. At times it spanned the entire area between the ends of the cartilage rings

while in other cases patches were found medial to both ends of the cartilage rings and pseudostratified epithelium was present between them. Occasionally it was located dorso-laterally rather than directly above or between the ends of the cartilage rings. In places where the transitional epithelium was stretched the cells became flattened and appeared similar to the cells in stratified squamous epithelium. The amount of transitional epithelium varied at different levels, but no definite trend could be established. The transition between the two types of epithelia is often abrupt (Plate V) but in many instances it is more gradual. In agreement with the findings of Florey et al. 1932, cilia and goblet cells are absent in the transitional-type epithelium thus accounting for the decreased amount of these elements in the dorsal region. Adjacent to the junction of the epithelial transition, the pseudostratified epithelium as well as the cilia it bears are usually lower than elsewhere in the trachea. The average thickness of the epithelium is greater in the ventral area than in the lateral and dorsal regions.

By examining a longitudinal section through the ventral part of the trachea another interesting variation in the epithelium becomes apparent. The epithelium is thicker and the goblet cells more numerous over the glandular areas than

over the cartilage rings (Plate VI). Table III shows that there is an average difference in thickness of about 4 μ between the epithelium covering the two areas. The difference between the epithelial thickness over the two areas was found to be analytically significant at a 1% level in the cats. The epithelium above the concentrated glandular areas bulges into the lumen (Plates VI and VIIa). A change in the height of the epithelium and number of goblet cells is not recognizable in the dorsal region where the cartilage rings overlap and the glands are more evenly dispersed.

Leucocytes are frequently found among the cells of both types of epithelium and can be easily mistaken for epithelial cell nuclei. Lymphocytes are the most numerous but polymorphonuclear leucocytes were seen frequently (Plate VIII). Lymphocytes are occasionally concentrated in nodules in the submucosa and invade the epithelium in large numbers. Many times they appear to erode it away (Plate IX). Lymphoid infiltration of the epithelium does not occur to the same extent in each animal. Lymphocytes are usually more numerous in and below the epithelium in the ventral and lateral regions than in the dorsal area which is in agreement with the findings of Paul (1913). Lymphoid infiltration occurs to a greater extent in the epithelium that lies over concentrated gland areas. Andrew and Burns (1947) reported that in the rat most of the leucocytes were found at or below the

level of the epithelial nuclei; the ones near the surface of the epithelium are usually pycnotic. This is also true in the tracheal epithelium of the cat.

Lamina Propria and Elastic Membrane

The lamina propria in the trachea of the domestic animals has been defined by Trautmann and Fiebiger (1952) as the area between the basement membrane and the elastic layer. It is composed of elastic fibers, a few fine collagenous fibers and usually many lymphocytes. It varies in thickness from 15 to 40 μ and does not blend with the submucosa. The elastic layer is often considered as a deeper or external part of the lamina propria.

The elastic layer or band consists of many longitudinally oriented elastic fibers closely associated into a compact layer (Plate X) which varies in average thickness from 28 to 33 μ . The band is thickest in the dorsal region, however, the fibers in this area are less closely packed; a fact which appears to be related to the number of glands in the underlying submucosa as well as the thickness of the submucosa. The elastic layer is thinnest in the lateral areas. In longitudinal section through the ventral region it is observed that the fibers over the bulging gland areas are more tightly packed than they are over the areas in between.

The individual elastic fibers average $2.7\ \mu$ in diameter and no large amount of variation in average fiber size is distinguishable in the various areas around the lumen. The fibers are not all the same size however; the smaller ones are found in greatest numbers on the medial surface of the membrane and are scattered through the lamina propria. Fibers extend from the membrane on both surfaces, many extend up to the basement membrane and a few mingle with fibers in the submucosa and annular ligaments. A few fine collagenous fibers could be distinguished scattered among the heavier elastic fibers of the membrane. Lymphocytes are frequently found migrating through the elastic membrane often in large numbers (Plate IX). The fibers bend around gland ducts which traverse the membrane.

Submucosa

This area is bounded internally by the elastic membrane and externally by the cartilage rings and annular ligaments. It is composed of a network of collagenous and elastic fibers, blood vessels, fat cells, glands and leucocytes. In longitudinal section through the ventral region the submucosa is much thicker in the area of the glands between the cartilage rings, than directly medial to the rings (Plate VIIa).

Stowe and Calhoun (1961) described this characteristic in the mink trachea. Averaged measurements derived from both longitudinal and cross sections show the submucosa to be thickest ventrally, thinnest laterally and of medium thickness dorsally.

The glands in the cat compose a large percentage of the submucosa and, as stated by Oppel (1905), increase in abundance dorsally to laterally to ventrally and are concentrated in areas medial to the annular ligaments (Plates VI & VIIa). They are so abundant in the ventral area that the mucosa protrudes into the lumen (Plate VI). In the dorsal region the glands are not concentrated in specific areas but are scattered along the entire length of the tube (Plate VIIb).

Both mucous and serous acini are present independently as well as mucous acini with serous demilunes (Plate XVIII). By counting the number of acini with and without mucus, the percentage of mucus secreting acini was roughly estimated to be about 25 percent.

The gland secretions reach the surface by means of numerous ducts. The ducts vary in size and the walls of the larger ones are often composed of a stratified layer of cells while the smaller ones are usually lined by a single layer of pyramidal cells. As Oppel (1905) explained, the

ducts are narrowed as they pass through the elastic membrane but often enlarge as they open on the epithelial surface. Cilia are found lining the duct openings and in the larger ducts they often extend as far as the acini. Collagenous fibers could be seen surrounding and scattered among the gland acini. Elastic fibers are less frequently seen among the glands.

Lymph nodules often occur in the submucosa especially in the ventral and lateral regions and are most frequently situated in the glandular areas.

Sussdorf (1911) reported that gland acini are occasionally found in the adventitia outside the cartilage rings. An example of this is shown in Plate XII. Acini are also rarely found in the lamina propria (Plate XIII) and in the area of the annular ligaments (Plate XIV). Acini were lacking outside the trachealis muscle which agrees with the reports of Stirling (1883) and Paul (1913).

The Cartilage Rings and Annular Ligaments

Plate II is a drawing illustrating the change in shape and relationship of the cartilage rings as they surround the tracheal lumen. Examination of the sections and measurements reveal that the rings decrease in width ventrally to laterally to dorsally, and that they are heavier in the proximal portion

of the trachea than in the distal part. In longitudinal section the rings appear more or less oval shaped in the ventral area having a flattened external surface and a rounded inner surface. Von Hayek (1960) described this characteristic in man and observed that the convexity of the inner surface of cartilage rings permits supportive action similar to that of the perpendicular ridge of a T-beam. The rings appear elliptical in the lateral area and spatulate dorsally (Plate II). This is similar to the description given by Stowe and Calhoun (1961) for the mink. In the dorsal area where the rings become greatly flattened they overlap each other in random fashion (Plates II & VIIb). Because of this it is common, in cross section, to see two plates of cartilage adjacent to one another in the dorsal lateral region (Plate XV).

The cartilage rings are hyaline in nature and surrounded by a perichondrium which is composed primarily of collagenous fibers. This contradicts the statements of Paul (1913) and Oppel (1905) who described the perichondrium as composed primarily of elastic fibers and the cartilages as somewhat elastic in composition. In agreement with Paul (1913) the external perichondrium is thicker than the internal one. Elastic fibers are found in the outer perichondrium and are present in small amounts in the inner one. The collagenous

fibers penetrate the periphery of the rings in large numbers. Spanning the area between the ends of the cartilage rings is a rather heavy collagenous sheet which appears continuous with the perichondrium and annular ligaments. Bifurcation of the rings does occur but not frequently as it does in man (Miller 1947).

The annular ligaments are observed best in longitudinal section through the ventral area as they link the cartilage rings to one another. They are composed primarily of collagenous fibers but many elastic fibers are present and appear more numerous in the external part of the ligaments. Between the rings the ligaments are thicker in the ventral area than in the dorsal region. They appear to be continuous with the perichondrium. Dorsally the ligaments can still be distinguished as they attach to the edges of the flattened, overlapping rings but they consist of relatively few bundles of fibers. Gland acini occasionally invade the area of the annular ligaments (Plate XIV).

Trachealis Muscle

The muscle is composed of bundles of transversely oriented smooth muscle fibers. In the cat the trachealis muscle lies external to the cartilage rings to which it attaches in the

lateral regions. Measurements indicate that the muscle is heaviest in the area near the larynx and decreases in size toward the bifurcation. This trend is contradictory to the one expressed by Paul (1913) who stated that the muscle increases in size from larynx to bifurcation. The muscle is thickest in the area between the ends of the cartilage rings and tapers at its point of attachment to the outer perichondrium and annular ligaments. The end of the muscle blends with transverse elastic fibers which attach to the outer perichondrium (Plate XV). Medial to the muscle the outer perichondrium is lacking in elastic fibers. External to the muscle is a thin sheet composed of collagenous and elastic fibers. Loose connective tissue is often found between this sheet and the muscle. This fibroelastic sheet blends with the outer perichondrium at the point of muscle attachment. In contradiction to Stirlings' (1883) report but in agreement with Paul (1913) no examples of longitudinally oriented muscle fibers or gland acini were found within or outside the muscle.

Adventitia, Nerves and Vessels

The adventitia is the outermost layer and is composed of loose connective tissue containing many blood vessels,

nerve trunks, ganglia and occasional lymph nodules. In accordance with the findings of Elftman (1943) and Honjin (1954) in the dog and rat respectively, the nerve trunks and ganglia are concentrated in the dorsal adventitia external to the muscle (Plates XV & XVI). Nerve trunks are quite frequently found in the lateral adventitia and occasionally in the ventral area. Ganglia are rarely seen ventrally but are more numerous in the dorsal and lateral regions. No nerve trunks or ganglia were observed medial to the cartilage rings. Blood vessels of varying size are found in abundance in the adventitia.

Sexual Differences

Comparative measurements of male and female animals show that differences between them are minimal. However, the averages of many measurements on both sexes indicate that in the females the epithelium, elastic layer, and submucosa are all of slightly larger proportions than in the males. The cartilage rings, on the other hand, are lighter and thinner in the females. The other factors remain unchanged between the sexes.

TABLE I[#]

THE CAT

TRACHEAL MEASUREMENTS IN MICRONS

		*a	b	c	DLV averages	Total average
Epithelial thickness	**D	33.9	37.4	42.6	37.9	
	L	35.6	40.4	37.8	37.9	40.2
	V	46.4	47.4	40.9	44.9	
Ciliary length	D	3.4	3.9	4.1	3.8	
	L	3.7	4.0	4.2	4.0	4.0
	V	3.8	4.5	4.5	4.3	
Goblet cell distribution	***D	1.9	2	2	2	
	L	2	2.2	2.3	2.2	2.1
	V	2.5	2.2	1.9	2.2	
Elastic layer thickness	D	32.2	35.6	32.1	33.6	
	L	25.5	27.3	21.6	24.8	29.0
	V	27.5	26.0	32.5	28.6	
Elastic fiber diameter		2.9	2.8	2.6	2.7	2.7
Submucosal thickness	D	124.8	94.1	150.5	123.1	
	L	96.5	92.6	117.8	102.3	136.4
	V	131.7	188.5	231.8	184.0	
Distribution of glands	***D	1	2	1	1	
	L	2	2	2	2	2
	V	2	3	3	3	
Cartilage thickness	D	133.6	131.8	119.5	128.3	
	L	403.1	302.7	336.4	347.4	319.3
	V	567.2	359.3	357.5	482.2	
Muscle thickness	D	98.0	87.4	33.7	73.0	73.0

TABLE I (Continued)

Every figure in the Table represents an average of four to six measurements obtained from each of ten animals.

