THE EYES AND EYESIGHT OF BIRDS, WITH ESPECIAL REFERENCE TO THE APPEARANCES OF THE FUNDUS OCULI.

CASEY A. WOOD, M.D., D.C.L., F.Z.S., Lond.
CHICAGO.

PRELIMINARY PAPER.

[Illustrated by two colored plates and eight illustrations in the text.]

The following studies of the eyes of birds were made chiefly from material supplied by the Gardens of the London Zoological Society, for which I am greatly indebted both to the Superintendent, Mr. R. I. Pocock, and the Prosector, Mr. F. E. Beddard, F.R.S., and from sections of birds' eyes and brains made for me by Professor Slonaker, now of Leland Stanford University. For the preparation of microphotographs from these I am indebted to Dr. Earl Brown, of Chicago. The paintings of avian fundi described in the text were drawn *ad naturam* by Mr. Arthur W. Head, F.Z.S., from birds examined ophthalmoscopically mostly by both of us. A portion of this paper was presented to the Ophthalmic Section of the American Medical Association at Boston (June, 1906), illustrated by streopticon slides prepared for me from his own drawings by Mr. Head.

If an apology be needed for an excursion into the little known and apparently unproductive domain of comparative ophthalmology it will be found in Treacher Collins' classic Erasmus Wilson Lectures on the Anatomy and Pathology of the Eye. He reminds us that "there is a law in biology to the effect that the various stages of development through which the individual passes typify the history of the race." Furthermore, as he again and again points out in the course of these lectures, pathologic changes, including arrest of development, often simulate anatomic arrangements that are normal in the lower animal. Speaking of the development of the eyelids, for example, he remarks that in a six weeks' human embryo these are absent, just as they are in eels and some other fishes, the skin of the head being continuous with the anterior layers of the cornea. At eight weeks the newly forming lids are seen as small buds of mesoblast covered with epiblast above and below. The same structural arrangement, permanent in character, is seen in the teleostean fishes. In these, little folds of tissue arise from the margin of the orbit, project toward the cornea, but do not reach that organ. Still later, as the dermal folds in the human fetus continue to grow into eyelids, they envelop the cornea, meet and adhere at their margins by union of their epithelial surface, so that the conjunctiva becomes a closed sac. As we know, separation takes place before birth in the human animal, but in our ancestors the snakes and in some lacertilia (lizards) the adhesion continues during life, these animals being obliged to see through their eyelids, as it were. The application of these embryologic facts is seen in cases of congenital absence of the lids and congenital ankyloblepharon in man.

If, then, a study of the eyes of the lower animals is likely to throw light upon the biology and pathology of the human visual apparatus, there is ample justification for the indulgence by the practical ophthalmologist in even the desultory observations and studies I have been able to make of the ocular organs in birds. I have said *birds* because in them we have the highest type of vision. The very existence of every bird depends upon good eyesight with which to obtain food and escape enemies. Some mammals, fishes, reptiles and amphibia get through life fairly well without eyes, but there are no blind bird families.

As an example of the visual capacity of some birds one has but to think for a moment of a hawk poised several hundred yards above a meadow in which a field-mouse or a small chicken is hidden. In a few seconds after the quarry is sighted it is seized by the bird, whose sharp sight has not only detected it, but whose wonderful accommodative apparatus permits of a sure and continuous fixation from hundreds of meters to less than a meter within an incredibly short space of time. Variations in the character of this acute vision are seen in many other birds; in the humming-bird that darts here and there so quickly that the human eye can not follow it, and yet comes suddenly to rest on an almost invisible twig; in the woodcock that flies through the thick woods, avoiding every tree, shrub and branch as if they were non-existent; in the owl that combines good diurnal with good nocturnal vision, and in the kingfisher that sees as well in the air as he does in water.

Bird vision, then, is not only the highest expression of eyesight both as to acuity and variety, but it repeats the oft-told tale of the correlation of sight in the animal to its life history as witnessed chiefly in the pursuit of food and escape from death or injury. If, then, as ophthalmologists we engage in the study of the physiology and mechanics of vision, surely a consideration of the ocular apparatus of birds—even in the superficial fashion in which I shall be obliged to present it to you here—will not be profitless.

The *size and shape of the eyeball* of birds must be noted. It is unusually large in comparison with that of other animals and in proportion to the size of the avian body. Of course, size alone is not the only consideration in determining effectiveness of function in an organ, but when one pursues the subject still further it will be seen that the cerebral and spinal parts of the ocular system are proportionately better developed and larger than in the great majority of other vertebrates. Almost all birds whose habits require the widest range of vision—eagles, hawks and vultures, for example—are noticeable for very prominent eyeballs, laterally placed. In the owl, whose eyes are adapted to searching only space in front of the globes and orbits, they are disposed as in man and the higher apes. Like them, the owl has the power and possesses the apparatus common to all animals that enjoy the privileges of binocular vision.

THE EYELIDS OF BIRDS.

First of all, let us consider their eyelids. There is something very human about the true lids of most birds. They have, as a rule, the same dermal folds, the same cilia, and much the same minute structure as we have—all employed in the same way for the same purpose.

The Nictitating Membrane.—The third eyelid found in reptiles, some mammals, and commonly seen as a vestigial remains in man (*plica semilunaris*) and the higher apes, finds its highest development in birds. It seems to act not only as a scraper of the cornea for cleansing purposes—like the true lid margins—but probably enables some birds, like the eagle, for example, to see through it, with a degree of distinctness, even in the blinding sunshine. When in the pursuit of food or when engaged in fighting, the bird may at short notice draw the curtain of his nictitating membrane and thus prevent serious damage to his cornea. When the eye is at rest and the true lids are separated, the avian nictitating membrane shows only at the inner canthus. Law[1] well describes this third lid as an "elastic fibrocartilage prolonged at its inner end as a thick prismatic stem and expanded anteriorly into a broad, thin expansion with a perfectly smooth, even border, fitting accurately on the rounded surface of the eyeball and covered by the mucosa. Its thick, deep extremity is continuous, with an abundant cushion of adipose tissue which fills the depth of the orbit and extends between the muscles."

In those mammals—the hoofed animals, for example—which are constantly grazing among thistles, nettles and other spiky plants, the cornea needs some protection other than lids, and this is probably found in the *membrana nictitans.* On the other hand, in the marine mammals—whale, seal, etc.—in which a third eyelid can serve no useful purpose, it is wanting. This shutter-like membrane is drawn over the cornea chiefly by the musculus pyramidalis, attached to it in much the same way as the true lids are moved by their muscles.

The Gland of Harder.—That the cornea of birds may be constantly disinfected and its surface cleaned of foreign bodies of all kinds, the gland of Harder, a supplementary lacrimal gland, furnishes a copious supply of tears, which are forced out and sprayed over the eyeball as the third eyelid sweeps over the anterior surface of the globe. This gland is placed beneath the *membrana nictitans* and functionates simultaneously with it.

