

# THE QUARTERLY REVIEW of BIOLOGY



## A HISTORY OF STUDIES OF VISUAL ACCOMMODATION IN BIRDS

ADRIAN GLASSER

*Section of Physiology, Cornell University  
Ithaca, New York 14853 USA\**

HOWARD C. HOWLAND

*Section of Neurobiology and Behavior, Cornell University  
Ithaca, New York 14853 USA*

### ABSTRACT

*Since 1813, when Crampton first described the ciliary muscle of the avian eye, there has been little agreement on how birds are able to change the focus of their eyes. Numerous later studies on the eyes of a variety of bird species contradicted earlier findings or proposed new accommodative mechanisms. The resulting confusion persists today, and a number of significant works on the avian eye perpetuate many of the myths developed during the 1800s. There is little consensus on avian accommodation; the early literature contains many accurate descriptions of the mechanisms, along with elegant experimental evidence to support them. Much of the early literature, however, is in German and has remained obscure. Further, among the mechanistic descriptions of avian accommodation are many that are incorrect. The current confusion can be attributed in part to the fact that some birds have both corneal and lenticular accommodation. It is unclear to what extent different bird species employ both mechanisms, or depend on one mechanism or the other. These facts, together with the diversity of bird species, their range of visual requirements, and the numerous anatomical differences in their eyes, make it impossible to describe a single avian mechanism of accommodation. Our own experience in studying accommodation in the chick eye has led us to review the historical literature in an attempt to provide a new foundation for future studies on visual accommodation in birds.*

\* Present address: Department of Ophthalmology and Visual Science, University of Wisconsin-Madison, Madison, WI 53792-3200 USA.

*While in relation to the anatomical arrangements [of the bird eye], these have led our knowledge pretty much to a conclusion. . . . There is among all these works no real difference of opinion. However, in terms of the accommodative mechanism of the bird eye, at the present time there are many different views of what is going on. Here the circumstances are very similar to what happened a few decades ago in the study of accommodation generally, but particularly with humans, when Helmholtz made the remark, "There is no other portion of physiological optics in which one finds so many differing and contradictory ideas as in the accommodation of the eye, where we have only recently actually made observations on what previously was left to the play of hypotheses" (Beer 1893:193).*

#### INTRODUCTION

**A** NORMAL, relaxed eye exhibiting no refractive error can form a sharply focused image on the retina for objects at optical infinity. Objects closer than infinity will remain unfocused unless accommodation occurs to increase the optical power of the eye. Accommodation is the process whereby the eye is able to change its focus from the relaxed state when viewing distant objects at optical infinity to viewing objects at a point closer to the eye. The need to accommodate differs greatly among animal species. Dogs, for example, have relatively poor optics and few requirements for fine visual tasks, and thus have little need for accommodation. Birds such as the cormorant, on the other hand, have an extraordinary accommodative range, which allows them to exploit both terrestrial and aquatic environments, a visual challenge that can be met by few other vertebrates. In humans, the true significance of functional accommodation is demonstrated through its loss following the inevitable onset of presbyopia, a condition of the aging eye that eventually leads to a total loss of accommodation.

#### AVIAN ACCOMMODATION

Avian accommodative mechanisms are of particular interest because of the diversity of visual behaviors that birds exhibit. The high optical quality and relative infrequency of refractive errors contribute to the remarkable ability of the avian eye. Birds have exploited a wider variety of habitats with greater visual demands than those experienced by probably any other animal group. Although many other species survive in spite of their vision, birds are perhaps successful *because* of their good visual abilities. There are no substantiated reports of the eyes of mature birds with significant refractive errors. Although farsightedness (hyper-

opia) has been measured in one bird species, the brown kiwi, this hyperopia was attributed to an artifact of the measurement techniques on the relatively small nocturnal eye of this species (Sivak and Howland 1987). Unlike the human eye, in which the normal resting point of focus is at optical infinity and drifts to a point closer to the eye in complete darkness, there are no reports of birds with a resting focus that differs from the normal focus of the eye. In general the bird eye provides a sharply focused image on the retina of objects at optical infinity (an emmetropic eye). A recent study confirms the excellent optical quality of the eyes of raptors and the absence of refractive errors (Glasser et al. 1996).

A good accommodative ability is by no means universal among birds, however. Many nocturnal birds (whose eyes are well adapted for low-light conditions) show little or no accommodation (Murphy and Howland 1983; Howland et al. 1991; Glasser et al. 1996). In order to utilize effectively a strong accommodative range, the visual system must have sufficient contrast sensitivity or sufficient sensitivity to high spatial frequencies with a small depth of focus, or both. In the absence of these conditions the visual system would be insensitive to defocus and have little need for accommodation. That is why a nocturnal owl with large pupils (and consequently a short depth of focus) in dim lighting conditions, looking for relatively large, moving prey from a distance of several meters, would not need a high acuity visual system or strong accommodation. A granivorous chicken pecking at small seeds at short working distances has very different visual demands.

#### OTHER ACCOMMODATIVE MECHANISMS

The wide variety of accommodative requirements among animals is paralleled by an equally wide variety of accommodative mecha-

nisms. For example, image focus on the retina can be improved by constricting the pupil and thereby increasing the depth of focus, by changing the distance between the retina and the lens, by changing the refractive indices of the optical media, or (most commonly) by changing curvatures of the optical surfaces. The human eye accommodates by increasing the curvature of the lens. In a normal, unaccommodated eye that is focused at infinity, the relatively elastic lens is held flattened by the meshwork of fine elastic elements (zonular fibers) stretched between the margin of the lens and the ciliary muscle. When the eye accommodates, the ciliary muscles contract to release the resting tension on the zonular fibers and the lens is allowed to round up.

It is now well established that some birds not only change the curvature of the lens during accommodation, but change the curvature of the cornea as well. From our own studies on chick eyes, we have found that corneal accommodation is accomplished by contraction of the ciliary muscle, which results in a flattening of the peripheral cornea and a steepening of the central cornea, and that lenticular accommodation is accomplished through a contraction of the iris musculature against the anterior equatorial surface of the lens (Glasser et al. 1994; Glasser et al. 1995). Although these mechanisms are described in the early literature for other bird species, more recently published studies on chicks (Levy and Sivak 1980; Subaru and Marcentoni 1983; Sivak et al. 1986; West et al. 1991) propose different mechanisms.

Our own findings on the chick eye have led us to undertake a comprehensive review of the literature on avian accommodation. Much of this historical literature dates back to German studies in the 1800s and, consequently, has remained relatively inaccessible or incompletely understood, particularly by investigators not fluent in German. The misinterpretations or inaccuracies in more recent reports can be attributed in part to the absence of reviews of the historical German literature. We have undertaken a systematic translation of the key articles on studies of avian accommodation between 1813, when Crampton first described the function of the ciliary muscle and 1942, when Walls published *The Vertebrate Eye and Its Adaptive Radiations*.

The volume by Walls, reprinted in 1967, is perhaps the single most frequently cited work on the subject of avian accommodation, and yet it contains no specific references to those early authors:

The book is not documented, i.e., loaded up with specific citations for every point of fact and reasoning which has originated outside of my own studies. The average reader will not miss them; and the earnest student who reads the book, and is led thereby to want to do research in its field, will have to devour all of the required reading listed in the bibliography anyway (Walls 1942:v).

Walls, however, failed to include many of the original seminal articles in the bibliography and, although he stated:

[T]he established investigator in the field . . . will readily know which of my pronouncements to blame on me alone. If not, he is free to write to me for specific bibliographic assistance, which I shall gladly furnish within the limitations of my time and ability (ibid.),

he did not anticipate the longevity of his work nor could he foresee the influence his writings would have in perpetuating the misunderstandings of the accommodative mechanisms of the avian eye.

#### INTERPRETATION OF THE EARLY AVIAN STUDIES

The extreme variability in avian ocular anatomy is a point requiring constant emphasis. The often contradictory descriptions of avian accommodative mechanisms can be attributed largely to the variety of species used in these studies and to the diversity these species show. For example, it is now well established that the eyes of aquatic birds that feed under water cannot benefit from corneal accommodation, because of the loss of refracting power at the water/cornea interface (Sivak 1980). These birds have hypertrophied ciliary muscles and a stronger lenticular accommodative ability than terrestrial birds, which overcome the loss of corneal power when the eye is submerged (Sivak and Vrablic 1981). In addition, the wide diversity of habitats, food items, and feeding habits necessarily place variable demands on the accommodative amplitude of

different species, thus making it impossible to define *the* avian accommodative mechanism. Besides their behavioral diversity, there are also vastly different eye shapes among bird species. Three distinct shapes are recognized: the tubular eyes of owls, the globose eyes of hawks and falcons, and the flattened eyes of chicks and pigeons. In describing the anatomical arrangement and function of the muscles, it is important to recognize how little leeway there is for generalization.

In the more recent literature on avian accommodation, no articles systematically address the early literature. Although at first glance the early literature may appear outdated or incorrect, it should be remembered that Young (1801) still remains the definitive reference for the absence of corneal accommodation in humans, and his work predates the avian literature. On the other hand, findings that are inconsistent with our own experimental evidence do exist in the early literature; many of these ideas have been perpetuated and are found in the modern literature on avian accommodation.

When viewed independently, many of the early studies may seem to bear little relevance to the current understanding of avian accommodation. This is largely because no single author was able to provide accurate descriptions of the mechanisms for both corneal and lenticular accommodation. When taken as a whole, however, these early studies contain important insights into the mechanisms of the avian eye, and have led us to what we believe are definitive descriptions of corneal and lenticular accommodation in the chick eye.

It is our intention here to provide a comprehensive historical review and critique of the most important articles on avian accommodation, starting with Crampton (1813). We will preface this review with a brief description of the anatomy and function of the accommodative apparatus of the chick eye as we currently understand it (Glasser et al. 1994; Glasser et al. 1995; Murphy et al. 1995; Glasser and Howland 1995). In providing this overview, we risk perpetuating the very errors that we hope to expose in the historical literature, and to avoid in this review. We must emphasize that, in describing the accommodative mechanism of a single species, it is impossible to generalize to

the full range of accommodative behaviors and abilities that occur in other birds. We have described previously the anatomy (Murphy et al. 1995) and mechanisms of corneal and lenticular accommodation in the chick eye in detail (Glasser et al. 1994; Glasser et al. 1995), and will provide only a brief synopsis below.

#### CHICKEN CILIARY BODY ANATOMY

The anterior segment of the chick eye contains the cornea, the lens, the ciliary muscles, the iris, and the tissues that hold them together (Figure 1). The sclera and associated scleral ossicles provide structural rigidity to the anterior segment of the eye. The ossicles constitute an overlapping ring of tiny scale-like bones that are embedded in the sclera at the limbus of the eye. Towards the anterior apices of the scleral ossicles, the scleral matrix organizes to form the cornea. Posteriorly, the scleral ossicles overlap with the scleral cartilage of the globe to provide some rigidity to the posterior globe. The striated ciliary muscle is associated with the sclera at the inner angle of the scleral ossicles and can be divided into two regional groups, an anterior group and a posterior group. Most of the ciliary muscle fibers originate in the region of the sclera associated with the scleral ossicles. Most fibers of the anterior ciliary muscle group insert on the inner lamella of the cornea either directly or indirectly through a stromal extension of the inner corneal lamella. The fibers of the posterior ciliary muscle group insert on the fibrous *pars plana* of the ciliary body. The tenacular ligament, an elastic fibrous tissue, connects the posterior ciliary body with the cartilaginous sclera of the globe. When the ciliary muscle and iris contract, the ciliary body is pulled forward, stretching the tenacular ligament. When the muscles relax, the tenacular ligament helps the ciliary body return to its rest position. Posteriorly, the ciliary body is continuous with the retina and associated layers, and anteriorly, the ciliary body is continuous with the ciliary processes that attach firmly to the anterior surface of the lens. The iris, which lies against the anterior surface of the lens, is continuous with the ciliary body at the region of the ciliary processes. The iris is composed of circumferential striated muscle fibers held together by the iridial stroma. These

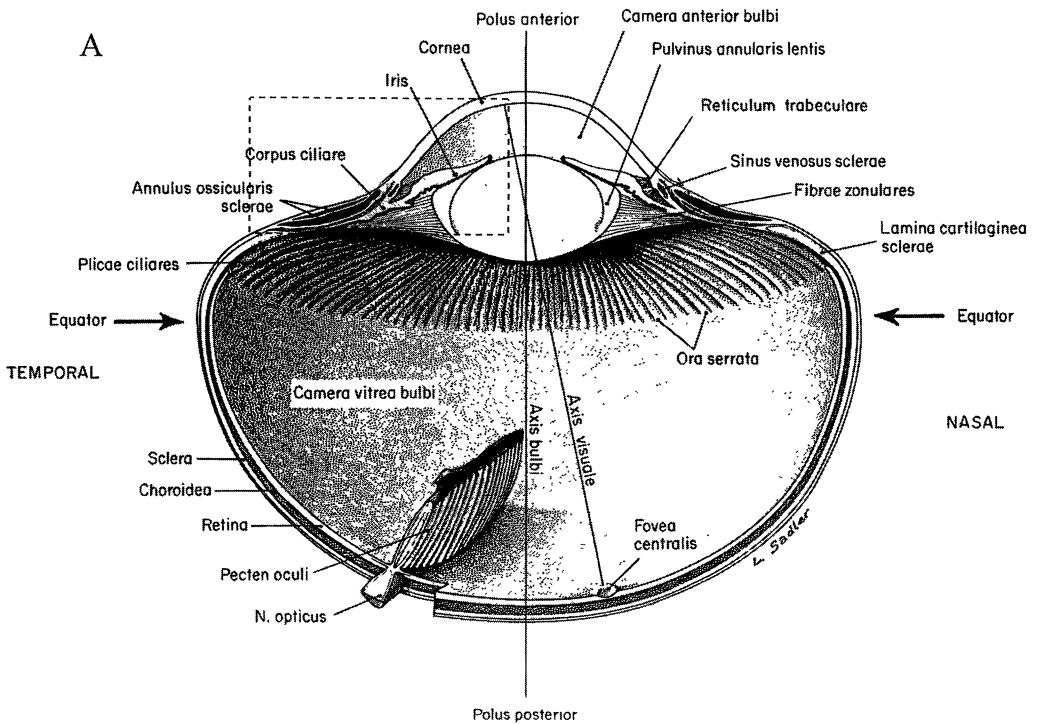


FIGURE 1A. DIAGRAM OF A CROSS SECTION AND INTERIOR OF A CHICK EYE SHOWING THE STRUCTURES INVOLVED IN ACCOMMODATION. THE RECTANGLE ENCLOSED BY DASHED LINES IS ENLARGED IN FIGURE 1B.

circumferential muscle fibers are predominantly located in the anterior two-thirds of the iris and are involved in both pupillary constriction and lenticular accommodation. Radial iris muscle fibers are found in the posterior iris adjacent to the pigment epithelium against the lens. These serve to dilate the pupil. The pectinate ligament connects between the inner lamella of the cornea and the anterior aspect of the iris. This is a meshwork of elastic fibers constituting one side of the triangular ciliary cleft, bordered on the other two sides by the ciliary body and the sclera, and associated ciliary muscle. The pectinate ligament is stretched during pupillary constriction and accommodation, and then aids in returning the iris to its rest position when the iris is relaxed.