*a--Proximal level

b--Middle level

c--Distal level

**D--Dorsal

L--Lateral

V--Ventral

***1--Scarce

2--Average

3--Abundant

TABLE II[#]

THE DOG

TRACHEAL MEASUREMENTS IN MICRONS

		a	b	c	DLV averages	Total average
Epithelial thickness	**D	42.3	35.8	41.7	39.9	
	L	41.1	38.2	42.8	40.7	40.9
	V	48.1	39.1	42.3	43.1	
Ciliary length	D	6.0	6.0	5.2	5.7	
	L	5.4	6.4	5.6	5.8	5.7
	V	6.2	5.5	5.9	5.8	
Goblet cell distribution	D	***2	2	2	2	
	L	2.5	2.3	2.3	2.3	2.2
	V	2	2.2	2.5	2.2	
Elastic layer thickness	D	155.8	84.8	62	100.8	
	L	68	55	87.8	70.2	94.3
	V	83.7	110	142.7	112.1	
Elastic fiber diameter		2.9	3.4	2.9	3.0	3.0
Submucosal thickness	D	426.6	369.4	290.1	362.0	
	L	309.7	308.8	280.8	299.7	328.9
	V	406.9	348.5	220.0	325.1	
Distribution of glands	D	***1	1	1	1	
	L	2	1	1	1	1
	V	1	1	1	1	
Cartilage thickness	D	303.7	221.8	216.2	247.2	
	L	700.0	555.1	492.5	582.5	538.2
	V	998.0	722.3	634.6	784.9	
Muscle thickness	D	433.2	319.5	273.4	342.0	342.0

TABLE II (Continued)

Every figure in the table represents an average of four to six measurements obtained from each of ten animals.

*a--Proximal level

b--Middle level

c--Distal level

**D--Dorsal

L--Lateral

V--Ventral

***1--Scarce

2--Average

3--Abundant

II. THE TRACHEA OF THE DOG

In the following pages the histology of the dog trachea will be discussed and compared to that of the cat. The measurements of the various structural elements of the trachea referred to below are in Table II.

Epithelium

Pseudostratified ciliated columnar epithelium containing goblet cells is also found in the trachea of the dog. The cells are very similar to those of the cat. The average thickness of the epithelium is very nearly the same as in the cat. It decreases in thickness ventrally, laterally to dorsally which agrees with Loginoff (1911) who reported that the epithelial cells of the dog are shorter over the membranous part of the trachea than elsewhere. The cilia are longer in the ventral area than in the dorsal region but there is no consistent modification in their length between the proximal and distal areas. The cells are covered on their distal surface by microvilli. Goblet cells are found in relatively the same quantity in the dog trachea and are similarly less abundant over the dorsal area. Intermediate and basal cells could also be identified. The basement membrane appears as an indistinct transparent border along the base

of the epithelial cells. It is often obliterated by longitudinal elastic fibers that are most obvious in a longitudinal section.

A modified type of epithelium similar to transitional is also found in the dorsal area of the dog trachea but in much smaller amounts than in the cat (Plate XVII). When present it is most often found directly medial to the tips of the cartilage rings and is lower than the pseudostratified epithelium. Occasionally it spans the entire distance between the ends of the rings and at times it is absent altogether. Cilia and goblet cells are not found in the transitional-type of epithelium. The pseudostratified epithelium is usually highly folded in a longitudinal direction over the membranous part of the tube where it protrudes into the lumen of the fixed specimen. This folded epithelium displays the characteristic pattern of alternating ridges and creases as seen in cross section on Plate XVII. The folds are smaller and more numerous than in the cat.

In the ventral region the epithelial lining is thicker in the area of the annular ligaments than in the region medial to the rings (Table III). The difference in epithelial thickness between the two regions is less in the dog (significant at a 10% level) than it is in the cat (significant at a 1% level).

Goblet cells generally do not appear more numerous in the epithelium over the annular ligaments and the epithelium in this area does not ordinarily bulge into the lumen as it does in the cat. In the dorsal region the epithelium is uniform in thickness.

TABLE III

MEASUREMENTS OF EPITHELIAL THICKNESS IN LONGITUDINAL SECTION*

	Epithelial thickness in microns	
	Over annular ligaments	Over cartilage rings
Cat number 1	45	41
2	44	40
3	62	59
4	40	35
Average	48	44
Dog number 1	40	32
2	57	55
3	42	41
4	35	36
Average	43	41

*Each figure represents an average of eight measurements taken from the ventral area of the trachea of each animal. Using the analysis of variance test on the original measurements, the difference between the epithelial thickness in the two areas was found to be significant at a 1% level in the cats but at a 10% level in the dogs.

Leucocytes appear in the epithelium and are usually found at the level of or below that of the epithelial nuclei; those near the surface are often pycnotic.

Lamina Propria, Elastic Layer, and Submucosa

It is in these areas that some of the greatest differences exist between the trachea of the dog and cat. For an illustration of these differences refer to Plates X and XI. The lamina propria cannot be identified as a distinct and separate area in the dog as it is in the cat. The area directly below the epithelium composed of fine collagenous and elastic fibers, many leucocytes and other connective tissue cells may be considered as the lamina propria, however, this area blends with the submucosa (Plate XI).

The elastic layer is not a compact band as in the cat but consists of numerous, loosely arranged, longitudinal fibers scattered through the lamina propria and submucosa. The layer varies greatly in thickness but is usually narrowest in the lateral region and becomes wider in the ventral and dorsal areas. No trend in the thickness of the elastic layer is evident among the various levels. Just beneath the epithelium in the dog trachea are two single layers of longitudinal elastic fibers separated from each other by approximately 10 - 20 μ (Plate XI). The medial layer is composed of fibers measuring about 1.5 μ in diameter which lie in close contact with the basement membrane. The external layer is composed of coarser

fibers having an average diameter of 3 μ or more. Between the two layers is a small portion of the lamina propria containing a network of fine collagenous and a few small elastic fibers. Both layers are not always distinguishable.

External to these layers the elastic and collagenous fibers gradually increase in size and density toward the cartilage rings. Occasionally the elastic layer extends through the entire width of the submucosa. Most often it extends about one third of the distance from the basement membrane to the perichondrium, however, the relationship between the submucosa and the elastic layer is subject to great variation. The heavier elastic fibers are most numerous in the lateral part of the layer where they appear to branch often and are frequently oriented in an oblique or transverse direction. The area external to the elastic layer and internal to the perichondrium and annular ligaments is relatively free of large elastic fibers but is very rich in collagenous tissue. The width of this area varies with the extent of the elastic layer and the width of the cartilage rings as seen in longitudinal section.

Strands of collagenous fibers are found among and around the gland acini often fusing with the perichondrium and annular ligaments. Blood vessels, fat cells, occasional nerve

trunks, leucocytes and glands are scattered through the submucosa. Lymph nodules are not as abundant in the submucosa of the dog as in the cat and consequently lymphoid invasion of the epithelium, which usually occurs near a nodule, is less frequently seen. The submucosa is thinner in the lateral region than it is dorsally and ventrally. It also decreases in thickness proximally to distally. Ventrally and laterally it is widest in the area of the annular ligaments.

Stirling (1890) noticed that the tracheal glands in the cat are more numerous than in the dog. Sussdorf (1911) reported that of all the domestic animals tracheal glands are most numerous in the cat and least numerous in the dog. Comparison of Plate VII and XIX illustrates that the tracheal glands are much more numerous in the cat than the dog. The gland acini are the same type as those found in the cat. Stirling (1883) mentioned that the mucous acini in the cat are more granular than in the dog. This difference, if it exists, is very minute. The percentage of mucus secreting acini in the dog was estimated to be about 42 percent which is greater than in the cat. The gland acini are scattered through the submucosa and lamina propria, many are embedded in the elastic layer (Plate XI) while others are situated lateral to it. There is no visible difference in the quantity

of glands between the ventral and dorsal regions, however, they are more numerous in the area of the annular ligaments than elsewhere. The small groups of acini are usually separated by expanses of collagenous and elastic tissue. Rarely are acini found outside the cartilage rings or in the annular ligaments. No acini were seen outside of the trachealis muscle which agrees with the report of Oppel (1905).

The gland ducts although less numerous have the same construction as those of the cat. The walls of the larger ones are often composed of a stratified layer of cells and are lined for long distances with cilia (Plate XX). The smaller ducts consist of a single layer of pyramidal cells. Some ducts become narrow as they open on the epithelial surface others enlarge at their openings. The ducts do not become narrowed in the area of the elastic layer as they do in the cat.

Cartilage Rings and Annular Ligaments

The cartilage rings in the dog trachea are similar to those of the cat in shape (Plate II) but differ in size (Plate I). They are thicker in the ventral region and decrease in size dorsally. A similar decrease in size is observed from the proximal part of the trachea to the distal end. The rings have the same general shape as those of the

cat in cross section: oval ventrally (flattened exterior surface, rounded interior surface), elliptical laterally and spatulate dorsally where they overlap each other. There apparently is no definite order or pattern in which they overlap.

The rings are composed of hyaline cartilage and are surrounded by a collagenous perichondrium which is thicker on the external surface than the internal one. Elastic fibers are present in small amounts in the perichondrium of both surfaces. A heavy sheet of collagenous tissue which appears continuous with the perichondrium and annular ligaments spans the ends of the incomplete rings.

In some of the dogs and cats the central portion of the rings in the ventral area appeared degenerated, highly vacuolated and stained very lightly with hematoxylin and eosin stain. This was first assumed as indicative of calcification, however, the results of von Kossa's stain showed that no significant amount of calcification had taken place in any part of the cartilage rings of either the dogs or the cats used. It should be noted here that the exact age of many of the animals was not known.

The annular ligaments are heaviest between the rings in the ventral area and are heavier in the dog than the cat.

They are composed of numerous collagenous fibers, few elastic fibers, and seem to blend with the perichondrium. In longitudinal section the ligaments are often seen folded inward toward the mucosa. In the gross specimen lengthwise tension on the trachea causes movement in the area of the annular ligaments. Thus the ligaments not only connect the cartilage rings but allow movement between them. In the dorsal area the ligaments can be discerned connecting the overlapping edges of the flattened rings.

Trachealis Muscle

The transverse smooth muscle bundles are located outside the cartilage rings and attach to the external perichondrium in the lateral areas by means of elastic fibers. The average width of the muscle is $269\ \mu$ thicker than in the cat which does not agree with Stirling (1883) who reported that the trachealis muscle of the dog did not seem to be as thick as in the cat. The muscle decreases in thickness from the larynx to the bifurcation. The area of muscle attachment is similar to that of the cat. Outside of the muscle lies a thin sheet of fibroelastic tissue similar to that in the cat, which blends with the outer perichondrium at the point of muscle attachment. Loose connective tissue is frequently found between this sheet and the muscle. The muscle is widest

in the region between the ends of the cartilage rings and tapers to its point of attachment. No examples of longitudinal muscle fibers were found outside the transverse bundles and no gland acini were found within or outside the trachealis muscle.

Adventitia, Nerves and Vessels

The adventitia is composed of loose connective tissue and contains numerous blood vessels, nerve trunks, ganglia and occasional lymph nodules. Blood vessels of varying sizes and oriented in both transverse and longitudinal planes are found here.

Nerve trunks and ganglia are concentrated in the dorsal area external to the muscle like in the cat. Nerve trunks are found occasionally in the lateral area but only rarely in the ventral adventitia. Ganglia are found only in the lateral and dorsal adventitia. Occasionally large nerve trunks are found in the submucosa of the dorsal area (Plate XXI).

