

MACROSCOPIC AND MICROSCOPIC ANATOMY OF THE
CANINE EYE FROM BIRTH TO TWO YEARS OF AGE

SF7167
D6
W587M
c. 2

by

Robert Daniel Whiteford

A Thesis Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
MASTER OF SCIENCE

Major Subject: Veterinary Anatomy

Signatures have been redacted for privacy

Iowa State College

1956

1495411

TABLE OF CONTENTS

	Page
I. INTRODUCTION	1
II. REVIEW OF LITERATURE	2
A. General	2
B. Fibrous Tunic	3
C. Vascular Tunic.	3
D. Neural Elements	5
E. Refractive Media of the Eye	7
III. MATERIALS AND METHODS.	8
A. General	8
B. Collection and Fixation of Specimens.	9
C. Macroscopic Methods	11
D. Microscopic Methods	12
IV. OBSERVATIONS	14
A. General Anatomic Scheme	14
B. Fibrous Tunic	18
C. Vascular Tunic.	27
D. Neural Elements	34
E. Chambers of the Eye	37
F. Refractive Media of the Eye	42
G. Post-natal Development of the Eye	44
V. DISCUSSION	53
A. General Anatomic Scheme	53
B. Fibrous Tunic	53
C. Vascular Tunic.	54
D. Neural Elements	56
E. Chambers of the Eye	57
F. Refractive Media of the Eye	58
VI. SUMMARY AND CONCLUSION	59
VII. SELECTED REFERENCES.	61
VIII. ACKNOWLEDGMENTS.	66

I. INTRODUCTION

The anatomy and physiology of the eye have attracted the attention of scientific investigators since the dawn of medicine. This inherent interest has produced a vast amount of literature dealing with virtually all classes of vertebrates. Many writers have described isolated structures or groups of structures in the canine eye; others have made comparative studies of various structures in conjunction with special problems in human ophthalmology. Unfortunately, however, a complete, concise anatomical study of the canine eye is lacking.

This work has a two-fold purpose: (1) to study the canine eye from birth to 2 years of age, in an effort to determine at what age the eye is structurally mature; (2) to provide a detailed description of the mature eye.

While this thesis is essentially a contribution to veterinary anatomy, it is hoped that it will be of value to the clinician and pathologist. At the same time it is hoped that it will be of value to the research ophthalmologist, who is handicapped by a lack of thorough, comparative, anatomical studies of the eye.

II. REVIEW OF LITERATURE

A. General

A review of the available literature in anatomy and ophthalmology produced no evidence that the canine eye has been completely described prior to this writing.

Michaelis (1796) described the fundus of the eye of the dog, calf, and swine. Schultze (1866), and Cajal (1894), described the histology of the canine retina in their classical works on the mammalian retina. Slonaker (1897) and Johnson (1901) described the macroscopic anatomy of the fundus of many animals including the dog. Duke-Elder (1934) and Wolff (1954) include brief discussions of the comparative anatomy of the eye in their texts.

In veterinary literature, Nicolas (1924), Ellenberger and Baum (1943), Bradley and Grahame (1948), Sisson and Grossman (1953), and Miller (1954), and Trautmann and Fiebigger (1952) describe the anatomy and histology of the mammalian eye in generalities.

Contemporary research has been reported by Dvorak-Theobald (1934), Troncoso and Castroviejo (1936), Swindle (1937), Walls (1942), Rechon-Davigneaud (1943), Uyama (1951), and Parry (1953).

B. Fibrous Tunic

The sclera, according to Duke-Elder (1934), Walls (1942), Trautmann and Fiebiger (1952), Sisson and Grossman (1953), and Wolff (1954), has the same general structure in all mammals. Trautmann and Fiebiger (1952) and Sisson and Grossman (1953) describe a scleral venous plexus which corresponds to the canal of Schlemm in the human. Swindle (1937), describing the principle drainage areas of the eye in various animals, including the dog, also describes this scleral venous plexus. Duke-Elder (1934) describes the sclera of animals as being more highly pigmented than the human.

The cornea was described by most authors as being essentially a circular meniscus. Nicolas (1924) stated that the cornea was slightly elliptical in its horizontal plane. Walls (1942) and Trautmann and Fiebiger (1952) state that Bowman's membrane was seldom discernible and that Descemet's membrane was always present.

C. Vascular Tunic

Walls (1942) stated that the iris of carnivores was essentially the same as in man. He pointed out that there is histological evidence of a dilator muscle. Sisson and Grossman (1953) described the color of the iris as light-brown or

yellow-brown; they stated that blue was not uncommon and that the color may differ in the two eyes. Johnson (1901) stated that the pupil was usually round and pointed out the shape of the pupil and that of the optic papilla usually coincide.

Walls (1942) stated that the choroid was essentially the same in all vertebrates except in those having a tapetum. According to Duke-Elder (1934) and Walls (1942) the thickness of the choroid varied among the different species, being thickest in the human. Walls (1942), Trautmann and Fiebiger (1952), Sisson and Grossman (1953), and Wolff (1954) described the tapetum as being cellular in type. Walls (1942) observed that the tapetum was composed of ten layers of endothelial cells. Johnson (1901) and Trautmann and Fiebiger (1952) noted that the tapetum was avascular. The majority of writers described the color of the tapetum as green to greenish-yellow. Johnson (1901) agreed with this in general, but noted that the Chinese Chou-Chou has an orange-yellow tapetum. This writer suggests that the variations in color may be genetic and linked to breed characteristics or to coat color. Johnson (1901) stated that the tapetum was remarkable by the absence of blues and violets and for the prominence of reds, greens, and yellows.

According to Sisson and Grossman (1953) the ciliary muscle of the canine eye was better developed than in other domestic animals. Other authors consulted made no mention

of the ciliary muscle in the canine eye. Their treatment of this portion of the vascular tunic was in general common to the carnivore as a group.

D. Neural Elements

Schultze (1866) and Cajal (1894) described the canine retina as having ten histological layers conforming generally to the plan typical of all mammals. This description was supported by Duke-Elder (1934), Ellenberger and Baum (1943), Trautmann and Fiebiger (1952), Sisson and Grossman (1953), and Parry (1953). Parry (1953), in his study of retinal degenerations in the dog, stated that the canine retina was not fully mature until 6 weeks of age.

The retinae of mammals contains an area that is specialized for the function of acute vision. The writer has chosen the term "area centralis" as the term of choice in describing this specialized portion of the retina. Other terms equally popular would have to be modified in definition in order to be applicable to the canine eye.

The area centralis was first described by Francesco Bruzzi (1789) in the human eye. He called this area the macula lutea or "yellow spot". v. Sommering (1791) discovered a depression or fovea near its center. These discoveries stimulated intensive study of the retinae of other mammals.

Michaelis (1796) described the area centralis of the dog, calf, and swine and was unable to find a macula lutea or a fovea in these species. Schultze (1866), Krause (1891), and Cajal (1894) were also unable to demonstrate a fovea in the dog. The retinal studies of Schultze (1866) and Cajal (1894) further indicated that the area centralis and fovea in man and simians was rod-free. They found that in other mammals there was no rod-free portion of the retina. Duke-Elder (1934), Trautmann and Fiebiger (1952), and Wolff (1954) also state that a macula and fovea are present only in the primates.

The area centralis of the dog was first described in detail by Chevitz (1890). Slonaker (1897) noted that the area centralis was characterized by a thickening of the retina and sometimes by increased thickening of the tapetum. Parry (1953), on the other hand, stated that the area was only noticed by a slight reduction in the density of secondary retinal blood vessels. Sisson and Grossman (1953), and Parry (1953) located the area centralis medial (nasal) to the optic papilla. They described its shape as round to roundly triangular.

Trautmann and Fiebiger (1952) stated that the cone-cells and rod-cells were increased in the area centralis and suggested that rod-cells may be entirely lacking in rat terriers

and in dogs hunting by sight. Parry (1953) could find no difference in the rod-cone complement of the area centralis in dogs hunting by sight and in those hunting by scent. In fact, he found the rod-cone complement to be strikingly constant throughout the retina with exception of the anterior tenth (in the region of the ora serrata).

The optic nerve, according to Bradley and Grahame (1948) enters the eye slightly lateral and ventral to the posterior pole of the eye. It emerges on the inner surface of the eye as the optic papilla. Johnson (1901) stated that the papilla was round.

E. Refractive Media of the Eye

The refractive media of the eye, consisting of the lens, vitreous body, and aqueous humor, received no specific mention in connection with the dog. The authors consulted treated these structures and fluids in generalities characteristic of the mammalia as a group. Nicolas (1924) did state, however, that the lens, in carnivores, was less sharply curved on its anterior surface than on its posterior surface. Duke-Elder (1934), on the other hand, described the lens of carnivores as being more sharply curved on its anterior surface than on its posterior surface.

III. MATERIALS AND METHODS

A. General

Ocular specimens for this study were obtained from dogs reared in the dog colony of the Department of Veterinary Anatomy, Iowa State College. Fourteen of the dogs were whelped in the colony; two were obtained from other sources.

The diet for these animals, after weaning, consisted of a dry, commercial dog food¹ which was fed free-choice, by means of a hopper type self-feeder. Fresh water was supplied by means of an automatic watering device. There was no evidence of nutritional deficiencies during the course of this study. The ration contained 25% protein, 7% fat, 48% carbohydrate, vitamins, minerals, and essential amino-acids. One pound of the feed supplied 1500-1600 calories.²

The colony did not appear to be excessively parasitized at any time. Intestinal parasites were controlled by daily cleaning of the animal quarters, and by treating the brood bitches with a commercial anthelmintic during early pregnancy.

¹Supplied by Gaines Dog Food Division, General Food Co., Kankakee, Ill.

²Feed analysis provided by the Gaines Dog Research Laboratories, Kankakee, Ill., October, 1954.

An isolation fence located 5 feet from the dog runs prevented the dogs in the colony from coming in direct contact with stray animals.

There was no clinical evidence of disease at the time the animals were destroyed.

B. Collection and Fixation of Specimens

The dogs used in this study were of mongrel breeding. Specimen material was collected from dogs of both sexes and representing the following age groups:

<u>Age</u>	<u>Breed characteristics</u>
Birth	Fox-terrier - X
1 week	Labrador - X
2 weeks	Labrador - X
3 weeks	Labrador - X
4 weeks	Labrador - X
6 weeks	Shepherd - X
8 weeks	Collie - X
10 weeks	Coonhound - X
12 weeks	Coonhound - X
16 weeks	Shepherd - X
20 weeks	Coonhound - X
24 weeks	Coonhound - X

28 weeks	Coonhound - X
12 months	Greyhound - X
24 months	Greyhound - X

The animals were destroyed by electrocution. The globes were enucleated immediately after death and placed in 10% neutral formalin. Later, during the process of dehydration, the globes were opened. Virtually all specimens showed some degree of retinal detachment. Subsequent inquiries indicated that formalin fixation caused extreme shrinkage of the globe with retinal detachment.¹

In an attempt to escape retinal detachment due to formalin fixation, globes used for macroscopic studies were fixed either in Bouin's or Zenker's fluids. The globes were fixed in toto. Specimens fixed in Bouin's fluid, which contains 5% formalin, still showed some evidence of retinal detachment. Globes fixed in Zenker's fluid did not show evidence of retinal detachment and were otherwise satisfactory. It would appear that of the fixatives used, Zenker's fluid would be the fixative of choice for ocular tissues.