#### CHICKEN ACCOMMODATIVE MECHANISM

The anterior ciliary muscle mediates corneal accommodation; the posterior ciliary muscle and the sphincter muscle of the iris

together are involved in lenticular accommodation. A contraction of the anterior ciliary muscle pulls backward on the inner lamella of the cornea to flatten the peripheral cornea. The biomechanical constraints of a deformable curved surface treated in this fashion result in an increased curvature of the central cornea. The posterior ciliary muscle pulls forward on the ciliary body and stretches the tenacular ligament. The forward pull on the ciliary body releases the outwards resting tension that the ciliary body imposes on the equator of the lens. The substantial peripheral musculature of the iris, lying on the ciliary processes against the anterior surface of the lens, constricts to push directly on the anterior equatorial surface of the lens through the ciliary processes. The contraction of the peripheral musculature of the iris represents the predominant force of lenticular accommodation and it causes an increased curvature of the anterior lens surface, an increased tension on the

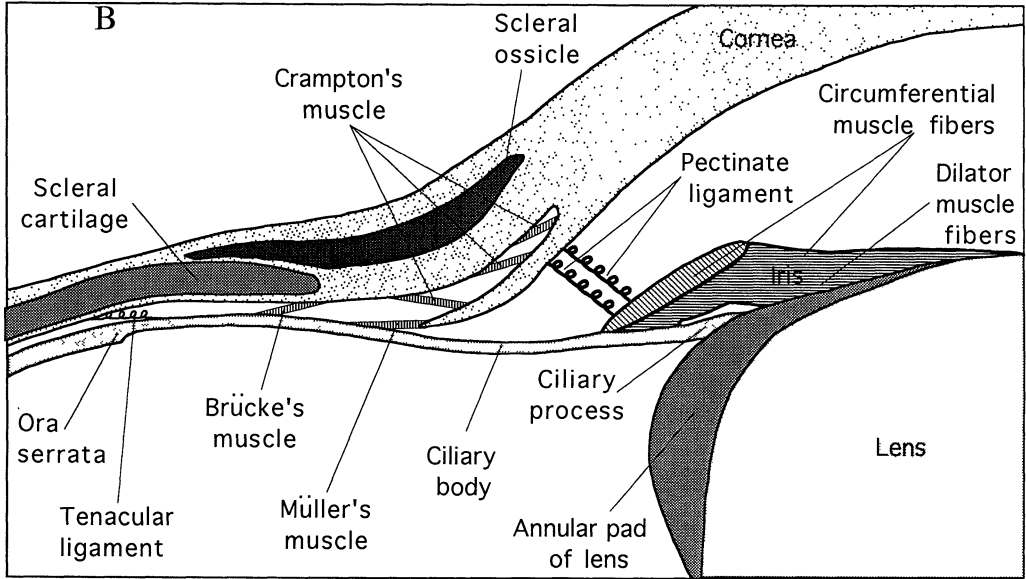


FIGURE 1B. DIAGRAM SHOWING THE CILIARY REGION OF THE NASAL SIDE OF A HORIZONTAL SECTION THROUGH THE MIDDLE OF A CHICK EYE.

One unique feature of the avian eye is the presence of the scleral bones or ossicles within the sclera of the eye. The scleral ossicles overlap with the most anterior edge of the scleral cartilage. The scleral cartilage is found within the fibrous sclera of the entire posterior pole of the eye and constitutes a scleral cup. The corneal epithelial matrix begins just beyond the anterior end of the scleral ossicles. The ciliary muscles are closely associated with the sclera of the eye beneath the scleral ossicles. As shown here, they are composed of an anterior division (Crampton's muscle) and a posterior division (Brücke's and Müller's muscles), each having different origins, insertions, and orientations. Only representative fibers of each of the muscle groups are shown. Crampton's muscle inserts on the inner lamella of the cornea and on a fibrous sheath that is continuous with the inner lamella of the cornea. The origin of Crampton's muscle is on the sclera beneath the scleral ossicles. Brücke's muscle shares the same origin, but it extends posteriorly to insert on the ciliary body. Müller's muscle has no fixed origin and insertion but extends between the fibrous sheath of the inner lamella of the cornea and the ciliary body. The action of all these muscles has been the subject of the long historical debate covered in this review. The ciliary body is attached to the sclera of the globe by the tenacular ligament near the insertion of the posterior ciliary muscle. The ciliary body also attaches to the annular pad of the lens via the ciliary processes. This constitutes a firm attachment of the ciliary body to the lens, unlike the mammalian eye. The peripheral edge of the iris is continuous with the ciliary body and lies on the ciliary processes. The iris is composed primarily of circumferential muscle fibers located in the anterior two-thirds of the iris. At the periphery of the chick iris there are dense circumferential muscle fibers that can play no role in pupillary constriction, but they provide the force for lenticular accommodation (shaded region of the iris). The few dilator muscle fibers are located adjacent to the posterior edge of the iris, which lies against the anterior surface of the lens. The pectinate ligament, an elastic meshwork of fibers, extends between the inner lamella of the cornea at the corneal spur and the angle of the iris at its junction with the ciliary body.

[Figure 1A is reprinted from *Handbook of Avian Anatomy: Nomina Anatomic Avium*, Second Edition, J J Baumel, A S King, J E Breazile, H E Evans, and J C Vanden Berge, editors, p 606 (1993), with kind permission from H E Evans; published by the Nuttall Ornithological Club, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, USA. Figure 1B is reprinted from *Vision Research*, Volume 35, A Glasser, C J Murphy, D Troilo, and H C Howland, The mechanism of lenticular accommodation in chicks, pp 1525-1540 (1995), with kind permission from Elsevier Science Ltd, The Boulevard, Langford Lane, Kidlington OX5 1GB, UK.]

ciliary body, and an increased tension on the pectinate ligament. The steepened curvatures of the cornea and the lens increase the optical power of the eye, allowing near objects to be focused on the retina. When accommodation is relaxed, the cornea is returned to its unaccommodated curvature through the positive intraocular pressure. The pectinate ligament pulls the peripheral musculature of the iris outward to its unaccommodated position, and the tenacular ligament pulls the posterior ciliary body and the posterior ciliary muscle backward to return them to their unaccommodated states. The elasticity of the pectinate ligament and tenacular ligament together result in an outward pull on the equatorial edge of the lens, returning it to its relatively flattened, unaccommodated state.

#### PHILIP CRAMPTON (1813)

Philip Crampton published the first investigations of the avian eye. His work appears at a time when controversial ideas about human accommodation were being discussed. Crampton's initial work on the ostrich eye was undertaken, almost certainly because of the large size of the ostrich eye, in the hopes of resolving some of the debates surrounding human accommodation. This is ironic because, rather than resolving the questions on human accommodation, Crampton's work began a debate on avian accommodation that has until recently remained largely unresolved.

Everard Home (1795) reported his experimental observations to the Royal Society of London, stating that the human cornea undergoes a change in curvature when the eye is accommodated to different distances. Six years later, Thomas Young (1801) presented results of extensive investigations and optical measurements on his own eye, again to the Royal Society of London, in order to refute Home's theories of corneal accommodation in humans. In 1813, Crampton addressed the uncertainties surrounding the mechanism of accommodation as follows:

It appears, then, that in the present state of our knowledge it must be difficult, if not impossible, to ascertain how much, if any, apparently optical effect is to be attributed to the mechanical constitution of the eye, and how much to the agency of the principle of

life. This cannot be better illustrated than by referring to the contradictory opinions, which have been maintained among the most distinguished natural philosophers, with respect to the faculty, which the eye is thought to possess, of adjusting its focus to the different distances of objects. All the hypotheses that have been framed to explain the means by which this adjustment is effected, have proceeded upon the supposition that it was necessarily connected with some change, either in the external configuration of the eye, or in the relative position of its internal parts. Now, although it is certain that to form a *perfectly* distinct image upon the retina, the focus of the eye must be accommodated to the distance of the object, still we have as yet no proof that such a *perfect* image is essential to distinct vision (Crampton 1813:170).

It is not difficult, therefore, to appreciate the position Crampton was in when he undertook studies of the accommodative capacity of bird eyes. Crampton summarizes the position with the following:

It would seem, then, that we are ignorant not only of the means by which the optical constitution of the eye is so changed as to be accommodated to the different distances of objects, but that we have not hitherto had satisfactory evidence that any such change takes place (ibid.:172).

With the recognition that:

[t]he strongest argument in favour of the internal changes of the eye seems to be drawn from the comparative anatomy (ibid.:171).

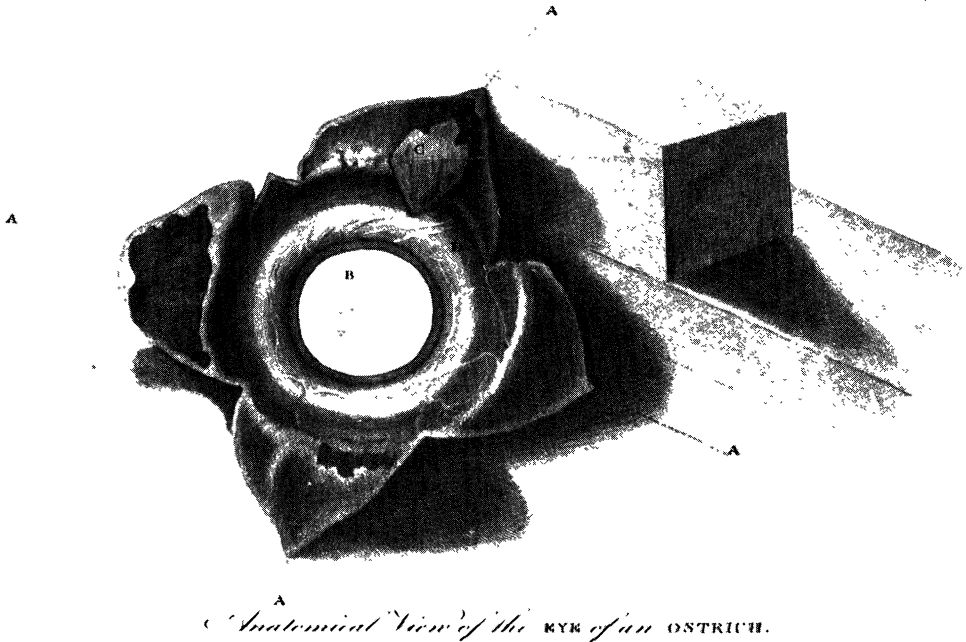
Crampton undertook an anatomical study of the eye of an eagle and an ostrich (Figure 2) and, with that, began what has become a 180-year-long study into the accommodative mechanism of the avian eye. He described:

[an] organ . . . which . . . is a distinct muscle, which arises from the internal surface of the bony hoop of the sclerotica, and is inserted by a tendinous ring into the internal surface of the cornea (ibid.:172).

Through gross dissection of the relatively large eyes, he concludes:

PLATE III.

Fig. 174



*Anatomical View of the* EYE of an OSTRICH.

FIGURE 2. CRAMPTON'S (1813) DISSECTION OF THE EYE OF AN OSTRICH.

The eye has been opened from the posterior pole, and the ciliary body and lens have been removed to view the ciliary muscle and the cornea. (A) shows four quadrants of the posterior sclera of the globe that have been cut and thrown open, (B) is the cornea, (C) is the pecten, which is attached to the sclera, and (D) is the ciliary muscle as revealed by removal of the lens and ciliary body. The innervation of the ciliary muscle is clearly seen when the ciliary muscle is viewed in this manner.

[A] mere inspection of the attachments of this muscle will be sufficient to suggest its action; for since the bony hoop, from which the fibers arise, must be considered a fixed point, the cornea into which they are inserted must be drawn inwards by their contraction (*ibid.*:173).

To observe the action of a contraction of the ciliary muscle, Crampton electrically stimulated a partially dissected eye of a turkey and noted that there is a concurrent motion of the cornea with every stimulation and contraction of the ciliary muscle fibers. The direction of this motion was better understood by pulling on the ciliary muscle fibers in the orientation of their contraction. Crampton noted that, upon doing this, the cornea became flattened and drawn closer to the iris. We now know Crampton was correct in this observation. The action of the anterior ciliary muscle does in-

deed flatten the peripheral cornea, the region that Crampton observed to move. He made no mention of what changes, if any, occur on the rest of the cornea. The peripheral cornea is of little optical significance, given that the iris blocks light rays that are refracted by the peripheral cornea and prevents them from reaching the retina. While Crampton surely recognized this, what he failed to observe was that the changes occurring at the peripheral cornea were not necessarily the same as those occurring on the more central cornea. So, although Crampton's observations were correct, he drew incorrect conclusions to account for the function of this muscle:

Since, then, it may be demonstrated that this muscle is in its action a depressor of the cornea, it seems scarcely necessary to add that its influence must tend to diminish the convexity of the eye (*ibid.*:173).



Crampton also assumed that the central cornea was flattened during accommodation and that this would allow the bird eye to adjust its focus to accommodate for distant objects, meaning that in the relaxed state the eye would have to be myopically focused. He concludes that the bird eye, therefore, is adapted for vision while on the ground, and that . . .

the focal length of the organ must be increased as the divergence of the rays decreases [while flying] (ibid.:173–174).

Crampton's historic description of the avian ciliary muscle and its function were largely accurate. Observing a flattening at the peripheral cornea, however, led Crampton to incorrectly conclude that birds accommodate for *distant* objects while remaining myopically focused at rest.

---

*In the following sections, all quoted passages have been translated from the German by Howard C Howland, with the exception of Cramer (1853), which is in High Dutch; also see the acknowledgments.*

#### ERNST BRÜCKE (1846)

Through gross dissection of the eyes of owls and emus (*Casuar*), Brücke made additional observations of the muscle that Crampton first described. Brücke recognized that the major function of this muscle was, in fact, to *increase* the curvature of the cornea. He contributed a more complete anatomical description of the insertion of this muscle to the inner lamella of the cornea by noting that, near its peripheral edge, the cornea could be divided into an inner and an outer layer, and . . .

in the region of the axis [of the cornea] these two layers are so bound up with each other that one can not find the borders between them. However, the further one goes from the axis, the more loose becomes this binding together and near the border it is very easy to separate the two layers, which are bound together with a very loose connective tissue-like fibrous layer. At this point, the outer layer goes into the sclera and anchors itself on the anterior rim of the bony ring so that it becomes one with the very strong fibrous membrane that covers the bones. On the inner layer is attached Crampton's muscle (Brücke 1846:371).

Brücke uses a geometrical argument to show how a contraction of Crampton's muscle would, in fact, increase the curvature of the cornea. The basis of the argument is that the curvature of the cornea is determined by different constraints, depending on the state of Crampton's muscle:

. . . if Crampton's muscle is flaccid, then the outer lamella of the cornea, whose circumference passes through the anterior surface of the bony ring, is the determining surface. On the other hand, if Crampton's muscle is contracted, then the important surface is that of the inner lamella and Crampton's muscle, which fastens it to the insertion on the bony ring (ibid.:372).

