THE COMPARATIVE MICROSCOPIC ANATOMY

OF THE TRACHEA OF THE

PIG AND HORSE

Ву

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A THESIS

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

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My Mother

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INTRODUCTION

Realizing the need of veterinary anatomists to establish general histological criteria by which a given organ or its counterpart peculiar to various species can be differentiated, histologists are actively engaging in research and comparing the results with those of earlier German investigations.

Other avenues of veterinary medicine are under consideration. For example, animals are potentially important as possible donors of tissue transplants to the human species. The production and distribution of food especially animal protein, is one of the major concerns in the world today. If such developments are to attain significance, the normal anatomy of experimental animals must be carefully examined. This can be accomplished only if students of veterinary and human medicine investigate the normal histology and cytology of domestic and laboratory animals. The normal morphology of individual species must be thoroughly mastered before physiological and pathological conditions can be differentiated.

This study is an attempt to supplement existing information by comparing the microscopic anatomy of the pig and horse trachea.

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REVIEW OF LITERATURE

Few textbooks, if any, contain a detailed microscopic study of the trachea of any domestic animal. As a result, teachers and researchers have to rely on the more complete material available on the human trachea or whatever scattered information is found on the various domestic animals. Today anatomists are trying to bridge this gap both by actively engaging in histological research and comparing the results with earlier German investigations.

Microscopic anatomy of the trachea of the following species have been reported: pig, horse, and cat (Paul, 1913); dog and cat (Niewenhuis, 1961); mink (Stowe and Calhoun, 1962); and ruminants (Miller, 1963).

Since the investigations by Niewenhuis (1961) and Miller (1963) contain a thorough review of the literature available on the trachea, the citations here are limited to publications on the trachea of the pig and horse. However, reference will be made to other animals where comparative or morphological differences are noted.

The tracheal wall of domestic animals is a composite of four main layers, namely: a) mucosa, b) submucosa, c) fibro-elastic membrane containing and connecting the cartilage rings, and d) muscularis present only dorsally. This has been substantiated by the investigations of many authors including Trautmann and Fiebiger (1957) and Niewenhuis (1961).

Miller (1963) does not consider the trachealis muscle as a separate layer. Trautmann and Fiebiger (1957) included the submucosa as a part of the mucosa. Stowe and Calhoun (1962) found the annular ligament (known as the fibroelastic membrane) in the ranch mink void of elastic fibers.

Paul (1913) listed the following components of the tracheal wall of the pig, horse, and cat: a) mucosal epithelium, b) basement membrane, c) tunica propria, submucosa, and elastic tissue (referred to as subepithelial layers), d) glands, e) muscle, and f) cartilage.

MUCOSAL EPITHELIUM

Paul (1913) classified the epithelium of the tracheal mucosa in the pig and horse as stratified, ciliated cylindrical. Prior to Paul's investigation, Verson (1868), Chauveau (1873), Frankenhauser (1879), Ellenberger and Baum (1908), and Sussdorf (1911) had used this classification to describe the tracheal epithelium of domestic animals (Paul, 1913).

The epithelium in the horse (Paul continued) is five to ten nuclear layers in depth compared to three layers in swine, and consists of the following cell layers: 1) ciliated cylindrical cells, 2) intercells, 3) basal cells, 4) goblet cells, and 5) leucocytes.

According to Paul (1913), the ciliated cells form the superficial layer of the tracheal mucosa. These cells have a clear cuticular border which is not as wide as that

found in swine. The cells vary from cylindrical to coneshaped. The cytoplasm is granular and homogenous. Its oval shaped nucleus is located near the cell base. The basal border of the ciliated cell is smooth in some areas or indented in others or even formed "foot-like" processes in some sections.

The intercells or wedge cells of Paul (1913) are spindle shaped and lie lateral and distal to the ciliated cells with their nucleus toward the cell base. Miller (1963) cited Miller (1932) who noted that these intermediate cells form a layer of cells. However, according to Paul (1913), these cells do not form a distinct layer.

Paul (1913) reported two layers of irregular, polyangular, spherical nucleated basal cells beneath the cylindrical cells. They are larger in the horse than in the swine. He noted that Verson (1868), Krause (1876), and Frankenhauser (1879) described two layers of basal cells in large animals and one layer in small animals.

Between the cylindrical cells, isolated or in groups, Paul (1913) found goblet cells in the dorsal and ventral regions of the pig and horse tracheal mucosa. Niewenhuis (1961) reported goblet cells in the dorsal part of the dog and cat tracheal epithelium. Miller (1963) found goblet cells decreasing in number from the ventral to lateral to dorsal region in the goat, sheep, and cow. Paul (1913) noted more numerous goblet cells in the horse than in the pig. Usually, goblet cells are more abundant toward the

lung and larynx.

Paul (1913) and Trautmann and Fiebiger (1957) observed lymphocytes in the tracheal epithelium of the pig and horse. Paul noted that Bauersachs (1910) described leucocytes in all layers of the sheep tracheal mucosa. Miller (1963) observed frequent lymphatic invasion of the epithelium in the trachea of the goat, sheep and cow.

Andrew (1959) recalled Mihalik's (1935) study on the origin of cilia in the respiratory epithelium of cats, dogs, and rabbits as follows: "In the basal replacing cells, the centrosomes multiply in number and group themselves about an intracellular vesicle which appears in the cytoplasm. Cilia then grow out into the lumen of this vesicle. Later, as the basal cells extend to the surface, the ciliated vesicles open out, giving rise to the free ciliated border." In Andrew's opinion, this seems to be a more efficient and rapid method of cilia replacement on the free surface than would be possible from migrating centrosomes.

Paul (1913) identified islands of flat "squamous" epithelium in the dorsal region of the ciliated cells in the swine trachea. Patches of this transitional type epithelium were reported in the dorsal region in dogs and cats (Niewenhuis, 1961); goat, sheep and cow (Miller, 1963). Paul reported that the transition from flat to cylindrical epithelium is abrupt.