The tissues spanning the membranous part of the dog and cat trachea from the lumen outward are: mucosa, submucosa, collagenous layer continuous with the perichondrium and annular ligaments, trachealis muscle, thin fibroelastic membrane

and loose connective tissue of the adventitia containing vessels and nerves (Plate XXII).

Sexual Differences

Sex variations in the dog trachea are in general less apparent than in the cat. The only trend which appears on the basis of measurements is the presence of thinner cartilage rings in the females than in the males. These sex differences in both the dog and cat are not of substantial importance because of the size variations among the various breeds of animals used in this study.

For an illustrated summary of some of the histological differences between the trachea of the cat and dog see Plate I.

SUMMARY AND CONCLUSIONS

Comparative histological studies of the trachea were made on fourteen dogs and eleven cats, all adults of both sexes. Routine techniques were used in preparation of the sections for microscopic study.

The tracheae of the dogs are larger in every respect than those of the cat. No substantial differences exist in the average thickness of the epithelium, the elastic fiber diameter and goblet cell distribution. Except for those characteristics mentioned, no changes were found among the various tracheal levels in either species.

Sex differences in both species are minimal but there is one trend in common, the cartilage rings are thinner in the females than the males.

A transitional-type of epithelium is commonly found in the dorsal tracheal wall of both species. It is present to a greater extent in the cat. Most frequently it is located directly medial to the ends of the cartilage rings and in the membranous region of the tube. The change from pseudostratified ciliated columnar to a transitional-type of epithelium is suggestive of continual movement of the mucosa in the membranous part of the trachea and especially so at the junction of the membranous and cartilagenous areas.

In the ventral area the thickness of the pseudostratified epithelium increases in the region of the annular ligaments

and decreases near the central portion of the cartilage rings. The difference is greater and more significant analytically in the cats than in the dogs. This variation becomes less obvious in the dorsal area of both species.

The cilia are shorter over the dorsal than the ventral and lateral areas in both species.

Goblet cells are found in decreased amounts in the dorsal epithelium of both the dog and cat. In the cat however, they are abundant in the epithelium over the concentrated gland areas in the ventral part of the trachea.

The lamina propria represents a distinct area in the cat and the elastic layer is a compact band composed of longitudinal elastic fibers located in the outer part of the lamina propria. In the dog the lamina propria blends with the submucosa and the elastic layer is a wide band of loosely associated fibers scattered through both areas. In both species the larger fibers are most numerous in the lateral part of the elastic band.

The submucosa decreases in thickness from the proximal to distal region in the dog but from the distal to proximal to middle area in the cat. In both species it is thinnest in the lateral region and in longitudinal section it is wider medial to the annular ligaments than medial to the cartilage rings. Shrinkage of the cartilage rings due to

fixation often modifies the width of the elastic layer and submucosa in the dorsal area.

Tracheal glands are very numerous in the cat and compose a large percentage of the submucosa. They increase in abundance dorsally to laterally to ventrally. Gland acini are occasionally seen outside of the cartilage rings, in the lamina propria and among the annular ligaments. In the dog the glands are scarce and collagenous and elastic tissues compose the bulk of the submucosa. The acini are more evenly dispersed around the lumen in the dog than in the cat and they are rarely seen outside the cartilage rings or among the annular ligaments in the dog. In both species the glands consist of mucous, serous and mixed acini. The percentage of mucus secreting acini is estimated to be less in the cat than the dog. Gland acini are not found within or outside the trachealis muscle. In both the dog and cat the glands are concentrated medial to the annular ligaments in the ventral and lateral areas.

The shape of the cartilage rings is the same in the dog and the cat. They are composed of hyaline cartilage and are surrounded by a collagenous perichondrium. In longitudinal section through the ventral area the rings have a flattened external surface and a rounded internal one.

They are elliptical laterally and flattened in the dorsal region where they overlap. The outer perichondrium is thicker than the internal one. The rings decrease in thickness proximally to distally as well as ventrally to dorsally. No significant amount of calcification was encountered in either species. Bifurcation of the rings does not occur frequently.

The collagenous annular ligaments are most dense in the ventral area in both species. Elastic fibers are present in small amounts. A collagenous layer apparently continuous with the perichondrium and annular ligaments spans the area between the ends of the rings.

The trachealis muscle lies external to the cartilage rings and attaches in the lateral region in both species. The muscle decreases in size from the laryngeal region to the bifurcation and is widest in the area between the ends of the rings. It becomes thinner where it attaches by means of elastic fibers to the external perichondrium.

In both the dog and cat the nerve trunks and ganglia are concentrated in the dorsal adventitia. Occasionally they are found laterally and ventrally. Only in the dog are nerve trunks seen in the dorsal submucosa.

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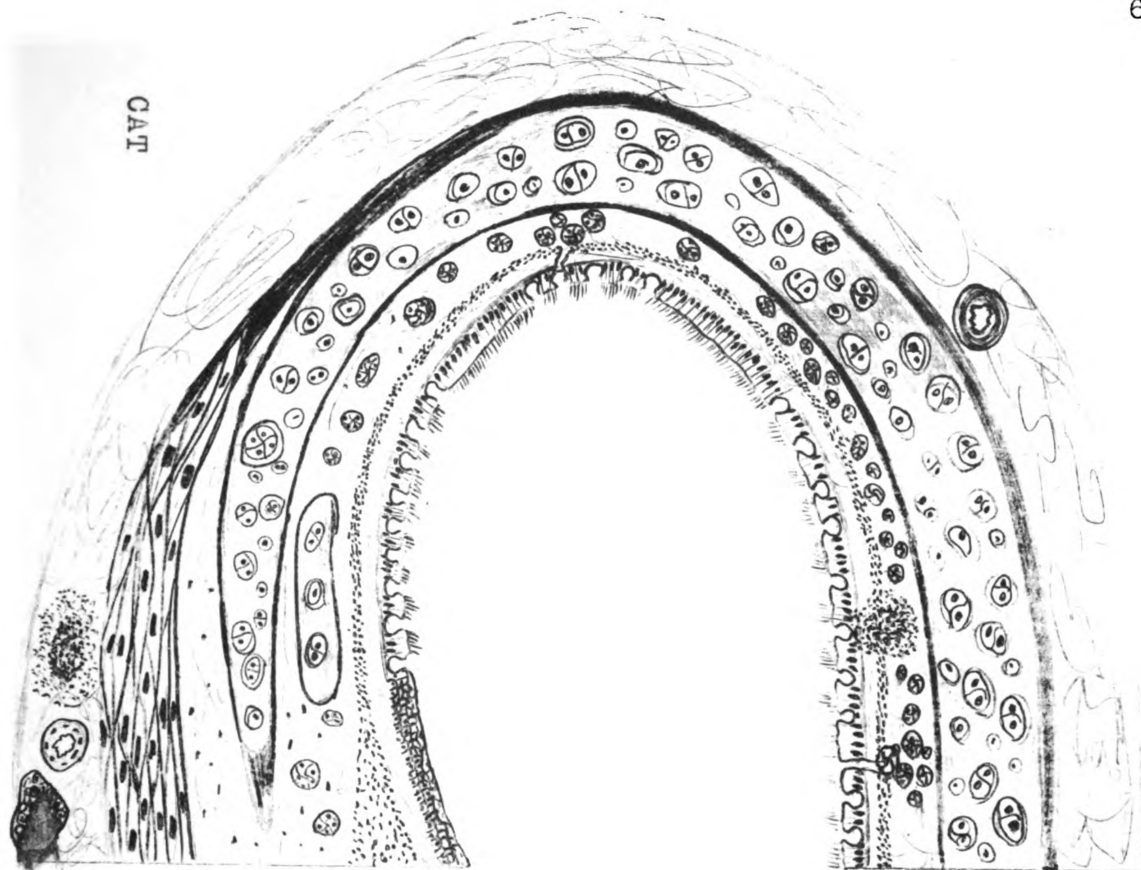
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PLATE I

A sketch to show some basic differences in various tracheal elements which exist between the dog and cat. Note variations in the dorsal epithelium, elastic layers, gland quantity, perichondrium thickness externally and internally and size of cartilage rings and muscle.

CAT



DOG

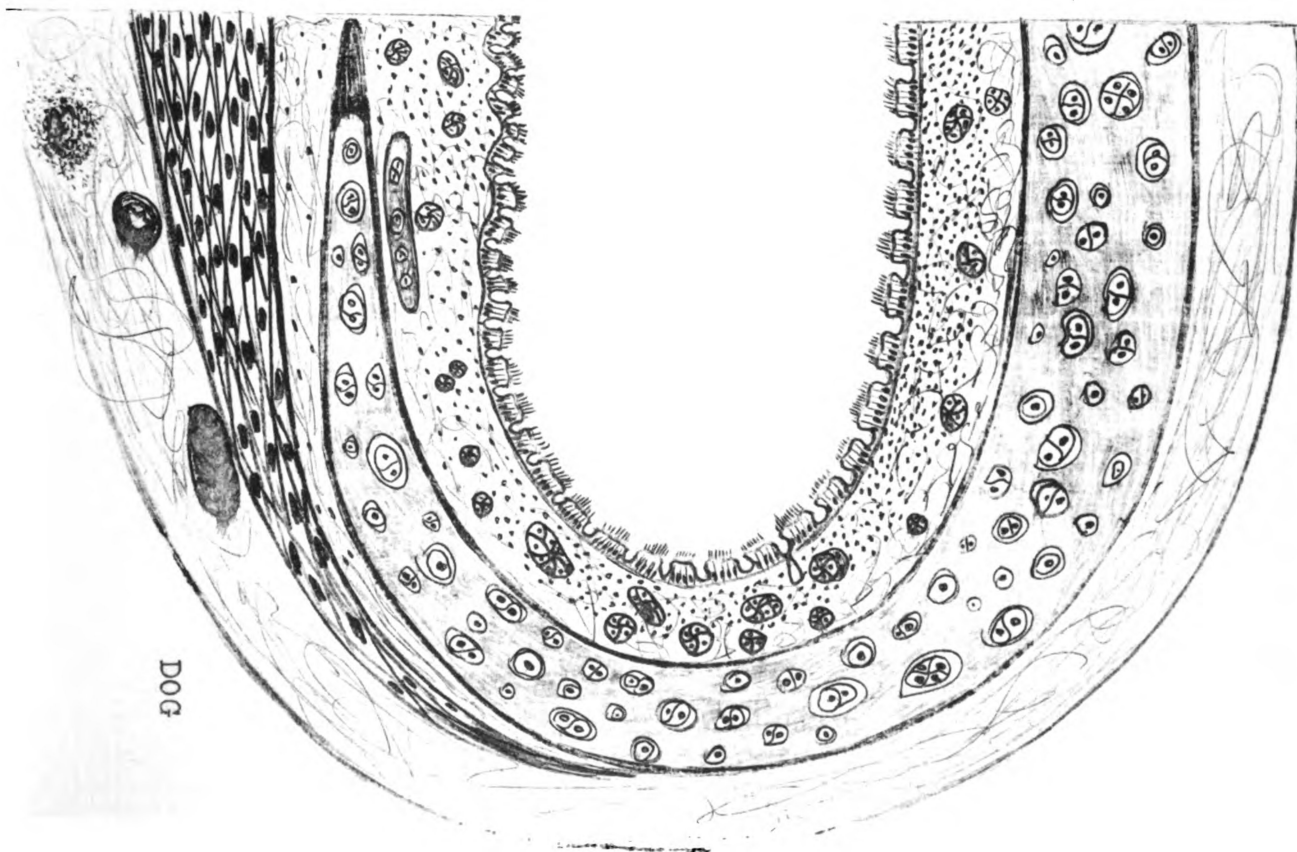


PLATE II

A drawing to show the change in shape of the cartilage rings as they surround the lumen. The rings become flattened in the dorsal area and overlap each other in random fashion. The shape and relationship of the cartilage rings is the same in both the dog and the cat.

