The Anatomy of the Ciliary Region of the Chicken Eye

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Purpose. To describe the detailed anatomy of the ciliary region of the chicken eye.

Methods. Fifty-two eyes from White Leghorn chickens were examined in the course of this study. Descriptions are based on specimens examined using microdissection and bright field microscopy of sections embedded in paraffin or epon. Microdissection was assisted through the use of an iodine-based stain.

Results. The ciliary region of the chicken eye is asymmetric through the horizontal plane, with the distance from the limbus to the equator of the eye being greatest temporally. This asymmetry is reflected in the relative development of the ciliary musculature. The nasal ciliary muscle fibers are the shortest of any of the quadrants, and the nasal quadrant lacks a well-developed scleral venous sinus. The ciliary musculature is approximately 2.5 mm in extent (temporally) and is composed of two regional groups (anterior and posterior) within which five distinct arrangements of muscle fibers can be recognized. The majority of fibers insert on fibrous elements associated with the inner or outer walls of the scleral venous sinus, which, in turn, are continuous with the inner stromal elements of the cornea.

Conclusions. The ciliary musculature of the chicken eye is composed of two major muscle groups within which five arrangements of muscle fibers have been identified. The anatomy of the ciliary muscle is consistent with the recently proposed functions of altering the corneal curvature for corneal accommodation and moving the ciliary body anteriorly as a part of the lenticular accommodative mechanism. The ciliary muscle also may serve in the regulation of aqueous dynamics within the eye. Invest Ophthalmol Vis Sci. 1995;36:889–896.

In the chicken eye, it has been demonstrated only recently that the iris muscle changes the curvature of the lens during accommodation, whereas the ciliary muscle is responsible for increasing the curvature of the cornea for corneal accommodation.[1,2] The ciliary muscle of the avian eye, however, has been the subject of numerous investigations since Philip Crampton[3] first identified it in 1813. Crampton[3] noted that the ciliary muscle attached to the inner lamella of the cornea and proposed that it flattened the cornea as part of the avian accommodative mechanism. Brücke,[4] however, thought that Crampton's functional interpretation was incorrect and proposed that Crampton's muscle must act to increase the corneal curvature. Brücke[4] also identified a posterior division of the ciliary muscle, which he named the tensor choreoidae. Müller[5] later described the posterior ciliary muscle as having two distinct origins. The outer part was as Brücke[4] had described it, originating on the sclera under the scleral ossicles and inserting on the pars plana of the ciliary body. A second, inner portion of the ciliary muscle, however, inserted on the fibrous sheet that forms the posterior extension of the inner lamella of the cornea.

In spite of these early, and largely accurate, descriptions of the anatomy and function of the avian ciliary muscle, there has been considerable confusion recently surrounding the accommodative mechanism of the chick eye and the role of the ciliary muscles. In addition, since the observation that chicks develop myopia in response to altered visual experience,[6] chicks have become extensively used as an animal model in the study of developmental myopia and emmetropization of the eye.[7,8] Despite this, studies detailing the functional anatomy of the ciliary muscle of the chick eye are few and are often contradictory.

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Two recent studies of the ciliary musculature of the chicken eye reported that two muscle groups were present.[9,10] These authors reported finding an anterior muscle group that inserted on the outer wall of the scleral venous sinus and a posterior muscle group that passed from the sclera posteriorly to insert on the uvea. In contrast to these studies, we report here for the first time that the ciliary musculature of the chicken eye is actually comprised of two muscle groups within which *five* distinct orientations of muscle fibers can be identified. We propose that four anatomically and functionally distinct muscles be recognized in the ciliary region of the chicken eye and propose new descriptive terminology for these muscles. A brief report of this work has been published.[11]