The basement membrane in the pig and horse lies between the epithelium and the connective tissue of the lamina

propria (Paul, 1913). In the horse it is clear, homogenous, irregular in thickness and at times filled with leucocytes. In the pig, Paul continued, the basement membrane toward the lamina propria contains small cells with elongated nuclei lying parallel to the nuclei of the connective tissue. Toward the epithelium, the basement membrane is indistinct. In some animals the basement membrane is rudimentary (Trautmann and Fiebiger, 1957); indistinct (Niewenhuis, 1961); faint but discernible, more refractile than cellular (Miller, 1963).

TUNICA PROPRIA, SUBMUCOSA AND ELASTIC FIBERS

Paul (1913) described a clear fiber containing matrix of elastic elements and lymphoid cells between the basement membrane and the submucosa in the swine. He recalled Frankenhauser's (1879) finding that the mucosa rests on connective tissue which contains elastic fibers and mixed lymphoid cells. In larger animals, Frankenhauser continues, an inner layer of lymphoid cells, a middle layer of strong elastic fibers and an outer layer of connective tissue can be differentiated. In smaller animals the inner and middle layers are fused. Ellenberger (1911) confirmed Frankenhauser's report that in cows and rats lymphoid cells are abundant.

In swine the lamina propria contains fine fibers and lymphocytes. A fibro-elastic layer of collagenous and longitudinal elastic fibers separates it from the underlying submucosa (Trautmann and Fiebiger, 1957).

Ebner (1902), cited by Paul (1913), compared the

elastic layer which divides the mucosa from the submucosa, to the muscularis mucosa of the intestine.

In the horse Paul (1913) described three subepithelial layers beneath the basement membrane: 1) a middle layer of elastic fibers, 2) a layer of glands, and 3) a subepithelial layer which blends into the submucosa. The superficial subepithelial layer, or "stratum granulosum," contains connective tissue cells, cell elements, blood vessels, and many lymphatic cells including some lymph nodules. The middle elastic layer is thick. Its superficial fibers are thin but become stronger and are arranged in bundles in its deeper part. Between these bundles are small gland acini and many blood vessels.

Przewosky, according to Paul (1913), reported an inner circular and an outer longitudinal elastic layer where the fibers anastomose forming large bundles. Niewenhuis (1961) noted two layers of longitudinal elastic fibers in the dog, the deeper layer containing coarser fibers than the medial layer. In the cat, Niewenhuis noted, the longitudinal elastic fibers form a single layer much thicker and more compact than in the dog. Miller (1963) observed a few scattered circularly coursing elastic fibers in the ventral region of the sheep trachea.

Trautmann and Fiebiger (1957) maintained that the submucosa in the pig contains many elastic fibers, fat cells, and mixed tubular glands. Paul (1913) reported numerous blood vessels and more submucosal fat ventrally. Bauersachs

(1910), according to Paul (1913), found fat cells, gland acini and a few scattered elastic fibers in the submucosa of ruminants. Near the musculature, he continued, the submucosal fat decreased with an increase in large glands. Parts of these glands are surrounded by thin elastic fibers and large lymph nodules.

GLANDS

According to Paul (1913), Frankenhauser (1879) noted the variation in the distribution of tracheal glands in domestic animals. They are most abundant in cats; cows, swine, sheep and horses follow in order of decreasing importance. They are scanty in dogs, mice, and guinea pigs, and absent in chipmunks. The ventral and dorsal regions contain more glands, Frankenhauser continued. These are generally located in the submucosa, seldom in the propria mucosa and outer fiber layer. In some animals, glands are found in the trachealis muscle.

Horse trachea contains fewer glands than swine trachea. These convoluted, coiled or tubular type glands appear isolated or in groups (Paul, 1913). They are equally distributed but occasionally appear more ventrally and laterally. Serous glands predominate, mucous glands are scanty and there are no mixed glands. Paul observed leucocytes around the glands in the horse but not in swine.

According to Paul (1913), gland distribution in the swine is irregular. Most of the glands are in groups located

chiefly between the submucosal fat cells, some among the longutidinal elastic fibers in the deeper part of the propria mucosa, and some dorsally between the smooth muscle bundles. The few isolated glands present lie in the upper subepithelial propria mucosa. Paul (1913) observed mucous, serous and mixed sero-mucous glands in a ratio of 3:2:1 respectively. Mucous glands predominate dorsally. Generally glands decrease in number toward the lung (Paul).

Paul (1913) classified the gland ducts as coiled tubular, simple alveolar or tubulo alveolar ducts. Waller and Bjorkmann (1882), according to Paul, reported tracheal glands in dogs, cats, and guinea pigs are predominately acinar. Niewenhuis (1961) confirmed this finding in dogs and cats.

Mucous glands in cross section have a relatively large lumen. The gland cells are cuboidal or cylindrical containing flat, elongated or spherical nuclei lying toward the cell base (Paul, 1913). He explained that the shape and position of the nuclei change according to the functioning condition of the cell. The lumens of the serous glands are very small. Their cells are much darker; the nuclei are spherical and lie more centrally. Paul noted that the end pits of the glands converge to form large excretory ducts which pierce the epithelium and open in the tracheal lumen. Cells lining these excretory ducts range from simple cuboidal to cylindrical, to "flat" epithelium.

CARTILAGE AND PERICHONDRIUM

Prior to Paul's (1913) investigation, many authors classified the cartilage of the trachea as hyaline. Using picric acid and acid fuschin, Paul (1913) observed a red network of elastic fibers in the cartilage of the horse trachea. He reported that the cartilage is impure hyaline and the elastic fibers come from the perichondrium. The cartilage rings, Paul added, are widest ventrally, decreasing dorsally. They are surrounded by elastic tissue.

Paul (1913) reported that the perichondrium of the pig and horse contains an irregular richness of elastic fibers and large cells. It is thicker in the horse than that of the swine. The external perichondrium is thicker than the internal and the size of the cartilage cells increase from the periphery toward the center. The cartilage rings are connected by "ligamenta annularia" which consists of connective tissue, elastic fibers, small flat cells and occasional glands.

MUSCLE

According to Paul (1913), Lyeh observed the presence of longitudinal and circular muscle fibers connecting the dorsally incomplete cartilagenous rings of mammalian tracheas. Cuvier (Paul, 1913), studying the trachea of lions, bears and ruminants, noted that the muscle insertion in lions and bears is outside the cartilage rings; in ruminants the insertion is inside the cartilage rings.