Both the *membrana nictitans* and Harder's gland occasionally suffer at the hands of would-be veterinary surgeons. In most acute diseases of the eye in birds and in many general conditions, the third lid falls down over the cornea. The ignorant operator, in his effort to relieve the sick animal, removes the "cataract" without, it

1. Ophthalmic Record, 1905, p. 440.

is needless to say, doing any good to his patient. The gland of Harder is also well developed in many mammals, and it, too, is occasionally mistaken for a diseased condition and summarily dealt with. A short time ago I saw a valuable bull-terrier from which the owner had, for cosmetic reasons, excised as much as was visible of these organs. The operation was followed by a large corneal ulcer and loss of sight in the affected eye.

The Cornea of Birds.—Practically every bird has a cornea much more conical than that of the human species. This largely accounts for the brightness of avian eyes, and is one of the factors in their wonderful power and range of accommodation.

The Avian Sclera.—The cone-like shape of the cornea is continued into the sclerotic, which is entirely unlike the same structure in most of the other vertebrates. The anterior segment of the bird's sclera is furnished with overlapping bony plates surrounded by connective tissue. These greatly strengthen the ocular walls, so that the marked pressure exerted upon them during accommodative efforts do not permanently affect the shape of the eyeball. The posterior half of the bird's eyeball is further strengthened by a cup of hyaline cartilage that extends to the bony plates in front.

The Iris of Birds.—Even the most superficial observer can not walk through an aviary without remarking the brilliancy and extraordinary variety of coloration in the irides of birds. Zoologists[2] have even built up a classification based upon variations in the color of the eyes in the genera of aves. The *sphincter pupillæ* in birds is unusually well devloped, as are also the radial fibers.

The Shape and Size of the Bird's Pupil.—This should receive some comment, since it, as in man, is closely related to the focussing apparatus, and forms an important part of the peculiar uveal tract of birds. The motility of the iris and pupil is most remarkable. In watching the yellow-eyed parrot, for example, one can not help believing that the size of the pupil must be under the control of his will, so quickly does it expand and contract without apparently any relation to variations in the distance of the object fixed. In the majority of birds the pupils are round, but in some nocturnal birds, like the owl, these, round at one moment, may be contracted

2. See, e. g., Th. Bruhin's Die Iris der Vögel als unterschiedenes Merkmal der Arten, etc., in *Zool. Garten,* 1870, p. 290. Also in *Ibis,* p. 207, 1859, On the Color of the Bird's Iris.

to a vertical slit, probably when the animal accommodates for a near object.

It must be confessed that not much is known about the size and shape of the avian pupil in the several conditions of accommodation, convergence, illumination, etc. In the London "Zoo" I spent considerable time trying to decide the extent to which the pupils of night birds are affected by light. There is no doubt but that the owl's pupils contract and expand in the presence and absence of light much as ours do. Flashing light into the eyes of all the owls had the same effect—an almost instant contraction of the pupil. Moreover, I was also able to determine a consensual contraction to light in several different species of owls. There are manifest difficulties in the way of exactly determining the effect of light upon birds' pupils, as it is almost impossible in most instances to eliminate the effect upon the pupil of accommodative efforts—a factor that probably exerts no little influence upon their size and shape.

The Anterior Chamber in birds is generally deep and the quantity of aqueous humor correspondingly large. The wide space between cornea and lens permits of greater antero-posterior movements of the crystalline in realizing the wide accommodative range needed by the bird in its frequent and extensive change of focus. Incidentally, also, it contributes to the peculiar brilliancy of the avian eye.

The Ligamentum Pectinatum is an elaborate and extensive organ in the eyes of birds. According to Collins,[3] it arises at the limbus corneæ a little in front of the root of the iris and extends backward between the striated muscle of Crampton and that part of the ciliary body attached to the ciliary processes.

The Canal of Schlemm is proportionately large, and in sections of the bird's eye is easily seen standing wide open. The presence of so capacious a lymph channel undoubtedly corroborates the view that the interior of the bird's eye is the scene of great nutritional activity, requiring a drainage canal capable of carrying off waste products in considerable amounts from organs constantly functionating.

The Ciliary Body of Birds, although well developed, is not, like that organ in man and most other animals, the only source of the

3. E. Treacher Collins: The Lancet Feb. 24, 1900.

intra-ocular fluids and the nutritive supply to the lens. As we shall later see, that peculiar organ, the pecten (the analogue of the falciform process of reptiles and some mammals) largely supplements the supply of nutritive fluid required by the intra-ocular tissues.

The chief muscle of accommodation in birds is probably that known as Crampton's. While variations in the shape of the globular lens of birds, under the influence of the ciliary fibers, undoubt-

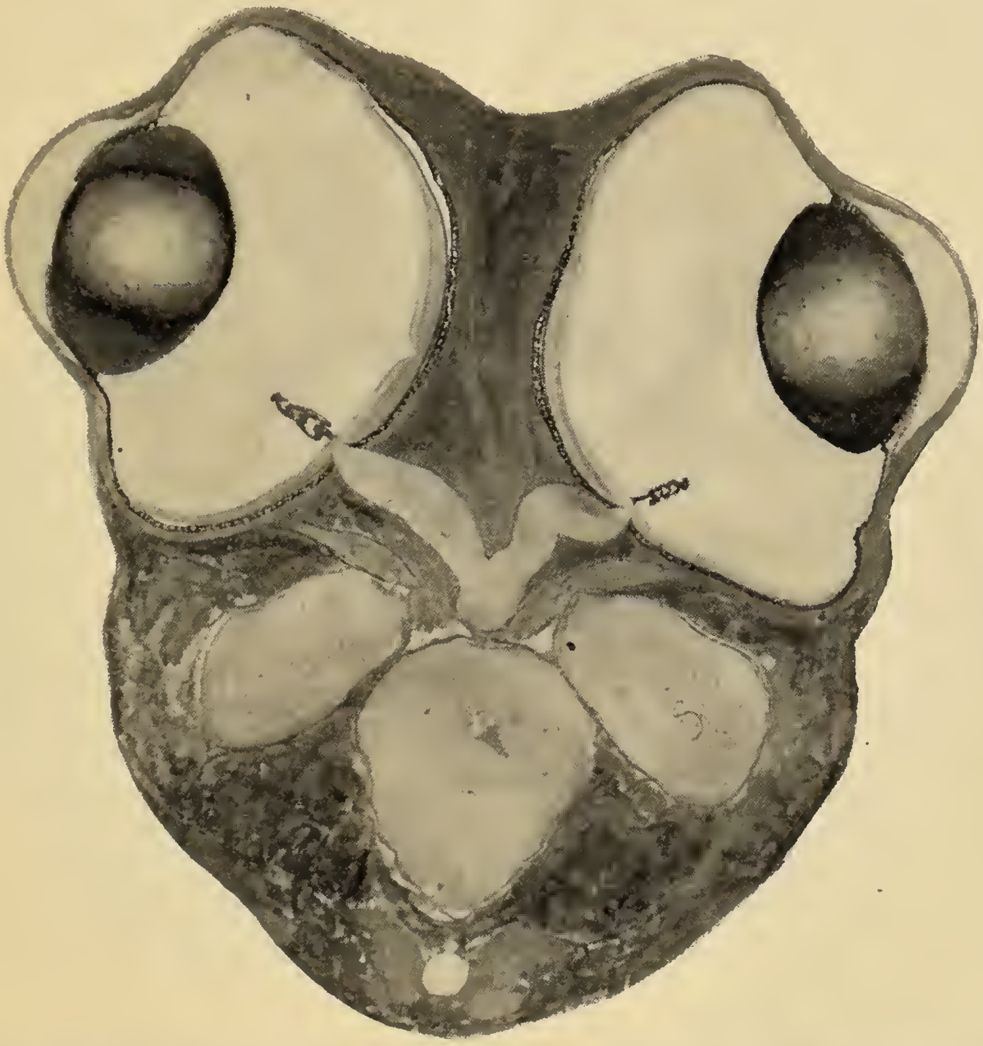

Fig. 1.—Cross section of the brain, orbits and eyeballs of the Kinglet (Regulus satrapa), showing the various ocular structures and their relations, especially the deep right fovea, the pectens, etc.