Retinal degeneration begins soon after death (Parry, 1953). Early and adequate fixation was therefore desirable. Considering this factor, three methods of preparing the globes for fixation were employed. The vitreous cavities of

¹Lindorfer, Katherine. 1955. Iowa City, Iowa. Celloidin technique for ocular tissues. (Personal communication.)

several globes were injected by means of a hypodermic syringe and needle. Other globes were incised either in the region of the limbus or equator. The remaining specimens were fixed in toto. Injection caused retinal detachment in the area of the injection. Limbal incisions made subsequent study of the anterior chamber angle difficult and occasionally impossible. Equatorial incisions caused escape of the vitreous with collapse of the globe and retinal detachment. Globes fixed in toto were quite satisfactory. This method of fixation was continued.

C. Macroscopic Methods

The basis of anatomical research has always been accurate observation and dissection. The delicate, complex structures of the eye, however, are too small for naked-eye observation. Simple magnification was found to be of great value. A standard, wide-field dissecting microscope was used to good advantage. To obtain a comprehensive view of the structures of the globe, a magnification of 15X was used. Finer details were studied at a magnification of 30X and 40X.

Globes were bisected transversely and sagittally for these purposes. Undesirable rotation of the globe segments was controlled by placing the segments in a concave depression cast in a paraffin block.

D. Microscopic Methods

The enucleated globes were allowed to remain in the fixative for 24-48 hours. They were then washed in running tap water for 24 hours, and stored in 70% ethyl alcohol. Dehydration was accomplished in graded ethyl alcohols and terminally in absolute alcohol-ether solution. During dehydration, vertical (sagittal), and horizontal (frontal) sections were prepared by bisecting the globes 1/8 inch on either side of the optic nerve head. This resulted in a ring-shaped section of ocular tissue which contained the central visual structures. The remaining "side-pieces" were discarded.

The globe segments were dehydrated and embedded in celloidin using the dry celloidin method currently employed by Lindorfer (1955). In this technique, the segments were dehydrated in graded ethyl alcohols and terminally in absolute alcohol-ether solution. Two solutions of commercial celloidin are used. The segments are infiltrated in 8% celloidin for 4 weeks and then in 15% celloidin for 4 weeks. The embedding mass was allowed to evaporate to partial hardness in the air at room temperature. When the block was hard enough to handle, it was transferred to cedarwood oil and chloroform to complete the hardening process (24 hours). The block was then cleared in cedarwood oil for at least 4 days. Celloidin sections were cut 10-15 micra in thickness using a standard rotary

microtome.

Sections were stained routinely with Harris' alum-hematoxylin and Eosin-Y and a modified picro-indigocarmine trichrome stain of Cajal. Van Gieson's acid fuchsin-picric acid stain was used to demonstrate collagenous fibers; Weigert's elastic tissue stain was used for elastic fibers.

IV. OBSERVATIONS

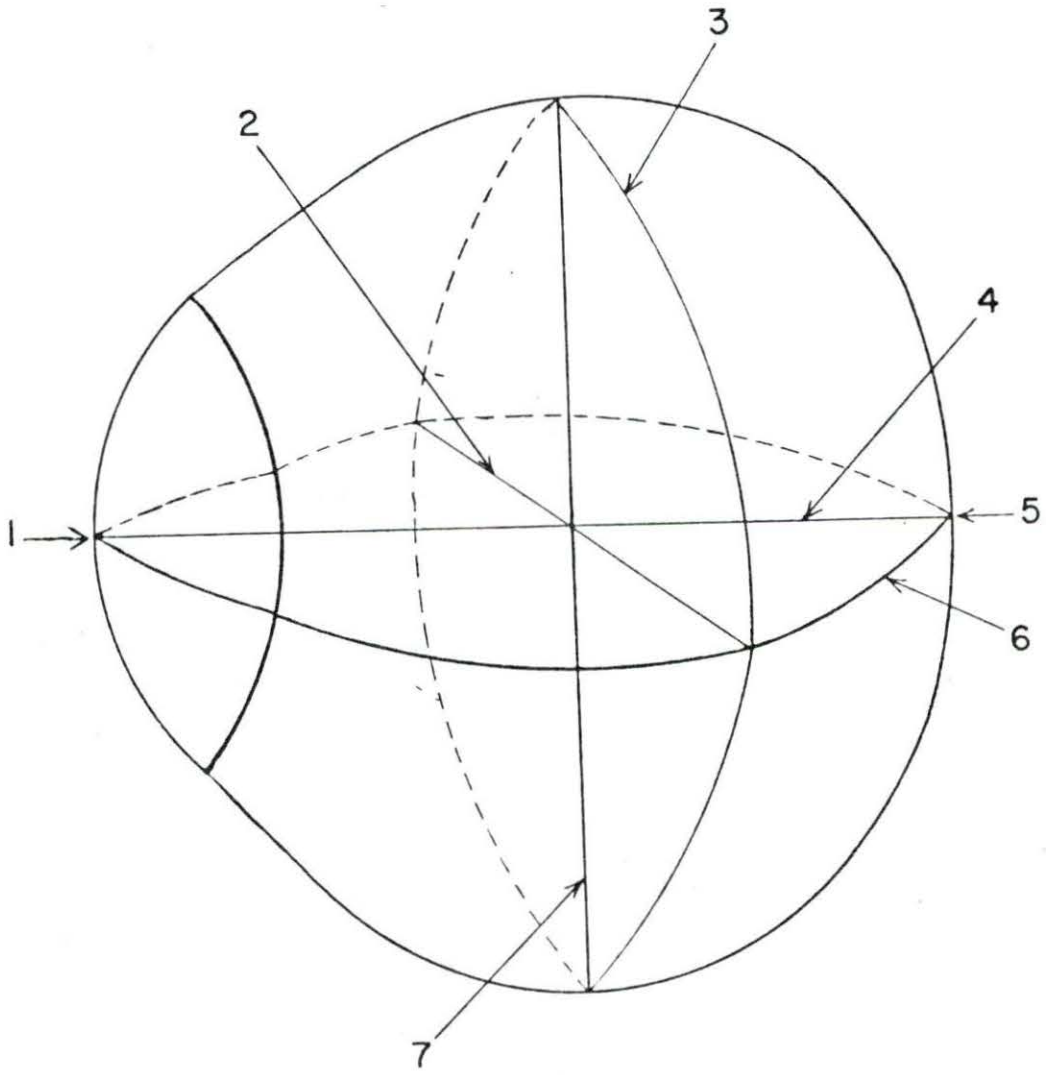
A. General Anatomic Scheme

The eye, protected by connective tissue and voluntary muscle, was situated in the anterior portion of the orbital cavity. It was composed of segments of two asymmetrical spheres, giving it the form of an oblate spheroid (Fig. 1). The anterior, transparent segment (cornea) had a radius of curvature $1/3$ smaller than the posterior opaque segment (sclera). The anterior segment therefore projected more strongly. The junction of the two segments was marked externally by a shallow groove, the external scleral sulcus.

Terms usually employed in describing a spherical structure were used in describing the surface of the eye. The central point on the anterior curvature of the cornea was designated the anterior pole; the corresponding point on the posterior curvature of the sclera, the posterior pole. An imaginary line connecting the two points was called the geometric axis. A circle executed over the surface of the globe equidistant from the two poles was called the equator. Circles passing over the surface of the globe, through the poles and at right angles to the equator, were designated meridians (Fig. 1). From these geometric points three diameters were determined: sagittal (anterior-posterior), horizontal, and

Fig. 1. Geometric orientation of the eye

1. Anterior pole
2. Horizontal diameter
3. Equator
4. Geometric axis
5. Posterior pole
6. Horizontal meridian
7. Vertical diameter



vertical.

The canine eye was found to be somewhat flattened from above down, hence the horizontal diameter was slightly greater than the vertical. The sagittal was greatest of all. In this study, the diameters of the adult eye were found to be: sagittal, 21.8 millimeters; horizontal, 21.4 millimeters; and the vertical, 21.0 millimeters.

The surface of the globe presented in its anterior $1/3$ the tendonous insertions of six of the extrinsic ocular muscles (four straight and two oblique). The exit of the vortex veins (one in each quadrant) emerged from the globe anterior to the equator. The optic nerve emerged from the globe slightly lateral to and below the posterior pole. The long ciliary nerves, four or five in number, entered the globe in this area also, forming an irregular circle about the optic nerve. The retractor muscle of the eye, which sheathes the optic nerve in its intraorbital course, inserted on the posterior $1/3$ of the globe. The insertions resulted from digitations of its fibers.

The eye consisted of three concentric tunics which contained the refractive media. From without inward they were: (1) the fibrous tunic, which is essentially protective; (2) the vascular tunic, which supplies nutrition to the nervous tunic (3) containing the peripheral end-organs serving the sense of vision.

B. Fibrous Tunic

The sclera, which was opaque, constituted the posterior $5/6$ of the fibrous tunic. It was dense in consistency and in general, had a dull-white color. The equatorial portion was thin, so thin in fact, that the underlying, heavily pigmented vascular tunic was visible through it. Here, the dull-white color took on a bluish-brown cast due to this underlying coat. The cut-surface of the sclera had a dense, glistening consistency similar to tendon. The inner surface was smooth; it was brown in color and dull in appearance due to the presence of pigment in its deeper layers.

The thickness of the sclera was not uniform. It was thickest (0.8 to 1.0 millimeters) at the corneo-scleral junction. This thickness was marked externally by a thickened band of fibrous tissue approximately 0.5 millimeters in width, which circled the globe on an equatorial plane. It was thinnest (0.3 millimeters) in the region of the equator. In the area of the junction of the anterior and equatorial thirds of the globe, the tendons of insertion of the ocular muscles blended with the fabric of the sclera. The posterior $1/3$ of the sclera increased to a thickness of 0.4 millimeters. The lateral aspect of the sclera was thicker in all regions than the medial aspect.

The sclera presented two so-called foramina, anterior and

posterior. The anterior scleral foramen was marked by the junction of the irregular fibers of the sclera and the regular lamellae of the cornea, forming the corneo-scleral junction. The external scleral sulcus has already been noted. At the corneo-scleral junction there was a corresponding internal scleral sulcus (Fig. 2C). The posterior margin of this junction projected forward and into the interior of the eye, forming the scleral spur. The ciliary muscle was attached to this spur and formed the anterior insertion ring of the vascular tunic. The posterior scleral foramen permitted the exit of the optic nerve. The inner layers of the sclera stretched across this opening but were fenestrated for the passage of the fibers of this nerve. The fenestrated area constituted the lamina cribrosa.