Brücke measured the radius of curvature of the outer ( $r = 12.801$  mm) and inner lamellas of the cornea of two owl eyes and found a difference of 1.426 mm. This would produce a 2.83 diopter increase in corneal refracting power as the cornea went from the curvature defined by the outer lamella to that defined by the inner lamella.

Brücke described an experiment to demonstrate the action of Crampton's muscle as he saw it:

Take a broad U-shaped tube that has unequal arms and hold it so that the openings are turned upwards. Then place on the shorter arm a softened bladder, and fill it through the longer arm until the bladder assumes a spherical shape. Press on this bladder a ring whose inner circumference is somewhat smaller than the base of the spherical segment, and you will see that the radius of curvature of the bladder inside this circle is smaller than it was before. This ring, which here presses from above, corresponds in the eye to the ring-shaped muscle that pulls it from underneath (ibid.:375).

While this experiment clearly illustrates Brücke's interpretation of the action of Crampton's muscle, it fails to provide a complete description of the mechanism. Brücke's model shows only an increase in corneal curvature, whereas Crampton's observation indicated that the action of the muscle was to flatten the cornea. The theories of Crampton and Brücke, when taken together, provide a complete and accurate description of the mechanism of corneal accommodation: the peripheral cornea

is flattened, which causes a steepening of the optically relevant central cornea. Perhaps because they were in apparent contradiction and perhaps because Brücke's explanation was largely theoretical, corneal accommodation may have been viewed with skepticism by subsequent authors.

Brücke made a further contribution to the anatomical description of the ciliary muscle. From his dissections, he observed that the ciliary muscle contains another group of fibers that, in contrast to the ones described by Crampton, course backward in the eye. This more posterior ciliary muscle is particularly evident in the eye of the owl, as drawn by Brücke, where it is quite distinct from the more anterior Crampton's muscle. Brücke describes its origin as being under the scleral ossicles, its orientation as running backwards in the eye, and its insertion as being onto the choroid. As for its function:

... it tenses the choroid with the included retina and vitreous body and from this I have given it its name ... the tensing muscle of the choroid [the *tensor choroidea*] (ibid.: 375–376).

Brücke notes that:

... its fibers are striated as in Crampton's muscle and the iris, and they are about the same thickness. This muscle is found not only in birds but also in those amphibians which have a bony ring, in turtles, in reptile-like amphibians including geckos and chameleons, and behaves in them just as it does in the bird eye. I have also found it in crocodiles, which lack a bony ring; it springs here from the anterior part of the sclera, and its fibers run backwards and attach to the choroid (ibid.:376).

Brücke also describes:

... a wreath of elastic fibers, which spring from the bony ring and run from the posterior to the anterior, a very small distance away from the attachment of the muscle [the *tensor choroidea*] onto the choroid, so that the contraction of this muscle works against [this wreath of elastic fibers], and by the relaxation of the choroidal muscle, the elastic fibers pull the choroid back into its original position (ibid.:375).

This "elastic tissue" is now known as the tenacular ligament. It is a connective tissue sheet,

continuous with the *pars plana* of the ciliary body, that attaches the posterior ciliary body to the scleral cartilage of the globe at the region of the *ora serata*. The posterior ciliary muscle, as described by Brücke, inserts to the anterior aspect of the tenacular ligament at the *pars plana* of the ciliary body. When the ciliary muscle contracts, the tenacular ligament stretches to pull the ciliary body, choroid, and retina forward, and when the muscle relaxes, the tenacular ligament returns these tissues to their relaxed position. Brücke provides no indication of the functional significance of having the choroid tensed, but as will be seen below, Cramer had by 1853 provided a logical explanation.

Brücke contributed to the understanding of avian accommodation by recognizing that the curvature of the central cornea was actually increased during accommodation by the muscle that Crampton claimed *flattened* the cornea. Brücke also provided an accurate description of the posterior ciliary muscle and proposed the function of tensing the choroid during accommodation.

#### ANTONIE CRAMER (1853)

It is ironic that Cramer begins his chapter entitled; "The lens becomes more curved on the anterior surface through the workings of the iris," with the quotation:

I may well say that no man if he take industry, impartiality, and caution in his investigations of science, ever works experimentally in vain—Faraday (Cramer 1853:86),

for it is possibly Cramer who first threw serious doubt on the belief that birds have the capacity to change the curvature of their corneas during accommodation. Cramer may have been the first to show that the iris is responsible for changing the curvature of the lens during accommodation, but his experimental observations of possible changes in corneal curvature, although doubtless industrious and cautious, were not sufficiently so to allow him to observe corneal accommodation.

Cramer observed the behavior of images reflected off the corneal surface of enucleated pigeon eyes. After stimulating the eyes using wire electrodes placed on the sclera on opposite sides of the cornea, Cramer concluded:

Never, however, have I been able to observe the smallest change in size [of the corneal images] . . . and (given the complete ease with which the obvious changes in size of the images can be seen or the capacity of the arrangement to measure the difference in size) can thus conclude that accommodation of the eye of birds must be brought about in the same manner as in man, [i.e.,] by a greater or lesser curvature of the front surface of the lens (ibid.:89).

Following Cramer's attempt, many other investigators have also failed to stimulate corneal accommodation in excised eyes, and even in more recent studies, the same conclusion—that birds do not have corneal accommodation—has been drawn from similar failures (Sivak et al. 1986). Had Cramer directly observed the ciliary muscle contraction during stimulation, as Crampton and Brücke had before him, he would have seen the ciliary muscle pulling on the inner lamella of the cornea. Cramer's attempts to induce naturally occurring corneal accommodation in excised eyes failed because of the loss of normal intraocular pressure. Therefore, he drew the conclusion that Crampton and Brücke were simply mistaken believing that the avian eye can accommodate by changing the curvature of the cornea.

In other matters, however, Cramer's investigations were not in vain. It was Cramer who first indicated that avian lenticular accommodation is controlled by the iris muscle. In pigeon eyes that were electrically stimulated after the cornea had been removed, Cramer observed the movement of Purkinje images reflected off the anterior surface of the lens. He writes:

Sometimes one could notice that during application of the current the pupil contracted and the [Purkinje] image decreased in size but that it became more noticeably intense. As soon as the current was interrupted, everything returned to the previously normal condition. When I, however, removed the iris carefully from the *orbiculus ciliaris* with small forceps, no change in size of the mirror image could be observed, with repeated observations, during the application of the electric current (ibid.:90–91).

As for the ciliary muscle, Cramer ascribed functional significance to Brücke's *tensor choro-*

*idea*. Cramer suggested that it applies a force behind the lens to prevent the lens from moving backward when the iris muscle constricts around the anterior lens surface. Furthermore, he also believed that Crampton's muscle served this function, thereby postulating a role for the avian ciliary muscle in lenticular accommodation.

#### HEINRICH MÜLLER (1857)

The mechanism of accommodation in birds has been the subject of recurrent confusion. This can in large part be attributed to the fact that many of the early studies were based on morphological findings only, without physiological support. Modern techniques have allowed more comprehensive investigations of the physiology of the avian eye than were possible in the 1800s and, as a result, new experiments have exposed many of the early misconceptions. Müller's principal work on the avian eye is remarkable in this regard, for despite the almost purely morphological nature of his work, Müller was able to identify several key features of the accommodative mechanism that had eluded earlier investigators.

Müller came close on the heels of Brücke and Cramer, but his work stands in sharp contrast to that of his predecessors. In fact, his style represents a transition from what might appear to be the writings of the merely curious to a substantive report of a systematic morphological study. Although lacking physiological support, Müller's descriptions have remained relevant largely owing to their accuracy and the scope and comparative nature of his studies. Müller's descriptions include comparisons of relative sizes of the ciliary body and angle of the ciliary region among vertebrates, and he notes particularly the striking difference between the globular eyes of raptors (Figure 3) and the tubular eyes of owls. The many morphological differences among the eyes of various bird species did not escape Müller's attention, and he is always cautious to indicate the species in which his observations were made.

In agreement with studies prior to his own, Müller found that the muscle fibers of the iris extend right to the pupillary margin. He also found that the thickness of the iris and the irideal muscle fibers diminish towards the pu-

pil. In contrast to earlier reports, Müller found that the full extent of the iris musculature is actually on the iris and does not extend onto the ciliary body as had previously been described. He finds that the iris is thickest at some intermediate point between the ciliary body and the pupillary margin.

By observing the iris contraction in a living falcon, Müller noted that the inner and outer muscle rings of the iris do not necessarily contract equally. A strong accommodative response causes a strong contraction of the outer iris muscle with little change in the pupil diameter:

indeed it appears that the outer muscle ring moves somewhat over the inner one. At other times, the width of the pupil shows very strong alterations without the outer part of the iris playing any role in it whatsoever. It is as if the outer part of the iris is primarily serving the accommodative movements and the inner one the pupil contractions. However, I won't make here a full division between these associated movements because I haven't really found a sharp border between the two muscle regions, even though in the living eye I have seen a line bordering the pupillary ring of the iris (Müller 1857:27–28)

And in a footnote to this text, Müller says:

If, on the one hand, the particular arrangement of the ring muscles on the anterior surface of the iris is shown to be for accommodation, and on the other hand, the analogy of those with a muscle ring on the ciliary body of humans is proven, then here is a strong argument that this ring muscle plays an important role in both [human and avian eyes]. It would, however, follow from this that Cramer's experiment on the irises of animals, and in particular of birds, was therefore not of telling significance in this relationship for humans (ibid.:28).

Müller summarizes the role of the iris in accommodation, thus:

Now concerning the function of the muscles in the bird eye, they can be described with certainty as follows: Only a very small portion of the musculature of the iris really serves the contraction and expansion of the pupil. The other portion of the iris, namely the ring muscle of its anterior lamella, which extends to the ciliary body, is cer-

tainly meant for accommodation. This same muscle must pull the relatively mobile end of the ciliary body with its extensions inwards and therefore cause a pressure on the edge of the lens. This pressure also reaches the peripheral portion of the anterior lens surface. It would therefore act on the lens to make it more curved in the middle portion of the anterior surface. This agrees with what Cramer found in his experiments on birds (ibid.:39–40).

Müller also describes the existence of a striated dilator muscle in the avian eye, which had been questioned by almost all his predecessors. Here again, displaying his scholarly nature, Müller provides a review of the previous works that had contributed to the confusion. In describing his own observations, Müller says:

At the most posterior layer of the iris, the dilator lies directly under the pigment and stretches from the ciliary margin outward, not quite to the edge of the pupil. Here the fibers vanish where the iris becomes thin and the ring fibers constitute the entire thickness of the iris (ibid.:30).

From his observations of many species, Müller notes:

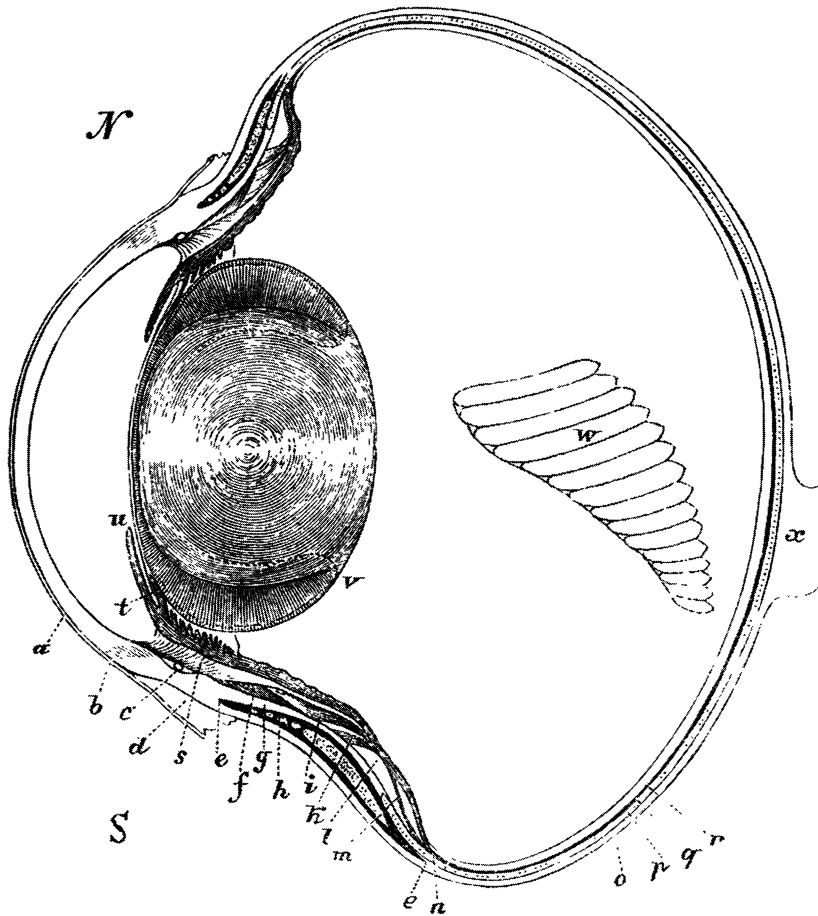
In particular, the dilator now shows considerable differences depending on the genus (ibid.:31).

And he concludes:

Therefore it seems to me that the appearance of a striated dilator is the general rule in birds. However, in any case, there are very large differences in their structure that are certainly worth looking into (ibid.:32).

Concerning the ciliary muscle, Müller summarizes by saying:

Donders (Onderzoekingen, Jaar VI, p 54) had described the [muscles of the ciliary region] correctly as having an unhappy history in which the arguments over their muscular nature was certainly accepted, but the arrangement was described differently by every observer. Crampton granted that the muscle, which carries his name, originated on the bony ring and through an oblique ring on the inner surface, inserts itself to the cornea. And he added that the muscle fibers also attach themselves to the choroid. After that, Treviranus (Beitraege zur Anatomie und Physiologie der Sinneswerkzeuge, p



Horizontaldurchschnitt des Auges von *Falco polumbarius*. 4 Mal vergrößert.

FIGURE 3. MÜLLER'S DIAGRAM SHOWING A HORIZONTAL SECTION THROUGH THE EYE OF THE FALCON.

Horizontal section of the eye of *Falco polumbarius*. Enlarged 4 times. (N) nasal, (S) temporal, (a) cornea, (b) transition between the cornea and the sclera, (c) blood vessel dividing the corneo-scleral venous sinus (canal of Schlemm), (d) conjunctiva and epithelium that is continuous with the cornea, (e-e) scleral ossicle, (f) Crampton's muscle, (g) fibrous sclera in which the scleral ossicles sit, (h) nerve in cross section, (i) inner, longer portion of the *tensor choroidea* muscle (Brücke's muscle), (k) the outer shorter portion of this muscle, (l) artifactual open space, (m) tenacular ligament, open spaces are also artifacts, (n) anterior end of the retina (*ora serata*), which thickens as it goes backward, (o) outer fibrous layer of the sclera, (p) (speckled) scleral cartilage, (q) (dark line) the choroid, (r) the retina, (s) tenacular ligament, (t) anterior protrusion of the ciliary processes, which is attached to the lens capsule, (u) the iris, (v) transition between the annular pad and the lens, (w) the pecten, (x) the optic nerve (the last two are not in the plane of this cross section) (Müller 1857:35).