edly result in increase of curvature and of refractive effect, yet the principal change in the direction of the light rays is produced by transforming a more or less round or ovoid globe into a tubular structure fitted with a conical lens. This alteration is brought about by the contraction of the circular muscle of Crampton—an intra-ocular band that encircles the bird's eye about the equator. The unyielding walls of the globe direct the pressure forward, the ciliary muscle relaxes, and the internal pressure pushes the crystalline into the anterior chamber. This movement is now assisted by the pectinate body, which fills with blood and occupies the space vacated by the lens; the cornea becomes more convex and the bird exerts his best efforts to fix a minute near object. Does he desire to see distinctly in the far distance, the converse is true; Crampton's muscle relaxes, the eyeball becomes more globular, the tense corneal cone becomes less prominent, the lens recedes and is less globular, the anterior chamber deepens, the pecten is flaccid, and the antero-posterior diameter sensibly diminishes. Thus the important function of accommodation in birds is a much more complex and extensive performance than in man. In this way the bird is able, as no other animal can, to convert his organ of vision, as Beebe remarks, "from a microscope to a telescope" in a fraction of a second—to see small objects a quarter of a mile away and to pick from the ground seeds so small that one would need a lens to distinguish them from surrounding grains of dust.

The crystalline lens in most birds has, as just remarked, a globular form. It is comparatively larger than the human crystalline, and in the nocturnal birds of prey has such a markedly convex anterior surface as to be almost round. In birds requiring chiefly good distant vision the round lens is a compound structure built up of concentric layers surrounded by a ring of radial fibers widest at the equator. This disposition of the lens fibers assists in producing the lenticular changes required by the active accommodation called for in birds. The globular lens, again, corresponds to the prominent cornea and deep anterior chamber. In water fowl the lens is flatter in front, i. e., more plano-convex in shape, and the cornea is not so conical.

In passing, it may be remarked that the postmortem appearances of the eyeball, especially of the cornea, are somewhat misleading, as there is always more or less rounding of the globe through sinking and retraction of the cornea shortly after the death of the animal. For this reason, also, microscopic sections of the globe generally fail to show the tubular-oval shape that the external eye generally maintains during life.

The Pecten.—This is the most peculiar organ in the whole ocular apparatus of birds. From the optic disc of every bird,[4] of their

4. The statement that the Kiwi, or Apteryx, is without a pecten (vide, e. g., Bernd, Die Entwicklung des Pectens, Inaug. Diss. Bonn, 1905, p. 8) is disproved by Lindsay Johnson. The same error is repeated in most text-books, as in Claus's Lehrbuch der Zoologie, 5th edition, 1891, p. 845.

first cousins the reptiles, and of some other animals, there projects into the vitreous to the posterior aspect of the lens (or nearly so) a remarkable, pigmented, corrugated or plicated, solid or fenestrated, erectile body long known as the pecten, marsupium or "ruff." It is composed of large vascular trunks, about which are arranged smaller vessels with cellular walls—all bound together loosely by connective tissue and covered with a smooth, thin, homogeneous, pigmented membrane. Treacher Collins regards the pectinate body as a prolongation of the chorioid (which it resembles structurally), containing, however, a finer capillary plexus. Most authors, in-

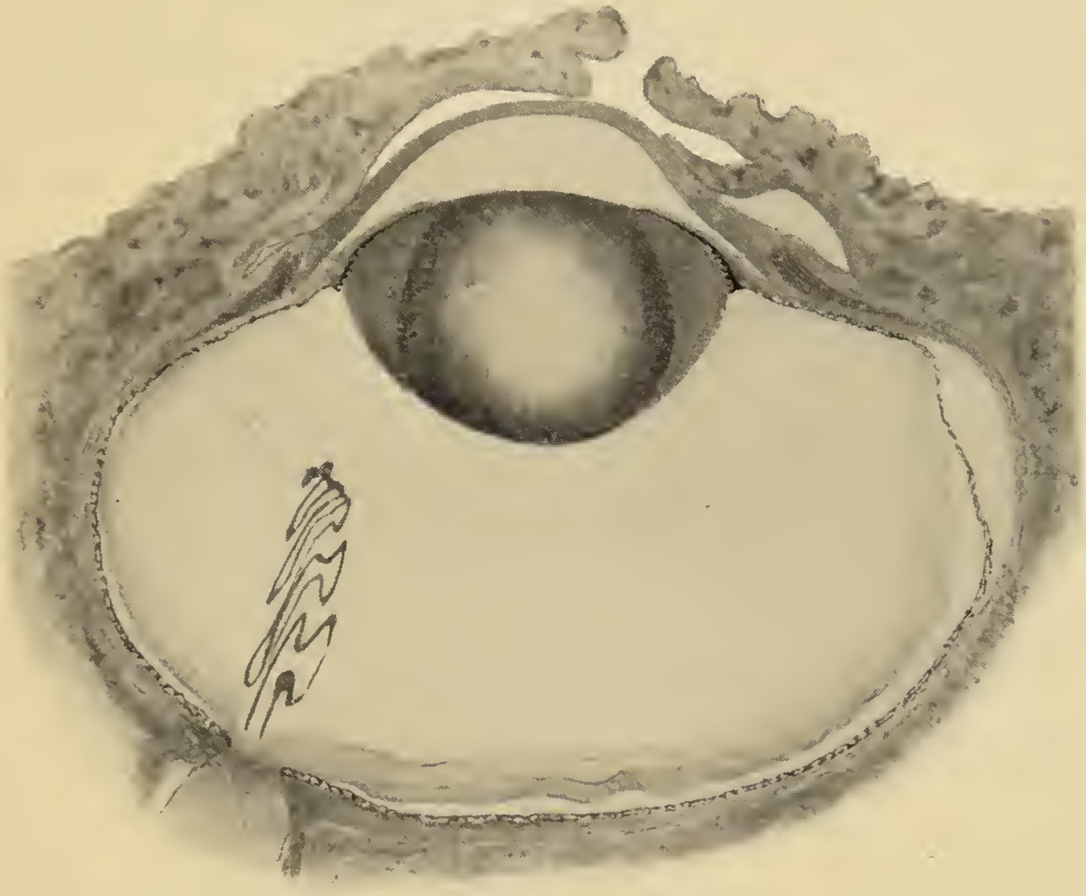

Fig. 2.—Section of the eye of the Golden-winged Woodpecker, showing especially the folds of the pecten, the ring fibers of the lens and nictitating membrane.

cluding Gegenbaur and Bernd, believe that it takes the place of the retinal vessels (which, in the avain fundus, are wanting), and arises from the optic tissues, having no direct connection with the chorioid. By this arrangement the percipient part of the bird's retina is rendered more sensitive to light rays, because the branches of the central artery and vein do not ramify, as in the mammals, in the substance of the retina, and so do not, to any extent, present an opaque obstruction to vision.