Microscopically, the structure of the sclera was uniform. Slight modifications were noted however which allowed it to be divided into three layers. From without inward they were: (1) the episclera, (2) the sclera proper, and (3) the lamina fusca.

The episclera was composed of collagenous and elastic fibers in a rather loose arrangement. It was attached above to the tissue fillings Tenon's space and below to the sclera proper. It was interesting to note the large numbers of small blood vessels here, in contradistinction to the sclera proper which was practically avascular.

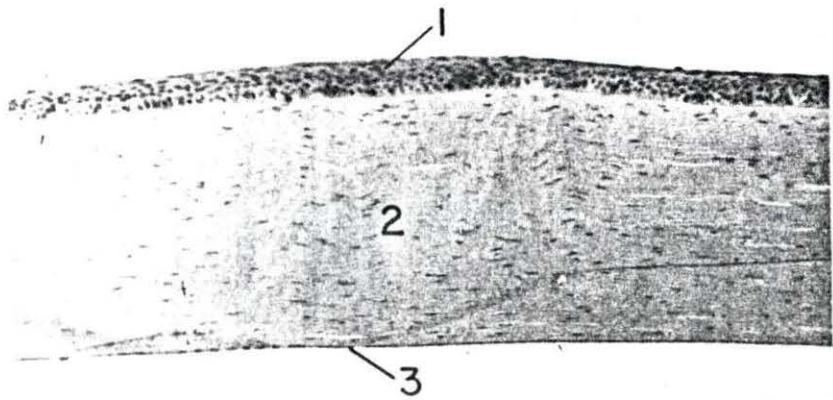
Fig. 2. Sections through the fibrous and vascular tunics of the mature canine eye

- A. Cornea in the region of the anterior pole (70X)
 - 1. Corneal epithelium
 - 2. Corneal stroma
 - 3. Descemet's membrane and the endothelium lining the anterior wall of the anterior chamber

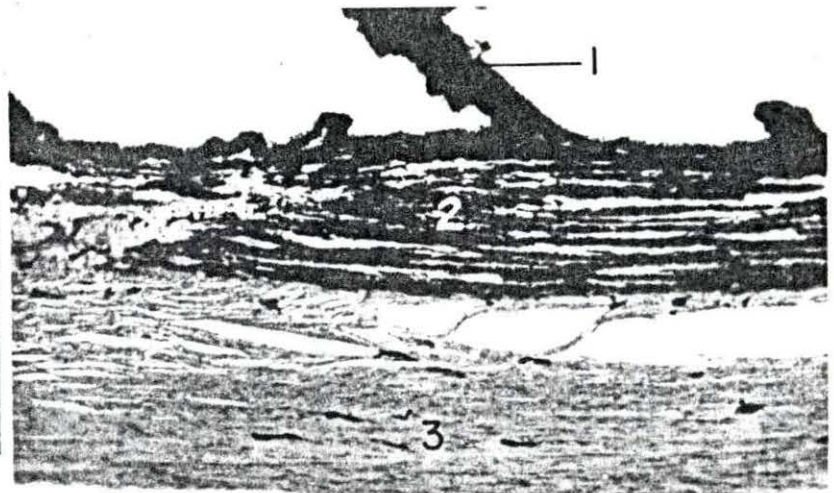
- B. Meridional section through the sclera in the region of the ciliary body (70X)
 - 1. Ciliary process
 - 2. Heavily pigmented ciliary body
 - 3. Sclera

- C. Meridional section at corneo-scleral junction (70X)
 - 1. Epithelium of the limbus
 - 2. Corneo-scleral junction

- D. Section of choroid and tapetum (115X)
 - 1. Tapetum
 - 2. Vascular layer of the choroid

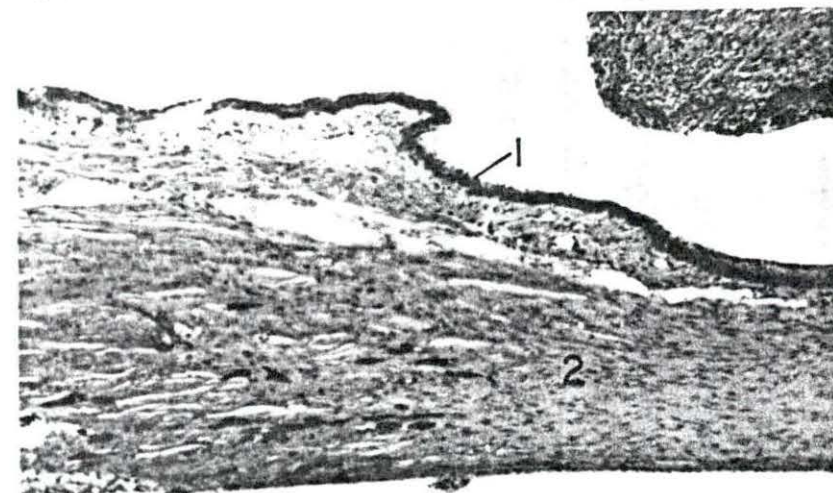


A

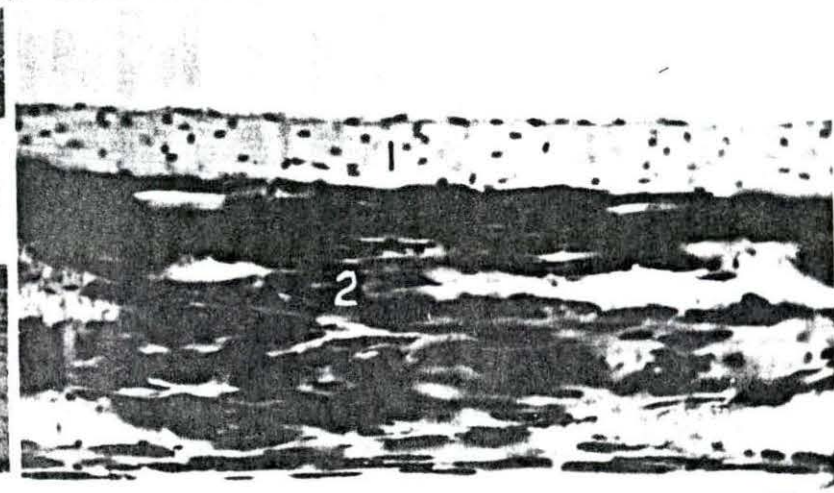


B

21



C



D

The sclera proper (Fig. 3A) was composed of collagenous fibers and a varying admixture of elastic fibers. The collagenous fibers were arranged in bundles lying parallel to the surface of the sclera and ran in all directions. They divided, reunited and crossed over each other forming a dense, interwoven meshwork. The elastic fibers were usually found on the surface of the collagenous fibers. The collagenous bundles were thickest near the surface of the sclera, becoming smaller in the deeper layers. The deeper layers also contained considerable amounts of pigment. The increasing density and pigmentation delineated the lamina fusca.

Cellular elements found in the scleral connective tissue were typical, flattened fibrocytes. Pigment cells (chromatophores) were plentiful. They were particularly evident at the corneo-scleral junction, the lamina cribrosa, and around the vessels entering and leaving the ciliary area. Moderate numbers of pigment cells were evident throughout the extent of the sclera, particularly in the deeper layers.

The sclera was practically avascular. Most of its blood supply seemed to reach it via the vessels located in the episclera. In the midscleral region, canals (the emissaria of Salzmann) were seen to contain the vessels going to and from the interior of the eye. These canals were lined by a loose connective tissue.

The cornea, the anterior segment of the fibrous tunic,

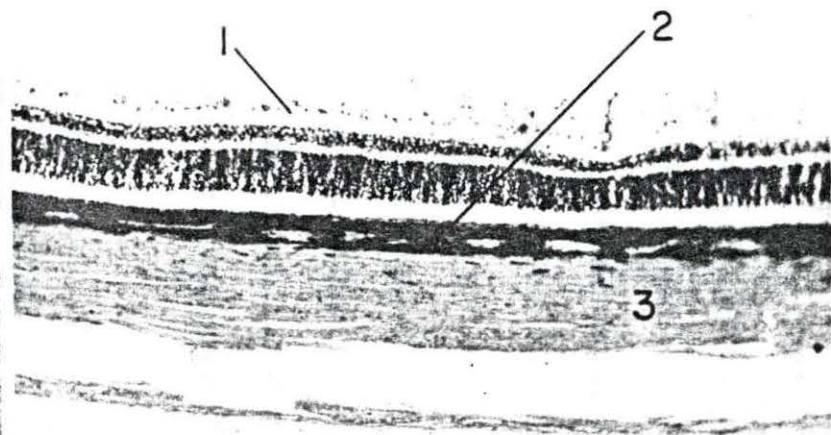
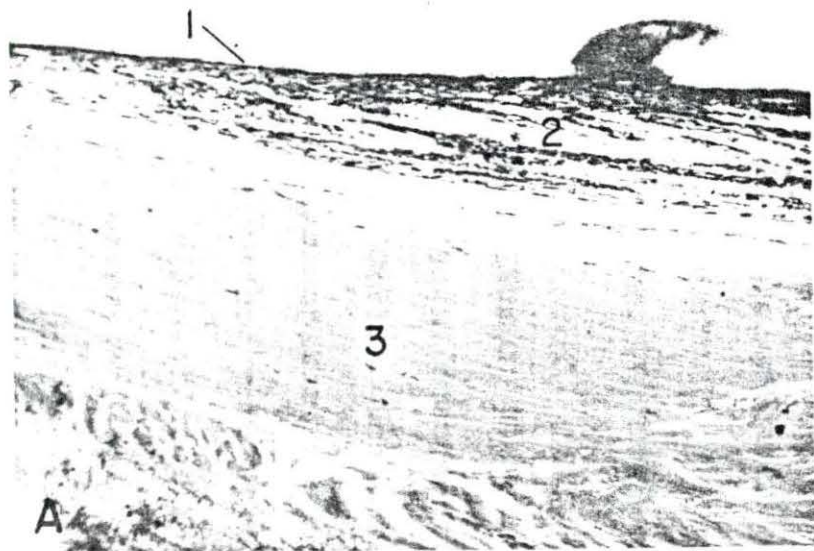
Fig. 3. Sections through various tunics of the eye

- A. Meridional section of ciliary body (70X)
 - 1. Pars plana of the ciliary body
 - 2. Ciliary muscle
 - 3. Sclera

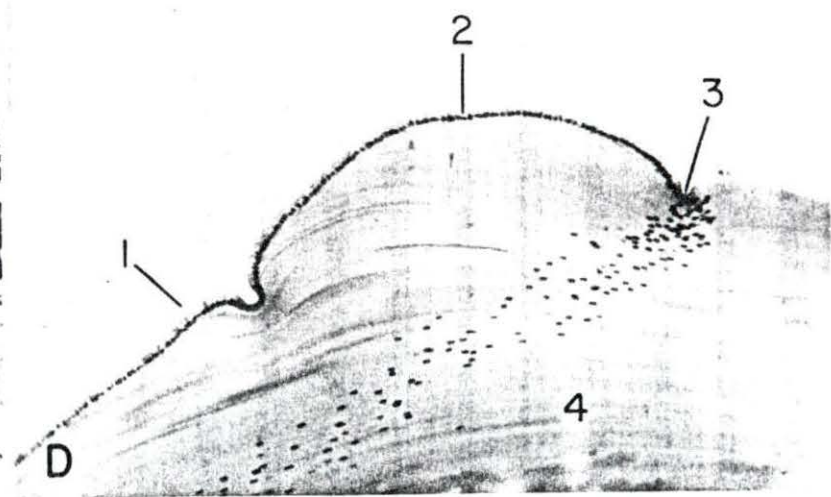
- B. Section through fundus of the eye (70X)
 - 1. Retina
 - 2. Tapetum and vessel layer of the choroid
 - 3. Sclera

- C. Meridional section through the optic nerve at the optic papilla (70X)
 - 1. Optic nerve
(NOTE: There is no central depression in the nerve head)

- D. Anterior-posterior section through the lens at the equator (115X)
 - 1. Lens capsule
 - 2. Subcapsular epithelium
 - 3. Lens vortex



24



was a clear, transparent tissue with a smooth and brilliant surface. It had the form of a strongly curved meniscus and was inserted with a beveled margin into the anterior scleral foramen. Viewed from the front, it was slightly elliptical on the horizontal plane. Due to its beveled insertion, it appeared circular from behind. The radii of curvature of the cornea was determined on a keratometer using formalin-fixed globes. These radii for the adult dog were found to be: horizontal, 715 millimeters; vertical, 619 millimeters. The thickness of the cornea at the anterior pole was 0.4 millimeters.