PLATE III

CAT

Oblique section through the bottom of an epithelial fold in the dorso-lateral area giving the appearance of an intraepithelial pocket lined with cilia. H & E; x 1215.

1. Bottom of epithelial fold.
2. Cellular debris.
3. Lamina propria.
4. Basement membrane.
5. Elastic fibers.



PLATE IV

CAT

Transverse section through a fold in the dorsal region showing both the transitional type of epithelium and the common pseudostratified ciliated columnar epithelium. H & E; x 183.

1. Pseudostratified ciliated columnar epithelium.
2. Transitional-type epithelium.
3. Tip of incomplete hyaline cartilage ring.
4. Lamina propria.
5. Submucosa.
6. Glands.
7. Elastic fibers in the lamina propria.

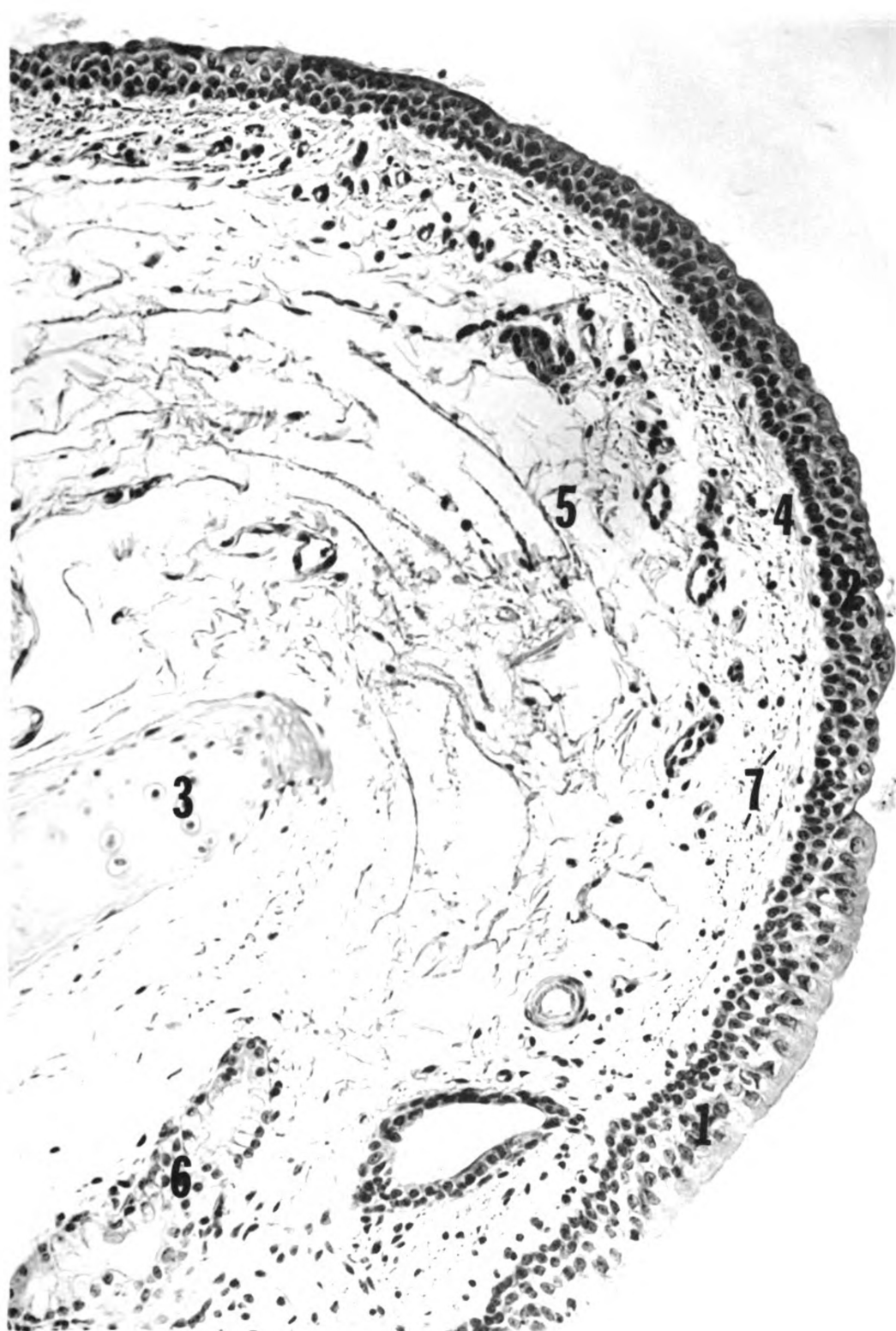


PLATE V

CAT

High power view of the abrupt transition between the two types of epithelia seen on Plate IV. H & E; x 1166.

1. Pseudostratified ciliated columnar epithelium.
2. Transitional-type epithelium.
3. Lymphocyte.
4. Elastic fibers.
5. Collagenous fibers.

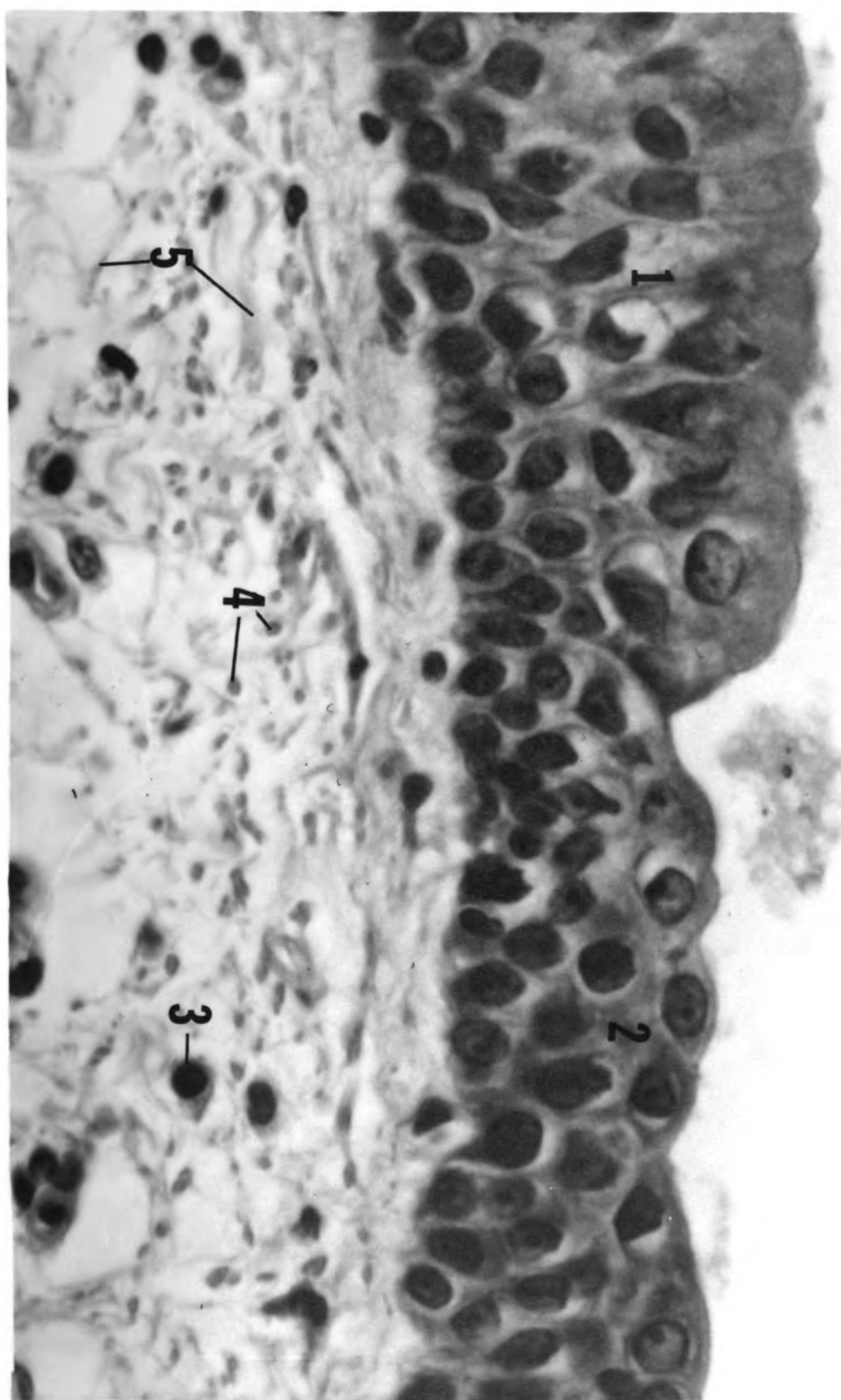


PLATE VI

CAT

Longitudinal section through the ventral area showing the difference in the number of goblet cells and height of the epithelium between the region medial to a concentrated gland area and the one medial to the center of a cartilage ring. Note how the epithelium protrudes into the lumen above the aggregation of glands which lie between the cartilage rings. H & E; x 157.

1. Thick epithelium with numerous goblet cells.
2. Relatively thin epithelium with few goblet cells.
3. Aggregation of glands between cartilage rings.
4. Elastic layer.
5. Blood vessel.
6. Cross section of a cartilage ring.