Ellenberger (1911) noted transverse muscle inside the cartilage rings in horse, cow, sheep, and swine. Paul (1913) confirmed this finding in horse and swine. In both of these species this muscle lies dorsally between the submucosa and the internal perichondrium. Mid-dorsally, the muscle is thickest. In the swine, Paul explained, the muscle inserts into the perichondrium by means of elastic fibers of irregular width. In the horse the muscle continued with the perichondrium by means of intermuscular connective tissue containing elastic fibers.

VESSELS AND NERVES

According to Paul (1913), Frankenhauser (1879), and Kölliker and Ellenberger (1911), reported that vessels of the tracheal mucosa form a large plexus outside the mucosa from which proprial and submucosal vessels developed and surrounded the gland acini. Most vessels are found in longitudinal section and they extend transversely to the submucosa where they form a capillary network and surround the glands. Niewenhuis (1961) observed blood vessels of different sizes, nerve trunks, and ganglia in the adventitia of the dog and cat. Blood vessels increase in size from the lamina propria to the submucosa to the adventitia. Nerve trunks lie in the adventitia of the lateral and dorsal regions of the goat, cow, and sheep (Miller, 1963).

MATERIALS AND METHODS

The nine horses and fourteen Yorkshire pigs used in this investigation were obtained from Lang Feed Company, Romulus, Michigan, and the Michigan State University slaughter house respectively. These twenty-three healthy animals included both males and females with ages ranging from six months to two years for the pigs and up to 20 years for the horses.

Immediately after the animals were slaughtered the entire trachea was removed. Three consecutive cartilage rings from each of the following areas were selected: a) upper level--two segments below the larynx; b) middle level; and c) lower level--two segments above the carina cartilage. These sections were then fixed in a solution composed of commercial formalin, 10 parts; ninety-five per cent ethyl alcohol, 50 parts; two per cent glacial acetic acid, 2 parts; and distilled water, 40 parts (Lavdowsky's Mixture, Guyer, 1949). After ninety-six hours, the tissues were removed from the fixative and stored in seventy per cent ethyl alcohol for four days.

From each of the three levels, cross and longitudinal sections were obtained from the ventral, lateral, and dorsal regions. The dioxane method was used for dehydrating the tissues, and the paraffin method for infiltrating and embedding (Guyer, 1949).

Sections cut seven to nine microns thick were stained either with: a) hematoxylin and eosin for general histology; b) toluidine blue for serous and mucous glands, for the shape of the goblet cell, and for identification of mast cells; and c) Weigert-Van Gieson connective tissue stain for differentiation of elastic tissue and collagenous fibers (Gridley, 1960).

Using a calibrated micrometer the following measurements were recorded in microns:

> Epithelium - height Cilia - length Elastic layer - thickness Elastic fiber - diameter Submucosa - thickness Cartilage - thickness Muscle - thickness

An average of three measurements was taken from the dorsal, lateral, and ventral regions at the upper, middle, and lower levels.

RESULTS AND DISCUSSION

Microscopically the tracheal walls of the pig and horse show three main layers. From the lumen toward the periphery these are: a) a mucosa consisting of an epithelium, a basement membrane, and a lamina propria; b) a submucosa consisting primarily of glands and blood vessels; and c) a fibroelastic cartilagenous layer (Plate 1).

MUCOSA

Epithelium

The tracheal mucosa of the pig and horse are lined by a pseudostratified, ciliated, columnar epithelium containing goblet cells. Intermediate, non-ciliated cells and basal cells complete the epithelial cell types (Plate 2).

The round to elongated basal cells located directly above the basement membrane extend not more than one-fourth the total epithelial length. Their conspicuous oval shaped nuclei lie horizontal to the basement membrane and occupy most of the cell space. They are arranged in two layers in the horse, as Paul (1913) had reported, but only one layer is present in swine (Plate 2).

The narrow spindle-like intermediate cells are the least obvious of the four cell types. They are found on a lower level between the lateral boundaries of the ciliated cells. This finding supports that of Paul (1913). Though

these cells span most of the epithelial thickness, they do not appear to reach the basement membrane. Toward the cell surface they taper and contain no cilia.

Dispersed between the ciliated columnar cells, goblet cells attached to the basement membrane, open onto the free surface of the tracheal lumen. As Paul (1913) observed, these cells may appear single or in groups. The shape of the cells and their nuclei fluctuates with their activity. They appear long and narrow with an oval nucleus in the latent stage, and flask-like with a flat basal nucleus in the filled state. In the horse and pig, goblet cells decrease from the ventral to the lateral to the dorsal surface, similar to their distribution in ruminants reported by Miller (1963). In agreement with Paul (1913), they are more abundant in the horse than in the pig and are least numerous at the middle level in both species.

The very numerous ciliated cells also extend the entire thickness of the epithelium. Each ciliated epithelial cell possesses a distinct cuticular border from which cilia protrude into the tracheal lumen. The nuclei of these cells are oval and lie midway or a little above in the cytoplasm.

Cilia in the pig and horse increase in length from dorsal to ventral regions. They are longer in the horse than in the pig. In the horse the length of the cilia is greatest laterally and ventrally, whereas in the pig there

is a gradual increase from dorsal to lateral to ventral regions. In both species cilia length increases from upper to lower level (Table 3).

Similar to the findings of Paul (1913), patches of a transitional type of epithelium are present in the mucosal epithelium of the pig. However, this flat epithelium is also present in the horse (Plate 3). This latter finding disagrees with the report by Paul (1913) who noted that the transitional type epithelium is not present in the horse. These patches appear more frequently in the pig but span longer distances in the horse. In both the pig and horse this transitional epithelium is found in the dorsal and lateral regions, though more frequently in the former area. Cilia and goblet cells are absent wherever this transitional epithelium is found.