Microscopically, the cornea (Fig. 2A) was composed of two zones: (1) the cornea proper and (2) the limbus.

The cornea proper consisted of five layers. From before backward they were: (1) epithelium, (2) Bowman's membrane, (3) corneal stroma, (4) Descemet's membrane, and (5) endothelium.

The epithelium of the cornea was of uniform thickness, varying in different specimens from 50 to 80 μ . Its contour was extremely regular, and structurally, was continuous with the conjunctival epithelium. The epithelium was stratified squamous in type and consisted of five to seven cell layers. These layers were divided into three zones based upon the general cell contour. The deepest zone, the basal-cell layer was composed of a single row of rather tall cuboidal elements.

The next zone also consisted of a single row of cells. These were polyhedral in outline and constitute the so-called "wing-cells". The most superficial zone was from three to five cell layers thick. The cells in this zone had the contour typical of squamous cells. They were flattened, with their long axes parallel to the surface of the cornea. The superficial layer showed no evidence of keratosis. The cells were united by intercellular bridges, which were very prominent in the basal-cell layer.

Bowman's membrane was not clearly discernible. This membrane was found immediately below the basal-cell layer of the corneal epithelium. It was represented by a uniformly structureless area that appeared to end abruptly at the limbus.

The stroma constituted about 90 per cent of the entire thickness of the cornea. Two structural elements were noted: connective tissue lamellae and corneal cells (corpuscles). The lamellae ran the entire length of the cornea, crossing back and forth with each other but running nearly parallel to the surface.

Between the lamellae were seen the corneal corpuscle. These cells seemed to be typical connective tissue elements, many of which were deformed by lateral pressure from the lamellae. Occasional leucocytes were seen scattered in the meshes of the lamellae. In many instances they were crushed

almost beyond recognition from the pressure exerted by the lamellae.

Descemet's membrane was a homogeneous structure which separated the corneal stroma from the endothelium. The membrane stained exceptionally well with van Giesson's stain.

The endothelium was a single layer of epithelioid cells arranged along the posterior border of Descemet's membrane.

The corneal limbus (Fig. 2C) marked the transition between the cornea on the one hand, and the conjunctiva, episclera, and sclera on the other. In the canine eye, the line of demarcation was very prominent because of the presence of a large number of pigment cells along the line of transition. It is also marked by the transition of the epithelium. The thinner, more regular corneal epithelium gradually is replaced by the thicker, papillated conjunctival epithelium. Bowman's membrane was seen to end abruptly at the conjunctival epithelium. The regularly arranged corneal lamellae goes over into the irregularly arranged scleral connective tissue. Descemet's membrane, and the endothelium were continued into the meshwork of the iris angle.

C. Vascular Tunic

The vascular tunic was divided into four regions on the basis of structural differences. From behind forward they

were: (1) choroid, (2) tapetum lucidum, (3) ciliary body, and (4) iris.

The choroid and tapetum lucidum were the most posterior parts of the vascular tunic. The choroid extended from the exit of the optic nerve, anteriorly to the ora serrata except for the area occupied by the tapetum. It had the appearance of a soft, brown membrane with the chief characteristics of extreme vascularity and a large amount of pigment.

Histologically, the choroid (Fig. 2D) was composed of the following layers from without inward: (1) epichoroid, (2) vascular layer, (3) chorio-capillaris, and (4) lamina elastica externa.

The epichoroid provided loose attachment for the choroid to the sclera. It was represented by a thin, delicate, loosely woven lamellae of elastic fibers. Large numbers of pigment-laden chromatophores were seen in the meshes of these fibers.

The vessel layer was the thickest layer in the specimens examined. It consisted of a dense vascular plexus suspended in connective tissue lamellae. Pigment cells, characteristic of this tunic were in great evidence in the area.

The chorio-capillaris and the lamina elastica externa were completely concealed by heavily pigmented chromatophores. Only in one or two areas were they bleached enough for the writer to hazard an assumption that these structures lay beneath.

The tapetum lucidum (Fig. 2D), a modification of the choroid, was essentially avascular and non-pigmented. It was approximately crescentic in outline, occupying the dorsal quadrants of the fundic portion of the choroidal layer.

Microscopically, the tapetum was composed of eight to ten layers of non-stratified, flattened, hexagonal cells. The cells contained relatively small amounts of cytoplasm; their nuclei were small and dense.

The ciliary body was recognized as the anterior continuation of the vascular tunic. It was situated between the ora serrata (the anterior termination of the retina) posteriorly, and the corneo-scleral junction, anteriorly. In meridional sections (Fig. 3A) it had the shape of a right-angled triangle, the apex of which was continuous with the choroid. The base or shortest side was directed anteriorly. It was attached by its outer angle to the scleral spur. Its external surface, bordering the sclera, was smooth; its internal surface was thrown into approximately 50-70 radiating folds, the ciliary processes.

The surface of the ciliary body presented an anterior and a posterior region. The posterior region (pars plana) was smooth and heavily pigmented. In the canine eye, this region was not nearly as wide as the same area in the human eye. The ciliary processes in many instances virtually encroached upon the ora serrata. Anteriorly, the prominent

folds of the ciliary processes were seen. These processes were pyramidal in shape; they were placed side by side in a radiating manner with their bases directed towards the lens, their apices toward the ora serrata.

The ciliary muscle (Fig. 3A) was of considerable bulk. It had the same triangular form characteristic of the rest of the ciliary body. Its right angle was internal and faced the ciliary processes; its apex blended with the choroid, the base was projected anteriorly.

Histologically, the ciliary muscle (Fig. 2B) was composed of smooth muscle fibers. The fibers were oriented in three directions: (1) meridional fibers were found to be the most external - from the choroid, they projected anteriorly forming a "muscle-belly" of good size; continuing forward, the muscle fibers became lost in the connective tissue of the scleral spur which provided attachment for the muscle, (2) radial fibers were seen internal and anterior to the meridional fibers and had a fan-like arrangement, and (3) circular fibers which appeared to be continuous with the radial fibers. This group of muscle fibers continued around the anterior edge of the ciliary body immediately behind the root of the iris.

The ciliary body as a whole was formed in a connective tissue stroma which supported a great number of vessels and pigment cells. The ciliary muscle contained a considerable amount of interstitial connective tissue. The internal surface

of the ciliary body was lined by pigment epithelium, the anterior continuation of the pigment layer of the retina; it continued anteriorly to cover the posterior surface of the iris.

The iris constituted the anterior limit of the vascular tunic. It was suspended between the cornea and the lens, having the form of a circular, contractile disc, perforated near its center by a circular aperture, the pupil. The iris presented two circular borders: the pupillary and the ciliary margins. The ciliary margin or root of the iris was attached to the middle of the anterior surface of the ciliary body. The ciliary margin was relatively thin; it became thicker towards the middle of the iris forming the collarette and then became thinner at the pupillary margin. The pupillary margin was unattached and moved freely over the anterior surface of the lens.

The anterior surface of the specimens studied were golden-brown in color. The surface was divided by an irregular ridge that was concentric with the pupil, the lesser arterial circle of the iris. A vascular anastomosis in the underlying stroma produced this ridge. The area lying between the lesser arterial circle and the pupillary margin was designated the pupillary zone. This zone in the iris of man is characterized by numerous excavations, the pupillary crypts. These crypts were not evident in the canine irises examined in this study. The

ciliary zone, the area between the lesser arterial circle and the ciliary border, was quite uniform. It contained, however, a number of linear defects that were concentric with the pupillary margin. No cryptiform excavations were evident in this area.

The posterior surface of the iris presented a uniformly dark-brown - almost black - color. With the magnifying lens, two systems of radiating furrows were visible; one in the pupillary zone and one in the ciliary zone.

Microscopically, the iris was divided into five layers. From before backward they were: (1) anterior endothelium, (2) anterior border layer, (3) stroma, (4) dilator muscle, and (5) posterior epithelium.

The anterior endothelium consisted of extremely delicate cells. These cells stained faintly with the staining techniques employed in this study. The cells were continuous with the endothelium of the cornea and scleral spur.

The anterior border layer was essentially a condensation of the anterior part of the stroma layer. It consisted of a dense meshwork of anastomosing processes of connective tissue cells and pigment cells. The connective tissue cells were stellate in outline, had the characteristics of primitive mesenchymal cells, and were arranged parallel to the surface of the iris.

The stroma of the iris consisted of loosely arranged

collagenous fibers and a few elastic fibers. The stroma cells for the most part were typical, flattened fibrocytes. Wandering cells (leucocytes) and plasma cells were very evident. The predominant cell-type, however, was the large, pigmented chromatophore. The pigment contained in these cells was yellow-brown in color. The cells were provided with two or three long, slender processes which united with processes of other chromatophores forming a syncytium. Numerous chromatophores in the region of the sphincter muscle and the ciliary border of the iris were atypical cells in that they were somewhat larger, more heavily pigmented, and lacked the processes which are characteristic of the chromatophore. These chromatophores were interpreted as the iris "clump cells" (Wolff, 1954). Suspended in the stroma of the iris were the radiating branches of the greater and lesser arterial circles. The adventitia of this group of arteries was quite thick, in some instances thicker than the lumen they surrounded. The veins appeared to have perivascular sheathes. Also present in the iris stroma was the sphincter muscle of the iris. This muscle was an annular band encircling the pupillary margin, and was composed of smooth muscle fibers. The peripheral border of the band blended with the dilator muscle of the iris.