The pecten varies in shape and size, as well as in the number (2 to 30) and the character of the folds of tissue that compose it, according to the genus to which the bird belongs. Indeed, such a striking and varied picture does the pecten exhibit, both when seen with the ophthalmoscope during life and as prepared macroscopical and microscopical specimens after death, that one might almost recognize the species by studying this organ and its relations to other parts of the bird's fundus.

While there seems no doubt that the pecten carries the nutrient vessels of the retina, and probably of other intra-ocular structures, its erectile character and its capacity for being alternately filled with and emptied of considerable blood at short notice raises the presumption that it takes an essential part in the function of accommodation, probably, as before stated, by pushing forward the lens by a sort of hydraulic pressure when it is filled with blood, and allowing it to recede when flaccid and empty. So far as I have noticed with the ophthalmoscope, although the free end of the pecten points toward the posterior surface of the lens, it is invariably found in the nasal half of the vitreous, and thus does not interfere with the passage of the light rays to the fovea or other visual areæ.

Slonaker,[5] whose macroscopical observations of the interior of hardened birds' eyes have so far corresponded closely to the ophthalmoscopic view of the living fundi of birds' eyes we have both examined, has noticed that a line joining the visual area in birds with a single fovea and the optic papilla forms about a right angle with the pecten.

That the hyaloid artery of fetal life is a vestigial pecten seems almost self-evident. No one who has examined a persistent hyaloid artery and its branches, particularly if he has been fortunate enough to see the vessels carrying blood to and from their termination in the vitreous, can fail to be reminded of the structures that occur normally in some mammalian, most reptilian, and all avian eyes. This arrangement surely carries us back in fetal evolution to those sauropsidian ancestors who have left their mark in our embryology. It is not improper for me to mention here the admirable anatomical description by Treacher Collins[6] of a case of persistent

5. A Comparative Study of the Area of Acute Vision in Vertebrates, Journal of Morphology, xiii, No. 3, p. 477.
6. The Anatomy and Pathology of the Eye, The Lancet, Feb. 24, 1900.

hyaloid artery carrying blood and anastomosing with the iris—the ciliary processes being absent.

Mittendorf has reported that about 1 per cent. of all patients coming to him for ocular affections exhibit minute dotted opacities on the nasal aspect of the posterior lens capsule. These dots are without the visual axis; they do not increase in size and do not interfere with vision. He regards them as remains of the fetal hyaloid artery or its connections on the posterior aspect of the crystalline.

The retina and optic nerve of birds are both highly developed

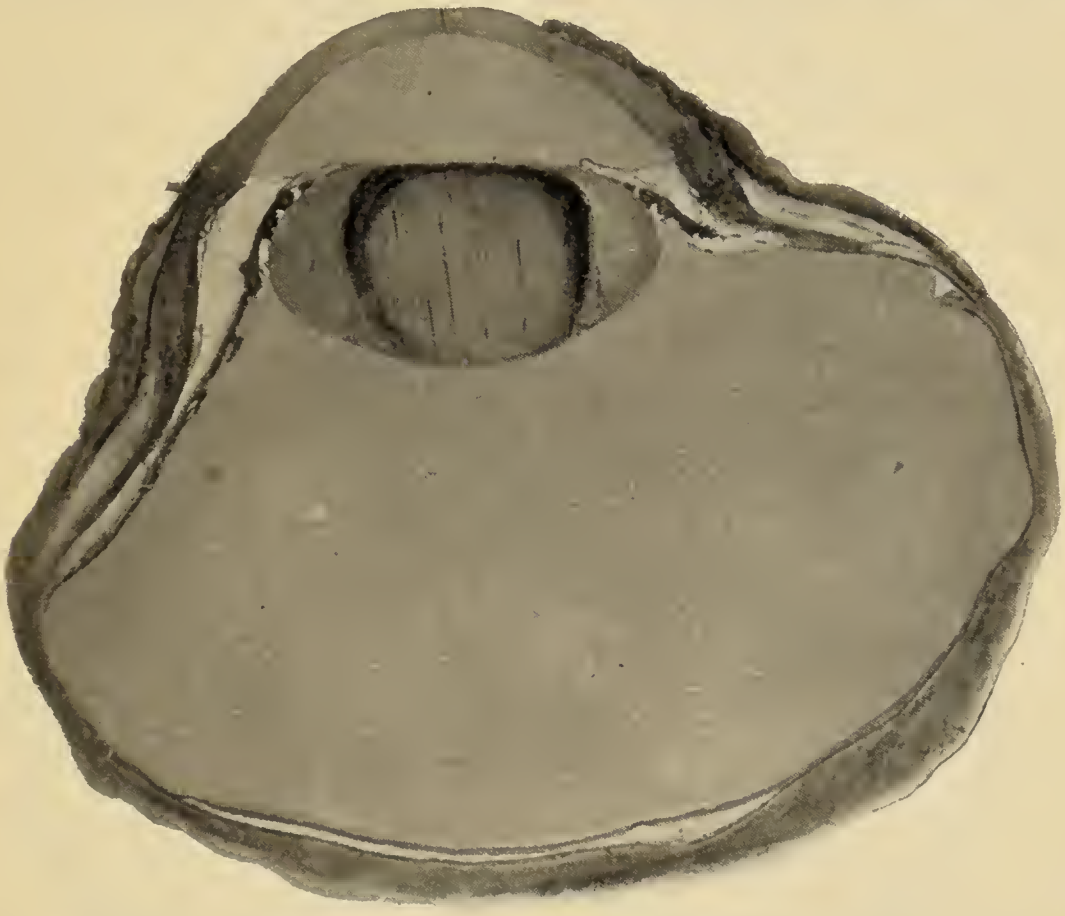

Fig. 3.—Section of the Red-tailed Buzzard's eye, intended to show (at the large white detachment), the nasal fovea.

and closely resemble the same organs in the Primates. The vascular supply to the retina is probably carried entirely by the pecten, although no direct connection with that membrane has been established.

The macular region or visual area is plainly differentiated from the rest of the retina, and macroscopic sections generally show at least one well-defined, deep fovea. Writers[7] on this subject generally refer to the *double macula* of certain birds. Of 102 species

7. Gegenbaur: Vergleichende Anatomie, Bd. i (1898). p. 937, remarks that many birds possess two foveas, one in the nasal, the other in the temporal aspect of the retina.

examined microscopically by Slonaker a distinct visual area was present in all; no fovea was discovered in one; a single, round area or macular region was found in 59; two round areæ (macular regions) in 11; while an additional band-like visual area was differentiated in 36. Seventy-two birds had a single, simple fovea, 11 had simple fovæ, and 22 had a trough-like fovea. The single fovea, almost invariably situated toward the nasal side of the animal, can generally be distinguished by means of the ophthalmoscope during life, but in birds with a double macula the second fovea, temporally placed, will, I believe, be more difficult to locate. Slonaker[8] found in most of the birds examined macroscopically after death a single fovea surrounded by a circular area—just as one sees them in man and the higher apes. In the goose and ring-neck plover he discovered a simple fovea in the center of a round macula, the latter area extending horizontally across the retina.