The epithelial height (Table 3) is greatest ventrally and least dorsally in both species. Overall height is greater in the horse than in the pig. The horse mucosa is uniformly wavy and the waves increase in height and width from the lateral to the dorsal region. In the pig the mucosal folds occur more often dorsally. Usually, the dorsal mucosal folds in the pig are larger and more uniform than those found ventrally and laterally. Short crypts appear only dorsally in the pig and occasionally in the horse. In sections where the cartilage was detached from the mucosa, no mucosal folds were present. This observation supports the report by Miller (1913) in which he attributed

tracheal mucosal folds to diminution in diameter of the tracheal lumen caused by contraction of the trachealis muscle and the inherent elasticity of the cartilage rings rather than resulting from the underlying elastic fibers.

As Paul (1913) observed, lymphoid cells are present in the tracheal epithelium of the pig and horse. They are more numerous among the basal cells but a few penetrate the epithelium to reach the lumen. The majority of these lymphoid cells are diffuse; others are found invading the epithelium from nodules present in the lamina propria.

Basement Membrane

The deepest layer of cells of the epithelial sheath rests on an acellular, clear, homogenous basement membrane (Plate 4). It is thinner and less obvious in the pig. In both species the basement membrane appears as a basal cuticular border formed by a condensation of the cellular cytoplasm in that area. This membrane does not appear continuous for any great distance, and in certain areas, it is obliterated by tiny fibers of the lamina propria.

Lamina Propria

The subepithelial layer (Paul, 1913), the lamina propria, is the deepest part of the mucosa. It lies beneath the basement membrane and above the submucosa. In the pig and horse, as Paul observed, this zone consists of elastic and collagenous fibers, connective tissue cells, gland acini and their ducts, diffuse lymphoid tissue and a few lymph

nodules, and capillaries.

The collagenous fibers are dispersed throughout the lamina propria. In the pig and horse, the diameter and compactness of these irregularly coursing fibers increase in the lower limits of the lamina propria; however, they are more abundant in the horse than in the pig.

The elastic fibers are the most conspicuous feature of the lamina propria. In the pig and horse, the elastic fibers course longitudinally forming adjoining bundles giving the appearance of an elastic membrane. This bundlelike arrangement was also observed by Paul (1913). The diameter of the elastic fibers and the thickness of the elastic membrane are greater in the horse than in the pig (Table 3). Here, too, the elastic membrane is thickest ventrally and thinnest laterally. In the pig the greatest diameter of the elastic membrane is on the lateral surface and least on the dorsal surface (Table 3). Compared to the horse, elastic fibers are more compact in the pig.

In a cross-sectional view of the pig trachea, circular elastic fibers are found in the superficial layer of the lamina propria (Plate 5). These fibers are not present in this area of the horse trachea. However, a few crosssections of the trachea of the pig and horse show circular elastic fibers underlying the longitudinal elastic fibers of the deep lamina propria (Plate 6). These circular fibers extend for a short distance but do not form a complete layer. They are more abundant in the horse than in the pig. In

the pig some of these circular elastic fibers extend obliquely blending with the fibroelastic layer of the cartilage rings.

SUBMUCOSA

The submucosa located between the elastic layer and the internal perichondrium consists predominately of glands, collagenous and elastic fibers, fat tissue and blood vessels. These components are also reported by Paul (1913). The fibers of this layer course in random directions. In the lower limits of the submucosa they blend with the fibroelastic membrane of the cartilage rings. The submucosa of the horse trachea is thicker than that of the pig with the greatest thickness on the lateral and dorsal surfaces. In the pig, the submucosa is deepest on the ventral surface and shallowest on the lateral surface (Table 3). Scattered lymph nodules are present in the submucosa of the pig and horse.

GLANDS

Glands in the trachea of the pig and horse (also reported by Paul (1913)) contain mucous and serous cells and are branched tubuloacinar type (Plate 7). As Paul also observed, the glands are found isolated or grouped in clusters chiefly in the submucosa. Some are located in the lamina propria, embedded in the muscle fibers of the dorsal region or extending as far as the area between the cartilage ends similar to the findings of Paul (1913). Either

isolated glands or clusters of glands may be all serous, all mucous, or a combination of sero-mucous glands. Glands are numerous in the pig and, as Paul (1913) noted, they generally decrease in numbers toward the tracheal bifurcation.

In agreement with Paul (1913), the glands of the horse are predominately serous (Plate 7); mucous glands are few and mixed sero-mucous glands are rarely present. Paul reported that there are no sero-mucous glands in the horse, but these are present occasionally (Plate 8). Although the glands in the horse trachea are smaller, isolated gland acini are more abundant than in the pig. These single gland acini are located in all levels of the lamina propria. They are more frequently seen dorsally. As Paul (1913) noted, larger gland clusters are found embedded between the longitudinal elastic fibers of the deep lamina propria, and in the submucosa. The glands appear uniformly distributed from ventral to dorsal regions but may be more numerous ventrally and laterally. Often no submucosal glands are found in the dorsal region of the horse (Plate 17). As Paul (1913) observed, diffuse and aggregated lymphoid tissue are found among and around the gland acini.

In agreement with the report of Paul (1913), gland acini in the pig may be all serous, all mucous, or of mixed sero-mucous type. Mucous type glands are more abundant dorsally. Isolated gland acini are few and are found with larger groups of glands in the deeper layer of the lamina

propria among the longitudinal elastic fibers. This finding agrees with that of Paul (1913). The submucosal glands are in larger clusters lodged between fat cells. In the pig glands are abundant ventrally and decrease in numbers laterally where the gland acini usually lie in the lower limits of the lamina propria (Plate 10a & 10b). Dorsally, the glands increase in numbers (Plate 10c), and as Paul (1913) observed, they extend between and outside the muscle fibers (Plate 11) as far dorsal as between the open ends of the cartilage rings.

In longitudinal section the submucosal glands in the pig may form a horizontal chain directly below the elastic fibers of the lamina propria (Plate 12), or may occupy the superficial part of the triangular-like spaces between adjacent cartilages, with the apex directed between the segments of the cartilage rings. Lymphoid cells are closely associated with glands in the pig (Plate 10). This finding does not agree with the report of Paul (1913) who reported that no lymphocytes are found in association with glands in the pig.