The dilator muscle of the iris was composed of myoepithelial cells whose fibers were arranged in a radial manner. The muscle appeared as a uniform layer in the posterior part

of the iris between the stroma and the posterior epithelium.

The pigment epithelium on the posterior surface of the iris was so heavily pigmented that histological study by routine methods was impossible. This layer is continuous posteriorly with the ciliary epithelium. Anteriorly, it ended on the expanse of the pupillary margin by forming a junction with the epithelium of the anterior surface.

D. Neural Elements

The neural elements of the eye that were considered in this study consisted of the retina and the intra-ocular portion of the optic nerve (optic papilla).

The retina was a soft-, non-elatic, translucent membrane. Its outer surface was in contact with the choroid; its inner, with the vitreous body. Posteriorly it was continuous with the intra-bulbar portion of the optic nerve; anteriorly, it terminated at or near the pars plana of the ciliary body. The anterior limit was noted by a dentate margin, the ora serrata. The retina was firmly attached to underlying structures at these points; elsewhere, it was loosely attached to the choroid. This attachment was probably aided by the mass of the vitreous body. The inner surface of the retina appeared to be finely granular, the density of which was most noticeable in older subjects. Between the granular-appearing

areas, dark, round or triangular areas of pigmented epithelium could be seen through the retina.

Histologically, the retina (Fig. 3B) consisted of ten structural layers. From without inward they were: (1) pigment epithelium, (2) layer of rods and cones, (3) external limiting membrane, (4) outer nuclear layer, (5) outer plexiform layer, (6) inner nuclear layer, (7) inner plexiform layer, (8) ganglion-cell layer, (9) nerve fiber layer, and (10) internal limiting membrane.

The pigment epithelium, on cross-section, was cuboidal in outline. The pigment was unevenly distributed from cell to cell causing an uneven staining reaction. In the region of the tapetum, the epithelium was entirely devoid of pigment. The granular appearance of the inner surface of the retina was interpreted as being due to the variation in the amount of pigment in this layer. The retinal surface of the epithelium exhibited delicate protoplasmic projections which interdigitated with the bases of the rod and cones.

The layer of rods and cones was approximately 30 micra in width and demonstrated a palisade arrangement.

The external limiting membrane was a delicate layer of filaments.

The outer nuclear layer was 30 micra in width and contained the nuclei of the rods and cones. The cone nuclei were located along the outer edge of the layer, resting on the

external limiting membrane. No portion of this layer was interpreted as being rod-free nor was there histologic evidence of a fovea centralis.

The outer plexiform layer was 10 micra in width and consisted of a rather dense reticulum of fine filaments.

The inner nuclear layer was 20 micra in width and three or four nuclei thick. The nuclei were closely packed and occupied most of the cell space; the cytoplasm formed an extremely thin canopy over the nuclei. The routine staining procedures employed could not be utilized to differentiate cell types.

The inner plexiform layer was approximately 50 micra wide and consisted of a fine reticulum of fibrous elements.

The ganglion-cell layer was 50 micra in width and two or three cells thick. The cells were of three sizes: giant, medium and small. In many fields the small ganglio-cells appeared to be in two layers. The cells comprising this layer were closer together in the peri-papillary area and were increasingly farther apart peripherally.

The nerve fiber layer was 10 micra wide peripherally, and increased gradually to a width of 60 micra at the optic papilla.

The internal limiting membrane was quite thin and delicate. It could not always be delineated.

The structure and width of the retina from the equator

posteriorly was uniform. Anteriorly from the equator, it decreased in width, slowly at first, then rapidly. In the region of the ora serrata, the thickness of the retina diminished rapidly until only the pigment epithelium remained. This was projected onto the ciliary body and the posterior surface of the retina as the pars ciliaris retinae and pars iridica retinae, respectively.

The optic papilla marked the beginning of the optic nerve, and was formed by the convergence of the nerve fiber layer of the retina. Viewed from within, it was a round or nearly round structure lying lateral to and slightly below the posterior pole of the globe. Fresh, unfixed specimens were light-pink in color. The color was interpreted as being due to the underlying retinal vessels.

Meridional sections through the papilla (Fig. 2C) indicated that it was not actually a papilla; the papillary area was in the same plane as the retina. The optic papilla in the human eye presents a physiologic depression near its center; the canine eyes examined in this study did not present this physiologic depression.

E. Chambers of the Eye

The iris, suspended between the lens and cornea, divided the anterior segment of the eye into two spaces; the anterior

and posterior chambers.

The anterior chamber was bounded by the posterior surface of the cornea in front; peripherally, by small segments of the internal surface of the sclera and anterior surface of the ciliary body; and posteriorly, by the entire anterior surface of the iris and the intra-pupillary portion of the lens. The surface of the chamber was lined by endothelium with the exception of the intrapupillary surface of the lens.

Histologically, the periphery of the anterior chamber (Fig. 4A and B) presented an acute angle between the iris and ciliary body on the one side, and cornea, sclera, and ciliary body on the other.

An extremely delicate meshwork of pigmented collagenous connective tissue fibers, covered by endothelium, was suspended across the chamber angle. The fibers of the meshwork were oriented in the following manner: (1) scleral fibers originated at the sclera near the scleral spur and terminated, for the most part, in the corneal stroma, (2) ciliary fibers originated between the fibers of the meridional, radial, and circular portions of the ciliary muscle. The meridional fibers terminated in the posterior corneal stroma, the radial and circular fibers near the end of, or blended with, Descemet's membrane, (3) iris fibers originated in or near the root of the iris and terminated in Descemet's membrane. This group of fibers constituted the pectinate ligament of the

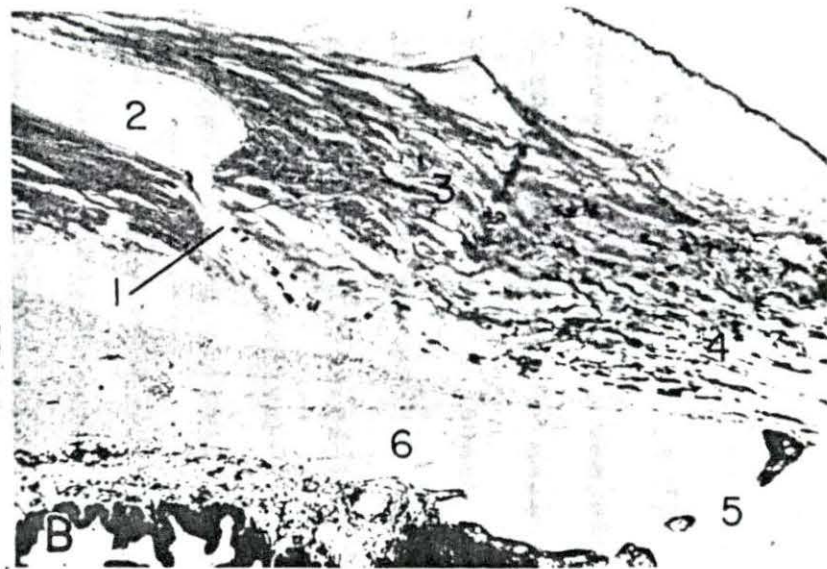
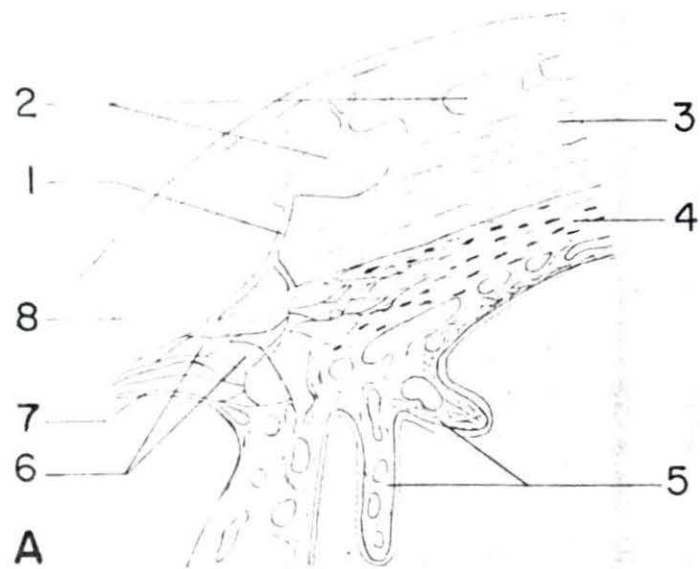
Fig. 4. The anterior chamber angle and age changes

- A. Schematic drawing of the anterior chamber angle and surrounding structures
 - 1. Aqueous canal
 - 2. Plexus of Hovius
 - 3. Sclera
 - 4. Ciliary body
 - 5. Ciliary processes
 - 6. Scleral and ciliary fibers of the meshwork of the chamber angle
 - 7. Pectinate ligament of the iris
 - 8. Cornea

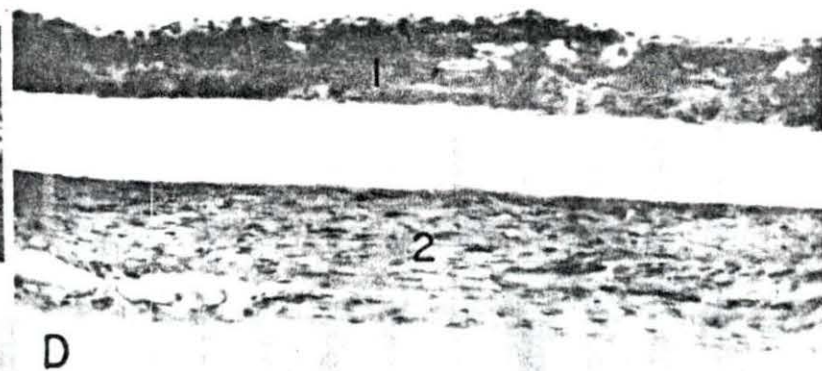
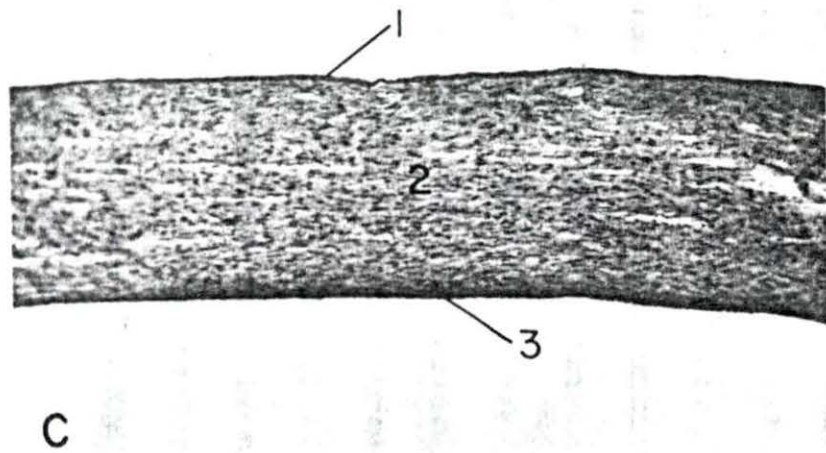
- B. Meridional section through the angle of the anterior chamber (70X)
 - 1. Aqueous canal
 - 2. Portion of plexus of Hovius
 - 3. Sclera
 - 4. Corneo-scleral junction
 - 5. Pectinate ligament of the iris
 - 6. Meshwork of the chamber angle

- C. Section through cornea at anterior pole (age: birth) (70X)
 - 1. Corneal epithelium
 - 2. Corneal stroma
 - 3. Descemet's membrane and endothelium

- D. Choroid, tapetum and sclera (age: birth) (70X)
 - 1. Choroid and tapetum
 - 2. Sclera



40



iris.