Two macular regions may be present, each with its fovea, joined by a short, band-like area, as in the sparrow-hawk, red-tailed buzzard, and kingfisher. He found the most complex arrangement of the visual areas in the tern. Here the *fovea temporalis* is surrounded by a small, isolated, circular macular region and is not connected with the narrow, band-like area. The latter, however, stretches across the fundus and near its middle widens out to enclose the *fovea nasalis* in a larger circle than that enclosing the temporal fovea.

So far, then, as concerns the shape and position of the areas of distinct vision in birds, a species may have one or two foveæ and from one to three visual areas.

The foveæ vary in depth and position. In the owls, which possess binocular vision, and in birds which require keen vision, the fovea is deep and clearly cut. According to Slonaker, in those birds that possess two foveæ, the *fovea nasalis* varies but little in position, while the locality of the temporal yellow spot depends largely upon the degree of divergence of the antero-posterior axes—the more divergence the greater the separation of the two foveæ. The more the eyes look forward the more dependence is placed upon a single, deep, sharply-defined nasal, macular region and the shallower, less distinct and more merged in it become the temporal fovea and

8. Loco. cit., page 458.

visual area. In hawks and other birds of prey—including insectivorous birds—which require binocular vision in each eye—the two foveæ are more widely separated and the temporal macular region again becomes better defined and resembles the nasal area.

A double macula, in one eye, furnishing stereoscopic vision and all the advantages of binocular sight, would help to explain the wonderful range and accuracy of the monocular eyesight of birds, especially in the eagles, hawks and vultures.

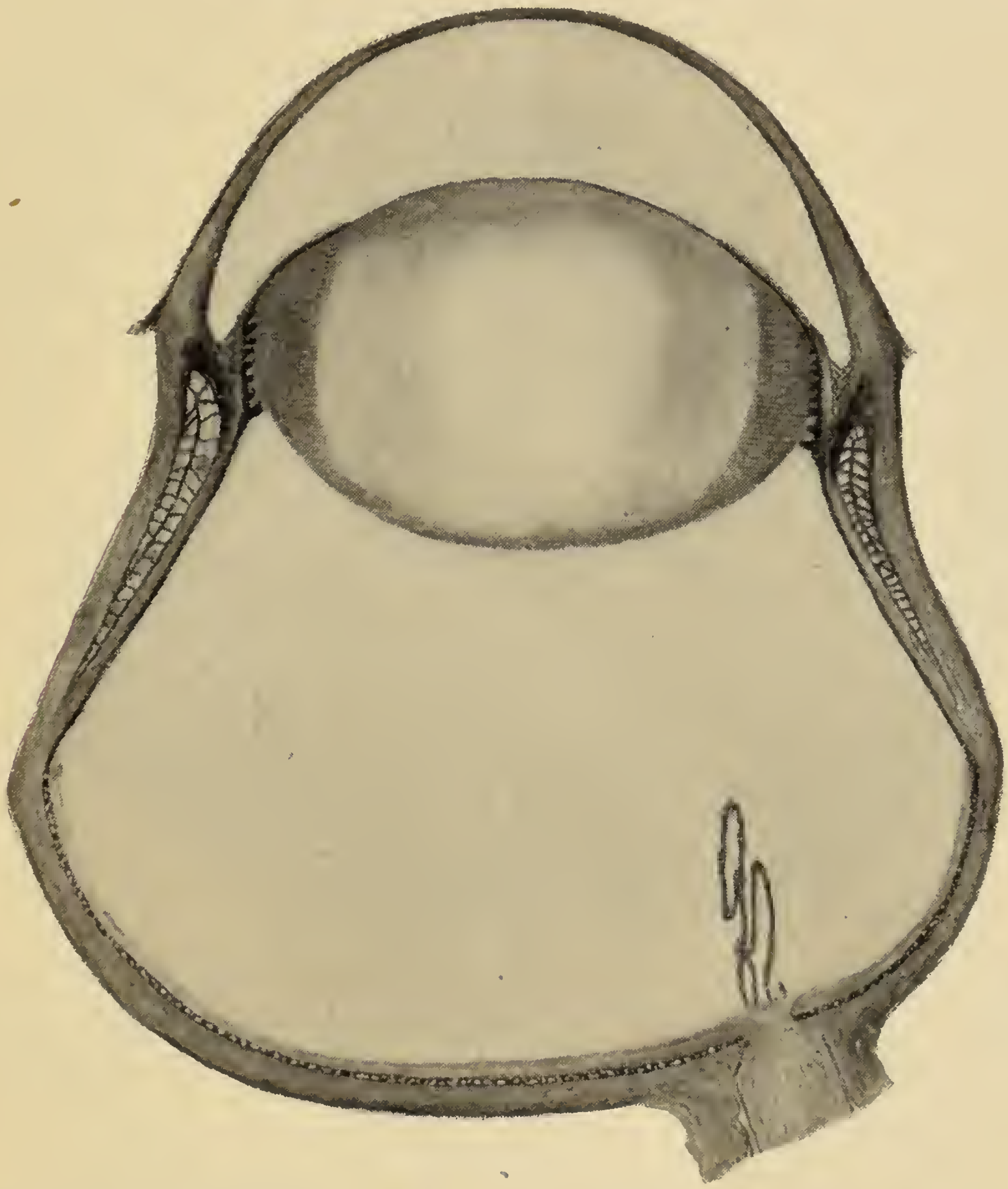

Fig. 4.—Vertical section of the American Screech Owl (Strix or Megascops asio), showing very plainly the accommodative apparatus, scleral plates, Crampton's muscle, etc., as well as the peculiarly-shaped eyeball of the owl family. Only a small portion of the pecten is depicted.

Color perception in birds. The color sense is supposed to be chiefly resident in the retinal cones; and this theory, Slonaker finds, is borne out in examining birds' retinæ. In the nocturnal birds he discovered few cones, while the proportion of rods to cones in mammals he found reversed in day birds, where the cones far surpass the rods in number. We may assume, as one might expect, that the appreciation of color is excellent in all avian species.

The extrinsic eye muscles in birds resemble those of the human eye, and, although the internal and external recti vary somewhat in their attachment to the globe, the purposes of these muscles are evidently the same in the avian as in the human eye. The pyramidal muscle that controls the nictitating membrane has not, so far as I know, an analogue in man.

The refraction of birds' eyes is generally hypermetropic. I have examined quite a number of them by skiascopy and find, just as Lindsay Johnson discovered in mammals, that *wild birds are invariably far-sighted, while domesticated species tend to become short-sighted, astigmatic, or both, and to present evidences of intra-ocular disease.* This was especially true of the large collection of owls in the London Zoological Gardens that I examined in the summer of 1905 with the ophthalmoscope and skiascope. Those owls, it matters not what variety, that had lived in the gardens more than two years were generally less hyperopic than those recently introduced, while in the case of the former it was difficult to find one that had not a more or less marked form of chorioiditis of the disseminate variety.