Gland ducts of both the pig and horse may be lined with either stratified squamous cells or pseudostratified, ciliated, columnar cells. The cells lining the deepest portion of the ducts are lower in height, and as the ducts traverse the epithelial length to reach the surface, the height of the epithelium increases. In the upper third of the duct the epithelium becomes pseudostratified, ciliated,

columnar or stratified squamous depending on the lining of the lumen in that particular area. As Paul (1913) observed, when glands are located between or beyond the muscle fibers, their ducts pierce the muscle layer, submucosa, and epithelium to reach the tracheal lumen.

CARTILAGE

The cartilage rings in the horse are larger in all aspects than those of the pig. The thoracic cartilages differ from those in the cervical region in that they do not overlap. All of the rings in the pig overlap with an increase of overlap toward the bifurcation. In the pig and horse the cartilage rings become thinner and narrower dorsally with the greatest thickness on the ventral surface. As Paul (1913) also observed, in the horse the cartilage width increases toward the lung (Table 3).

The cartilage in the pig and horse is hyaline in nature. The tracheal rings of the nine horses used in this study revealed no content of an elastic character, as reported by Paul (1913). The cartilage cells are oval and, as Paul (1913) noted, these cells increase in size from the periphery toward the center of the ring. These cells are larger in the horse than in the pig.

Longitudinal sections from the dorsal, lateral, and ventral regions were stained with methyl green and photographed grossly to show the cross-sectional appearance of the cartilage rings of the pig and horse tracheas (Plate

13). The overlying arrangement allows for maximum tracheal movements.

No calcification was observed in the pig trachea; however, some evidence of calcification was observed in the central area of the cartilage ring in the horse. A few of the chondrocytes were degenerating (Plate 14), and a few blood vessels were present in the deeper layer of the perichondrium. These factors may indicate that a degree of calcification does occur in the trachea of horses. Unfortunately, the exact ages of most of the horses used in this investigation were unknown.

PERICHONDRIUM

The perichondrium (Plate 15) is a layer of dense white fibrous connective tissue containing fibroblast-like cells. This membrane spans the entire circumference of the cartilage rings. Similar to the observation of Paul (1913), the perichondrium is thicker externally than internally. The cell nuclei lie parallel to the circularly oriented collagenous fibers. The "irregular richness of elastic fibers," Paul (1913) observed in the perichondrium of the horse trachea was not present in any of the specimens studied. Therefore, his suggestion that the elastic fibers in the cartilage substance of the horse migrated from the perichondrium is unlikely.

ANNULAR LIGAMENT

The annular ligament is a double sheath of collagenous

and elastic fibers that connects the cartilage rings one to another, and completely encloses them. This tube-like membrane is best seen in longitudinal section or in cross section where two or three cartilage rings lie parallel. The circularly disposed dense collagenous fibers are the chief components of the annular ligament. Elastic fibers are relatively few and show a random deposition. In a crosssectional view circularly and longitudinally directed elastic fibers are more concentrated between and covering the flat free ends of the cartilage rings (Plate 16). Here the circular elastic fibers extend for a short distance along the cartilage surface. This latter finding could have been the basis for Paul's (1913) report of the "elastic" character of the cartilage of the horse trachea. Elastic fibers are more abundant in the annular ligament of the horse than in the pig. The following relationships between the width of the cartilage rings and the thickness of the annular ligament were observed: ventrally, the cartilage rings and annular ligament are thickest in both the pig and horse. This thickness decreases from ventral to lateral to dorsal surfaces.

TRACHEALIS MUSCLE

Circular smooth muscle bundles span the incomplete cartilage rings of the dorsal tracheal wall. In agreement with the finding of Paul (1913), this muscle in the pig and horse lies inside the cartilage rings external to the

submucosal glands. As Paul observed, in the horse the muscle inserts into the lateral internal perichondrium. In the pig the insertion is more dorsad. Paul also noted that in the pig the muscle narrows laterally becoming spindlelike and attaches by means of a fibro-elastic tendon. The muscle attachment in the horse may be indirect or direct. In the former the muscle fibers do not taper laterally but course obliquely and dip into the peripheral substance of the cartilage ring (Plate 17). In the latter, the muscle fibers taper slightly and, as Paul (1913) observed, insert into the lateral internal perichondrium by means of a fibroelastic tendon (Plate 18). In both species the muscle is widest mid-dorsally. It is greater in the horse and decreases toward the lung. In agreement with the report of Paul (1913), in the pig the muscle decreases from the larynx toward the bifurcation. No longitudinal muscle fibers were observed in either species. Bundles of circular smooth muscle fibers were seen frequently in the ventral, lower level in the pig trachea but not in the horse.

BLOOD AND LYMPHATIC VESSELS

In the pig and horse blood vessels are located in the lamina propria, submucosa, between the open ends of the cartilage rings, and in the adventitia. Blood vessels in the lamina propria are of the smallest caliber. Here tiny networks are found directly beneath the basement membrane. In the elastic layer, the blood vessels have larger lumens

though their walls remain relatively thin. The submucosal blood vessels have thicker walls. The grouping of blood vessels in the submucosa as well as the networks found under the epithelium in the lamina propria suggest the plexus formation observed by Frankenhauser (1879) and Kölliker and Ellenberger (1911), as reported by Paul (1913). These vessels are closely associated with gland acini. Blood vessels of the largest caliber are found in the adventitia. A few thin walled blood vessels lie in the perichondrium in the horse. In agreement with the observations of Paul, the vessels in the horse are generally larger and more numerous than in the pig. Tiny collapsed lymphatic vessels are found in the submucosa and adventitia in both the pig and horse (Plate 20).

NERVES

Larger nerve trunks are more frequently found dorsally in the space external to the muscle fibers and internal to the cartilage rings, and the dorsal adventitia. A few smaller nerve trunks are found laterally. Ganglia are few and lie only in the dorsal adventitia. No nerve trunks or ganglia were observed ventrally.

ADVENTITIA

This layer is found outside the dense fibro-elastic membrane that invests and connects the tracheal rings, and is continuous with it. It is a layer of loose collagenous and areolar connective tissue containing fat cells. This

layer transports and lodges blood vessels, nerves, and ganglia which supply the trachea.