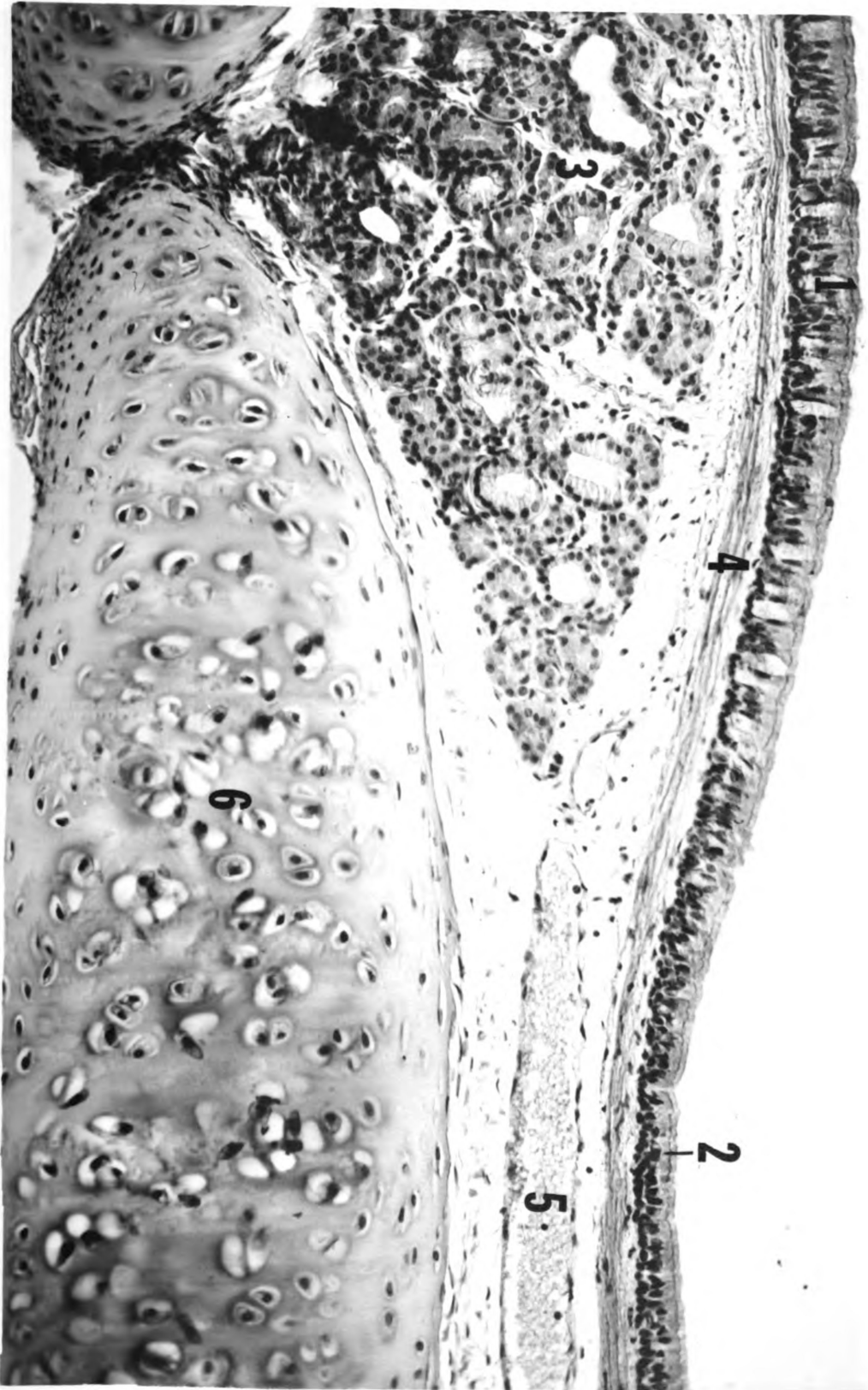


PLATE VII

CAT

a. Longitudinal section through the ventral area showing the gland-cartilage relationship and the shape of the cartilage rings. Note how the epithelium protrudes into the lumen above the gland aggregation. H & E; x 83.

b. Longitudinal section through the dorso-lateral region to show the difference in gland-cartilage relationship and the shape of the cartilage rings in this area as compared to a. H & E; x 83.

1. Gland acini.
2. Cartilage rings in cross section.
3. Epithelia.
4. Adventitia.

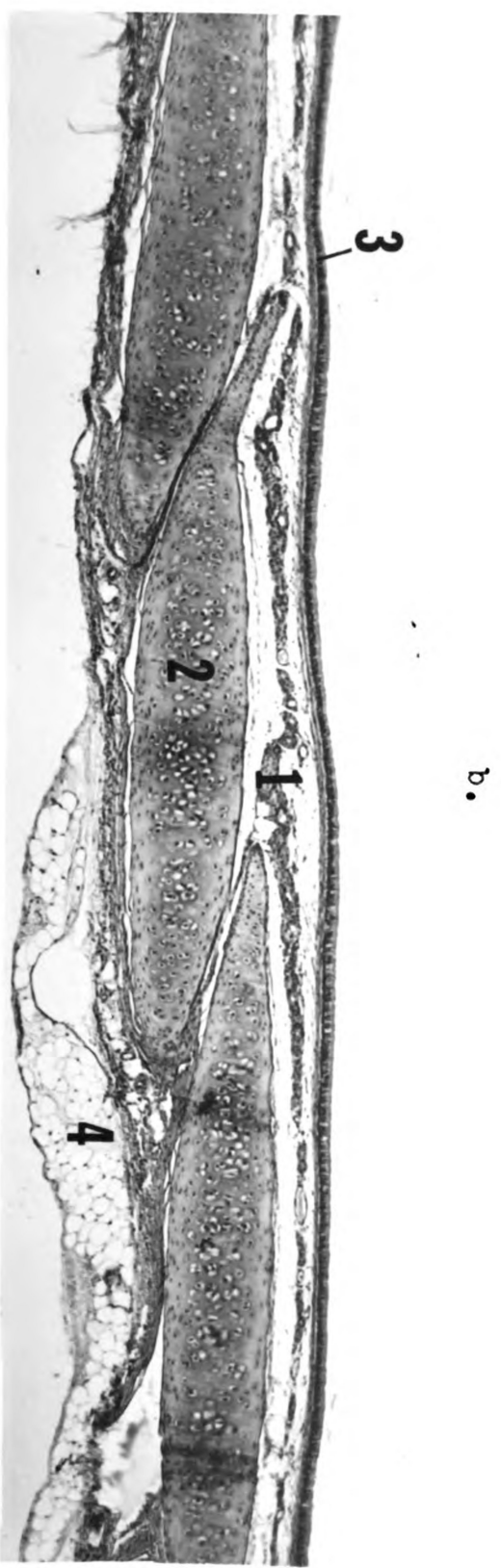
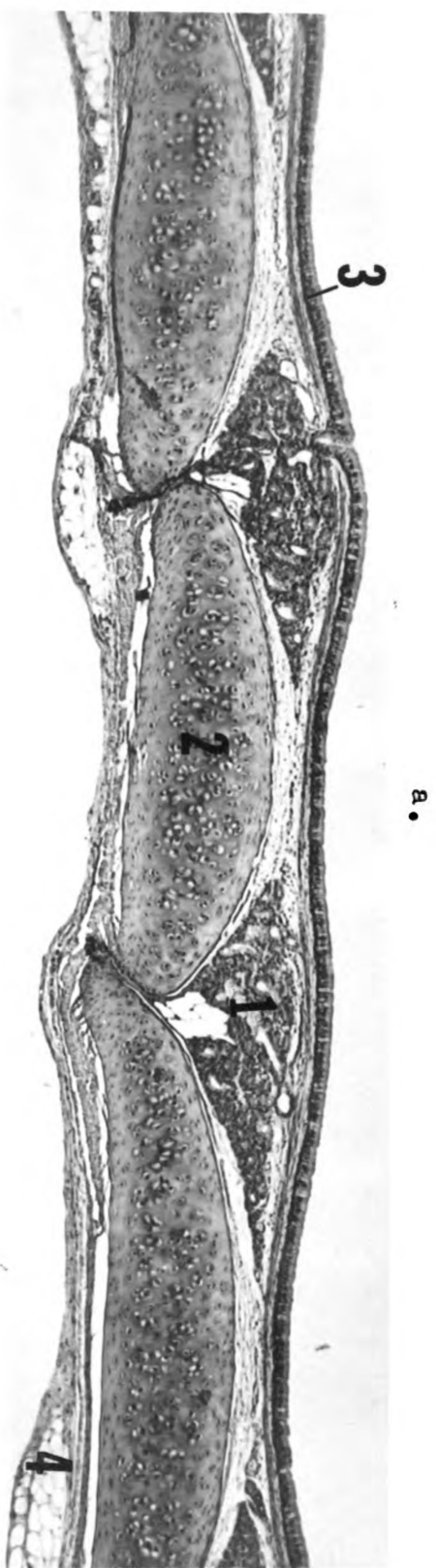


PLATE VIII

CAT

Transverse section through a fold of the mucosa in the dorsal region showing many leucocytes in the epithelium. The tracheal epithelium of either species normally does not contain as many leucocytes (especially neutrophils) as pictured here. H & E; x 1381.

1. Transitional-type epithelium.
2. Neutrophils.
3. Lymphocytes.
4. Tracheal lumen.

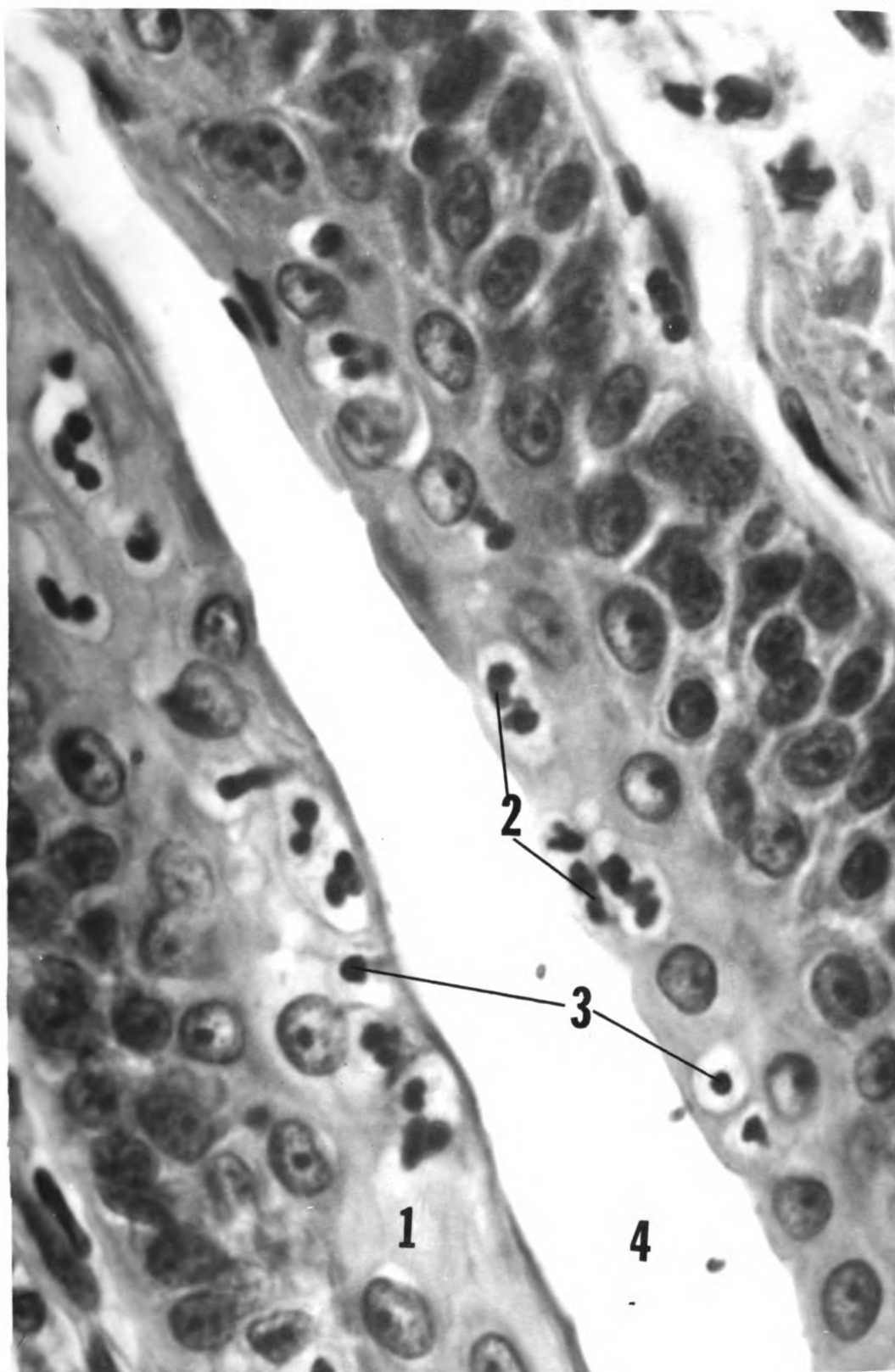


PLATE IX

CAT

Lymphoid invasion of the mucosa as seen in longitudinal section. H & E; x 205.

1. Aggregation of lymphocytes.
2. Elastic layer.
3. Lymphocytes in the lamina propria.
4. Epithelium, pseudostratified ciliated columnar.