METHODS

All animals were treated in accordance with the ARVO Statement for the Use of Animals in Ophthalmic and Vision Research. Fifty-two chicken eyes were examined in the course of this study. The ages of the animals ranged from 4 weeks to 2 years. Forty eyes were fixed in Bouin's solution, or 10% neutral buffered formalin. Eyes were opened in either a sagittal or a horizontal plane (relative to the optic axis) and examined under a dissecting microscope. Visualization of muscle fibers was aided by the use of an iodine-based stain.[12] The anterior segments of the eyes were processed routinely and embedded in paraffin. Eight-micrometer sections were obtained and stained with hematoxylin and eosin or with periodic-acid Schiff or Masson trichrome stain. Twelve eyes were fixed in 4% glutaraldehyde blocked in either the sagittal or horizontal plane to include the lens, decalcified in 10% ethylenediaminetetraacetic acid for 48 hours, dehydrated, embedded in EMbed 812 or JB4 polaron methacrylate embedding media (BioRad Polaron Instruments; Cambridge, MA), serially sectioned at 10 μm and stained with basic fuchsin and methylene blue. All sections were examined by bright field microscopy.

RESULTS

Anatomic

The anterior segment of the eye is asymmetric through the horizontal plane, with the distance from the equator of the globe to the limbus being greatest temporally (Fig. 1). This asymmetry is reflected in the relative development of the ciliary structures. The ciliary muscle fibers are shorter at the nasal quadrant than at any other quadrant of the eye, and the nasal quadrant generally lacks a well-developed scleral venous sinus (Fig. 2). All the ciliary muscle fibers identified are striated. All the fibers are arranged longitudinally. The ciliary musculature of the chicken eye is composed of two regional groups (anterior and posterior) within which five distinct arrangements of muscle fibers can be recognized (Fig. 3). The longitudinal extent of the combined ciliary muscle fibers is approximately 2.5 mm temporally. Terminology proposed for the ciliary muscles of the chicken eye is summarized in Table 1.

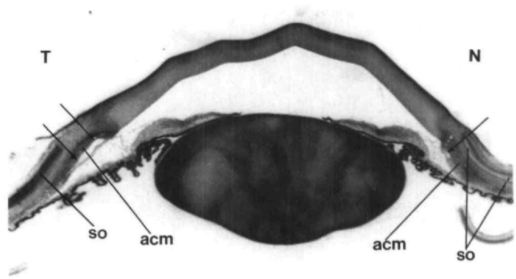
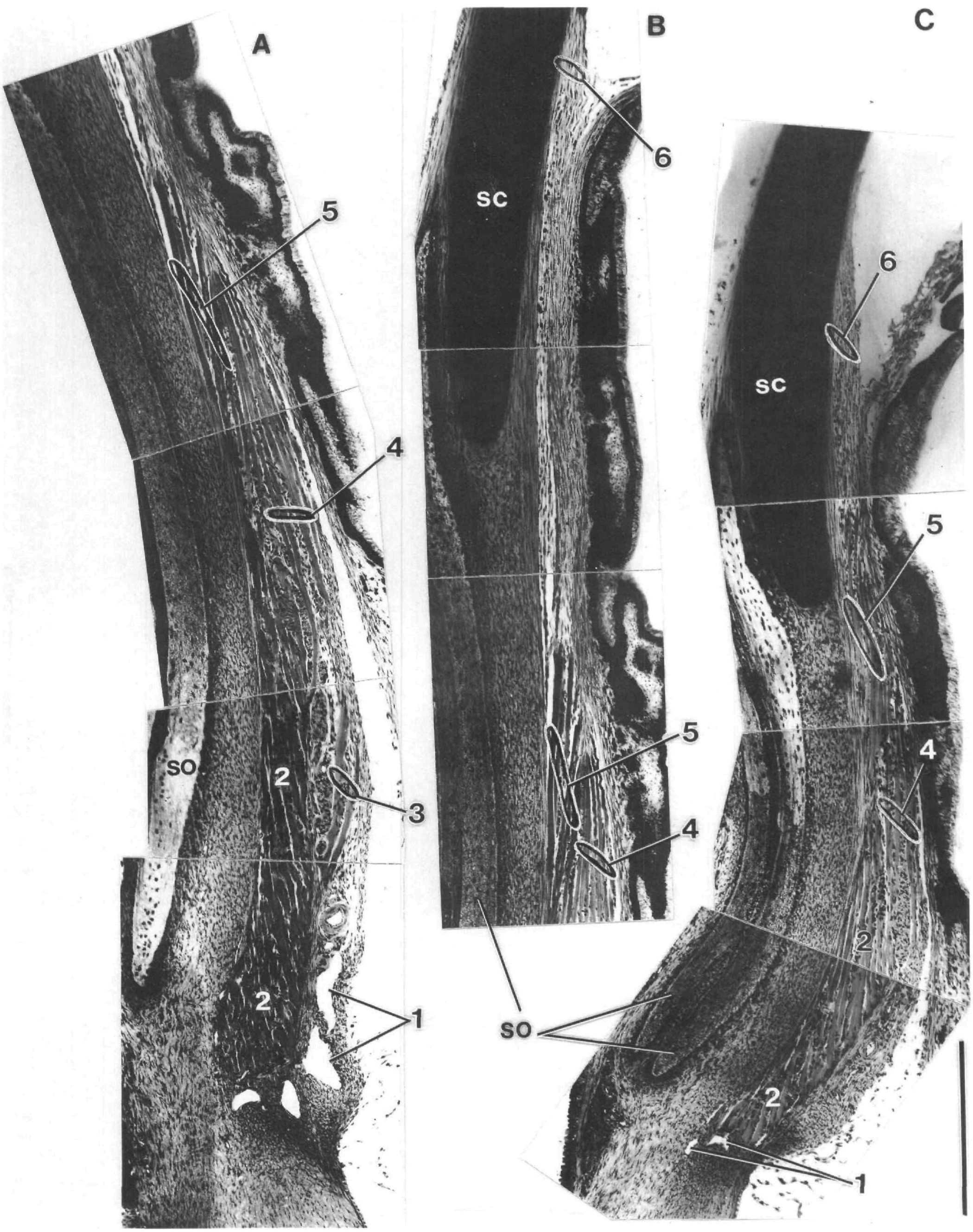