Ophthalmoscopic appearances of birds' ocular fundi. Probably the chief reason why the interior of the eyes of birds has been so little studied during life is the difficulty inherent in the employment of the ophthalmoscope and in reporting the results of the examination. As we are all well aware, the expert use of the instrument, as practiced on the human subject, requires months of patient application before the student is able to distinguish the ordinary variations in the normal appearances of the uveal tract, retinal vessels, chorioid, optic entrance, vitreous, etc., while the usual pathological alterations in the tissues call for additional months of close observation. The same assertion can be made of animals' fundi and of birds' backgrounds in particular. In the case of the last-named animals care must be taken to prevent injury to delicate specimens during an ophthalmoscopic examination, and the observer must protect himself from bill and claw while the examination goes on. I can assure any one who intends to pursue this study that the common barn owl, for example, can inflict severe wounds upon the hands that hold him, and imperil the vision of the ophthalmologist that places his eye too near his powerful beak. On the other hand, a little gentleness, combined with firmness, will suffice to enable the observer to make satisfactory explorations of the avian fundus. The main trouble lies with the pecten and the small, undilatable pupils of a great many birds. I have not yet had sufficient experience of some orders to speak with authority, but, in my experience so far, the best mydriatic for the examination of birds' fundi is the following mixture:

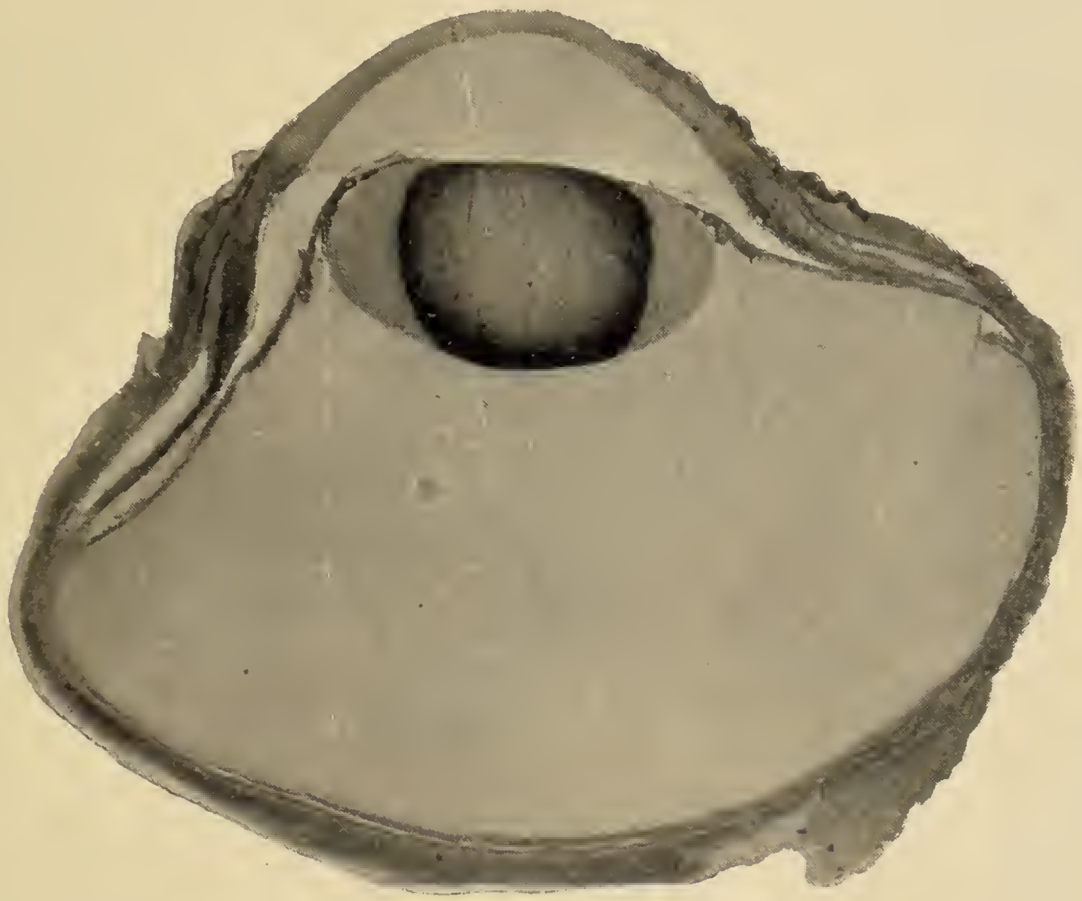

Fig. 5.—Section of the Red-tailed Buzzard's eye, to show the temporal fovea, the large ciliary muscle, Crampton's muscle and the locality of the bony plates in the bird's sclera.

Cocain mur.
Homatropin mur., of each, one grain.
Atropiæ sulph., half a grain.
Distilled water, half a fluid ounce.

The great majority of birds' pupils will be affected by one drop in each eye of this solution, one-half to one hour after instillation.

The ignorance that has hitherto prevailed with respect to the ophthalmoscopic appearances of the ocular fundi of birds has led to all sorts of curious mis-statements, even by those who ought to be better informed. The fact is that the postmortem—especially the microscopic—appearances of the ocular interior are, especially in birds, not the same as those seen during life. This is especially true of the vascular pecten, projected forward in the posterior chamber, and seen during life as a moving, ever-changing, black body. We see with the mirror the living *nerve-head,* of all possible shapes and sizes, nearly always white or whitish, and generally covered with the pecten, although sufficiently free of it to recognize its outlines and sometimes most of its surface. The *coloration of the fundus* in birds does not present that marked variety that one observes in the other sub-kingdoms, especially among the mammals and reptiles. It is, however, never "black," as alleged by some authors, but is generally gray, with a suspicion of red—the red color being more plainly seen and variously distributed according to the family to which the bird belongs. Within bounds more limited than in the mammalian fundi opaque nerve fibers are generally seen, and the foveæ can usually be distinguished. The macular region of the owls (following the rule that animals with binocular vision have this area ophthalmoscopically well marked) can be readily seen with the mirror, and it is generally observed as a well-defined reddish spot. (See Plate I.) During a fundus examination continual variations in the size, position and shape of the pecten will at first confuse the comparative ophthalmologist, but after a while he will make his exploration of the background and ignore these changes, just as he does some of the annoying corneal reflexes in man.

The examination by the erect image will, on the whole, be found the most satisfactory method, although, as in viewing the human fundus, it is advisable to use the indirect plan at the outset. The self-luminous ophthalmoscope is quite satisfactory for this purpose, and is the instrument preferred by my fellow-worker, Mr. Head. It does not require a totally dark room, and (of extreme importance sometimes), one is able to dispense with a separate source of light. The objections to its use are, as in picturing the fundus of man, the presence of the reflexes, macular, retinal and corneal, as well as the exaggeration of the number and whiteness of opaque nerve fibers in the background. Mr. Head believes, however, that it has enabled him to obtain fundus views through small pupils and to distinguish variations in some animal backgrounds that he failed to appreciate with the older instruments. It is, of course, not my purpose to discuss the whole subject here, but I would remind any of my readers

FUNDUS OCULI

(Erect image of right eye)

Of the Tawny Owl, Syrnium aluco. Painted by A. W. Head, F. Z. S. for Casey Wood.

who think of studying avian fundi that *it is the wild species of birds that present invariable ophthalmoscopic pictures.* It will be found that, after two or three generations of inbreeding, confinement and domestication, changes occur in the ocular apparatus coincident with variations in other parts of the organism. I shall refer to this matter again.