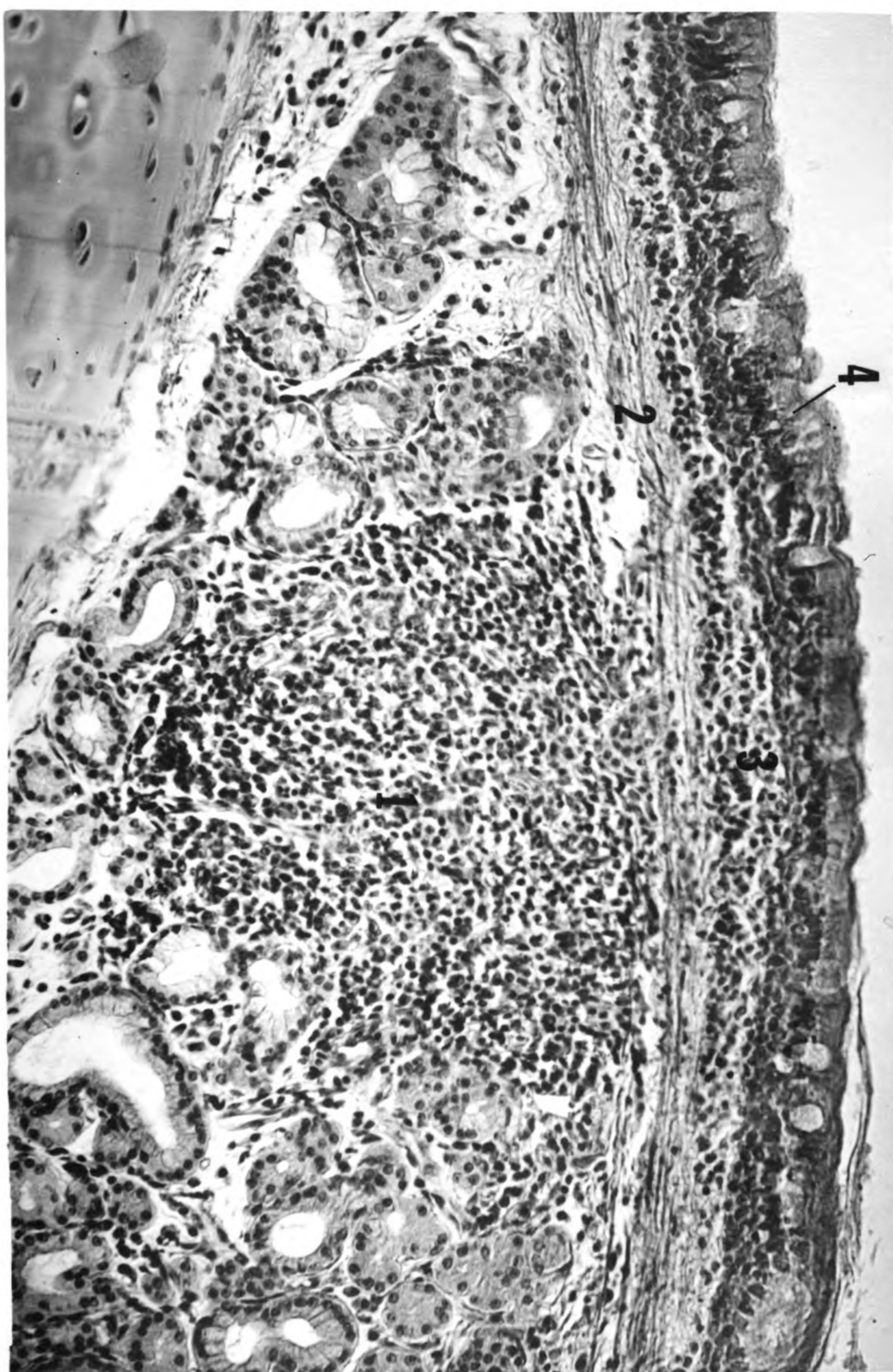


PLATE X

CAT

Transverse section from the lateral area showing the arrangement of various elements in the mucosa and submucosa. Compare with Plate XI. Weigert and Van Gieson; x 290.

1. Lamina propria and elastic layer.
2. Tracheal gland acini in the submucosa.
3. Loose elastic and collagenous tissues.

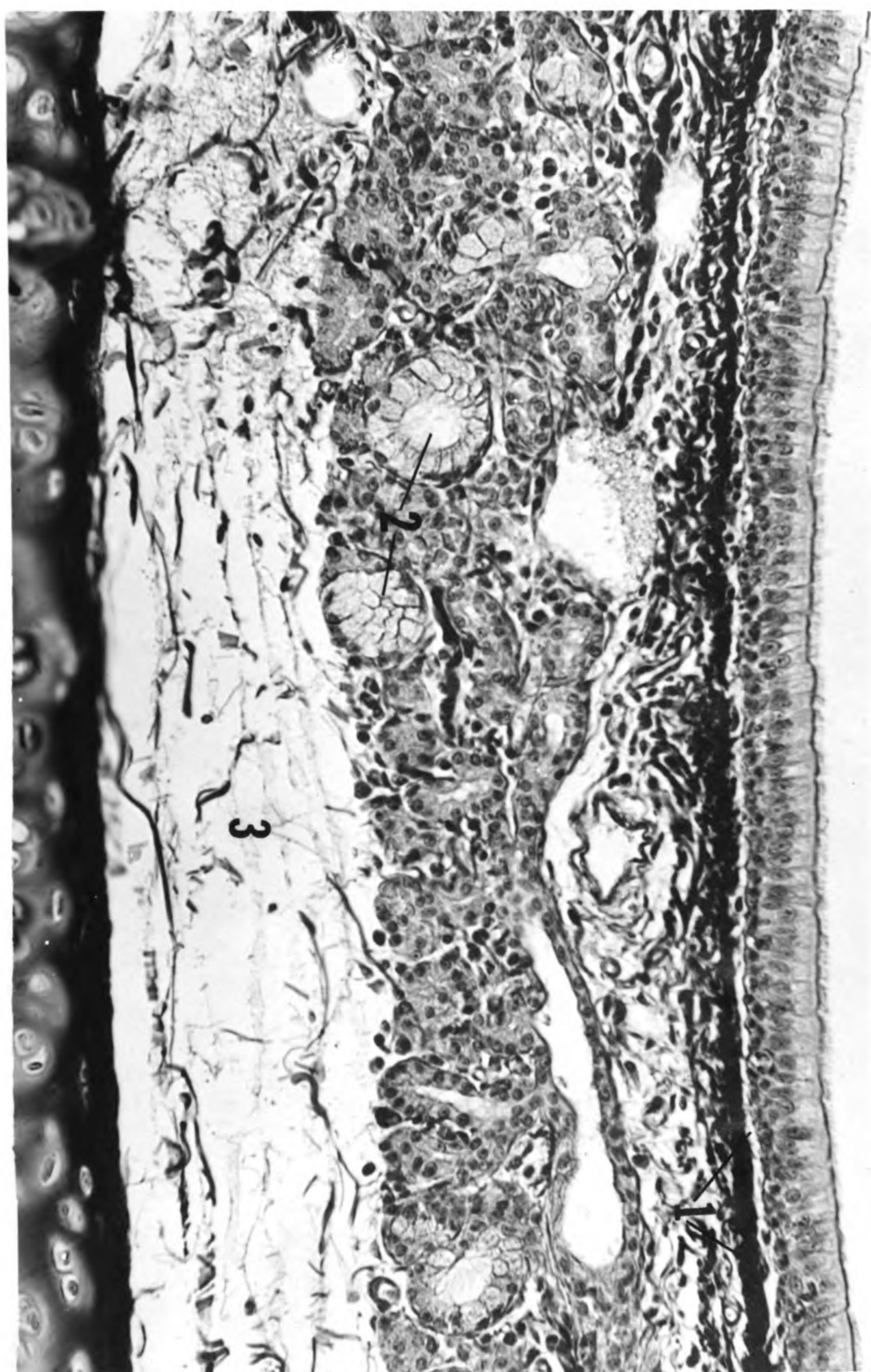


PLATE XI

DOG

Transverse section from the lateral area showing the arrangement of mucosal and submucosal elements in the dog trachea.

Compare with that of the cat in Plate X. Weigert and Van Gieson; x 300.

1. Area of the lamina propria which blends with the submucosa.
2. Two layers of longitudinally oriented elastic fibers separated by a small area of lamina propria.
3. Elastic layer which is a wide band of loosely arranged elastic fibers scattered through the lamina propria and submucosa. The larger fibers are concentrated in the deeper part of the band.
4. Gland acini.
5. Blood vessels.
6. Heavy collagenous fibers in the lateral part of the submucosa. Few large elastic fibers are found in this area.



PLATE XII

CAT

Transverse section showing acini external to a cartilage ring in the ventral region. This section is cut through the edge of a cartilage ring and therefore the perichondrium is seen as it blends with an annular ligament in the lower part of the plate. H & E; x 229.

1. Fat cells in the adventitia.
2. Gland acini external to the ring.
3. Outer perichondrium blending with an annular ligament.
4. Acini in the submucosa.

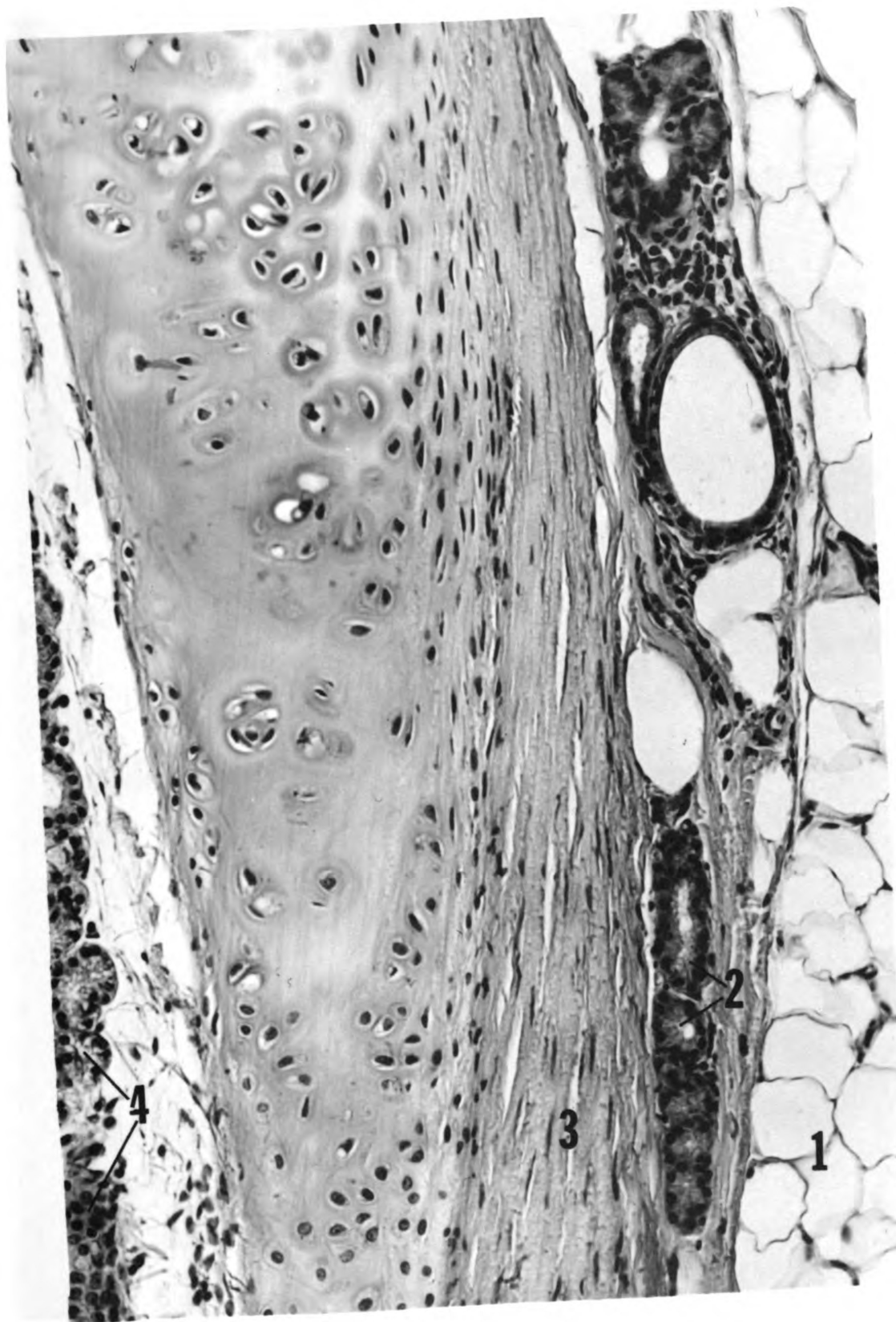


PLATE XIII

CAT

Gland acinus situated in the lamina propria as seen in longitudinal section. Note the distinct lamina propria and well defined elastic layer. H & E; x 640.