83), who didn't notice the striations and held the ring to be nonmuscular, divided it into an anterior and posterior division. Krohn remarked that in owls and to a certain extent in ospreys, both these parts were separated by a free intercalated area, but that in small birds, there was never an interrupted mass. Brücke (Müller's Archiv, 1846, p 370) characterized these two muscles by their origins and insertions and their function as different muscles, noting that these muscles are similar in all birds. According to Brücke, Crampton's muscle has its origin at the bony ring and attaches anteriorly to the inner lamella of the cornea. Brücke then calls the muscle that originates from the bony ring and goes backwards to the choroid the "*tensor choroidea*." Cramer found this latter muscle described by Brücke to be Crampton's muscle. However, separating himself from Crampton and Brücke, he stated that the origin was at the choroid and that it attached to the inner surface of the bony ring and onto Descemet's membrane. Finally, Donders (Onderzoekingen, Jaar VI, p 56) found from his researches that there was really only one muscle there, which, in a feathered arrangement, comes from the outer wall of Schlemm's canal and from the outer side of a fibrous string. This string runs backwards from the wall [of Schlemm's canal]. The most forward [muscle] fibers go outward and backwards and attach themselves to the sclera. The further backwards the [muscle] fibers arise from each fibrous string, the more they take a posterior direction, so the last ones attach to the choroid (ibid.:32-33).

Given this confusion over the anatomy and function of the ciliary muscle, Müller may have been particularly cautious in his work. Regarding Crampton's muscle, he writes:

I regret the fact that I have to add one more to the number of somewhat varying descriptions, since after my own investigations I simply cannot adhere to any one of the earlier descriptions. For this purpose, I particularly looked at the eye of the falcon (*Falco buteo*; *palumbarias*, *milvis*), but actually with other vertebrates I found primarily the same thing. . . . With respect to the anterior muscle part, which Brücke called Crampton's muscle, I don't have much more to add. . . . It arises from a fibrous sheath that comes from the inner lamella of the cornea (which earlier was called the outer or upper wall

of the Fontana's space [ciliary cleft]). This sheath is anteriorly quite strong, but thins as it goes backwards such that it is often lost before it reaches the midpoint of the bony ring. Inwards this sheath was attached to the outer surface of the ciliary body with a thin elastic tissue. Crampton's muscle springs outward from the sheath. The other insertion point of Crampton's muscle is to the fibrous sclera that covers the scleral ossicles. . . . The most forward fibers of this muscle, which often lie somewhat forward of the bony ring, are short and not so much directed rearward. The further back the fibers are from the sheath the longer they become, and they attach more and more rearward onto the sclera. Finally, they go pretty much entirely backwards and only slightly outward (ibid.:34).

Müller's most significant contribution, however, is his description of the posterior ciliary muscle. Brücke had described the *tensor choroidea* as originating at the scleral ossicles and inserting to the choroid, but Müller correctly noted that this muscle is actually composed of two groups of fibers:

Regarding this [muscle], I find that it has on the anterior portion two origins, the outer portion being attached to the sclerotica on the outer bony ring; the inner one, however, is on the same fibrous sheath that is also anterior to the inner insertions point of Crampton's muscle. This last portion behaves in the following manner: after the last fibers of Crampton's muscle extend backwards to the bony ring, the end of the sheath is literally a muscle crossing which attaches to the choroid. This is on its innermost side, no longer covered with a fibrous plate (ibid.:37).

So, in addition to the fibers that Brücke had described (whose origin is under the scleral ossicles and whose more posterior insertion is on the choroid), there exist a group of fibers suspended between the fibrous sheath continuous with the inner lamella of the cornea and the choroid. Müller concludes:

Because the description I have just given is rather different in terms of the individual portions of the muscle and because their function certainly cannot be regarded as identical, it appears to me that one should not regard the whole thing as one muscle (ibid.:39).

This, then, divided the ciliary muscle into the three components: (i) Crampton's muscle and the two posterior divisions, (ii) Brücke's muscle, and (iii) Müller's muscle.

Müller was certainly among the first to ascribe an accommodative function to the scleral ossicles of the avian eye. He recognized the significance of the location of the intraocular muscles within the ring of ossicles and the strength of the ossicles relative to the size of the muscles:

This ring itself can certainly be regarded as immovable and the function of the bone is certainly in part to ensure that the form of the eye is held constant against the action of the muscles that are right inside this bone (ibid.:40).

Interestingly, despite his thorough description of the posterior ciliary muscle, Müller failed to resolve the confusion about the function of the anterior ciliary muscle. This failure can be attributed in part to the purely morphological nature of his observations and in part to Cramer's claim against the existence of corneal accommodation. Without considering the possible existence of corneal accommodation, Müller proposes the following dilemma for the anterior ciliary muscle:

Should this muscle be regarded as one that pulls the anterior part of the ciliary body (with which it is only in contact through deformable elastic tissue), should it be regarded as one that pulls the ciliary body outward after the ciliary body had been pulled inwards by the iris, or should the muscle be regarded as one, which during accommodation for near vision pulls the . . . iris backwards and prevents the inner plate of the cornea from being pulled inwards by the iris (ibid.:41)?

His misconceptions of the anterior ciliary muscle aside, Müller's proposal for the role of the posterior ciliary muscles in accommodation was the most plausible for his time:

From the *tensor choroidea* the outer portion [of the muscle] has its fixed point on the sclera, and it appears that, through its action, the choroid must be pulled forward; and in this way the same function could be assigned to the larger inner portion of the muscle. It appears that both insertion points of these muscles approach each other and

that as in the manner of insertion of Crampton's muscle, the fibrous plate on which both of these are fastened cannot be regarded as immovable. It must support the function of the inner portion of the *tensor choroidea* as well as that of Crampton's muscle. However, here as with the human eye, perhaps more weight should be laid on the pressure rather than the movement effect. If the walls of the vitreous body are tensed around it, then a rearward movement of the lens would find a great hindrance and it would be interesting to find if in birds the position and form of the rear surface of the lens suffered only a very small alteration as is apparently true for humans, according to Helmholtz (ibid.:41–42).

As Brücke (1846) noted, the posterior ciliary muscle is attached to the sclera of the globe by an elastic fibrous tissue called the tenacular ligament. Müller added to this original description:

The antagonist of the *tensor choroidea* consists of a wreath of very fine elastic fibers which, however, do not spring from the bony ring, but rather from the cartilage of the sclera. The position of the elastic fibers defines the *ora serata*. This wreath then lies on the outer surface of the ciliary body and inserts itself from behind on the thick ring on which both portions of the *tensor choroidea* insert anteriorly. This ring corresponds approximately to the anterior end of the cartilage plate and is characterized on the inner surface of the ciliary body through a small alteration in the formation of the folds (ibid.:42).

The function Müller proposes for the tenacular ligament is implicit in his description, namely, returning the ciliary body/choroid to its rest position when the ciliary muscle relaxes.

Müller describes how the ciliary projections, the ciliary cleft (Fontana's space), the pectinate ligament, the structure of the crystalline lens, and the annular pad of the lens contribute to the accommodative mechanism and follows by saying that the iris is primarily responsible for changing the shape of the lens:

Given this arrangement of the ciliary projections, the pull of the ring muscles that go to the ciliary margin of the iris must act on the lens. Therefore it is not to be doubted that

the iris acts on the lens from its margin much more than it does in humans and that, through this, it increases the thickness of the lens, which is necessary for near vision (ibid.:44–45).

With no mention of corneal accommodation or explanation of a possible role for the anterior ciliary muscle in the accommodative mechanism, Müller closes with an overall perspective of the avian accommodative mechanism. While largely correct in the particulars he describes, Müller nonetheless misleads the reader because of his failure to recognize the true function of the anterior ciliary muscle:

Finally, if one views the accommodative apparatus of the bird eye in totality and brings this into perspective with the physical investigations whereby for near vision the anterior surface of the lens is more curved and moves forward, so one can hardly doubt that the mechanism rests primarily on two factors. First, through the force that the iris muscle exerts on the ciliary body at the border of the lens, which also in the most peripheral parts works on the anterior surface and causes a greater curvature of the lens. Second, due to the tension of the choroid and that of the vitreous, the expansion of the posterior lens surface is either prevented or reduced. So there is really a great difference in the particulars of the construction relative to the human eye, but in the general mechanism [of accommodation] there is really a great similarity and one could look at this as a proof for the arrangements we believe exist in the human lens (ibid.:54–55).

#### SIGMUND EXNER (1882)

Through the work of his predecessors, Exner had a clear understanding of the anatomy of the avian eye and of the differences that exist among species (Figure 4). Although Exner reviews the work of Crampton, Brücke, and Cramer, and refers to Müller's muscle, his theories on avian accommodation diverge markedly from earlier ones. Cramer and Müller had compiled considerable support for the involvement of the iris in lenticular accommodation, yet Exner believed that the ciliary muscle was entirely responsible for changing the curvature of the lens during accommodation.

Although clearly skeptical that the ciliary

muscle plays a role in corneal accommodation, Exner did not refute the possibility that the curvature of the cornea might be changed during accommodation. He even interprets Cramer's work to provide support for his own theory.

Cramer, indubitably had an incorrect view of the anatomical behavior of Crampton's muscle insofar as he allows the muscle to terminate not on the cornea but on the [ciliary body] where the ciliary projections sit, . . . found that electrical stimulation of the eye had absolutely no influence on the radius of curvature of the cornea. Königstein argued that the Crampton's muscle and the *sphincter pupillae*, by their joint action, indirectly influenced the wall of the canal of Schlemm, parting the walls from each other and thereby opening the canal of Schlemm. In the following, I bring forth an interpretation of the action of this unique muscle, which I believe is the simplest and the most plausible, but it does not rule out the action of Crampton's muscle either on the corneal curvature or the opening of the canal of Schlemm (Exner 1882:54).

However, Exner proposes that the entire action of the ciliary muscle is a part of the lenticular accommodative mechanism:

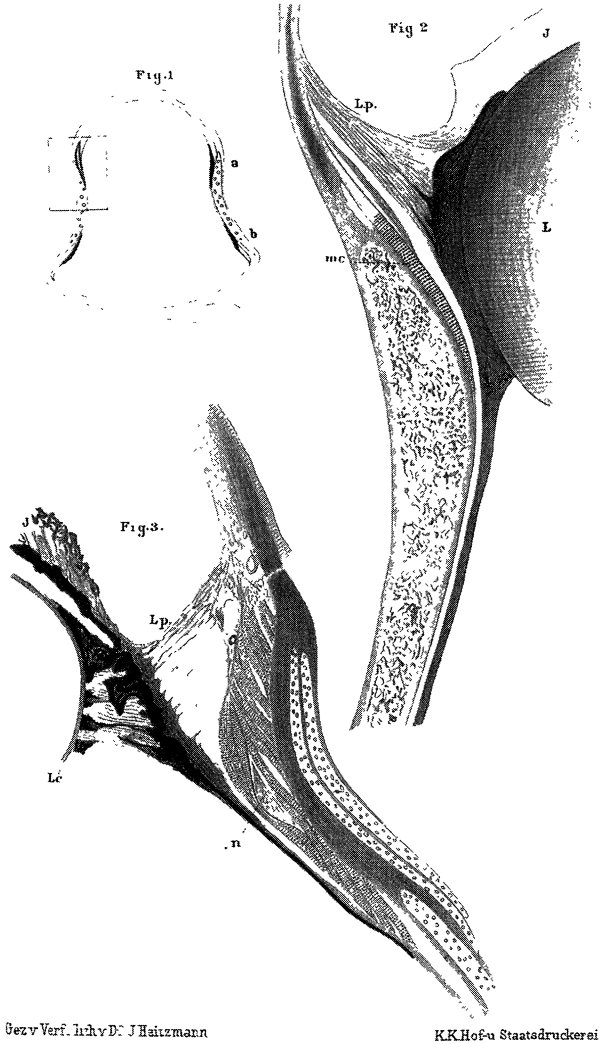
I hold that the three muscle groups, the *tensor choroidea*, Crampton's muscle, and Müller's portion, all constitute an accommodative apparatus that is definitely stronger in birds than in mammals, but in general performs the same function as the *tensor choroidea*, which in mammals acts alone (ibid.:54).

Exner describes the action of the ciliary muscle on the lens as acting both indirectly and through pressure changes in the eye. His proposed mechanism relies on assumed pressure gradients and fluid dynamics within the eye (Figure 5). The anterior ciliary muscle inserts around the scleral venous sinus. Investigators before Exner had suggested that the anterior ciliary muscle was involved in regulating fluid flow within the anterior chamber of the eye. Exner assumed that the positive pressure in the anterior chamber of the eye was required to maintain the lens in the flattened unaccommodated state.

I will assume that . . . the pectinate ligament forms a blockage so that the hydrostatic



S. Exner: Function d. Musc. Cramptonianus.



Özzy-Verf. lithvD: J. Heitzmann

KK Hof-u Staatsdruckerei

Sitzungsb. d. k. Akad. d. W. math. naturw. Classe LXXXV. Bd. III. Abth. 1881.

FIGURE 4. EXNER'S DIAGRAMS OF THE OWL EYE AND THE PIGEON EYE.

Exner's diagrams of the owl eye (Fig. 1), the region boxed in Fig. 1 (Fig. 2), and the pigeon eye (Fig. 3). Fig. 1: Section through the eye of an owl (after Brücke); (a) Crampton's muscle, and (b) the *tensor choroidea*. Fig. 2: The region enclosed by a box is at greater magnification to show the uveal tract and the lens (L); Crampton's muscle (mc) is shown with stippling. (J) is the iris, and (Lp) is the pectinate ligament. Fig. 3: The three muscle groups of the pigeon, with the muscle fibers also stippled; (j) is the iris, (Lc) is the lens capsule, (Lp) is the pectinate ligament, and (n) is a ciliary nerve branch squeezed between two branches of Müller's muscle.

This figure is instructive because it shows that the anatomy was well understood by Exner and that the diversity between species (the owl and pigeon eye shown here) was well characterized. Yet, despite this, Exner invoked a pressure-mediated mechanism of accommodation unlike any of his contemporaries. Further, Exner believed that in spite of the anatomical differences, a uniform accommodative mechanism applied across all bird species.

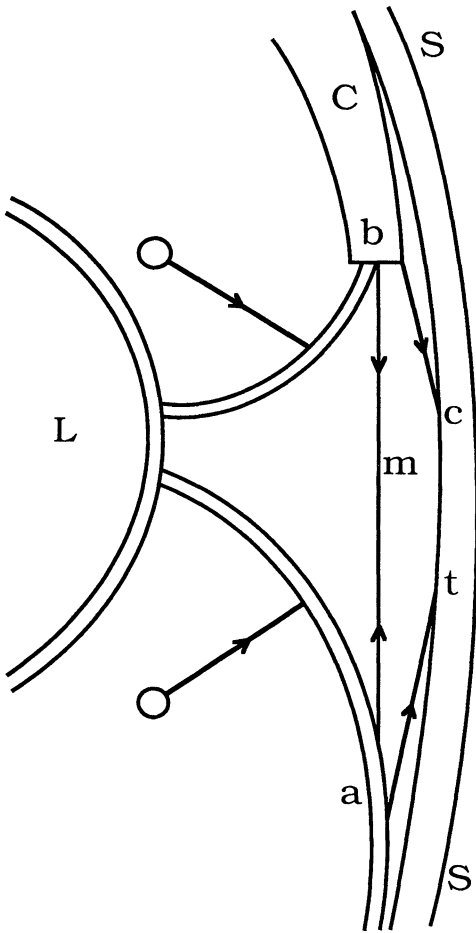


FIGURE 5. A TRACING OF THE DIAGRAM THAT EXNER USED TO DEMONSTRATE HIS PRESSURE-MEDIATED MECHANISM OF ACCOMMODATION IN THE BIRD EYE.