It has been noted that the sclera was found to be quite thick in this area (Table 3). This thickness was due to the presence of a large venous sinus, the plexus of Hovius (Nicolas, 1924). The plexus communicated with the anterior chamber by radially arranged "aqueous canals". The openings of the canals were found in the region of the scleral meshwork (Fig. 4A and B). The floor of the scleral sulcus, in the human eye, presents an endothelium-lined channel, the canal of Schlemm. The eyes examined in this study did not present a structure of this description.

The posterior chamber was somewhat smaller than the anterior chamber. It was bounded by the posterior surface of the iris, the equatorial portion of the lens, the anterior surface of the vitreous body, and the inner surface of the ciliary body. The posterior chamber was not as regularly formed as the anterior, therefore, it was divided into three parts: (1) the space bounded by the posterior surface of the iris, a portion of the anterior surface of the lens, the anterior leaf of the zonule, and the ciliary body was called the pre-zonular space, (2) the space bounded by the two leaves of the zonule and the equatorial zone of the lens constituted the circumferential space, and (3) the space between the posterior leaf of the zonule and the anterior surface of the vitreous body was designated the retrozonular space.

F. Refractive Media of the Eye

The space enclosed by the wall of the eyeball was occupied by the refractive media of the eye. These media consisted of: (1) an anatomical structure, the lens, (2) a gel-like mass, the vitreous body, and (3) a body fluid, the "aqueous humor".

The lens was a biconvex, transparent, semisolid body situated immediately posterior to the iris and suspended from the ciliary body on all sides. It presented two surfaces and one border. The anterior surface was more convex than the posterior surface. The midpoints of the two surfaces constituted the anterior and posterior poles, respectively. An imaginary line connecting the two poles was designated the axis. The border or equator, was the point where the anterior and posterior curvatures met. The border was not smooth; a series of dentations was seen that corresponded to the attachments of the suspensory apparatus. A thin, easily removed capsule was present. The mature lens diameters were found to be: anterior-posterior diameter, .4 millimeters; vertical (circumferential) diameter, .9 millimeters.

The fresh, unfixed lens was putty-soft, and pliable. It was transparent, colorless, and sparkled with the brilliance of a diamond.

The cut-surface of the lens indicated that it was com-

posed of at least three layers of laminated lens material. The external layer was soft, almost fragile; the middle layer was firmer but quite pliable; the central mass, the nucleus, was hard and firm.

Microscopically, the lens (Fig. 3D) consisted of: (1) lens capsule, (2) subcapsular epithelium, and (3) lens fibers.

The capsule formed a transparent, structureless, highly elastic envelope surrounding the lens proper. It was thicker anteriorly (70 micra) than posteriorly (10 micra). Diagonal striations were visible on its surface; these were interpreted as the points of attachment for the zonule fibers.

The subcapsular epithelium consisted of a single layer of cuboidal cells on the anterior surface of the lens only. In the equatorial region, the epithelium was arranged in a serpentine pattern, the lens vortex of Duke-Elder (1934).

The lens fibers were not intact in the specimens described in this study. Histologic technique so hardened the lens material that it tore on sectioning. However, the remnants indicated that they were long, prismatic, six-sided fibers. They originated at the equator and converged at the poles, tapering during their progress.

The lens was maintained in position by a suspensory apparatus, the zonule of Zinn. Macroscopically, the zonule was a thin membrane which originated near the equator of the lens and disappeared in the folds of the ciliary processes.

Microscopically, the zonule appeared to have two "leaves", an anterior one and a posterior one. The anterior leaf was almost perpendicular to the equator. The posterior leaf described a long sweeping curve which was concave backwards, blending with the substance of the pars plana and ciliary processes.

The vitreous body occupied the greater part of the interior of the eye. This structure or substance, in the freshly enucleated globe, was a colorless, highly transparent, gel-like mass. Unfortunately, the vitreous body did not lend itself to any of the techniques of preparation employed in this study.

The aqueous humor, a clear, colorless, water-like fluid was found in the anterior and posterior chambers. This fluid was of necessity lost during technical procedures.

G. Post-natal Development of the Eye

The form of the eyeball at birth was essentially spherical (Table 1). The horizontal, sagittal, and vertical diameters from 2-28 weeks of age indicated that the growth pattern of the eye was subject to considerable variation and that the direction of growth was inconstant. From 28 weeks to 2 years of age, the gross measurements of the globe followed a more stable pattern. The slight variations in the measurements

Table 1. Gross diameters of canine eyes from birth to 2 years of age (recorded in millimeters; formalin-fixed)

Age	Horizontal	Sagittal	Vertical
Birth	8.3	8.9	--
2 weeks	9.8	9.9	--
4 weeks	14.0	12.9	--
6 weeks	13.8	13.9	13.4
8 weeks	16.6	16.5	14.8
10 weeks	15.7	15.8	16.0
12 weeks	16.0	16.8	--
16 weeks	14.9	15.0	--
20 weeks	17.1	19.9	--
24 weeks	19.0	20.0	18.0
28 weeks	21.0	21.8	19.0
12 months	20.7	21.8	--
24 months	21.4	21.8	21.0

were probably due to breed differences. The eye seemed to grow more rapidly during the first 8 weeks and reached its average size at about 28 weeks of age.

The cornea at birth (Fig. 4C) was transparent, relatively large, and was considerably more flattened than the adult cornea. The corneal epithelium was thin (10 micra) and consisted of only two layers of cells. The stroma was relatively thin (40 micra) and contained large numbers of corneal corpuscles. Bowman's membrane was not visible; Descemet's membrane and its accompanying endothelium were present. From 2-6 weeks of age (Table 2), the corneal epithelium increased

Table 2. Thickness of the cornea from birth to 2 years of age (corneal measurements in millimeters, epithelium measured in microns; formalin-fixed)

Age	Cornea	Corneal epithelium
Birth	0.40	10
2 weeks	0.35	10
4 weeks	0.37	40
6 weeks	0.35	50
8 weeks	0.30	50
10 weeks	0.45	60
12 weeks	0.38	60
16 weeks	0.48	60
20 weeks	0.38	60
24 weeks	0.40	80
28 weeks	0.50	60
12 months	0.40	60
24 months	0.40	60

in thickness and in the number of cell layers. The stroma became increasingly fibrillar at the expense of the corneal corpuscles. Bowman's and Descemet's membranes presented no apparent changes. At 8 weeks of age the cornea had the appearance of maturity (Fig. 1A).

The sclera increased in thickness from birth (Table 3). The thickness characteristic of the mature eye was not attained until 28 weeks of age. The cellular components reached maturity at 6-8 weeks of age, e.g., the fiber content increased and connective tissue cells decreased until the sclera had the appearance of a mature collagenous connective

Table 3. Thickness of the sclera in three regions from birth to 2 years of age (recorded in millimeters; formalin-fixed)

Age	Posterior pole	Equator	Anterior one-third
Birth	0.1	0.2	0.3
2 weeks	0.1	0.15	0.3
4 weeks	0.1	0.1	0.4
6 weeks	0.3	0.2	0.3
8 weeks	0.3	0.2	0.6
10 weeks	0.3	0.15	0.6
12 weeks	0.2	0.2	0.75
16 weeks	0.35	0.3	0.95
20 weeks			
24 weeks	0.4	0.3	1.0
28 weeks	0.4	0.2	0.7
12 months	0.4	0.3	0.9
24 months	0.4	0.3	0.8

Table 4. Thickness of the retina and choroid from birth to 2 years of age (recorded in millimeters; formalin-fixed)

Age	Retina		Choroid
	Fundus	Peripheral	
Birth	0.25	0.25	0.2
2 weeks	0.2	0.2	0.1
4 weeks	0.2	0.2	0.1
6 weeks	0.2	0.15	0.1
8 weeks	0.2	0.15	0.1
10 weeks	0.35	0.15	0.1
12 weeks	0.2	0.15	0.1
16 weeks	0.3	0.2	0.1
20 weeks	0.25	0.1	0.1
24 weeks	0.3	0.15	0.1
28 weeks	0.3	0.1	0.1
12 months	0.2	0.1	0.1
24 months	0.2	0.1	0.1

tissue. At birth, pigmentation of the sclera was scanty (Fig. 5B) although the cells which were to contain the pigment were present. Pigmentation was fairly complete at 8 weeks of age.

The limbus was evident at birth but was located opposite the ciliary body. During the first 6-8 weeks it had moved forward to the normal position at the corneo-scleral junction. The relocation was due to growth in the sagittal diameter and increased sharpness of curvature on the part of the cornea.

The corneo-scleral junction and scleral spur were not visible at birth. These areas were well-defined at 2 weeks of age by pigmentation at the zone of junction and by modification of the corneal stroma.

The several components of the vascular tunic were present at birth. The tapetum was considerably thinner than at maturity. The choroid was almost twice as thick at birth (0.15-0.2 millimeters) as at maturity (0.1 millimeters at 6 weeks of age). The thickness was due to an extremely vascular chorio-capillaris (Fig. 4D). Pigmentation was not heavy at birth but by 2 weeks of age it was as heavily pigmented as the adult eye.