The task of picturing the ocular background for the purpose of conveying an intelligent idea of its appearance is a serious one; indeed, with all the work done upon the eyes of birds, this has been almost entirely neglected. The ophthalmologist may be a good observer but a poor artist; conversely, an expert in the use of brush and pencil may not be sufficiently conversant with normal and pathological, human and comparative ophthalmoscopy and ophthalmol-

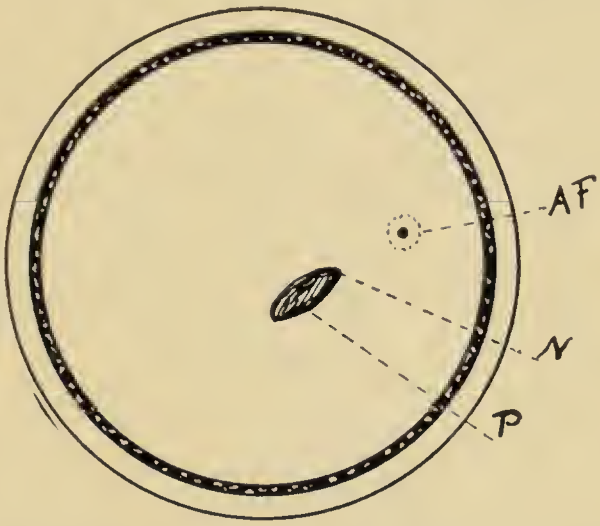

Fig. 6.—Diagram of the fundus (macroscopical, postmortem view) of the barred owl (*Syrnium nebulosum*). N, optic nerve; P, pecten; AF, macula and central fovea. (Slonaker.)

ogy to enable him to make an intelligent use of his artistic talents. These difficulties are, I trust, largely met by an arrangement which I have been able to make with Mr. Arthur Head, the well-known London artist, who for some fourteen years past has been painting both human and animal fundi for *confrères* here and abroad. In conjunction with Mr. Head I have examined many ocular fundi of birds, and propose to continue this work until we gather a sufficient number of such observations upon the ocular apparatus of birds and fishes—particularly of their fundi—as may constitute some slight addition to our knowledge of this rather large subject. Inasmuch as little or nothing has been so far published in the way of the comparative illustration of piscean or avian fundi, I am led to believe that the task thus set for Mr. Head and myself may be well worth the time and labor spent upon it, and that side lights may, in this way, be thrown upon some of the problems (as yet unsolved) of human ophthalmology.

The following description of a few of these fundi will serve to show the variations in avian backgrounds, and is published as a note preliminary to further investigation of the subject.

THE RATITÆ.

The ocular fundus of the Kiwi or Apteryx Mantelli. (Plate II.) This is the only background of the sub-class Ratitæ, or birds with functionless wings, that I have to exhibit. It is one of the oddest of the Australian birds—something like a thin little Cassowary with thick legs, no visible wings, and a long bill like a snipe. The nostrils are placed at the very tip of this slender beak, which the bird deeply plunges into the soft ground, smelling about for worms, which, when discovered, are drawn out and eaten. Kiwis are nocturnal in their habits and for that reason are rarely seen by visitors to our zoological parks and gardens. If aroused from their straw during the daytime they open their mouths several times in long-drawn and very human yawns and then fall asleep again.

The fundus of the Apteryx, in comparison with that of most carinate birds, suggests its nocturnal life. Indeed, all animals that prowl, run about or feed at nighttime have brilliant yellow, orange or yellow red fundi.

The almost uniform red, mottled background of the Apteryx, shows no blood vessels in his retina whatever. The chorioidal pigment is less plainly seen in a concentric area surrounding the remarkable optic nerve entrance. Here the brilliant, white, round disk surrounded by short, opaque nerve-fiber rays is not entirely covered by the fenestrated base of the long, large and regularly conical pecten which reaches almost to the lens. If one were allowed to stretch his imagination, the combined picture of pecten and nerve-head might be said to resemble a black rubber teat from a nursing bottle, partly stretched over a white sea-urchin. How the Kiwi's pecten could have remained undiscovered for so many years is difficult to explain, except that it emphasizes the difficulties in the way of a satisfactory exploration of birds' fundi in general and the differences between the erect, vascular, functionating pecten of the live

FUNDUS OCULI

(Erect image of right eye)

Of the Kiwi or Apteryx Mantelli. Painted by A. W. Head, F. Z. S. for Casey Wood.

bird and the blanched specimen that may easily escape recognition after death. To Mr. Head and Dr. Lindsay Johnson are due the discovery—as yet unheeded by text-books—that every bird, the Kiwi included, has a well-developed pecten.

THE CARINATÆ.

The ocular fundus of the common Blackbird—Merula vulgaris. Everyone is acquainted with this member of the large order of Passeres—his yellow bill, his yellow-edged eyelids, and his jet-black body. I have chosen him as a fair example of a quick-sighted, insectivorous bird, with monocular vision and daylight habits. These are all reflected in his beautiful uniform, bluish-gray fundus, his canoe-shaped, whitish optic nerve entrance, and his black-brown, club-shaped pecten. A lateral view of his pectinate body shows that

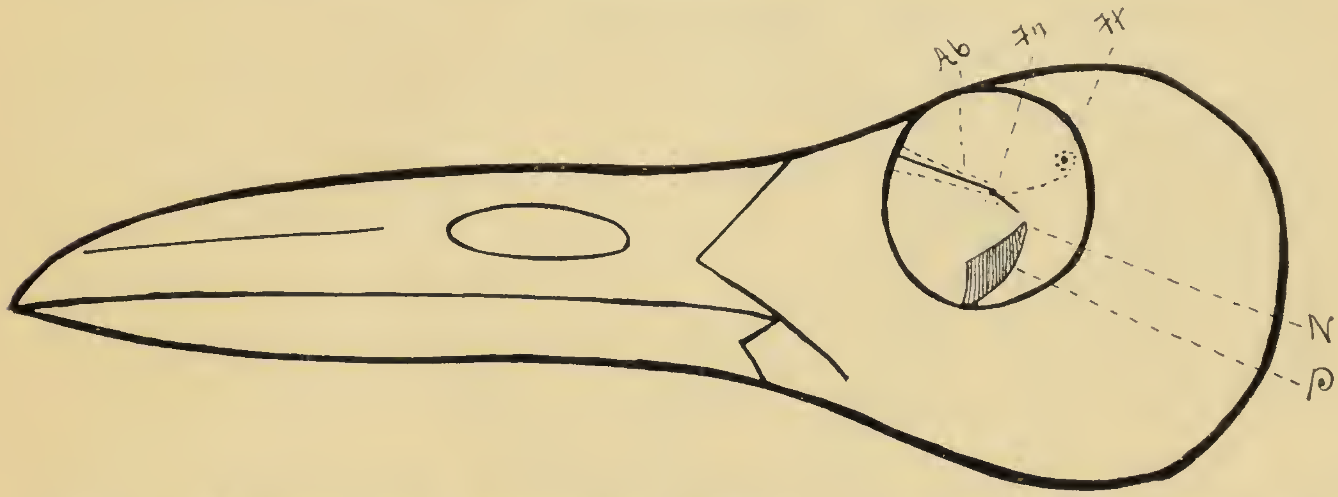

Fig. 7.—Macroscopical, postmortem diagram of the left eye and orbit of the tern (*Sterna hirundo*). N, optic nerve entrance; P, pecten; Ft, At, fovea and area temporalis; Fn, An, fovea and area nasalis; Ab, band-like area. (Slonaker.)

it arises by a rather slender pedicle that covers less than one-half the optic papilla. The body then spreads out and, projecting toward and almost reaching the posterior surface of the crystalline lens, gradually enlarges until it presents to the ophthalmoscope a dumb-bell or "nine-pin" appearance. One will also observe the regularly placed opaque nerve fibers covering the whole fundus, as well as the streaks of reddish chorioidal vessels showing through the gray-white background. There is no macular region differentiated from the general fundus coloration, although, in common with other birds, *Merula vulgaris* has a microscopically deep and well-defined fovea.