At rest, the lens (L) is maintained in a relatively flattened state by the intraocular pressure (open circles with arrows) pushing on the two suspensory elements of the lens: the upper bowed line (the pectinate ligament) and the lower bowed line (the ciliary body). (S) is the sclera of the globe, which at its anterior point (top) forms the outer lamella of the cornea. (C) is the inner lamella of the cornea to which two muscles are attached. One muscle (m), extending between (b) on the inner lamella of the cornea and (a) on the ciliary body, depicts Müller's muscle. A second muscle, extending between (b) on the inner lamella of the cornea and (c) on the sclera, depicts Crampton's muscle. A third muscle extending between the ciliary body at (a) and the sclera at (t) depicts Brücke's muscle. Exner argued that a contraction of any of these three muscles (arrows) would act to draw the points (a) and (b) closer to-

pressure, which is obtained [in the anterior chamber] helps the lens to be flattened (*ibid.*:57).

Had Exner undertaken any experiments, he would have realized his theory was wrong. His entirely theoretical argument can be paraphrased as follows: The lens is held flattened near its equator by two suspensory elements, the pectinate ligament and the ciliary body. Both are stretched by the intraocular pressure to maintain the relaxed lens in its flattened state. Every muscle action that reduces the distance between the pectinate ligament and the ciliary body also reduces the pull that the suspensory elements exert on the lens. All three portions of the ciliary muscle act to reduce this distance: Brücke's muscle pulls the ciliary body forward, Crampton's muscle pulls the pectinate ligament backward, and Müller's muscle pulls the pectinate ligament and the ciliary body towards each other. When the tension on the suspensory elements is relieved by the muscular contractions, the lens would, through its own elasticity, ball up to take on its accommodated form.

So sure was Exner of his theory that he wrote:

I will once again state that different cuts through a bird's eye, and even more cuts through the eyes of different birds, show many modifications in the muscle apparatus that we have been discussing, as has often been described before. Two extremely different types, that of the owl and the pigeon, I have already discussed, but there is no modification known to me which could not easily be placed in the scheme I have outlined above (*ibid.*:59).

Although Exner saw the anatomical differences, he failed to comprehend the functional implications. It is clear that the accommodative mechanism does differ widely among bird species. In spite of this, and even though his view of accommodation did not agree with the earlier findings of Müller and Cramer, Exner

together. This would relieve the resting tension on the pectinate ligament and the ciliary body and so allow the lens to ball up under its own elasticity (in a manner similar to that in the mammalian eye). When the ciliary muscles relax, the lens would again be stretched into its more flattened state through the tension applied by the intraocular pressure to the pectinate ligament and the ciliary body.

still reinterpreted Cramer's results to provide further support for his own theory.

This particular view finds support in an old experiment of Cramer's, which showed that the lens of the bird eye ceases its accommodative movements when the iris is removed. After what has been said, we are dealing here not only with the iris but also with the pectinate ligament, which is cut through with the iris removal. In this way, the entire suspensory apparatus of the lens is destroyed, and it is no longer possible to release the tension through muscular action (ibid.:60).

Exner's pressure theory was clearly incorrect, since Cramer had shown that it was possible to stimulate lenticular accommodation in enucleated eyes from which the cornea had been excised. Once the cornea is removed, the intraocular pressure is lost, yet Cramer still observed lenticular changes. It is surprising that Exner did not see this as an indication that pressure changes are not necessary to induce accommodation. While some aspects of Exner's theory are accurate, the overall mechanism fails, based on the empirical facts.

Exner's failure to address Müller's findings, to recognize species differences, to acknowledge the existence of corneal accommodation, or to provide empirical evidence, all throw serious doubt on his theory that intraocular pressure controls accommodation in birds.

#### THEODOR BEER (1893)

Beer was the first to undertake a truly comprehensive experimental study of the accommodative mechanism in different bird species. He recognized the inadequacies of the earlier morphological studies and designed some creative experiments to explore the accommodative mechanism. Like those before him, Beer was fully conversant with the anatomy of the avian eye and the anatomical differences that exist from one species to another (Figure 6). In spite of this, however, Beer apparently assumed there was no difference in the accommodative mechanism across species. No doubt many of the inaccuracies in Beer's work can be attributed to this oversight. Nevertheless, we will quote at length from Beer's work because of the clarity of his writing and the elegance of his experiments.

Following Cramer's work, Beer electrically stimulated the eyes of curarized birds:

Neither on the hen nor the pigeon (the experimental animals actually used by Cramer), was I able, by stimulating the ciliary region, to get an alteration of the behavior of the two reflections of the gas light flames in the cornea (Beer 1893:207).

This is where Beer's predecessors had stopped and concluded that birds had no corneal accommodation, but Beer persisted:

Therefore I tried at least to demonstrate the tension on the inner layer of the cornea, which I felt was unquestionably there by virtue of the anatomical arrangements. I turned to animals that had a very well developed Crampton's muscle. On a curarized owl [in Beer's words: "a middle size, but adult tawny owl, *Syrnium aluco*, of the gray kind"], I removed the cornea, leaving a 2-3 mm wide rim. By electrical stimulation of the ciliary region, I could observe a clear in and out movement of the corresponding corneal parts (ibid.:207).

Beer then attached a thread between the cut edge of the cornea and a kymograph needle. Every stimulation of the eye caused a deflection of the kymograph needle as the cornea was pulled by a contraction of the ciliary muscle. For most, this may have been sufficient evidence, but Beer continued:

I convinced myself that Crampton's muscle, through its contraction, caused the pulling in of the cornea, by virtue of taking a sickle-shaped dissection needle and placing it between the cornea and the iris, thereby cutting the [ciliary] muscle where it was fastened to the cornea. Later more careful cuts through the eye convinced me that, outside of the few filaments of the pectinate ligament, no other part of the eye was injured. Repeated stimulation now had no effect with no movement to see, and the kymograph needle described an absolute parallel line during the stimulation. As soon as one put the connection to the kymograph needle on another intact position [of the cornea] the kymograph registered again (ibid.:209).

Although Beer was unable to see the movement of Purkinje images on the cornea of the intact eyes, he was able to use the kymograph to demonstrate the action of the ciliary muscle

on the peripheral cornea of several bird species.

Thus it seemed to me proven that Crampton's muscle, by its contraction, exerts a pull on the inner lamella of the cornea. In order to prove the same thing on unoperated corneas, I arranged the following experiment with a tawny owl. I inserted into the cornea, approximately 2 mm from the edge of the cornea, a long thin needle so that the needle tip went a bit into the anterior chamber. If I stimulated it in the same way in this situation, the outer end of the needle moved towards the anterior end of the axis of the eye. It was a very pretty picture to observe two needles, which were inserted diametrically opposite to each other. During the stimulation, their outer free ends moved towards each other.

I now inserted needles on different parts of the cornea and observed the behavior of these during the stimulation of the ciliary muscle. By and large, the farther the needle was from the periphery, the less movement it showed towards the center. . . .

Therefore, this description of the motion of the inner lamella of the cornea can be regarded as a regular and integral part of the accommodative apparatus of the bird. . . .

Now I turned my attention to the optical behavior of the cornea and found the following. During electrical stimulation of the eye of a tawny owl (*Syrnium aluco*), I saw the intact cornea flatten itself near the position where the electrode lay [at the periphery]. . . . The explanation of this phenomenon was easy to understand. The inner lamella of the cornea . . . was pulled inwards. If the inner and outer lamella were not completely separate from each other, but as the anatomical preparation shows, connected through loose connective tissue, then even a small pull has to reach the outer lamella, and here it must act to decrease the corneal curvature.

In the apex of the cornea, however, the region that is important for vision, one could

not see any change in curvature with the naked eye when looking at the images of two gas flames.

Only when I looked at the corneal curvature with an ophthalmometer could I repeatedly see in the apex of the cornea, during the stimulation, a clear reduction of the corneal radius. . . .

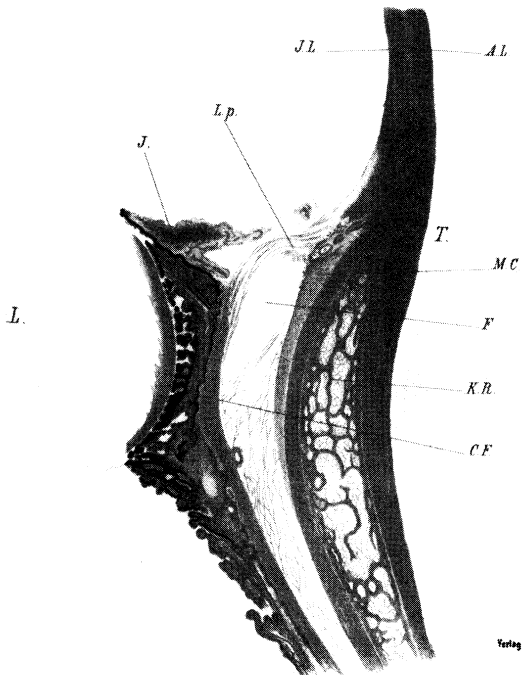
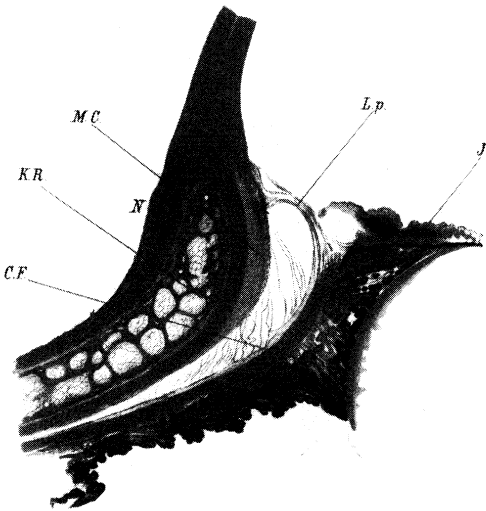
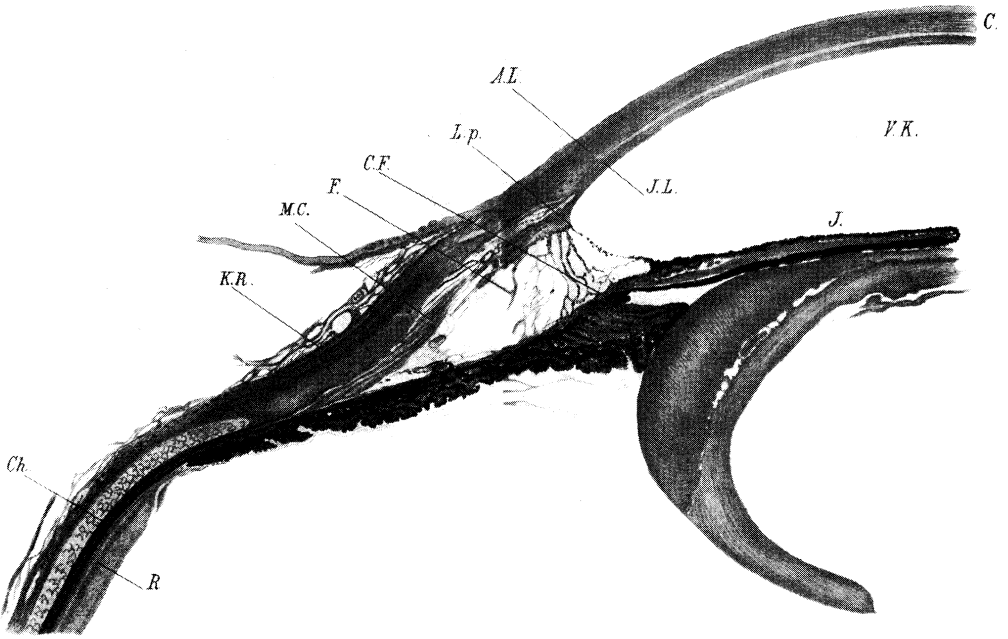
Neither in the house hen nor in the seed crow (*Corvus frugilegus*) could I observe an alteration of the behavior of the center of the cornea during stimulation. I did not think to observe the behavior in the periphery, but I would assume that because I found this [flattening of the peripheral cornea] in many different types of birds, the behavior would be the same. This flattening of the periphery could also be observed in the house pigeon, but no alteration of curvature could be seen in the center of the cornea. . . .

Particularly interesting was the following experiment on a buzzard. For another experiment 12 days earlier, I had destroyed the pectinate ligament and also a part of Crampton's muscle in the left eye, and I now went with a sickle-shaped dissection needle into the anterior chamber, and pressing it against the bony ring, cut these portions. The operation was conducted under aseptic conditions, and the animal took it well. Other than a small point on the cornea where the needle had been inserted, the operated eye looked absolutely normal. During the stimulation of the right, intact eye, the peripheral cornea showed a flattening while the central cornea showed an increase in its curvature. In the left eye, where Crampton's muscle had been totally destroyed, the same stimulation led to no alteration in the images on the cornea. This was true both on the periphery and in the center (ibid.:209–214).

Here, and again in the following paragraph, Beer incorrectly assumed that his inability to see changes in curvature of the central cornea meant that these birds have no functional corneal accommodation. It is unlikely that a cili-

FIGURE 6. BEER'S DEPICTION OF HORIZONTAL SECTIONS THROUGH THE EYES OF (A) A COCKATOO (*PLICTOLOPHUS LEUCOCEPHALUS*) AND (B) AN OWL (*BUBO IGNAVUS*).

(AL) outer corneal lamella, (C) cornea, (CF) ciliary process, (Ch) choroid, (F) Fontana's space [ciliary cleft], (J) iris, (JL) inner corneal lamella, (KR) bony ring [scleral ossicles], (L) lens, (Lp) pectinate ligament, (MC) Crampton's muscle, (N) nasal, (R) retina, (T) temporal, (VK) anterior chamber. The eye of the cockatoo bears the same flattened eye shape as that of the chick and pigeon. Note the striking anatomical differences between the tubular eye of the owl and the flattened eye of the cockatoo.



ary muscle contraction that caused a flattening of the peripheral cornea would occur without changes in curvature of the central cornea. As Beer recognized, it is the central cornea that is optically significant, so it is likely that movements at the peripheral cornea indicate the presence of functional corneal accommodation.

The series of experiments that I have just described seem to me to prove that in some owls and other raptors, the contraction of Crampton's muscle causes a reduction in the radius of curvature of the cornea and therefore an accommodation for near, just as Brücke postulated on the basis of anatomical considerations.