FIGURE 1. Photomicrograph of the chicken eye opened in the horizontal plane showing the nasal (N)–temporal (T) asymmetry evident at the ciliary region of the eye. Note that the scleral venous sinus (*arrows*) is considerably larger temporally than nasally. Note also that the anterior ciliary muscle (acm) extends beyond the apices of the scleral ossicles (so) temporally but not nasally. Scale bar = 2 mm.

Scleral Venous Sinus and Associated Stromal Elements

The scleral venous sinus typically consists of two to three large venous spaces divided by an annular artery and its associated stromal elements. A degree of variation is commonly encountered, and three or more venous spaces may be seen. Nasally, the sinus is poorly developed, with several smaller channels being typi-

FIGURE 2. Photomicrographs comparing the temporal (A, B) and nasal (C) quadrants of the chicken eye. (A) A representative section of the anterior ciliary region of a temporal quadrant of the eye. (B) An overlapping micrograph of the posterior ciliary region of the same temporal quadrant shown in A. The posterior insertion of the posterior ciliary muscle to the pars plana of the ciliary body can be seen in both A and B. (B) The tenacular ligament of the temporal segment, where the ciliary body attaches to the scleral cartilage of the globe. In comparing A and C, it can be seen that the scleral venous sinus is less well developed and the intermediate ciliary muscles are absent: 1 = scleral venous sinus; 2 = anterior ciliary muscle; 3 = intermediate ciliary muscle; 4 = sinociliary muscle; 5 = sclerociliary muscle; 6 = tenacular ligament; sc = scleral cartilage; so = scleral ossicles. Scale bar = 400 μm.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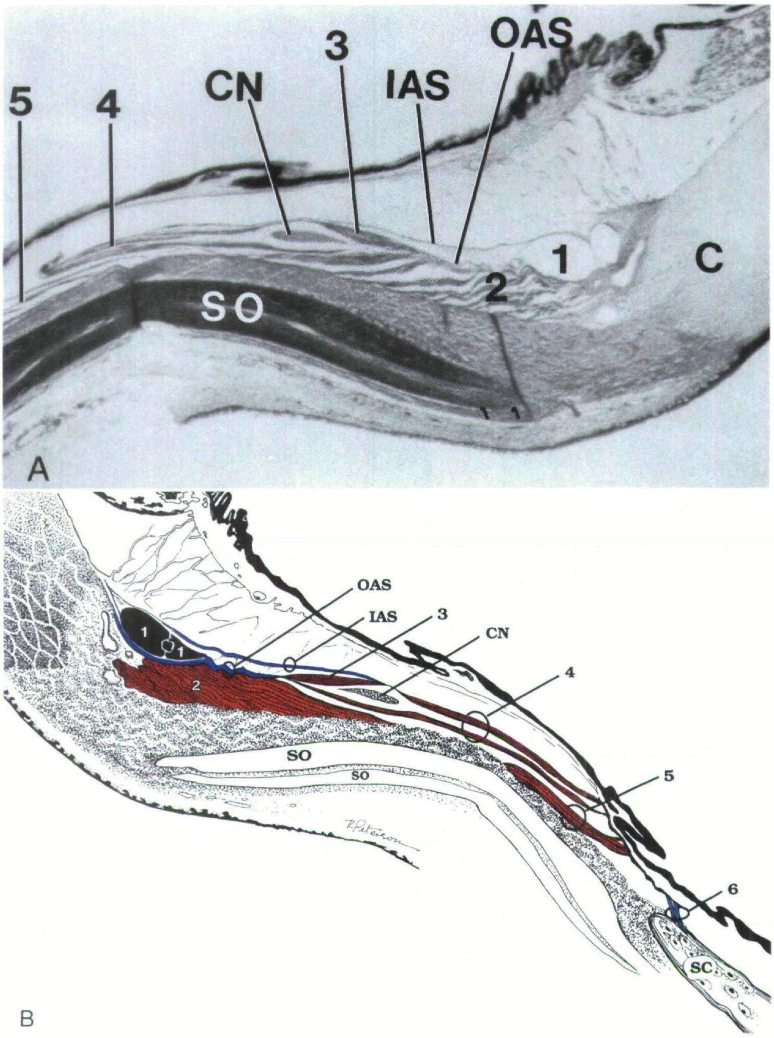

FIGURE 3. Photomicrograph (**A**) and illustration (**B**) of the ciliary musculature of the temporal quadrant of the chicken eye: 1 = scleral venous sinus; 2 = anterior ciliary muscle; 3 = intermediate ciliary muscle; 4 = sinociliary muscle (note the distinct origins from the inner and outer aponeurotic sheets which extend posterior to the scleral venous sinus); 5 = sclerociliary muscle; 6 = tenacular ligament; C = cornea; CN = ciliary nerve; IAS = inner aponeurotic sheet; OAS = outer aponeurotic sheet; SC = cartilagineous sclera; SO = scleral ossicles.

TABLE 1. Proposed Terminology of the Ciliary Musculature of the Chicken Eye *(together with previously used terminology)*

Anterior Ciliary Muscle Group	*Posterior Ciliary Muscle Group (Brücke's Muscle)**
Anterior ciliary muscle *(Crampton's muscle, anterior ciliary muscle)*	Sinociliary muscle† *(Müller's muscle, intermediate muscle, radial fibers)*
Intermediate ciliary muscle *(Lord's temporal muscle)*	Sclerociliary muscle *(Brücke's muscle, posterior ciliary muscle)*

* Brücke[4] originally described the posterior ciliary muscle group, recognizing that it differed from the anterior ciliary muscle group described by Crampton.[3] Müller[5] subsequently identified two arrangements of fibers in the posterior ciliary muscle group based on their distinct origins. This divided Brücke's muscle into two divisions, henceforth given the eponyms Brücke's muscle and Müller's muscle. Even after this distinction was made, however, many authors continued to refer to the combined posterior ciliary muscle group as Brücke's muscle.