1. Gland acinus.
2. Epithelium.
3. Lamina propria.
4. Elastic layer.
5. Submucosa.

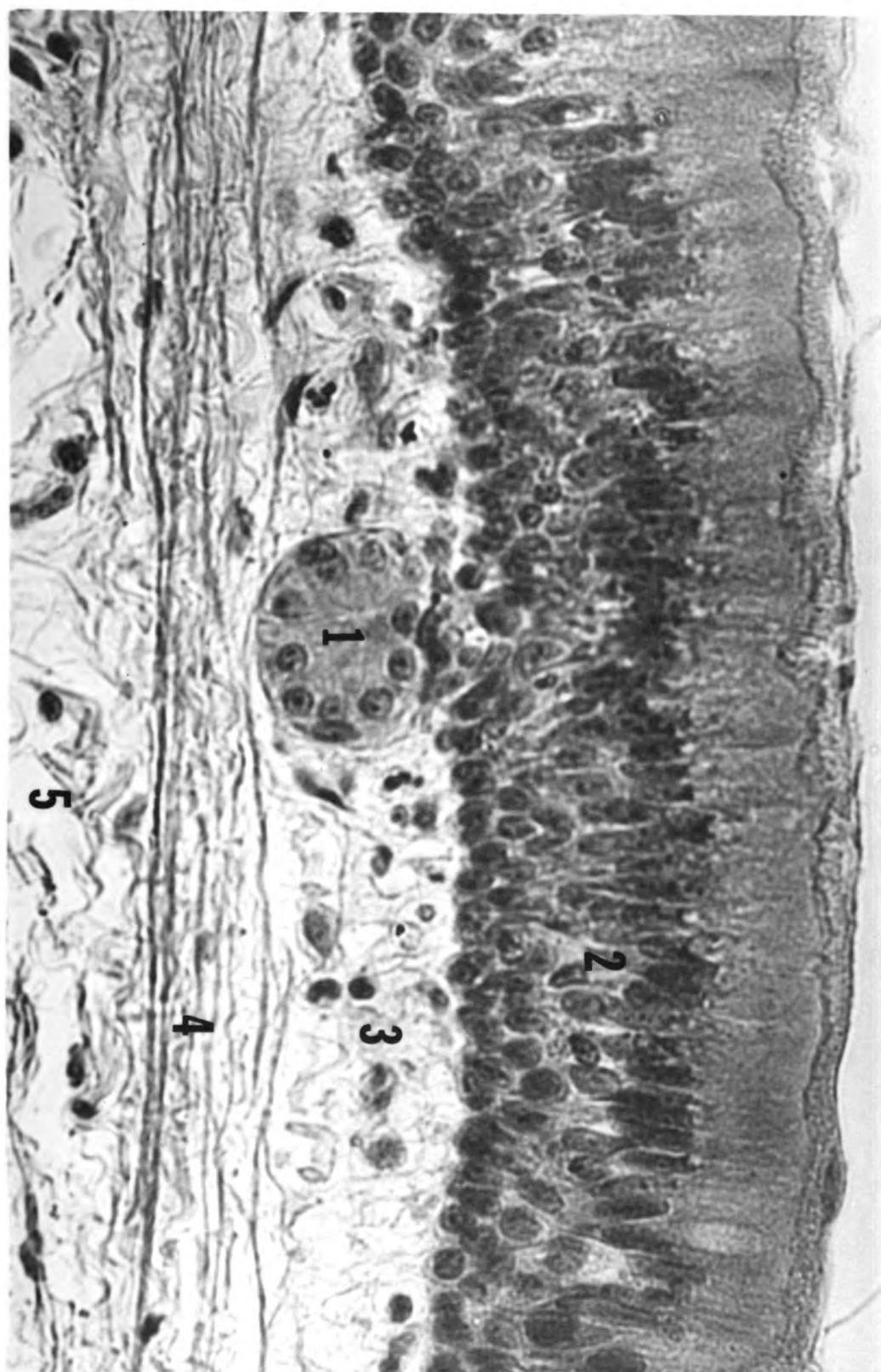


PLATE XIV

CAT

Gland acini situated in the area of the annular ligaments;
longitudinal section. H & E; x 159.

1. Elastic layer in the lamina propria.
2. Gland duct.
3. Mucus secreting cells.
4. Serous acini.
5. Blood vessel filled with blood.
6. Remaining part of the annular ligament.
7. Adventitia.

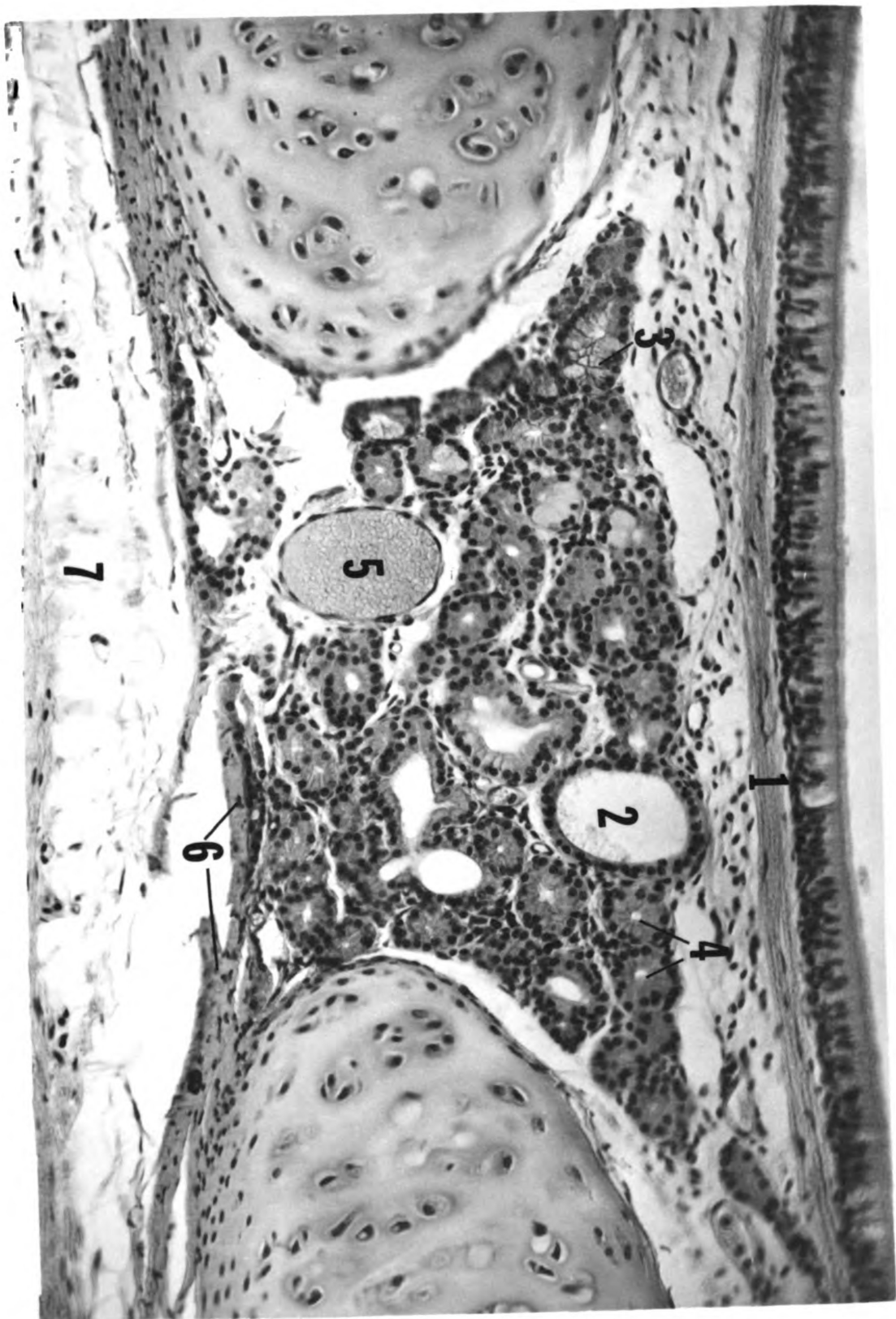


PLATE XV

CAT

Transverse section from the dorso-lateral region showing two adjacent cartilage plates and the muscle attachment to the outer perichondrium by means of elastic fibers.

Weigert and Van Gieson; x 63.

1. Adjacent cartilage plates.
2. Muscle fibers.
3. Elastic fibers.
4. Outer perichondrium.
5. Adventitia containing adipose tissue, blood vessels and nerve trunks.



PLATE XVI

DOG

Transverse section through the dorso-lateral region showing the relationship of ganglion, muscle and cartilage. H & E; x 223.

1. Tracheal lumen.
2. Cartilage ring.
3. Trachealis muscle.
4. Nerve ganglion in the adventitia.



PLATE XVII

DOG

Transverse section through the area medial to the cartilage-membranous junction showing a patch of transitional-like epithelium. Note the highly folded epithelium. H & E; x 245.

1. Transitional-like epithelium directly medial to the cartilageneo-membranous junction.
2. Folded pseudostratified ciliated columnar epithelium lining the membranous portion of the trachea.