Unfortunately, in my earlier experiments I had contented myself with qualitatively observing the reduction of the corneal radius in the apex of the cornea only, and I later had difficulty getting the appropriate animals to make the measurements. So I can only say that the increase in curvature of the cornea and the corresponding alteration of the images were in some cases certainly large enough to be measured or at least estimated as Helmholtz had done, by observing the change in curvature of the posterior surface of a human lens during accommodation.

On the other hand, the reduction of the corneal radius was certainly not as much as Brücke had imagined on the basis of his theoretical deductions. In any event, his explanation of the total accommodation of the bird eye through the reduction of the corneal curvature, which he explicitly stated for all types of birds, is certainly not correct because I showed in a number of birds that there was no alteration in corneal curvature at the apex of the cornea (*ibid.*:216).

Beer's observation that not all bird eyes have corneal accommodation may be accurate. In diving birds, for example, where the refractive significance of the cornea is neutralized when the eye is under water, corneal accommodation would be of no value. Beer's experiments, however, failed to show changes in curvature at the apex of the cornea of terrestrial birds such as chicks and pigeons, both of which have relatively well-developed ciliary muscles. Beer, with his newfound knowledge of the ciliary muscle, reviews the earlier descriptions of its function.

Crampton's opinion that the contraction of the muscle he discovered causes a flattening of the cornea has been proven to be true, but in a completely different fashion than Crampton thought. Namely, flattening occurs only at the periphery of the cornea. In no way is Crampton's view of accommodation for distance correct, because for vision, the alteration of the periphery of the cornea is irrelevant. In the apex of the cornea, there is either an increase in the curvature or no change at all, but never is a flattening of the cornea observed. If such were observed, which I never saw in any of the eyes that I looked at, it would in all probability still not cause an accommodation for distance because as I will show in the following section, Crampton's muscle causes an increase in the curvature of the anterior lens surface, which would compensate for any possible flattening at the apex of the cornea.

On the basis of his negative experiments (whose value can be estimated from the fact that he worked only on dead animals of one species and without the use of ophthalmic methods), Cramer abandoned the idea that Crampton's muscle had any influence on the cornea. Indeed, he denied that the cornea had any role in accommodation. My own experiments are sufficient to show that this view is incorrect. Also, regarding the strong curvature of the anterior lens, Cramer again drew incorrect conclusions from a negative experiment, which I will discuss more in the following section (*ibid.*: 216–217).

Beer's summary represents what we now believe to be an accurate interpretation of Crampton's and Brücke's findings on the role of the ciliary muscle in changing the corneal curvature. Beer continues:

It was impossible for me, in part from other causes and in part because the animals were difficult to come by, to use a large number of birds of different species to research the behavior of the cornea during accommodation. But it seemed to me that on the basis of anatomical observations primarily in raptors, the curvature at the apex of the cornea would increase during accommodation. It would have to be the object of further research to follow this phenomenon through the entire class. It would be particularly important to make quantitative measurements on the reduction of the corneal radius of

curvature in the apex, and after having done that, to make a judgment over the range of accommodation caused by Cramp-ton's muscle and its influence on the cornea (ibid.:217–218).

It is interesting, given the elegance of Beer's work on corneal accommodation, that he was unable to similarly define the mechanism of lenticular accommodation. As has already been shown, he was fully conversant with the literature and theories of the day.

However well known it is that the human iris plays no important role with respect to accommodation, and particularly with respect to the change in shape of the anterior surface of the lens (observations from people whose irises have been removed, or who were born without irises, etc.), nevertheless, in the bird eye, the dominant view is that the increase in curvature of the anterior lens surface is brought about by the active compression of the iris on the lens (ibid.:218).

Through electrical stimulation and observations of naturally occurring accommodation in a variety of bird species, Beer was able to convince himself that the anterior surface of the lens increased in curvature during accommodation and that the anterior surface of the lens moved forward to decrease the distance between it and the cornea. As for the mechanism by which this is accomplished, Beer writes:

As a paradigm for the accompanying series of experiments, I report this: in a young, but fully grown hawk (*Astur palumbarius*), the cornea was removed and the electrodes were put onto the anterior surface of the bony ring. . . . During the stimulation, the behavior of the anterior lens image . . . given by two gas flames . . . was observed ophthalmometrically. The middle images showed a definite parting from one another in the sense of an increased curvature of the anterior lens surface. If I now took the iris carefully with a fine pair of scissors or Wecker's pincettes and removed it, it showed, in exact contradiction to Cramer's assertion, that the effect of the stimulation was not in the slightest reduced through the removal of the iris. This experiment was conducted on a very large number of other birds with the same results. . . . The negative results that Cramer obtained after removing the iris can

be explained in part by the fact that he worked on a dead animal and in part by his really inadequate methods of observation that allowed him to overlook very small alterations. They can be explained in the largest part in that when ripping out the iris with pincettes, he removed other parts, such as the pectinate ligament, which I will show in the following section to be very important for the accommodation of the bird eye. Hence he ascribed this lack of accommodation in the iridectomized eyes as being due to the lack of the iris (ibid.:220–221).

Having argued against a possible role of the iris, Beer describes a role for the pectinate ligament and the ciliary muscle in lenticular accommodation:

After I had shown that the accommodative change in curvature of the anterior lens surface was independent of the contraction of the iris, I went on to show an experimental proof of the hypothesis that was put forth by Exner.

If Exner's assumptions were correct, then if the lens is removed from the elastic tension apparatus by which it is suspended, it must take on a smaller radius of curvature than would be observed in a normal situation. My ophthalmological apparatus and observations showed that, in fact, if you cut the pectinate ligament, then the anterior lens surface will curve appreciably (ibid.:221–222).

Beer measured the curvature of the anterior surface of the lens of a curarized hawk eye (from which the cornea had been removed) both before and after the pectinate ligament had been cut. The results showed that, after cutting the pectinate ligament, there was an increase in the curvature of the lens, and Beer concludes:

Through these experiments . . . I hold it proven that the anterior surface of the lens of the bird eye, during accommodative rest, has a larger radius of curvature than it does when the pectinate ligament is cut through. I am therefore justified in making the conclusion that the bird lens is held in a relatively flattened position by the pectinate ligament when it is in a resting state (ibid.:226).

It was possible that Beer had not induced the full iris-mediated accommodative response. Beer himself admits this:

As we said above, during the stimulation of the accommodative muscles, there results a strong curvature of the anterior surface of the lens in the intact eye. The behavior of the image of the lens can easily be seen. However, if the cornea is removed, one can only see . . . the reduction of the radius of curvature of the anterior lens surface with an ophthalmometer (*ibid.*:226).

Beer then invokes Exner's pressure related theory as an explanation for the reduced accommodative response.

This is because, as a consequence of opening the anterior chamber and, by this, the reduction of the intraocular pressure on the anterior lens surface, the cornea, and on the anterior attachment of the pectinate ligament (all of which were acted upon by the intraocular pressure), the anterior lens surface undergoes a stronger change in curvature than it would have in the unoperated eye. Therefore, when the lens is in this position, the contraction of Crampton's muscle can affect only a small increase in the curvature of the anterior surface of the lens through the reduction of tension of the pectinate ligament, so one can only see these alterations clearly with an ophthalmometer (*ibid.*:226-227).

Beer proposes the following mechanism for lenticular accommodation:

It is the pectinate ligament that is responsible for this reduction of tension [of the lens] during a contraction of Crampton's muscle and, hence, allows the lens to come to its equilibrium [accommodated] state. This can be seen by the cutting of the pectinate ligament in an otherwise unaltered experimental arrangement, and [afterwards], during the stimulus, no alteration in the behavior of the anterior lens surface can be seen under these conditions (*ibid.*:227).

The mechanism of accommodation that Beer proposes for "the bird eye" is not as broadly applicable as he implies above. Beer, himself, went some way towards recognizing this when he described the owl eye.

The eye of *Syrnium aluco* requires a separate consideration. In the eye of this bird, the pulling in of the corneal margin, the shearing of the inner corneal layer (determined with needles, which had been inserted through the cornea), and the flattening of

the periphery of the cornea could all be seen very clearly. The reduction of the radius of curvature in the apex of the cornea was either very small or not there at all.

However, concerning the behavior of the lens in three experiments on animals of this species: by observing the lens surface from the side in intact eyes, it was never possible to see an increase in the curvature, as could be seen so clearly in many other bird species. Regarding the anterior lens image during the stimulation, I was not able to see any clearer alteration in its form, whereas in other birds, the minification of this image and the fact that the image became sharper was easy to observe. Only with the ophthalmometer could we observe a very small reduction in the radius of curvature of the anterior lens surface. After removal of the cornea, it was impossible to see any change in the anterior lens surface (*ibid.*:229-230).

Beer also describes the results of an experiment in which he surgically cut the pectinate ligament in two owl eyes (*Syrnium aluco*). He did this by inserting a specially curved surgical needle through the center of the cornea and making a circumferential cut through the pectinate ligament. Beer expected the eye to become myopic from the increased curvature of the lens; however, he found no difference in refractive state before and after the surgery.

Beer addresses the possibility that the posterior surface of the lens also changes curvature. His attempts to observe such changes through movements of the fourth Purkinje images failed, largely because he was unable to see them clearly after the pupil had constricted.

Finally, Beer addressed the function of the *tensor choroidea*. He attempted to observe movements of the choroid through a small window cut in the sclera in the hopes of demonstrating that the choroid was pulled forward during stimulation. Although these attempts failed, he agreed in essence with the function that Brücke and Müller had proposed for this muscle. Beer was able to observe increases in pressure in the vitreous chamber by watching the behavior of the choroid through the scleral window.

I find it interesting and important to note that each time during the stimulation and also when the electrodes were placed on the eye in a rather remote position, there ap-



peared during this stimulation a very large bowing out of the membranes of the eye at the position of the scleral window—a sign that during this stimulation, an increase in the intraocular pressure took place (*ibid.*: 233–234).

Beer uses this finding as a verification that the corneal changes he observed were due to an active contraction of Crampton's muscle rather than a passive result of changes in intraocular pressure.

I just wanted to mention one thing: as Helmholtz noted for the human eye, namely that “an increase in the hydrostatic pressure of the eye makes the cornea flatter,” may also be true here [in the avian eye]. Thus, in some birds, the observed reduction of the radius of curvature in the corneal apex then must, *a fortiori*, come from the pull of the Crampton's muscle (*ibid.*:234).

Beer summarizes his findings as follows:

- (1) Crampton's muscle exerts a pull on the inner lamella of the cornea.
- (2) This flattens the peripheral cornea and increases the curvature of the central cornea, thus accommodating the eye for near objects.
- (3) The major component of accommodation comes from an increased curvature of the anterior lens surface. The pectinate ligament holds the lens in a flattened state, and a contraction of the ciliary muscle releases this tension when it pulls the inner lamella of the cornea inwards, thus allowing the lens to take on its more curved accommodated shape.
- (4) Cutting the pectinate ligament also allows the lens to take on its accommodated form.
- (5) After cutting the pectinate ligament, no further changes in lens curvature occur with electrical stimulation.

Beer believed his evidence supported both Exner's observations of accommodation in the bird eye and Helmholtz's observations of accommodation in the human eye, and therefore concludes:

[T]o put the matter another way, the fundamental idea [of Helmholtz's theory] has received, from my investigations on the bird eye, a new support (*ibid.*:236).

#### CARL HESS (1909 & 1913)

Hess's writings on accommodation are numerous and extensive. His findings on the accommodative mechanism of diving birds (Hess 1909) were based on sound empirical evidence. Although the descriptions given are detailed and almost certainly accurate, they too have been misinterpreted.

Hess's description of intraocular pressure changes during accommodation are important because of the emphasis that Exner and Beer placed on the role of intraocular pressure in avian accommodation. Hess, however, begins with the statement:

[I will] look at the question of the influence of accommodation on the intraocular pressure (Hess 1909:88).

He therefore recognized at the outset that the accommodative mechanism caused the pressure changes rather than the pressure changes causing accommodation.

Hess used a Hering manometer to make his measurements. This apparatus consists of a fine capillary tube partially filled with saline. Once the tip of the capillary tube is inserted into either the anterior or vitreous chamber of the eye, very small pressure changes can be observed by a movement of the meniscus. Hess then placed enucleated eyes on needle electrodes and was able to induce contractions of the intraocular muscles for up to half an hour.

Hess was able to observe an increase in intraocular pressure in both the anterior and vitreous chambers of a wide variety of bird eyes. Even among nocturnal birds with a small accommodative range, there was an increase in pressure. The pressure increased on the order of 0.5 mmHg and always returned to baseline when the stimulus was terminated. Hess found no such pressure changes in the eyes of mammals and concludes with the speculation:

The fact that an accommodative pressure increase can not be demonstrated in the eye of the dog does not prove that pressure is unimportant for accommodation [in the mammalian eye], because the absence of a pressure change in an eye with so little accommodation does not allow one to draw the same conclusion as for an eye with a much larger accommodative range. This

objection, however, is no longer tenable since we have been able to demonstrate an accommodative pressure rise in the eye of a nocturnal bird whose accommodative range is, by our investigation, no larger than that of a young dog. The accommodative range of the monkey eye, which showed no increase in pressure during accommodation, is approximately three times that of the above mentioned nocturnal bird.

An interesting and closely related question is whether the rise in intraocular pressure that accompanies accommodation in vertebrates such as reptiles and birds, is in some way related to the fact that these animals have the unusual accommodative mechanism of changing the shape of the lens through the force of the intraocular muscles on the anterior surface of the lens (*ibid.*:94-95).

Hess (1913) began his review of accommodation in the bird eye with a description of the ciliary processes and their attachments on the anterior surface of the lens. He observed that, during electrical stimulation of a partially dissected eye, the ciliary folds appear to push on the lens. Hess was able to demonstrate that there was an increase in curvature of the lens by observing the movement of Purkinje images reflected off the anterior lens surface. It was evident from the following experiment that this was due to a contraction of the iris muscle:

If one takes a fine scalpel, and starting on the edge of the pupil, removes more and more of the iris so that, finally, only a narrow (about 1 mm wide) band of the iris root remains, this remainder still contracts strongly when stimulated. With most of the iris thus removed, so that the ciliary projections on the front surface of the lens are clearly seen, with every stimulation it may be observed how they, apparently pressed from the contraction of the remaining iris, push forward and inward and press on the front surface of the lens. . . . If the iris is fully removed down to its root, then one sees, with stimulation, a clear but diminished motion of the ciliary projections, and no longer any changes of the lens images.

In a chicken, we removed approximately two-thirds of the iris down to the root, the last third remained almost untouched. After several hours, the eye was quickly enucleated and observed from behind immedi-

ately after opening the globe at the equator. In the iris-free parts, the curvature changes of the front surface had essentially ceased with stimulation. In that sector, in which the iris remained, one saw with every stimulation abundant iris movements, and on the corresponding spots of lens, the lengthening, pulling out, and doubling of the distance of the images made by the anterior surface of the lens, in a manner similar to that in the normal eye (Hess 1913:810).