† This muscle has two distinct origins (as described here) that were not mentioned in Müller's original description and have not been identified in subsequent studies.

cally observed (Fig. 2). There is a thin sheet of dense stroma associated with the external wall of the scleral venous sinus that continues posteriorly as an aponeurosis (Fig. 3). The outer surface of this aponeurosis serves as a site for the attachment of anterior ciliary muscle fibers and, more posteriorly, the site of origin of some of the posterior muscle fibers. Associated with the inner wall of the sinus is a thin condensation of stromal elements. As with the stromal elements of the outer wall, the sheet composing the inner wall continues posteriorly as an aponeurosis approximately twice as far as the outer aponeurosis (Fig. 3). The posterior end of this aponeurosis serves as a site for insertion of a subgroup of the posterior ciliary muscle fibers. The aponeurotic sheets, which extend posterior to the inner and outer walls of the sinus, are themselves tenuously connected by loosely arranged connective tissue as well as by the distinct attachments of three to eight intermediate ciliary muscle fibers. The muscle fibers and the intervening connective tissue may serve to "yoke" loosely the two sheets mechanically. Loosely arranged stromal elements also are found associated with the inner wall of the scleral venous sinus, and they connect the inner and outer walls of the sinus, surrounding the annular artery.

Anteriorly, the stromal elements associated with the inner and outer walls of the scleral venous sinus are continuous with the stroma of the most internal aspect of the cornea. The stroma of the cornea in this region is more loosely arranged than the more externally situated corneal stroma and forms a posteriorly projecting corneal spur. The corneal spur is approximately 0.2 mm in longitudinal extent and abuts the inner wall of the anterior channel of the scleral venous sinus. This spur serves as a direct insertion site for the most anteriorly situated ciliary muscle fibers.

Anterior Muscle Group

The anterior ciliary muscle group is composed of a substantial *anterior muscle* and a diminutive *intermediate muscle*, the latter of which is absent in the nasal quadrant of the eye.

Anterior Ciliary Muscle. The anterior muscle is approximately 1.2 mm to 1.5 mm long (temporally) and is approximately 0.1 mm thick. All these fibers have as their origin the most internal aspect of the fibrous sclera located near the anterior apices of and within the ring of scleral ossicles. The fibers are arranged in "shingle-like" fashion, with the more posterior fibers residing external to the fibers that have a more anterior origin. The most posterior fibers originate from the sclera in a region that approximates the most internal bowing of the curvilinear scleral ossicles.

In the temporal segment, the most anterior of the muscle fiber insertions extend approximately 0.25 mm beyond the anterior apices of the scleral ossicles (Fig. 2). In the nasal segment, this anterior insertion is at the anterior apices of the scleral ossicles. Nasally, from 5 to 10, and temporally, from 10 to 20, of the most anterior fibers insert on the stroma of the inner cornea at the corneo-scleral spur.

The more posterior fibers of this muscle insert on the aponeurosis that is continuous with the inner lamella of the cornea. This aponeurosis is considerably more pronounced in the nasal quadrant of the eye, where the scleral venous sinus is all but absent. In the remainder of the eye, where the sinus is more pronounced, this aponeurosis forms the outer wall of the scleral venous sinus. The great majority of fibers of the anterior muscle insert directly along the stromal elements of this aponeurosis.

Intermediate Muscle Fibers. In the best-preserved specimens, a distinct group of fusiform muscle fibers could be delineated that connect the thin aponeurotic sheets, which extend posterior from the inner and outer walls of the scleral venous sinus (Figs. 2, 3). These fibers were not present in all specimens and were never seen nasally where the aponeurosis is pronounced and does not constitute the inner and outer walls of the scleral venous sinus. These muscle fibers are approximately 0.2 mm in longitudinal extent and are typically only three to eight fibers thick (Figs. 2, 3).

Posterior Muscle Group

The fibers of this muscle group share a common insertion on the outer wall of the pars plana of the ciliary body (Fig. 2). This region of the ciliary body constitutes the anterior aspect of the tenacular ligament (see Tenacular Ligament). The posterior ciliary muscle fibers have three distinct origins (Figs. 2, 3). The majority of fibers arise from the inner wall of the sclera in the region of the most medial bow of the scleral ossicles, approximately 2.2 mm anterior to the most anterior edge of the scleral cartilage. Fibers also originate from the aponeurotic sheet continuous anteriorly with the inner wall of the scleral venous sinus, and a few long fibers originate from the posterior portion of the aponeurotic sheet continuous anteriorly with the outer wall of the scleral venous sinus. These fibers originate in the region adjacent to the site of origin of the fusiform intermediate muscle fibers.