COMPARATIVE HISTOLOGY

It is important that the veterinary histologist recognize normal organ histology, noting individual species specifications before physiological and pathological conditions are differentiated. A summary of this study, as well as those of Niewenhuis (1961), and Miller (1963), are in a chart (page 29). It is a concise report of those histological characteristics regarded as the distinguishing features of the trachea of the dog, cat, cow, goat, sheep, horse and pig.

Sheep, Horse, Pig Cat, Cow, Goat, the Dog, the Tracheas of Comparison of ፈ

Mucosa

Pseudostrat- ified ciliated columnar epi- thelium with goblet cells	Patches of transitional- like or stratified squamous epithelium	Crypts	Basement membrane	Elastic membrane (fasiculated, longitudinal fibers)	Trachealis muscle (smooth and circular)
o Present	Transitional-like	Present	Indistinct	Thin, compact, non-fasiculated	External attachment
bresent	Less amount of transitional epithelium than dog	Present	Indistinct	As above but fibers loosely arranged	External attachment
o Present	Moderate patches of stratified squamous epithelium	Absent	Distinct	Thick, diffuse near epithelium, dense near sub-	Internal attachment
p Present t	Occasionally stratified squamous epithelium	Usually absent	Distinct	mucosa Relatively thick, compact	Internal attachment
e Present	Occasionally stratified squamous epithelium	Usually absent	Distinct	A s above but diffuse	Internal attachment
Present t	Moderate patches of transitional-like epithelium	Usually	Distinct	Thick, circular fibers near sub- mucosa	Internal attachment
g Present	Less amount of transi- tional-like epithelium than horse	Only dorsally	Distinct	Thicker than pig; circular fibers near epithelium	Internal attachment

and elastic fibers, lymph nodules, glands, blood and lymphatic vessels; mixed tubuloacinar glands in the lamina propria and submucosa; dorsally incomplete, hyaline cartilage rings with a thin internal and a thick external perichondrium; an annular ligament of collagenous fibers and scattered elastic fibers; an adven-titia of blood and lymphatic vessels, nerve trunks and ganglia. (Dog and Cat, Niewenhuis, 1961; Cow, Goat and Sheep, Miller, 1963). a submucosa of collagenous Similarities for all species exist in the following: NOTE:

Measuremen	ts (in micro	ns) of the	Microscol	oic Structur	es of th	e Trachea of	the Pig
		Upper leve	1	Middle lev	el	Lower level	
Structure	Region	Range	Mean	Range	Mean	Range	Mean
Epithelium (height)	<pre>D (dorsal) L (lateral) V (ventral)</pre>	24-60 21-65 24-65	44 42 46	18-55 23-59 18-68	38 41 6	23-55 25-52 18-60	36 36 36
Cilia (length)	0 1 >	2 °5 - 5 °0 2 °5 - 5 °0 2 °5 - 5 °8	4.9Ω •4.9Ω	2 • 5 - 5 • 6 2 • 5 - 5 • 6 2 • 5 - 6 • 0	44 5.7 2.0 6.0 6.0	2.5-5.8 2.5-5.8 3.0-6.0	4 n n 0 0 0
Elastic membrane (thickness)	012	80-278 60-294 75-300	175 180 187	47- 278 70-353 50-278	148 202 192	57-171 65-171 50-128	117 125 101
Elastic fibers (diameter)	고나>	1 •5-6•2 1 •5-6•2 1 •5-6•2	4.0 4.0 0.9	1、5-6、2 1、5-6、2 1、5-6、2	4 4 4 5 4 2 4 5 4 4 4 4 4 4 4 4 4 4 4 4	1.5-6.2 1.5-6.2 1.5-6.2	ი ფ ფ ო ო ო
Submucosa (depth)	0 1 7	86-792 125-524 160-819	2667 304 464	100-578 75-182 150-321	285 147 234	150-578 96-251 43-417	279 165 235
Cartilage (thickness)	0 1 >	103-712 250-1081 588-2284	519 788 1253	100-749 250-1006 400-856	378 572 609	150-685 300-855 460-1070	4 21 582 726
Muscle (thickness)	Q	87-500	277	53-530	226	50-364	164

Table l

Measurement	s (in micron	s) of Micro	oscopic St	uructures of	the Trach	ea of the l	lor se
		Upper leve	21	Middle lev	el	Lower leve	21
Structure	Region	Range	Mean	Range	Mean	Range	Mean
Epithelium (height)	<pre>D (dorsal) L (lateral) V (ventral)</pre>	30-62 49-68 72-85	46 59 79	23-60 35-58 42-55	35 43 47	30-64 58-63 41-50	51 61 47
Cilia (length)	0 - 1 >	2.3-5.0 7.1-7.5 6.2-7.0	3.7 7.3 6.6	4.3-5.0 5.0-6.2 5.8-7.5	4.7 5.7 6.3	3.8-6.2 7.0-7.5 5.0-7.5	5.3 7.2 6.7
Elastic membrane (thickness)	0 - 1 >	355-717 305-546 325-610	536 426 468	265-460 263-642 350-439	327 375 376	173-342 206-535 300-453	271 311 376
Elastic fibers (diameter)	0 1 >	4。1-5。0 4。1-5。0 4.1-5.0	444 0.0	3.5-7.5 3.5-7.5 3.5-7.5	ល ល ល 	4.2-7.5 4.2-7.5 4.2-7.5	5.7 5.6 6
Submucosa (depth)	01>	332-1655 1120-2610 733-1894	994 1865 1314	321-1715 1374-2500 1070-1626	1035 1873 1355	268-2140 1542-2810 246-1310	1368 1995 587
Cartilage (thickness)	0 1 >	760-770 600-980 1705-1926	765 790 1816	407-930 1016-2617 1947-2761	645 1769 2294	519-1070 1370-2533 1816-2854	806 1823 2495
Muscle (thickness)	Q	395-1378	1157	762–1119	1003	851-1177	1044

Table 2

Table 3

Comparison of the Mean Values (in microns) of the Structural Dimensions of the Tracheas of the Pig and Horse at Dorsal, Lateral, and Ventral Regions and at the Upper, Middle and Lower Levels