All of these observations show that: (1) the musculature in the iris root . . . pulls itself together strongly when there is only an approximately 1 mm wide band of basal iris remaining, and (2) the contraction of this iris musculature is without doubt of great importance for the curvature changes of the lens. Its influence in different species may be varyingly large; however, that removing even some of the iris in great measure impairs the ability of change in curvature in the front surface of the lens is after our findings no longer to be doubted (*ibid.*: 810-811).

Hess goes on to describe other elements involved in the accommodative mechanism, among them the tenacular ligament, which as Hess describes it, can be found by bisecting the globe of the eye at the equator. If the retina and choroid are separated from the sclera at the edge of the cut . . .

one finds an approximately 1 mm wide band constructed of very fine, brilliant, elastic fibers that run towards the lens approximately 1-1.5 mm anterior to the equator. From the outside, it is bound to the middle portion of the ciliary body or may go entirely into the ciliary body. During stimulation, this band increases by about 1/3 or more in length. The scleral origin is unmoved and remains in its place, but the ciliary insertion is moved forwards towards the lens. After the cessation of the stimulation, this band, which we can call the "ciliary elastic ring band," returns, due to its very great elasticity, rapidly to its original width. This band is easy to see in ordinary sections. It apparently has the job of pulling the ciliary body backwards into its resting state after it has been moved forwards and of preventing too strong a forward movement of the middle and rear choroid during accommodation. The muscle that pulls the ciliary body forwards, and to a certain extent is hindered

by this band, works as the *tensor choroidea* (ibid.:811).

Although Hess makes no mention of the possible existence of corneal accommodation, he inadvertently observed the effects of a contraction of the anterior ciliary muscle on the cornea. He describes removing the retina, ciliary body, and lens from the otherwise intact globe that had been cut in half at the equator. It appears, he says, as though this consists only of the cornea and sclera.

However, if this is placed on electrodes and stimulated, one will be astounded by the lively bending movements at the corneal scleral border, which is apparently moved towards the inner portion of the eye. Thus, in such a preparation, Crampton's muscle remains attached to the sclera, and its influence on the shell of the eye can hardly be demonstrated more clearly and beautifully than through this experiment. Because we could successfully stimulate these muscles four hours(!) after enucleation, such an object might be of interest to muscle physiologists (ibid.:812).

Hess observed and described an elegant demonstration of the effect of Crampton's muscle on the cornea, evidently without appreciating its implications for corneal accommodation. He also describes another elastic fiber, the pectinate ligament, that spans the ciliary cleft between the corneo-scleral spur and the angle of the iris. He writes:

[When] the cornea was removed up to a portion near its border, then one saw from the scleral margin a large number of the finest transparent fibers running obliquely backwards and attached to the root of the iris. When stimulated, the entire iris contracted, particularly its basal portion, and the entire tissue moved noticeably towards the anterior surface of the lens; by this, the fibers were very strongly tensed and bent, and on cessation of the stimulus, they shortened themselves again, whereby the iris root was pulled backwards. If one cuts these fibers with a Graefe's knife, the iris sinks noticeably backwards (ibid.:812).

In this review, Hess describes the similarities between his earlier observations of accommodation in the cormorant eye and those described here. He reiterates that in the cor-

morant the accommodative range of the eye is sufficient to produce an emmetropic (objects at optical infinity are focused on the retina) or even a myopic refraction underwater and that these changes are due to the effects of a hypertrophied iris sphincter muscle. On observing the ciliary body at the root of the iris, Hess says that it is clear that this edge of the ciliary body is being pulled axially into the eye through the contraction of the peripheral edge of the iris, and it is this action that causes the active deformation of the lens.

The most astounding thing about the lens is the enormous change in shape of its anterior surface with electrical stimulation. The anterior lens image moves forward through the pupil and becomes much smaller. Upon cessation of the stimulation, it moves backwards to its old magnification. I could not see any clear reduction in the posterior lens image. The entire posterior lens surface in an eye that had been opened and stimulated moved somewhat backwards, and the equatorial diameter of the lens became clearer but not smaller [Figure 7]. By observing the opened globe of the eye from the rear, one can look through the lens and see that when stimulated those portions of the iris nearest the pupil are not arranged in a perpendicular plane as they are in a resting eye, but rather they are pushed forwards towards the cornea and make an open funnel. Also, those accommodative alterations, which I talked about [earlier]—the doubling of the anterior lens image, etc.—can be seen particularly easily in the cormorant eye. The lens is remarkably soft and a slight push on the lens with a needle suffices to take it out of its normal form. It is the softest lens I have seen among birds and only in turtles have I seen a lens that is comparably soft (ibid.:813–814).

Hess recognized the similarities in the lenticular accommodative mechanism among the species he studied.

The accommodative alterations I found in the other birds I investigated differed from the cormorant only by degree and certainly not in kind (ibid.:815).

He also accounted for the superior accommodative range of the cormorant eye:

The suitability of the accommodation apparatus for the much greater demand in div-

ing is brought about in the following way in the cormorant eye. (1) The lens is considerably softer in the cormorant than in other birds. This interesting fact conforms with what we have found in a large number of species, namely that the lens is much softer in those animals that have a greater range of accommodation. (2) The inner musculature of the eye, which either directly or indirectly causes the alteration of form of the lens, is particularly strong. In particular, we should mention the muscles in the neighborhood of the root of the iris. The function of the latter as the *compressor lentis* is very clear both in the fixated cormorant eye and in the living eye. (3) The great mobility of the circumlental tissue parts which, through their approach to the lens and iris root, allow the movement of the iris during accommodation. . . . The most important accommodative events in the bird eye have been explained by these findings. One can speculate as to how things might be; our studies show for the first time how things really are. With our methods we can let the entire process play itself out before our eyes. Rather than simply deducing the changes in curvature of the lens, we can see them directly (ibid.:815).

Hess explains the role of the ciliary muscles in lenticular accommodation as follows:

The increase in curvature in the lenses of birds and reptiles follows primarily from the pressure of the ring musculature of the iris root and the ciliary prominence that lie behind the iris on the periphery of the lens anterior surface. Elastic elements, which we can easily demonstrate in the circumlental ciliary portion, support this movement but by themselves cannot call forth any appreciable change in curvature. In order for this pressure to be possible, the ciliary prominence has to move inwards towards the axis of the eye. This is achieved through the contraction of the two other intraocular muscles. Crampton's muscle has the job of moving the corneal scleral border and the fibers that go from there to the ciliary body inwards towards the iris root and the lens border, and so allows an effective contraction of the iris. The *protractor corporis ciliaris* [the name Hess gave to the posterior ciliary muscle] stretches the elastic ciliary ring band [the tenacular ligament] that we talked about above and pulls the ciliary body forwards and towards the axis of the eye. It functions

in a very similar manner as Crampton's muscle does on the circumlental part of the ciliary body. Without it the elastic forces of the ciliary body and the contraction of the iris musculature would not exert the same pressure on the lens (ibid.:815-816).

Hess suggests that the zonular fibers in the bird eye are not relaxed during accommodation, as they are in the mammalian eye, but are in fact tensed. The zonular fibers extend from the ciliary processes to the anterior lens surface between the ciliary folds. Hess proposes that they strengthen the attachment of the ciliary body to the lens so that, during accommodation, the lens is squeezed rather than simply pushed backward in the eye. Although he provides no proof of this assertion, it is clear that the zonular fibers cannot serve the same function as they do in the mammalian eye. This and the other unique features of the avian eye led Hess to a different conclusion than Beer.

The accommodative events in the eyes of reptiles and birds are totally different from what has been assumed until now. They are totally different in principle from those in the human eye, indeed in a most important point they are exactly opposite! During accommodation in reptiles and birds, the lens is under increased pressure and therefore changes itself from its less curved resting form. In humans, during accommodation the lens is under a lessened pressure and therefore approaches its resting form of increased curvature. The mechanism that we find in ape and human eyes therefore is not as one originally assumed, namely, an old, inherited part of the vertebrate series, but rather it is a much more recent discovery that we encounter for the first time in the mammalian eye (ibid.:817).

In reconciling the different theories that his predecessors formulated, Hess observed:

In the older literature we find almost entirely theoretical writings about the accommodative changes in the bird eye that are founded on anatomical investigations. . . . So of the anatomical arrangements, one author had developed a compression theory and the other author had developed a relaxation theory of accommodation. This is, among other things, of interest because recently the opinion was published that one

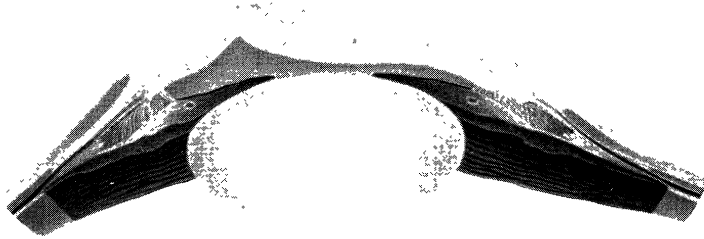


Fig. 4



Fig. 5

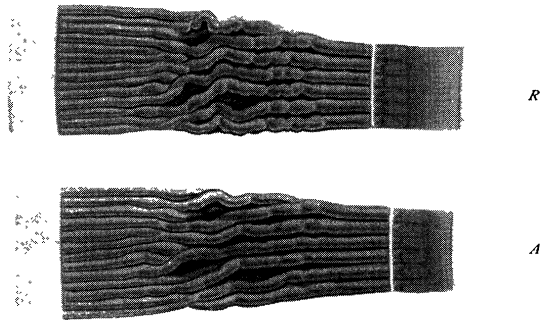


Fig. 6.

W. Freytag gez.

C. Heß, Akkomodation bei Tauchervögeln.

Verlag von S. Hirzel in Leipzig

FIGURE 7. HESS'S DIAGRAM SHOWING THE ANTERIOR LENTICONUS CAUSED BY NICOTINE STIMULATION OF A CORMORANT EYE.

The eyes were enucleated; one was placed in saline (Fig. 4), while the other was placed in a nicotine solution (Fig. 5). The eyes were then fixed and bisected. The nicotine caused a contraction of the iris, which applies a sphincter-like force to the anterior surface of the lens. The direct force of the iris on the lens causes a marked increase in the curvature of the anterior lens surface. The ciliary body undergoes an increase in tension after nicotine stimulation (Fig. 6). In the relaxed eye (R), the ciliary folds have a loose and wavy appearance. In the nicotine-treated or accommodated eye (A), the ciliary body is stretched by the iris contraction and the ciliary folds take on a more parallel arrangement.

could obtain a sufficient knowledge of the physiology of accommodation simply by looking at morphological arrangements (ibid.: 817,818).

Conspicuous only by their absence are any of Hess's own ideas on a mechanism for corneal accommodation. While he never denied the possibility that birds use corneal accommodation, he unequivocally expresses his doubts of its existence when addressing other studies prior to his 1913 paper.

Franz was in error with the statement that "the accommodation of the lens according to Hess is accomplished without the collaboration of Crampton's muscle. This muscle is far more important for the corneal accommodation." I have never said anything like this. Rather, the significance of the muscle in question for accommodation of the lens . . . I have formulated in an entirely different way. . . . Franz believes that the bird eye is better equipped for accommodation than any other eye because, in addition to the accommodation of the lens, it also has corneal accommodation. Contrary to that, may I say that Beer in a series of really strongly accommodating birds (for example hens, crows, and pigeons) could find no active accommodation at the apex of the cornea. Further, according to my investigations on diving birds, after removal of the cornea, that is, solely through the accommodation of the lens, I was able to find a change in refraction of approximately 50 diopters (ibid.:818-819).

Although Hess observed as much as 50 diopters of accommodation in the cormorant eye, he recognized that not all birds have such a large accommodative range. Nocturnal birds can capture their prey at night without using visual cues. Hess cites this fact to support his observation that accommodation is often considerably reduced or absent in nocturnal birds. The need for accommodation is also reduced in raptors, since these birds dive to capture their prey on the wing. Hess notes that the high visual acuity of these birds says nothing about their accommodative abilities, for there is no accommodative demand in diving from great heights until the predator is within 5 to 6 meters of the prey. These birds capture their prey with their talons and use their beaks only for ripping meat from the carcass, an act that can be accomplished without accommo-

modation. (Falcons can, after all, feed while hooded.) Hess maintains, therefore, that the strong accommodators are the seed feeders, such as chicks and pigeons, and that the large accommodative range of these foragers cannot be generalized to all birds.

Hess concludes his article with a discussion of both the annular pad and the significance of the relative softness of the lens. In the latter case, Hess notes that among the bird species he examined, the stronger the accommodation, the softer the lens. This relationship held among all the *Sauropsida* he observed, where the turtle had the softest lens followed by the cormorant, the bird with the strongest accommodative range. In general, the lenses of the nocturnal species were firmest among the birds, reflecting their reduced accommodative ability. Hess agrees with Müller that the annular pad serves as a more rigid surface around the lens through which the muscles and ciliary body can force a change in curvature of the lens. The annular pad is only found in those species that accommodate by changing lens curvature. According to Hess, the annular pad tends to be more prominent in birds that have a large accommodative range, but this is not the only factor that determines its size.

## CONCLUSIONS

### SUMMARY OF THE FINDINGS IN THE HISTORICAL LITERATURE

Crampton, through his anatomical and physiological investigations, determined that the anterior ciliary muscle originated on the sclera of the globe and inserted on the inner lamella of the cornea. He believed that a contraction of this muscle would pull on the inner lamella of the cornea to flatten the peripheral cornea. Crampton failed to see that this effect was not carried through to the more central cornea, and formulated the belief that corneal accommodation was a mechanism of flattening the cornea to allow the normally myopic eyes of birds to accommodate for distant objects.

Following Crampton, Brücke, through his anatomical investigations, argued that the corneal curvature was actually increased during accommodation, rather than flattened as Crampton had suggested. Brücke concen-

trated his attention on the central cornea and believed that Crampton's muscle was sufficient to cause an increase in the optical power of the cornea. Brücke described the posterior ciliary muscle and the tenacular ligament against which this muscle works. He also found muscle fibers with an origin on the sclera that coursed backward in the eye to insert on the choroid. He believed this muscle would pull the choroid forward during accommodation, but gave no indication of what purpose this may serve.

Cramer was unable to induce movements of corneal Purkinje images in enucleated eyes that were electrically stimulated. He concluded that Crampton and Brücke were incorrect in their descriptions of corneal accommodation. Cramer believed that the entire ciliary muscle served the role that Brücke had attributed to the posterior ciliary muscle, namely pulling forward on the choroid. Cramer thought that this pulled the vitreous forward against the posterior surface of the lens to prevent the lens from moving backward during accommodation. Cramer was thus the first to ascribe a role for the entire ciliary muscle in lenticular accommodation. Cramer was also the first to observe that the iris sphincter muscle contracted around the anterior surface of the lens to actively squeeze the lens to induce lenticular accommodation.