Tenacular Ligament

The tenacular ligament forms the posterior attachment of the ciliary body to the sclera of the eye just posterior to the anterior edge of the scleral cartilage (Fig. 2b). This fibrous structure is located posterior to the posterior ciliary muscle and is continuous with the stromal element of the pars plana of the ciliary body. It passes posteriorly from the point of insertion of the posterior ciliary muscle fibers to its origin on the thin inner fibrous scleral layer of the cartilage. It shows an asymmetry in horizontal section being longer in the temporal quadrant of the eye (approximately 1.2 mm in length) than in the nasal quadrant (Fig. 2). Nasally, its entire extent lies beneath the anterior edge of the cartilaginous cup. Temporally, the insertion of the posterior ciliary muscle fibers onto the anterior aspect of the tenacular ligament is approximately 0.5 mm anterior of the edge of the scleral cartilage. The ora serrata is located internal to the site of attachment of the tenacular ligament to the scleral cartilage.

DISCUSSION

Nomenclature

The literature pertaining to the avian ciliary musculature is confusing. Recently, the musculature was reported to consist of one to four unique muscles.[13] Most commonly, the ciliary musculature of the avian eye is said to be comprised of an anterior muscle and a posterior muscle. A third muscle is variably reported to be present. This last group of muscle fibers is located posteriorly and is also referred to as Müller's muscle and radial fibers by some authors.[13,14] Some of the confusion is doubtless due to species variation. A single author, for example, recognized from one (meadowlark) to four (red-tailed hawk) distinct ciliary muscles, depending on the species.[14] Further confusion is caused by the tendency of some investigators to split the posterior muscle group into the intermediate muscle (Müller's muscle or radial fibers) and the posterior muscle (Brücke's muscle), whereas others simply lump them as a single posterior muscle (Brücke's muscle) with minor variations in origin. Lord[14] described a fourth muscle, present in some species, that he named the temporal ciliary muscle. He stated that this muscle had its greatest development temporally, though a few fibers could be found in the nasal quadrant.

We propose the following terminology for the ciliary musculature of the chicken eye (Table 1): The ciliary musculature of the chicken is comprised of two regional muscle groups, namely an *anterior ciliary muscle group* and a *posterior ciliary muscle group*. The anterior group can be subdivided into a robust *anterior ciliary muscle* and a diminutive *intermediate ciliary muscle*. The anterior ciliary muscle is identical to that originally described by Crampton.[3] It originates from the sclera and inserts predominantly on the fibrous elements associated with the outer wall of the scleral venous sinus. Between five (nasally) and 20 (temporally) of the most anterior of these fibers insert directly on the stromal elements of the inner cornea.

The intermediate ciliary muscle is identical to that described by Lord[14] to be well developed in the eyes of red-tailed and sparrow hawks and, in a less robust condition, present in other species. It is best developed temporally in the chicken but is also present superiorly and inferiorly.

Muscle fibers that constitute the *posterior ciliary muscle group* have three distinct origins and share a common insertion on the pars plana of the ciliary body. We propose the term *sinociliary muscle* be used to designate those muscle fibers that take origin from the aponeurotic sheets continuous anteriorly with the stromal elements of the inner and outer walls of the scleral venous sinus. Although these fibers have two distinct origins (inner and outer stromal elements), a single descriptive designation seems appropriate because they both originate from sinus-associated structures and would have similar actions. This term designates muscle fibers that have been referred to as Müller's muscle, intermediate ciliary muscle, and radial fibers. These terms are inadequate descriptors. The term sinociliary also implies that these fibers require the presence of the scleral venous sinus. These fibers are absent in nasal sections that lack a sinus.

We propose the term *sclerociliary muscle* be used to designate the most posteriorly located muscle fibers of this group that pass from the sclera to the ciliary body. This term would designate fibers commonly referred to as Brücke's muscle or as posterior ciliary muscle.