Structure	Region*	Pig	Horse	Level**	Pig	Horse
Epithelium	D	40	44	a	44	61
(height)	L	40	54	b	42	42
	v	<u>43</u> 41***	<u>57</u> 52***	c	36	53
Cilia	D	4.5	4.6	a	3.9	5.9
(length)	L,	4.6	6.7	b	4.6	5.6
	v	$\frac{4.6}{4.6}$	$\frac{6.4}{6.0*}$	C **	5.3	6.4
Elastic	D	147	378	a	181	477
membrane	L	169	371	b	181	359
(thickness)	v	<u>160</u> 159 ***	<u>407</u> 385***	С	114	319
Elastic	D	4.1	5.3	a	3.9	4.5
fibers	L	4.0	5.2	b	4.2	5.4
(diameter)	V	$\frac{4.0}{4.0}$ **	* <u>5.2</u> 5.2*	с **	3.8	, 5.6
Submucosa	D	277	1132	a	345	1391
(depth)	L	205	1911	b	222	1421
	V	<u>311</u> 264***	<u>1085</u> 1376***	С	226	1317
Cartilage	D	439	739	a	853	1124
(thickness)	L	647	1461	b	520	1569
	V	<u>863</u> 650***	2202 1467***	С	576	1708
Muscle	D	223***	1068***	a	277	1157
(thickness)				b	226	1003
				С	164	1044
* D - dorsal L - lateral V - ventral		• a - up b - mi c - lo	oper .ddle ower	*** tota	l mean	

SUMMARY AND CONCLUSIONS

Routine histological techniques were employed to study the comparative histology of the tracheas of fourteen pigs and nine horses, including both sexes. A range and mean (in microns) were obtained for each of the structures measured.

Microscopically, the tracheal wall of the pig and horse show three main layers, namely: 1) a mucosa consisting of an epithelium, a basement membrane, and a lamina propria; 2) a submucosa consisting primarily of glands, and blood vessels; and 3) a fibro-elastic cartilagenous layer containing and connecting the tracheal rings.

The tracheal mucosae of the pig and horse are lined by a pseudostratified, ciliated, columnar epithelium containing goblet cells. Intermediate, nonciliated cells and basal cells are also present. The spherical basal cells are located directly above the basement membrane. They form two layers in the horse but only one layer is present in the pig. The intermediate cells are spindle shaped located between the lateral boundaries of the ciliated cells. They do not appear to reach the basement membrane or the tracheal lumen. The goblet cells extend the entire length of the epithelium. In the pig and horse goblet cells decrease from the ventral to the lateral to the dorsal surfaces. They are more abundant in the pig than in

the horse. The bases of the ciliated cells attach to the basement membrane and their apices protrude into the tracheal lumen. Cilia length in the pig and horse increases from dorsal to ventral regions. They are longer in the horse than in the pig.

At intervals, patches of a transitional type of epithelium are present in the lateral and dorsal regions in the epithelium of the pig and horse. These patches appear more frequently and span longer distances in the horse. Whenever present they lack cilia and goblet cells.

Epithelial height is greatest laterally and least dorsally in both species. Overall height is greater in the horse than in the pig. The horse mucosa is uniformly wavy. In the pig mucosal folds occur more often dorsally. Usually, the dorsal mucosal folds in the pig are larger and more uniform than those found ventrally and laterally. Short crypts are present dorsally in the pig.

Lymphoid cells are numerous among the basal cells of the tracheal epithelium in the pig and horse. A majority of these are diffuse; others invade the epithelium from nodules present in the lamina propria.

In the pig and horse, the longitudinally directed elastic fibers of the deep lamina propria form adjoining bundles giving the appearance of an elastic membrane. Circular elastic fibers are found in the superficial layer in the lamina propria of the pig. Lymphoid tissue including nodules are present in the lamina propria and submucosa.

Some of these lymphoid cells are closely associated with gland acini of both the pig and horse.

The submucosa consists predominately of glands, loose collagenous fibers, and fat cells coursing in random directions. The submucosal depth is greater in the horse than that of the pig with the greatest thickness on the lateral and dorsal surfaces. In the pig it is deepest on the ventral surface and shallowest on the lateral surface.

The branched, tubuloacinar type glands in the lamina propria and submucosa in the trachea of the pig and horse contain mucous and serous cells. In the pig gland acini may be all serous, all mucous, or a combination of seromucous glands. In the horse gland acini are predominately serous, mucous glands are scarce, mixed glands are practically absent. Glands are more numerous in the pig than in the horse. They are more abundant ventrally, and decrease in numbers laterally. Dorsally the glands increase in numbers extending between and outside the muscle fibers as far dorsad as between the open ends of the cartilage rings.

The epithelial cells of the gland acini in both the pig and horse vary from low columnar to cuboidal. Gland ducts may be lined with either stratified squamous cells or pseudostratified ciliated, columnar cells. When glands are located between or beyond the muscle fibers, their ducts pierce the muscle layer, submucosa, and mucosa to reach the tracheal lumen.

The dorsally incomplete cartilage rings in the pig and horse are hyaline in character. In the horse the thoracic cartilages differ from the cervical cartilages in that they do not overlap. All of the tracheal rings in the pig overlap. In both species the cartilage rings become thinner and narrower dorsally with the greatest thickness on the ventral surface. A slight degree of calcification was observed in the tracheal cartilage of the horse. The internal and external perichondrium consist of dense collagenous fibers.

In the pig and horse the annular ligament, composed of dense collagenous and elastic fibers, connects and completely encloses the cartilage rings.

Circular smooth muscle bundles, the trachealis muscle, spans the dorsal tracheal wall and is located inside the cartilage rings of the pig and horse. In the pig the muscle tapers laterally and inserts by means of a fibroelastic tendon into the internal perichondrium of the cartilage rings. In the horse the muscle fibers may dip directly into the lateral internal perichondrium or may taper laterally and insert by means of a fibroelastic tendon. In both species the muscle is widest mid-dorsally.

Blood vessels of the smallest caliber form networks in the lamina propria directly beneath the basement membrane. The submucosal network of blood vessels have thicker walls. The largest caliber blood vessels are found in the adventitia. Blood vessels in the horse are larger and more

numerous than in the pig. Smaller nerve trunks are found in the lateral adventitia. Larger nerve trunks appear more frequently dorsally in the space external to the trachealis muscle and internal to the cartilage rings, and in the dorsal adventitia. Ganglia are few and are found only in the dorsal adventitia.