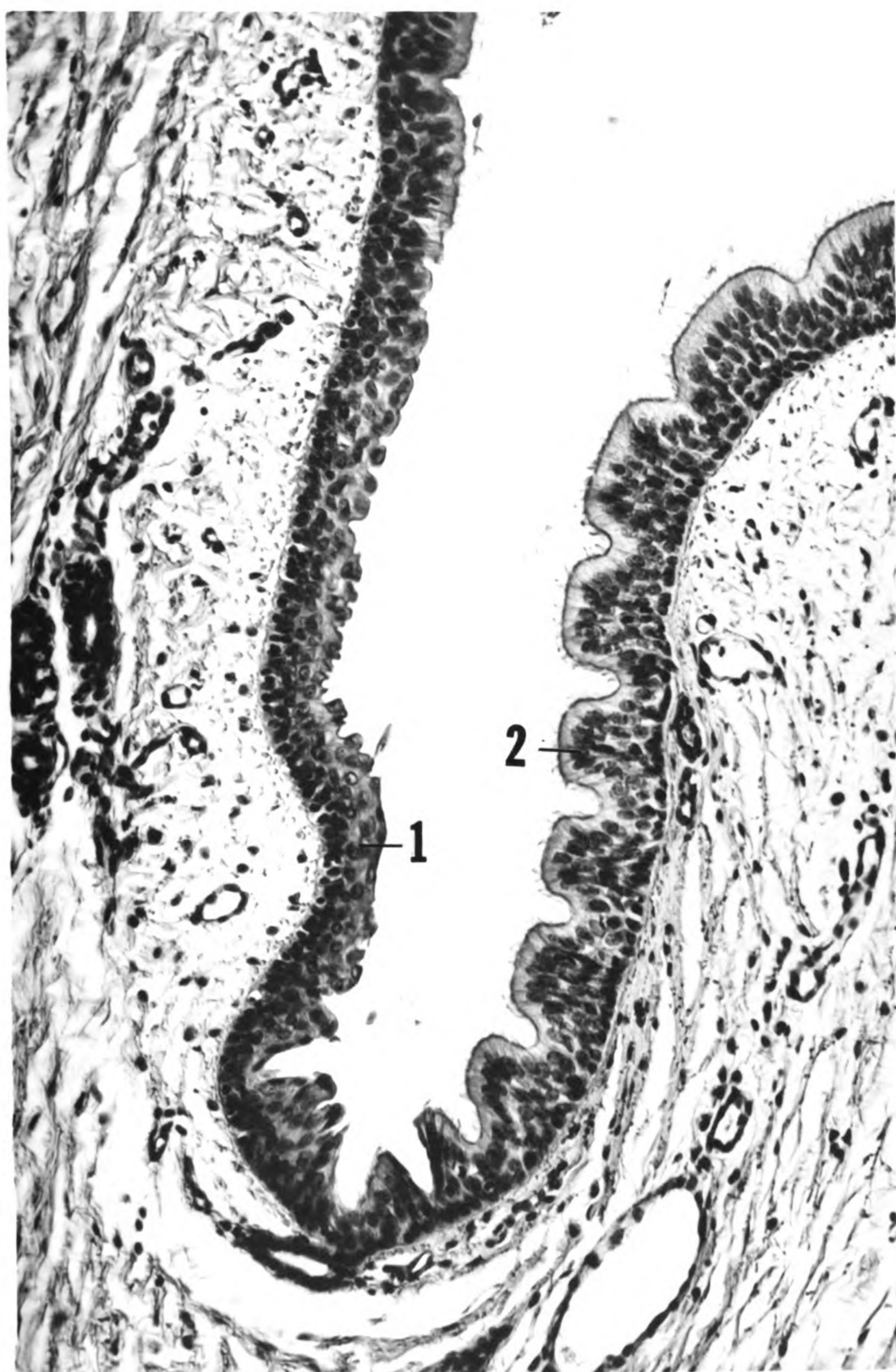


PLATE XVIII

CAT

Transverse section showing mucous, serous, and mixed acini.

H & E; x 950.

1. Mucus secreting cells.
2. Serous acinus.
3. Mucous acini with serous demilunes.

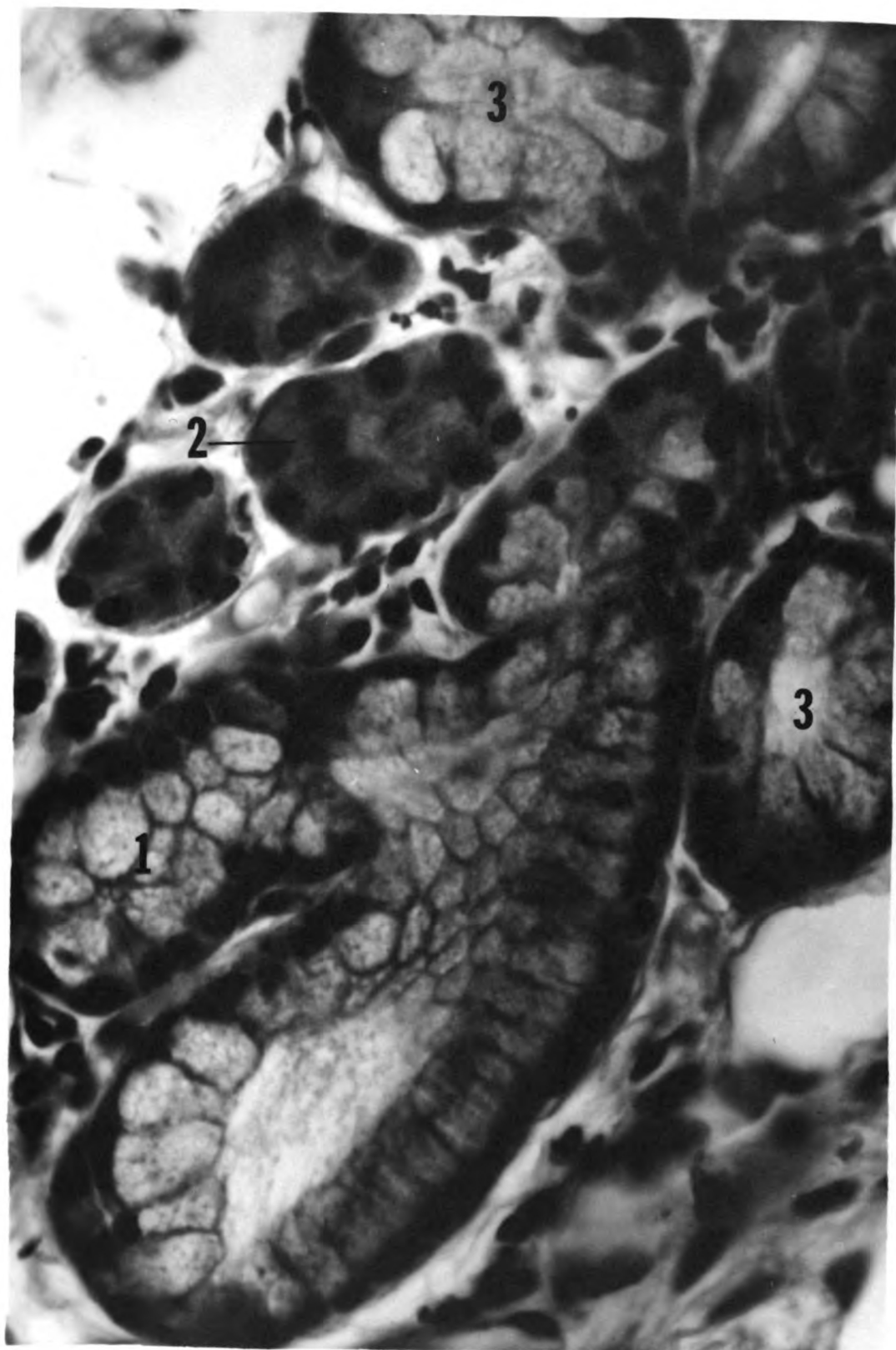


PLATE XIX

DOG

Longitudinal section through the ventral region of the trachea.
Note the difference in size and gland quantity from that of
the cat in Plate VII a. H & E; x 71.

1. Gland acini.
2. Cartilage rings.
3. Annular ligament.



PLATE XX

DOG

Typical large gland duct characteristic of both species, seen in a transverse section. Note the cilia and stratified duct epithelium. H & E; x 560.

1. Gland duct.
2. Stratified epithelium with cilia lining the duct.
3. Stratified epithelium lining the tracheal lumen.
4. Submucosa.

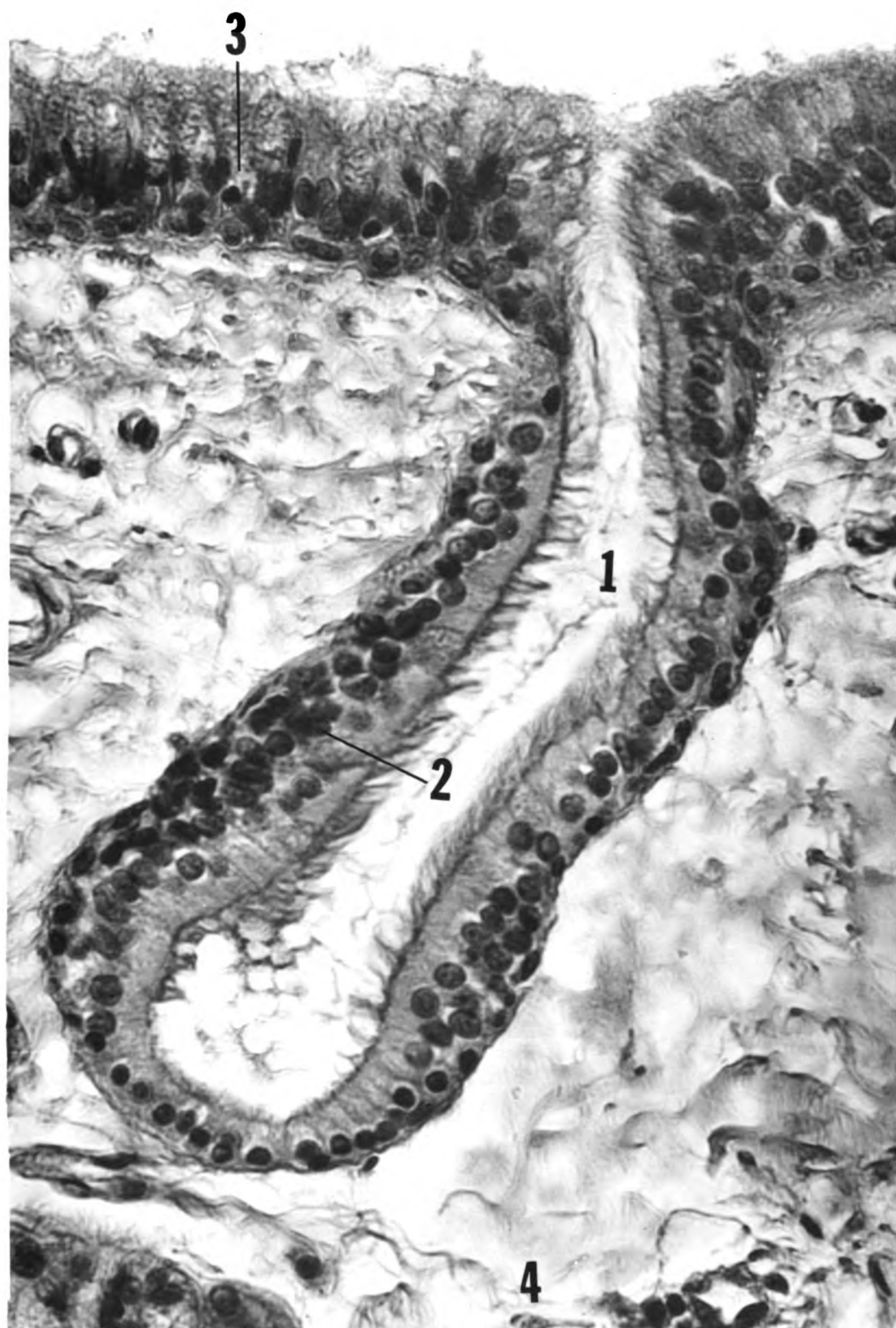


PLATE XXI

DOG

Transverse section through the dorsal submucosa showing nerve trunks. Note the irregular epithelium. H & E; x 162.

1. Tracheal lumen.
2. Folded or clumped epithelium.
3. Nerve trunks in submucosa.
4. Blood vessels.
5. Cartilage.
6. Approximate lateral limit of the lamina propria.



PLATE XXII

DOG

Longitudinal section through the membranous part of the trachea showing the relationship of tissues in this area.

Weigert and Van Gieson; x 266.

1. Epithelium.
2. Submucosa with scattered elastic fibers of the elastic layer.
3. Collagenous sheet continuous with the perichondrium and annular ligaments.
4. Trahcealis muscle.
5. Thin fibroelastic layer external to the muscle.
6. Adventitia.



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