Effects of Muscle Contraction

Anterior Muscle Group. The possible actions of the anterior muscle fibers are to draw the inner lamellae of the cornea posteriorly and internally[1] and to pull the outer wall of the scleral venous sinus externally and posteriorly.[15] It should be noted that the anterior muscle fibers have origins that reside far posterior to the anterior apex of the scleral ossicles. A contraction of the anterior ciliary muscle would impart an inward rotation of the peripheral cornea about the fulcrum provided by the anterior apex of the scleral ossicles. The effect would be to flatten the peripheral cornea while increasing the curvature of the central cornea during accommodation for near.[1]

The effect of dilating the scleral venous sinus also would be augmented during accommodation by the trabeculae of the pectinate ligament and the uveal meshwork, which have attachments to the inner wall of the scleral venous sinus.[15] During accommodation, the tension on the pectinate ligament is increased through a contraction of the peripheral iris sphincter muscle.[1,2] This would act to pull the pectinate ligament and the uveal meshwork of the scleral venous sinus inward, further acting to dilate the sinus. During accommodation, there is an increase in intraocular pressure on the order of 3 mm Hg.[1] It is possible, therefore, that the fibers of the ciliary muscle, in direct association with the venous sinus and the increased tension on the fibers of the pectinate ligament, are acting to prevent the collapse of the sinus under the impact of the increased intraocular pressure.

The action of the intermediate ciliary muscle fibers seem to "yoke" together the fibrous sheets associated with the inner and outer walls of the scleral venous sinus. The outer wall of the sinus remains fixed, and the fibrous sheet associated with the inner wall is pulled anteriorly. This may relieve some of the tension on the inner wall of the sinus when the posterior ciliary muscles are contracted. This action may aid blood flow through the sinus when the eye is in the accommodated state.

Lord[14] proposed that this muscle served as a *depressor corneae,* with its greatest effect occurring temporally. Given the diminutive extent of this muscle compared to the anterior ciliary muscle as a whole, a major action of which is that of a *depressor corneae,* the intermediate muscle would contribute relatively little in this regard. The presence and relative development of the intermediate ciliary muscle coincides with the relative development of the scleral venous sinus and the sinociliary muscles, so it seems more likely to serve a regulatory function on the scleral venous sinus.

Posterior Muscle Group. The combined action of these muscle fibers pulls posteriorly the stromal elements of the scleral venous sinus and, hence, the inner corneal lamellae to which they are associated, and it moves the posterior circumference of the ciliary body anteriorly.

Posteriorly directed tension applied to the aponeurotic sheets would be directly transmitted to the inner lamellae of the cornea with which they are continuous. This would augment the action of the anterior ciliary muscle to rotate the inner lamellae of the cornea posteriorly and inward around the fulcrum of the anterior aspect of the scleral ossicles. By pulling on inner and outer walls of the scleral venous sinus simultaneously, forces would be applied that would tend to flatten, and possibly collapse, the sinus.

The function of the posterior ciliary muscle group in moving the circumference of the ciliary body anteriorly serves as a part of the lenticular accommodative mechanism.[2] In the unaccommodated chicken eye, there is a resting tension on the ciliary body that serves to maintain the lens in a flattened state, similar to the mammalian eye. A contraction of the posterior ciliary muscle would relieve some of the resting tension on the ciliary body to allow the lens to "round up" under its own elasticity. This, however, represents only a relatively minor component of the lenticular accommodative mechanism of the chick eye. Lenticular accommodation in chicks has been shown to be mediated primarily through the action of the peripheral iris musculature.[2] The peripheral iris muscle, located at the root of the iris, directly squeezes the lens during accommodation. This action of the peripheral iris musculature would further stretch the ciliary body in the accommodated eye. The simultaneous contraction of the posterior ciliary muscle would relieve some of this tension to allow the peripheral iris musculature to act on the lens directly rather than against the tension of the ciliary body.

In summary, the ciliary musculature of the chicken eye is composed of two distinct muscle groups within which five distinct muscular arrangements can be identified. Contraction of these muscles play a role in changing corneal curvature, lens curvature, and aqueous dynamics.

Key Words

avian, chicken, bird, eye, anatomy

Acknowledgments

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