Continuous with and external to the dense fibroelastic membrane of the pig and horse is the adventitia. It is a layer of loose collagenous and areolar connective tissue containing fat cells. It lodges blood vessels, nerves and ganglia which supply the trachea.

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^{*}For further references on the microscopic anatomy of the trachea see the literature cited in Niewenhuis (1961) and Miller (1963).



Plate 1. Comparative histology of a) horse and b) pig trachea; cross section, ventral region, middle level. Note relative thickness of each layer. 1. epithelium; 2. elastic membrane; 3. submucosal fat; 4. collagenous fibers; 5. cartilage; 6. annular ligament; 7. adventitia. Hematoxylin and eosin stain; x54.



Plate 2. Epithelial cell types; pig trachea; cross section, ventral region, lower level. 1. ciliated cell; 2. intercell; 3. goblet cell; 4. basal cell; 5. lymphocyte; 6. monocyte. Note single layer of basal cells. Hematoxylin and eosin stain; x1095.



Plate 3. Transitional-type epithelium; horse trachea; cross section, dorso-lateral region, middle level. 1. pseudostratified, ciliated, columnar epithelium; 2. transitional-type epithelium; 3. mast cells; 4. trachealis muscle; 5. collagenous fibers. Hematoxylin and eosin stain; x272.



Plate 4. Basement membrane; horse trachea; cross section, lateral region, middle level. 1. cilia; 2. goblet cell; 3. intercell; 4. ciliated cell; 5. basal cell; 6. basement membrane; 7. lamina propria. Note double layer of basal cells. Hematoxylin and eosin stain; x1043.



Plate 5. Circular elastic fibers in superficial lamina propria; pig trachea; cross section, lateral region, upper level. 1. epithelium; 2. circular elastic fibers; 3. longitudinal elastic fibers; 4. elastic membrane; 5. glands. Note variation in diameter of elastic fibers. Weigert-Van Gieson stain; x308.



Plate 6. Circular elastic fibers underlying elastic membrane; horse trachea; cross section, lateral region, upper level. 1. epithelium; 2. elastic fasiculus; 3. gland acini; 4. circular elastic fibers; 5. collagenous fibers. Weigert-Van Gieson stain; x180.



Plate 7. Branched, tubular glands; horse trachea; cross section, ventral region, upper level. 1. networks of blood vessels in lamina propria; 2. branched, tubular glands; 3. gland duct; 4. submucosa blood vessels. Note serous nature of glands. Toluidine blue stain; x156.



Plate 8. Mixed sero-mucous gland acini; horse trachea; cross section, dorsal region, middle level. 1. elastic layer; 2. mucous cells; 3. serous cells. Note variation in size of blood vessels and elastic fibers. Hematoxylin and eosin stain; x226.



Plate 9. Duct of mixed sero-mucous gland; pig trachea; cross section, dorsal region, middle level. 1. epithelium; 2. mast cells; 3. patent duct; 4. duct of mixed sero-mucous glands; 5. muco-serous acinus; 6. blood vessel; 7. trachealis muscle. Toluidine blue stain; x173. Plate 10. Gland distribution; pig trachea; cross section, a) ventral; b) lateral; c) dorsal regions; middle level. Hematoxylin and eosin stain; x95.

- 1. epithelium
- 2. superficial lamina propria
- 3. elastic membrane
- 4. glands 5. lymph nodule

Note association of lymphatic tissue with glands.





Plate 11. Gland acini outside muscle fibers; pig trachea; cross section, dorsal region, upper level. 1. elastic layer; 2. glands; 3. trachealis muscle; 4. glands outside muscle fibers. Hematoxylin and eosin stain; x71.



Plate 12. Glands in relation to intercartilagenous area; pig trachea; longitudinal section, ventral region, upper level. 1. epithelium; 2. elastic membrane; 3. layer of gland; 4. adipose tissue; 5. cartilage. Hematoxylin and eosin stain; x77. Plate 13. Appearance of cartilage rings; a) horse and b) pig trachea; longitudinal section; c) dorsal, d) lateral, e) ventral regions; middle level. Note arrangement of car-tilage rings. Methyl green stain; x7.

1. cartilage rings 2. annular ligament

For orientation sections near arrows and letters c, d, e are ventral; opposite sections are dorsal.





Plate 14. Cartilage degeneration; horse trachea; cross section, ventral region, lower level. 1. degenerated chondrocytes; 2. calcified cartilage. Weigert-Van Gieson stain; x222.



Plate 15. Relative thickness of perichondrium; pig trachea; cross section, ventral region, lower level. 1. elastic layer; 2. glands; 3. submucosa; 4. internal perichondrium; 5. cartilage; 6. external perichondrium. Hematoxylin and eosin stain; x231.



Plate 16. Elastic character of annular ligament; horse trachea; cross section, dorsal region, middle level. 1. annular ligament; 2. elastic fibers; 3. perichondrium; 4. cartilage. Weigert-Van Gieson stain; x417.



Plate 17. Indirect muscle attachment; horse trachea; cross section, dorsal region, lower level. 1. trachealis muscle; 2. fibroelastic tendon; 3. perichondrium; 4. cartilage. Weigert-Van Gieson stain; x185.



Plate 18. Direct muscle attachment; horse trachea; cross section, lateral region, upper level. 1. epithelium; 2. lamina propria; 3. trachealis muscle (Note how it dips into cartilage substance); 4. cartilage. Hematoxylin and eosin stain; x256. Plate 19. Comparison of muscle-gland distribution; horse and pig tracheas; cross section, dorsal region, lower level. Note scarcity of glands in horse trachea. Hematoxylin and eosin stain; x84.

- épithelium
 elastic layer

- 3. glands
 4. trachealis muscle
 5. collagenous fibers
- 6. cartilage





Plate 20. Blood and lymphatic vessels; pig trachea; cross section, lateral region, middle level. 1. epithelium; 2. lamina propria; 3. artery; 4. vein; 5. lymphatic vessel; 6. gland acini. Toluidine blue stain; x270.