Müller made additional observations of the role of the iris in lenticular accommodation adding substantially to the anatomical description of the iris. He noticed that it was the peripheral musculature of the iris that served the predominant role in squeezing the lens during accommodation. Müller found a third component of the ciliary muscle that had not been described by Crampton or Brücke. He noticed fibers in the posterior ciliary muscle group that did not terminate in the sclera as Brücke had described, but passed forward to terminate on the inner lamella of the cornea in the same manner as fibers of Crampton's muscle. These fibers formed an intermediate group, which serves the dual purpose of pulling backwards on the inner lamella of the cornea in the same manner as Crampton's muscle, and pulling forwards on the choroid in the same manner as Brücke's muscle. Although not entirely convinced of the function of the

ciliary muscle, Müller suggested that the three separate components all pulled the choroid forward against the posterior surface of the lens to prevent the lens from moving backwards during accommodation. Thus Müller believed that the iris and the ciliary muscle were both serving a role in lenticular accommodation. Müller made almost no mention of the possibility of corneal accommodation, neither refuting nor accepting its existence.

Exner proposed an entirely new hypothesis for accommodation in birds that he believed to apply universally across all species. He was under the impression that the lens was held in a flattened state by the positive intraocular pressure, and that a contraction of each of the three divisions of the ciliary muscle would act to release this tension on the lens, thus allowing the lens to assume a more spherical, accommodated shape.

Beer's observations of corneal accommodation brought together Crampton's and Brücke's findings. Beer observed the flattening of the peripheral cornea and the increased curvature of the central cornea. Beer recognized that for the ciliary muscle to have any effect on accommodation in the eye, it was necessary that changes must occur in the central region of the cornea. However, in many of the birds that Beer studied, he was unable to see movements of the central cornea, even though he could clearly observe a flattening of the peripheral cornea. Beer concluded that these birds simply did not have functional corneal accommodation.

From his observations of lenticular accommodation, Beer noticed that the curvature of the lens increased when the pectinate ligament was cut and that the extent of lenticular accommodation was reduced when the cornea had been removed. Beer's experiments also led him to conclude that a removal of the iris had little effect on the amplitude of the lenticular changes. This led Beer to depart from the irideal theories of Cramer and Müller and to invoke Exner's pressure theory to explain lenticular accommodation. Beer believed, as had those before him, that the posterior ciliary muscle served the function described by Brücke and Cramer, namely, pulling the choroid and the vitreous forwards against the posterior surface of the lens.

After the emphasis that Exner and Beer placed on pressure-related theories, Hess did the obvious experiments of measuring pressure changes in the eye of many vertebrates during accommodation. He concluded from these studies that the pressure changes in bird eyes were caused by the accommodative mechanism rather than *vice versa*.

Hess described the action of the posterior ciliary muscle against the elastic tenacular ligament and the action of the iris against the elasticity of the pectinate ligament. Although he observed the effect that a contraction of the anterior ciliary muscle had on the peripheral cornea, Hess argued against the existence of corneal accommodation, pointing towards Beer's negative experiments and the fact that the cormorant had 50 diopters of lenticular accommodation alone. Hess failed to recognize the species differences and the fact that for an aquatic bird such as the cormorant, corneal accommodation would be of no value. Hess believed that the anterior ciliary muscle served the same function as the posterior ciliary muscle in releasing the resting outward tension that the ciliary body imposed on the lens.

#### HISTORICAL FINDINGS IN LIGHT OF RECENT EVIDENCE

Recent descriptions of the anatomy of the avian ciliary muscle (Glasser et al. 1994; Murphy et al. 1995; Pardue and Sivak 1996) agree in large part with the three separate divisions described by Crampton, Brücke, and Müller. The action of the anterior ciliary muscle of the chick eye in mediating corneal accommodation by pulling backward on the inner lamella of the cornea is in agreement with the independent observations of Crampton and Brücke. Beer subsequently provided a more comprehensive description bringing together these two theories. Our own observations are essentially similar to those described by Beer. Beer, however, failed to observe corneal movements in chicks, the subject of our investigations, and so believed that chicks and some other terrestrial birds did not have corneal accommodation.

While the role of the posterior ciliary muscle has been less contentious than that of the anterior ciliary muscle and the iris, a complete description of the function of the posterior ciliary muscle was not provided in the histori-

cal literature. The roles we have described for the posterior ciliary muscle in the chick eye are in agreement with functions initially proposed by Crampton, Brücke, and Cramer combined. The posterior ciliary muscle in the chick eye assists in lenticular accommodation by pulling forwards on the choroid to pull the vitreous up against the posterior surface of the lens. We have found that the posterior ciliary muscle serves an additional function in pulling forwards and axially on the posterior ciliary body. This releases the outward tension that the ciliary body imposes on the lens. Through this action the peripheral musculature of the iris can act directly on the lens rather than having to pull against the outward tension of the ciliary body. A description of this function of the posterior ciliary muscle is not to be found in the historical literature. Our observations of the role of the posterior ciliary muscle in lenticular accommodation in the chick eye are in sharp contrast to the descriptions given by Cramer, Müller, and Exner of the entire ciliary muscle involvement in lenticular accommodation in the bird species they studied.

The descriptions that Cramer and Müller provided for the role of the iris in lenticular accommodation, and Müller's anatomical descriptions of the iris, are similar to our own findings in chicks (Glasser et al. 1995; Glasser and Howland 1995). The pressure-related ideas put forward by Exner and later expounded by Beer, however, are clearly in error. Substantial changes in lens power can be induced in the chick eye in the complete absence of intraocular pressure (Glasser and Howland 1995). Exner's misguided theories probably stem from the absence of experimental support. Had he undertaken physiological experiments similar to those conducted by Cramer before him, he would have seen that lenticular accommodation could still occur after the cornea had been removed from the eye and that his pressure theory could not be correct.

Beer supported Exner's theories because he saw that the tension on the pectinate ligament pulled the lens into a flattened state and also because he saw small changes in lens curvature even after the iris had been removed. Our results in the chick eye also show that the pectinate ligament pulls the lens into a flat-



tened state, but this is due to the elasticity of the pectinate ligament and the rigidity of the globe from the scleral ossicles rather than a consequence of the intraocular pressure. In addition, it is possible that the small changes in lens curvature that Beer observed during stimulation after the iris had been removed were caused by a contraction of the posterior ciliary muscle as we have described previously. In the chick eye we observed dramatic changes in lens curvature during stimulation when the iris is intact. After removal of the iris, small changes in lens power still occur. We attribute this to an incomplete removal of the iris, as well as the effect of the posterior ciliary muscle on lenticular accommodation.

Our own work on the role of intraocular pressure in accommodation in the chick eye (Glasser et al. 1994) agrees well with the conclusions arrived at by Hess from his pressure experiments on a variety of bird species. An increase in pressure in the globe, most likely due to a contraction of the posterior ciliary muscle pulling on the choroid, would provide a force against the posterior lens surface to prevent a backward movement of the lens during accommodation.

Hess observed the iris sphincter muscle to be pushing directly on the anterior surface of the lens. Our own results of Edinger-Westphal stimulated accommodation in partially iridectomised chick eyes (Glasser et al. 1995) show the same results. It is clear that when the more central iris muscle fibers are removed, the remaining muscle fibers are clearly acting directly on the lens.

#### GENERALIZATIONS ABOUT CORNEAL ACCOMMODATION

Cramer, Exner, Müller, and Hess believed that the anterior ciliary muscle served the same function as the posterior ciliary muscle; i.e., pulling the posterior ciliary body forward against the tenacular ligament. Based on our anatomical observations, this function is not possible in the chick eye. The fixed posterior origin of the muscle fibers are on the sclera of the globe inside the scleral ossicles. The anterior insertions of these fibers are on the inner lamella of the cornea. Therefore, when these fibers contract, they can only pull backwards on the inner lamella of the cornea. That both

early and subsequent authors missed this action of the anterior ciliary muscle can be attributed to several causes:

- (1) Once the intraocular pressure of the globe has been lost through death or enucleation, the normal curvature of the cornea is no longer sustained, and hence a contraction of the anterior ciliary muscle may not have any visible effect on the central cornea (Glasser et al. 1994). This may have misled Cramer into believing that all birds did not have corneal accommodation, and Beer into believing that some of the terrestrial birds he studied did not have corneal accommodation. Beer reported seeing movements at the peripheral cornea, but no movements of the central cornea. It is unlikely that the physiological action of a flattening of the peripheral cornea could have evolved without a resultant optical effect.
- (2) It is unlikely that nocturnal birds, such as some owls, which may have little or no accommodation (Murphy and Howland 1983; Glasser et al. 1996), would have evolved functional corneal accommodation. The shape of the eye, the anatomical structure of the ciliary region, the diminished size of the anterior ciliary muscle, and the reduced accommodative ability all suggest that these birds may not in fact have functional corneal accommodation. It is therefore possible that in studying birds such as these one could only conclude that no such accommodative mechanism exists.
- (3) Aquatic birds can have no use for corneal accommodation, since the optical power of the cornea is neutralized when the bird is submerged. If birds such as the cormorant are to chase and capture prey underwater, they must have a substantial accommodative capacity that is entirely lenticular in nature. This is exactly what Hess found in the cormorant, and it led him to conclude that corneal accommodation was neither necessary nor did it occur in birds.

#### GENERALIZATIONS ABOUT LENTICULAR ACCOMMODATION

It is necessarily true that generalizations cannot be made about the lenticular accommodative mechanisms in different bird spe-

cies. Because of the varied accommodative requirements of birds, the varied eye shapes, and the varying degrees of irideal musculature (Glasser and Howland 1995), it is just as likely there is considerable diversity in the mechanism of lenticular accommodation. Whether birds with diminished iris musculature employ different lenticular mechanisms or whether they simply lack lenticular accommodation can only be accurately determined by systematic histological, anatomical, and physiological investigations.

## SUMMARY

One cannot help but admire the enormous effort that went into understanding the accommodative mechanisms of the avian eye. Nevertheless, one also cannot help but notice that the scientific dialogue was often a monologue and that, time after time, the work of predecessors was simply ignored. Furthermore, attempts to interpret the function of an-

atomical arrangements without using physiological experiments often came to grief. While *in vitro* experiments often gave useful results, such as in studies of lenticular accommodation, this was not always true. A perfect example was the failure to find corneal accommodation when the globe is opened and the intraocular pressure has fallen. Lastly, the investigators cited in this review have shown a tendency to seize on a single simplifying hypothesis for all birds, when, in fact, nature is far more complicated.

## ACKNOWLEDGMENTS

We would like to thank Ari Van Tienhoven for assisting in the translation of Cramer's (1853) Dutch writings. We owe tremendous thanks to Terri Natoli for patiently transcribing dictated translations and to Lani Peck for editorial suggestions on the manuscript. The authors gratefully acknowledge the two anonymous referees and the editors of the *QRB* for their helpful comments and suggestions. Portions of this work were supported by NEI grant #EY02994 to HCH from NIH.

## REFERENCES

- Beer T. 1893. Studien über die accommodation des vogelages. *Archive Gesamte Physiologie* 53:175–237.
- Brücke E. 1846. Ueber den musculus Cramptonianus und den spannmuskel der choroidea. *Archiv für Anatomie, Physiologie und Wissenschaftliche Medicin* 1:370–378.
- Cramer A. 1853. Het accommodatievermogen der oogen, physiologisch toegelicht. *Hollandische Maatschappij der Wetenschappen te Haarlem*. Haarlem: De Erven Loosjes. pp 1–139.
- Crampton P. 1813. The description of an organ by which the eyes of birds are accommodated to the different distances of objects. *Thompson's Annals of Philosophy* 1:170–174.
- Evans H E. 1993. Organa sensum [Organa Sensoria]. In J J Baumel et al., editors. *Handbook of Avian Anatomy: Nomina Anatomica Avium*. Second Edition. Cambridge (MA): Nuttall Ornithological Club. pp 585–612.
- Exner S. 1882. Über die function des *Musculus Cramptonianus*. *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften* 85:52–61.
- Glasser A, Howland H C. 1995. *In vitro* changes in back vertex distance of chick and pigeon lenses: species differences and the effects of aging. *Vision Research* 35:1813–1824.
- Glasser A, Murphy C J, Troilo D, Howland H C. 1995. The mechanism of lenticular accommodation in the chick eye. *Vision Research* 35:1525–1540.
- Glasser A, Pardue M T, Andison M E, Sivak J G. 1996. Accommodation in raptors. *Journal of Comparative Physiology, A* In press.
- Glasser A, Troilo D, Howland H C. 1994. The mechanism of corneal accommodation in chicks. *Vision Research* 34:1549–1566.
- Hess C. 1909. Vergleichende Untersuchungen über den Einfluss der Accommodation auf den Augendruck in der Wirbelthierreihe. *Archiv für Augenheilkunde* 63:88–95.
- Hess C. 1913. Gesichtssinn. In H Winterstein, editor. *Handbuch der Vergleichenden Physiologie*. Volume 4. Jena: Gustav Fischer. pp 789–840.
- Home E. 1795. The Croonian lecture on muscle motion. *Philosophical Transactions of the Royal Society of London* 85:1–23.
- Howland H C, Howland M J, Schmid K, Pettigrew J D. 1991. Restricted range of ocular accommodation in barn owls (Aves: Tytonidae). *Journal of Comparative Physiology, A* 168:299–303.
- Levy B, Sivak J G. 1980. Mechanisms of accommodation in the bird eye. *Journal of Comparative Physiology, A* 137:267–272.
- Murphy C J, Glasser A, Howland H C. 1995. The anatomy of the ciliary region of the chicken eye. *Investigative Ophthalmology and Visual Science* 36:889–896.
- Murphy C J, Howland H C. 1983. Owl eyes: accom-

- modation, corneal curvature and refractive state. *Journal of Comparative Physiology* 151:277–284.
- Müller H. 1857. Ueber den accommodations-apparat im auge der vogel, besonders der falcken. *Archiv für Ophthalmologie* 3:25–55.
- Pardue M T, Sivak J G. 1996. The functional anatomy of the ciliary muscle in four avian species. *Brain Behavior and Evolution* In press.
- Sivak J G. 1980. Avian mechanisms for vision in air and water. *Trends in Neurosciences* 12:314–317.
- Sivak J G, Hildebrand T E, Lebert C G, Myshak L M, Ryall L A. 1986. Ocular accommodation in chickens: corneal vs lenticular accommodation and effect of aging. *Vision Research* 26:1865–1872.
- Sivak J G, Howland H C. 1987. Refraction of the eye of the brown kiwi (*Apteryx australis*). *Canadian Journal of Zoology* 65:2833–2835.
- Sivak J G, Vrablik O E. 1981. Ultrastructure of intraocular muscles of diving and nondiving ducks. *Canadian Journal of Zoology* 60:1588–1606.
- Suburo A M, Marcantoni M. 1983. The structural basis of ocular accommodation in the chick. *Revue Canadienne de Biologie Experimentale* 42:131–137.
- Walls G L. 1942. *The Vertebrate Eye and Its Adaptive Radiation*. Bloomfield Hills (MI): Cranbrook Institute of Science. [Reprinted 1967. New York: Hafner Publishing Company.] pp 247–289.
- West J A, Sivak J G, Doughty M J. 1991. Functional morphology of lenticular accommodation in the young chicken (*Gallus domesticus*). *Canadian Journal of Morphology* 69:2183–2193.
- Young T. 1801. On the mechanisms of the eye. *Philosophical Transactions of the Royal Society of London* 91:23–88.