The mature features of the ciliary body were absent at birth. The three parts of the ciliary muscle were present but mesenchymal connective tissue was dispersed through its fibers. The ciliary processes were adherent to the posterior

Fig. 5. Age changes in the canine eye

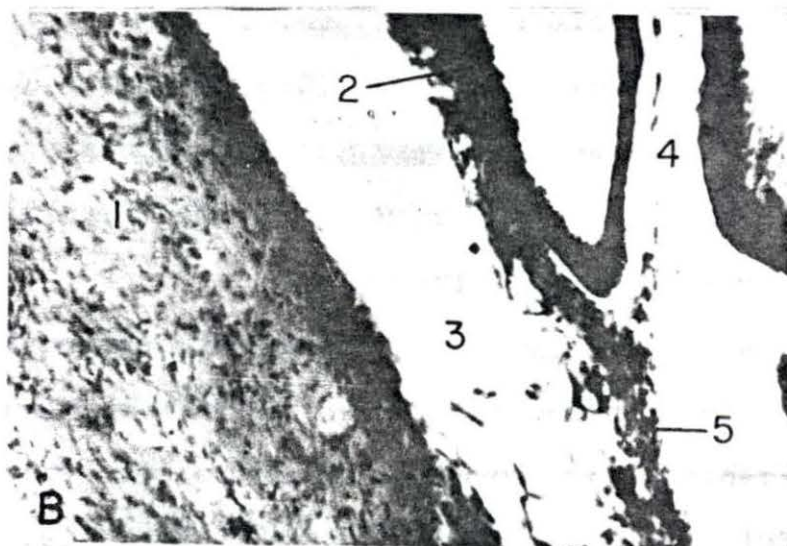
- A. Retina (age: 2 weeks) (115X)
 - 1. Ganglion cell layer and vessels
 - 2. Undifferentiated inner nuclear layer
 - 3. Undifferentiated outer nuclear layer 2 and 3 constitute the combined nuclear layer referred to in the text; in this section, it has just begun to divide

- B. Anterior chamber angle (age: birth) (231X)
 - 1. Sclera
 - 2. Root of the iris
 - 3. Chamber angle showing the meshwork beginning to bridge the angle
 - 4. Ciliary process
 - 5. Primitive pectinate ligament

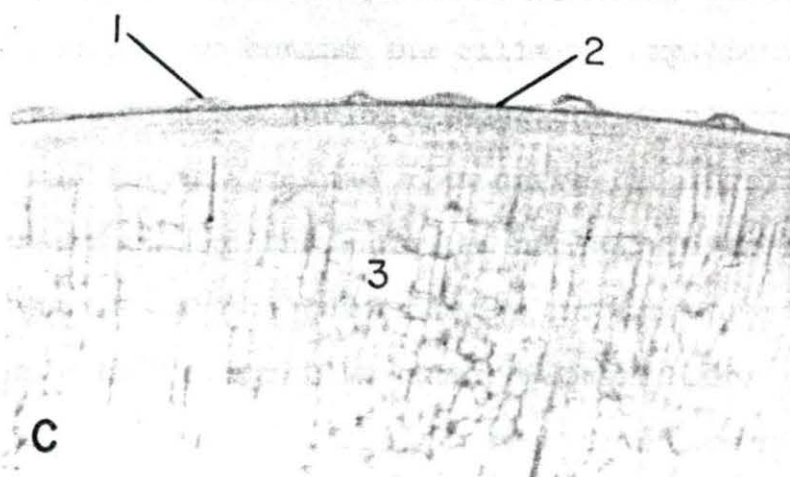
- C. Equator of lens (age: birth) (231X)
 - 1. Capillary of fetal hyaloid vessel system
 - 2. Lens capsule
 - 3. Growing lens fibers



A



B



C

surface of the iris and the epithelium of the processes was smoother than in the adult. At 6-8 weeks the ciliary body appeared mature.

The muscles of the iris were present at birth. Pigmentation of the iris was scanty although numerous chromatophores were present. The anterior epithelium was present and many fetal blood vessels were seen in the stroma.

The anterior chamber was shallow and its angle quite narrow. The meshwork of the angle was adherent to the anterior boundary of the angle (Fig. 5B). The pectinate ligament was formed and visible. At 2 weeks of age, the meshwork filled out the angle and by 6-8 weeks of age the chamber angle had the general structure of maturity.

The retina was the least well-developed structure of the eye. The scalloped margin of the ora serrata was barely visible. From birth to 6 weeks of age, the ora serrata was marked by a fold, the fold of Lange (Duke-Elder, 1934). The pars plana of the ciliary body was so narrow that the retina terminated immediately behind the ciliary body.

The inner and outer nuclear layer could not be distinguished nor was there evidence of a nerve fiber layer (Fig. 5A). At 2 weeks of age the combined nuclear layer had divided and by 6 weeks of age the retina had a mature structure.

The lens was spherical at birth; its anterior curvature pushed the iris forward producing the shallow chamber that

was previously described. The anterior-posterior diameter at birth was 0.35 millimeters; this value had changed only slightly at 8 weeks of age (0.4 millimeters). This figure remained reasonably constant to 2 years of age. The equatorial diameter at birth was also 0.4 millimeters. This measurement gradually increased with age. The equatorial diameter at 8 weeks of age was 0.9 millimeters and remained unchanged at 2 years of age.

Histologically, the anterior lens epithelium was present at birth; the posterior lens epithelium was incorporated in the lens nucleus. The lens capsule was considerably thinner at birth than at maturity (Fig. 5C).

V. DISCUSSION

A. General Anatomic Scheme

Walls (1942) suggested that the eyes of placental mammals conformed to a basic structure irrespective of species and that the differences that occurred were in specific details and not in gross generalities; e.g. all placental mammals normally have a ciliary body, however, its size, muscular components and the form of the ciliary processes will vary depending upon the visual requirements of the species in question. The canine eyes described in this work conformed to this basic structure characteristic of the placental mammal.

Nicolas (1924) stated that the canine eye was spheroidal in form and presented sagittal, horizontal, and vertical diameters to support his observations. The measurements of these diameters in this study compared favorably with Nicolas' findings and indicated that the canine eye has the form of an oblate spheroid.

B. Fibrous Tunic

The canine sclera was found to be thinner than the human sclera. The human sclera was thickest at the posterior pole (Salzmann, 1912); the canine sclera was quite thin in this

region. The thinness was due in all probability to the presence of the retractor muscle of the eye which inserted in the immediate area and provided additional thickness and support. Histologically, the most striking difference between the canine and human sclerae was the presence of considerable amounts of pigment in the canine sclera, particularly at the corneo-scleral junction and the lamina cribrosa.

The radii of curvature of the human cornea (Wolff, 1954) were not as sharp as those values obtained for the canine. Grossly, the cornea of the dog appeared larger than the human which was in keeping with the observations of Rechon-Davigneaud (1943). Histologically, the cornea showed no great difference from the human cornea. The only noteworthy item of interest was that the stroma might have been slightly more cellular than the human.

C. Vascular Tunic

The most striking difference in the vascular tunics of the canine and human eye were the presence of a tapetum and extremely heavy pigmentation of the non-tapetal portions of the vascular tunic of the dog. The tapetum was a cellular type and conformed to the description given by Walls (1942). Walls (1942) stated that the vascular part of the choroid was essentially the same in all vertebrates. The choroid of the

canine eye had the same general features as the choroid of the human eye except that it was thinner and more heavily pigmented. The role of the tapetum in the visual process may be related to the heavy pigmentation of the surrounding choroid.

Walls (1942) stated that the iris of carnivores is essentially the same as in man. The iris of the dog, a canid carnivore, was constructed in this manner. The color of the iris received no special attention in this work. cursory examination at the time the specimens were collected showed no difference in the color of the two eyes. The colors ranged from light-brown to yellow-brown. Browns were the most common colors noted by Sisson and Grossman (1953). The pupil was practically round and coincided with the shape of the optic papilla. Johnson (1901) stated that this was usually the case.

The structure of the ciliary body differed in some respects from that of the human. The muscle tissue did not stain as strongly as the human; this was interpreted to indicate that it was not as functional. Duke-Elder (1934) stated that the ciliary body of lower mammals was not as efficient as it is in the human. A considerable amount of connective tissue was included in the structure of the ciliary muscle which would indicate further that the functional efficiency was lower than the human ciliary body.

D. Neural Elements

The scope of this work precluded the possibility of a cytologic study of the canine retina. For specific details of structure, the reader is referred to the classical works of Schultze (1866), Cajal (1894), and more recently to Parry (1953).

The canine retina was composed of ten histological layers which conformed in general, to the structural plan typical of the mammalia as a group. There was no evidence of a macula lutea or fovea centralis in the specimens examined. Johnson (1901) pointed out that these structural modifications were present only in the primates. Trautmann and Flebeiger (1952) stated that the retinae of dogs hunting by sight may have a rod-free area centralis or, that the cone-cells may be increased in the area centralis. Parry (1953), on the other hand, could find no histologic difference in the retinae of dogs hunting by sight and those hunting by scent. In this work, no evidence of a rod-free zone was observed.

The optic papilla presented no noteworthy feature other than the absence of a physiologic depression. The mammalian eye is usually under a certain intra-ocular pressure. Salzmann (1912) stated that, in the human, the sclera is weakest at the lamina cribrosa and that the optic nerve, in passing through the globe, is rather securely attached to the walls

of the fenestrae of the cribrosal plate. He stated further that the intra-ocular pressure pushed against this part of the globe causing it to bulge posteriorly; the attachment of the optic nerve to the lamina cribrosa would then pull the optic papilla backwards and produce the depression so characteristic of the human optic papilla. Wolff (1954) stated that the depression is severely exaggerated by glaucoma. This observation would tend to support Salzmann's explanation of the depression. The writer suggests that the absence of a physiologic depression in the canine eye is due, at least in part, to the retractor muscle of the eye which inserts in the posterior hemisphere of the globe, and thereby adds strength to the cribrosal area.

E. Chambers of the Eye

The importance of the anterior chamber, and in particular the chamber angle, in the drainage of the aqueous humor and the control of intra-ocular pressure is emphasized by the critical study this portion of the mammalian eye has received in the past 50 years. Braley, Burian, and Allen (1955) described the anomalies of the chamber angle of the human and compared them with the chamber angle of the dog. The structure of the chamber angle of the dog described in this study follows essentially the description presented by these workers. The canal

of Schlemm is absent in the floor of the internal scleral sulcus in the chamber angle of the dog. It is probably replaced functionally by the plexus of Hovius (Nicolas, 1924). The literature does not designate the channel which allows communication between the anterior chamber and the plexus of Hovius (Fig. 4A and B). The writer suggests the term: aqueous canal. From the structural point of view, the chamber angle of the canine eye appeared to be highly functional. However, extensive physiologic studies are planned to definitely substantiate this observation. The posterior chamber presented no significant structural differences from that observed in the human.

F. Refractive Media of the Eye

Nicolas (1924) stated that the lens of carnivores is more flatly curved on the anterior surface. Duke-Elder (1934) maintained that the anterior surface is more sharply curved. In this work, the anterior surface of the lens was found to be more sharply curved than the posterior surface.

Technical difficulties prevented more than a casual description of the vitreous body. Kronfeld (1949) stated that there are no anatomical procedures presently available that are entirely satisfactory for vitreous studies.

VI. SUMMARY AND CONCLUSION

The eyes of 16 dogs were studied macroscopically and microscopically to determine the structure of the mature eye, and to describe the growth changes that occurred from birth to 2 years of age. The results of this study indicate that the canine eye is structurally mature at 6-8 weeks of age. At birth the eye had the form of a sphere; at the age of 6 weeks it had the form of an oblate spheroid, the form typical of the mammalian eye. The direction of growth was not constant. The eye grew most rapidly the first 8 weeks of post-natal life and reached growth maturity at 28 weeks of age.

There were specific details of structure that varied from the human eye. The most outstanding of these were:

1. A larger, more sharply curved cornea.
2. A cellular type of tapetum lucidum subserving acute vision.
3. Pigmentation was more conspicuous than in the human.
4. A macula lutea and fovea centralis were absent in the retina; a rod-free zone in the retina was also absent.
5. A physiologic depression as seen in the human eye was absent in the optic papilla and a theory for its absence was advanced.
6. The anterior chamber angle contained a meshwork

partially filling the angle and the absence of a true canal of Schlemm was noted.

7. The probable function of the plexus of Hovius was stated and the aqueous canals connecting the anterior chamber with the plexus of Hovius was described.

VII. SELECTED REFERENCES

- Arey, Leslie B. 1942. Numerical relationship between the ganglion cells of the retina and the fibers of the optic nerve in the dog. *J. Comp. Neur.* 77:609-616.
- _____, Breush, S. R. and Castanares, S. 1942. Relationship of eyeball size and the number of optic nerve fibers in the dog. *J. Comp. Neur.* 76:417-422.
- Barkhan, Otto. 1936. Structure and function of the anterior chamber angle and Schlemm's canal. *Arch. Ophth.* 15: 101-110.
- Bensley, Robert R. and Bensley, S. H. 1938. Handbook of histological and cytological technique. University of Chicago Press, Chicago, Ill.
- Bradley, O. Charnock and Grahame, Tom. 1948. Topographical anatomy of the dog. 5th ed. Oliver and Boyd, Edinburgh and London.
- Braley, Alson E., Burian, Hermann M., and Allen, Lee. 1955. Iowa City, Iowa. Gonioscopic visualization of Schwalbe's ring. (Personal communication.)
- Bruzzi, Francesco. 1789. (Original not available for examination; cited by Slonaker, J. R. 1897. Comparative study of the area of acute vision in the vertebrates. *J. Morph.* 13:445-502.)
- Callahan, A. 1946. Photography of the eye. *Medical Photography and Radiography.* 24:46-53.
- Chevitz, J. H. 1890. ^UÜber die Entwicklung die Area und Fovea Centralis retina. *Arch f. Anat. u. Entwickl.* heft 5 and 6:232-260. (Original not available for examination; cited by Slonaker, J. R. 1897. Compara-
- Davson, Hugh. 1949. *Physiology of the eye.* Blakiston Co., New York, N.Y.
- Detwiler, S. R. 1937. Nature of the so-called "droplets" found between the rod outer-segments of the vertebrate eye. *Anat. Rec.* 63:295-303.

- Dostolewsky, J. 1886. Über den Bau des Corpus Ciliare und der Iris von Saugtieren. Arch. f. mikr. Anat. 28: 91-121.
- Duke-Elder, W. Stewart. 1934. Textbook of ophthalmology. Vol. 1. C. V. Mosby Co., St. Louis, Mo.
- Dvorak-Theobald, Georgiana. 1934. Schlemm's canal - its anastomoses and anatomic relationships. Trans. Am. Ophth. Soc. 32:574.
- Ellenberger, W. and Baum, H. 1943. Handbuch der Vergleichenden Anatomie der Haustiere. 19th ed. Julius Springer, Berlin.
- Finkbeiner, F. 1855. Vergleichenden untersuchungen der Struktur des Glaskorpers bei dem Wirbeltieren. Z. Wiss. Zool. 6:330-348.
- Friedenwald, Jonas S. and Pearce, H. F. 1931. Circulation of the aqueous humor. Johns Hopkins Hospital Bulletin no. 40:259-270.
- Gowan, Alf and Fry, W. F. 1932. Hyaloid membrane of the vitreous. Am. J. Ophth. 15:428-432.
- Gunter, R. and Harding, H. G. W. 1951. Spectral reflection factors in the cat's tapetum. Nature. 168:293-294.
- Johnson, George Lindsay. 1901. Comparative anatomy of the mammalian eye. Philos. Trans. Roy. Soc. (London). 194B: 1-82.
- Kinsey, W. F. and Jackson, B. 1945. Development of secretory function in the ciliary body in the rabbit eye. Arch. Ophth. 34:415-417.
- Krause, W. 1891. Die Retina. Internat. Monatschrift für Anat. und Physiol. Bd. 8:414-415. (Original not available for examination; cited by Slonaker, J. R. 1897. Comparative study of the area of acute vision in vertebrates. J. Morph. 13:445-502.)
- Kronfeld, Peter C. 1949. Further gonioscopic studies on the canal of Schlemm. Arch. Ophth. 41:393-405.
- _____ and McHugh, Gladys. 1948. Human eye in anatomical transparencies. Bausch and Lomb Press, Rochester, N.Y.

- Langham, M. 1951. Secretion and rate of flow of the aqueous humor in the cat. *Brit. J. Ophth.* 35:409-415.
- Lightbedig, W. H. 1867. Observations on the comparative anatomy of the cornea of vertebrates. *J. of Anat. and Physiol.* 1:15-43.
- Lindorfer, Katherine. 1955. Iowa City, Iowa. Celloidin technique for ocular tissues. (Personal communication.)
- Lowenstein, A. 1949. Glomus cells in the human choroid. *Nature (London)*. 163:4132.
- Michaelis, P. 1796. Über einer goldenen Fleck und ein Loch in der Nervenhaut des Menschlichen Auges. *J. der Erfindungen, Theorien u. Widersprüche in der Natur- und Arznet-Wissenschaft.* Bd. 15:3-17. (Original not available for examination; cited by Slonaker, J. R. 1897. Comparative study of the area of acute vision in vertebrates. *J. Morph.* 13:445-502.)
- Michaelson, I. C. 1954. Retinal circulation in man and animals. Charles C. Thomas Publishers, Springfield, Ill.
- _____ and Stedman, H. F. 1949. Injection of the retinal vascular system of enucleated eyes. *Brit. J. Ophth.* 33:376-379.
- Miller, Malcolm E. 1954. Guide to the dissection of the dog. 4th ed. Edwards Bros. Inc., Ann Arbor, Mich.
- Modes, E. 1936. Das Blutgefässt das Augenhintergrundes bei den Haustieren (Pferd, Rind, Schaf, Ziege, Schwein, Hund, Katz, und Konnchen). *Arch. für Wissen. und practische Tierheil.* 70, no. 6:449-473.
- Moffat, D. E. 1952. Regulatory mechanism in the posterior ciliary arteries of the dog. *Nature (London)*. 169:1015.
- Moller, H. 1910. Lehrbuch der Augenheilkunde für Tierärzte. Stuttgart.
- Nicolas, Eugene. 1924. Veterinary and comparative ophthalmology. (Edited and translated by Henry Gray.) H. and W. Brown, London.
- Parry, H. B. 1953. Degenerations of the dog retina. I. Structure and development of the retina of the normal dog. *Brit. J. Ophth.* 37:385-404.

- Polyak, S. L. 1941. Retina. University of Chicago Press, Chicago, Ill.
- Ramon y Cajal, Santiago. 1893. La Retina des Vertebres. La Cellule. 9:119-258.
- Rechon-Davigneaud, André. 1943. Les yeux et la vision des vertebres. Masson et C. Editeurs, Paris.
- Salzmann, Maximillian. 1912. Anatomie und Histologie des Menschlichen Augapfels im Normalzustande. Franz Deuticke, Leipzig und Wien.
- Schultze, Max. 1866. Zur Anatomie und Physiologie der Retina. Arch. f. mikr. Anat. Bd. 2:175-286.
- _____ 1873. Retina. In Manual of human and comparative histology. (Edited by Striker.) Vol. 3 (translated by Powers). New Sydenham Press, London.
- Schwalbe, G. 1870. Untersuchungen über die Lymphbahnen des Auges und ihre Begrenzungen. Arch. f. mikr. Anat. 6:261.
- Seidel, E. 1922. Weitere experimentelle untersuchungen über die Quelle und die Verlauf der interokularen Saftstromung. Arch. f. Ophth. 108:420.
- Sisson, S. and Grossman, J. A. 1953. Anatomy of the domestic animals. 4th rev. ed. W. B. Saunders Co., Philadelphia, Pa.
- Slonaker, J. R. 1897. Comparative study of the area of acute vision in vertebrates. J. Morph. 13:445-502.
- Sommers, I. C. 1949. Histology and histopathology of the eye and its adnexa. Grune and Statton, New York, N.Y.
- Sonderman, R. 1933. Über Entstehung, Morphologie, und Funktion der Schlemmshen Kanals. Acta Ophth. 11:280.
- Sugar, H. S. 1942. Anatomic factors that influence the depth of the anterior chamber, their significance. Am. J. Ophth. 25:1341-1351.
- Swindle, P. F. 1937. Principle drainage areas of the eye. Arch. Cphth. 17:420-443.

- _____ 1942. Morphology and function of the scleral vessels. Am. J. Ophth. 25:991-995.
- Trautmann, Alfred and Fiebiger, Josef. 1952. Histology of domestic animals. (Translated by Habel, Robert and Biberstein, Ernst L.) Comstock Publishing Associates, Ithaca, N.Y.
- Troncoso, M. and Castroviejo, R. 1936. Micro-anatomy of the eye with the slit-lamp microscope. I. Comparative anatomy of the angle of the anterior chamber in living and sectioned eyes of mammals. Am. J. Ophth. 19:371-384; 481, 583.
- Uyama, Yasuo. 1951. Mammalian retina. II. Summarized description based chiefly on my own investigations. Med. J. Osaka Univ. 2:113-157.
- Walker, Ernest P. 1938. Eyes that shine at night. Smithsonian Inst. Rep. 1938:349-360.
- Walls, Gordon Lynn. 1932. Hot celloidin technique for animal tissues. Stain Tech. 7:135-148.
- _____ 1936. Microtechnique of the eye with suggestions as to materials. Stain Tech. 13:69-72.
- _____ 1936. Rapid celloidin technique for the rotary microtome. Stain Tech. 11:89-93.
- _____ 1937. Significance of the foveal depression. Arch. Ophth. 18:912-919.
- _____ 1939. Significance of "Kilmer's droplets" of the vertebrate retina. Anat. Rec. 73, no. 3:373-388.
- _____ 1940. Pigment of the vertebrate lens. Science. 91:172.
- _____ 1942. Vertebrate eye. Cranbrook Institute of Science. Bloomfield Hills, Mich.
- Wolff, Eugene. 1954. Anatomy of the eye and orbit. 7th ed. Blakiston Co., New York, N.Y.
- Wood, E. H. 1948. Normal optic nerve; classification of the optic disc based on branching of the central retinal artery. Arch. Ophth. 39:305-313.

Wybar, R. C. 1955. Study of the choroidal circulation in
the eye of man. J. Anat. 88:94-98.

VIII. ACKNOWLEDGMENTS

The writer wishes to extend his sincere thanks and appreciation to Dr. Robert Getty for guidance and constructive criticism given during the course of this investigation; to the medical staff of the Department of Ophthalmology, University Hospitals, Iowa City, Iowa, for their guidance in technical problems and many helpful suggestions; to Dr. John G. Bowne for the excellent photomicrographs; and to Dr. George C. Christensen for his many helpful criticisms and suggestions.

The writer appreciates the support of the Gaines Dog Food Division of General Foods Corporation, Kankakee, Ill., who generously supplied the feed for the animals utilized in this investigation.