The ocular fundus of the Tawny Owl. Syrnium aluco. The eye-sight of the whole owl family should be of consuming interest to the ophthalmologist because of the almost human arrangement of his ocular apparatus. First of all, the owl has his eyes placed in front of his skull, looking straight forward, just like man and the other Simiæ. Like the higher apes, also, he has a well-defined macular region and binocular vision. At the outset let me say that the popular notion regarding the owl's daylight vision is incorrect. That he does see better at night than other birds is quite true, as the coloration of his fundus amply proves, but that he is blind by day is far from the truth. From observations made by myself in the London Zoo, from the experience of the keepers and other observers, I think we may conclude that almost all the owls have good vision both by day and night. Bendire,[9] for instance, remarks: "The Barred Owl is nocturnal in its habits, but nevertheless sees well enough, and even occasionally hunts in the daytime, especially during cloudy weather. I believe that owls in general prefer to remain hidden during the daytime on account of attracting the attention of nearly every feathered inhabitant of the vicinity, who instantly attack and annoy them in every possible manner the moment they leave their retreats." Although owls live almost exclusively on grasshoppers, mice, frogs, etc., yet few of them are able now and then to resist the attractions of a nice downy chicken or other bird—habits that justify the warfare carried on against them whenever or wherever they are found by other birds. As the owl has practically no noctural bird enemies he does not need to see behind him. His ocular apparatus is accordingly arranged to intercept with the highest degree of efficiency all the light rays, however faint, that fall upon his retina from the front. He is thus able to sit at night entirely motionless and watch for his prey without exposing himself to view.

The background of the Tawny Owl's eye (See Plate I) at first glance reminds one of the light-haired Caucasian. It is yellowish-red with the chorioidal vessels conspicuous. The macular region is a round, red disk surrounded by a bright reflex ring of silver-gray. The latter is often so marked that it resembles an exaggerated "bull's-eye-lantern" macula—occasionally seen in human eyes—and the reflex may be so dazzling as to interfere with a clear view of the region itself. Surrounding the red macula is a very large, concentric area (which reaches to the nerve-head) that looks like a gray haze.

9. Life Histories of North American Birds, 1892, p. 336.

There are few traces of chorioidal vessels here; probably we look at only the translucent retina against the underlying chorioidal pigment. The optic disk is a long, whitish, ovoid figure surrounded by the reddish chorioidal vessels. Springing from the whole length of the papilla and almost covering it is the pecten. Seen with the ophthalmoscope this organ presents the appearance seen in the picture—a smooth, black, corrugated, grub-like body slightly pointed at the papillary end. Viewed laterally the owl's pecten closely resembles the dorsal view of a partially clenched hand.

Below both papilla and macula is a rather large area, abundantly supplied with large chorioidal vessels, between which are masses of pigment. The nerve-head occupies the center of a smaller, much lighter, yellow field. On the whole, this nocturnal bird of prey

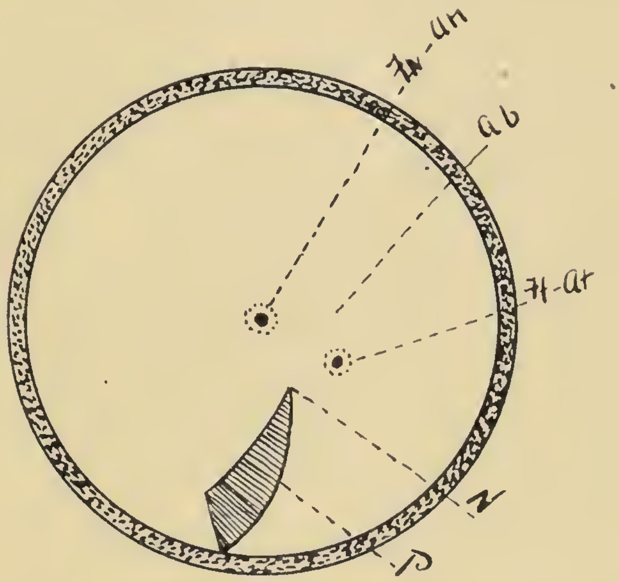

Fig. 8.—Postmortem and diagrammatic view of the double maculæ, double fovea and third visual area of the Red-tailed Buzzard (*Buteo borealis*). N, optic nerve entrance; P, pecten; Ft, At, fovea temporalis and area temporalis; Fn, An, fovea and area nasalis; Ab, band-like area. (Slonaker.)

shows a background such as we would expect from what we know of the fundi in mammals of similar habits. The refraction of this owl is about 3 diopters of simple hypermetropia.

The Cape Eagle Owl (*Bubo Capensis*) has, in half-lights, large round pupils. He shows, with the ophthalmoscope, the same reddish background, the oval optic nerve and the pepper and salt area about the disk-like macular region seen in the Tawny Owl. In one specimen that had lived in the London Zoological Gardens three years, the refraction (as determined by the skiascope) was only + 2 D., and I found several well-defined, pigmented, chorioiditic exudates in each eye. In the chorioid, around at least three of these spots, there was distinct evidence of absorption of the epithelium.

The fundus of the British Barn Owl (*Strix flammea*) is more grayish-red than that of the foregoing. In ordinary daylight and even after flashing the light from the ophthalmoscopic mirror into his eyes the pupils continue to be round. In a specimen recently presented to the London Zoo I could find no trace of chorioidal disease, and the refraction without a cycloplegic was highly hypermetropic.

The so-called winking owl of Queensland shows an ovoid papilla almost entirely obscured by a pecten, from whose apparently perforated base a corkscrew-like body extends almost, if not quite, to the crystalline lens.

The eyegrounds of the gulls are well worth examining. These birds have excellent monolateral vision, which I have spent some time in studying. Although web-footed, the hind toe is free, like the other longipennes, and their pointed wings are well fitted for rapid flight. The visual aim of the average gull is as accurate at close range as that of any of the raptores. A gull will swoop down from a considerable distance and catch unerringly, by means of his long, compressed beak, a very small piece of meat or bread thrown into the air long before it reaches the ground or surface of the water—thus simulating in a small way the exploits of the true birds of prey. I have examined, among others, the fundi of several specimens of the British Herring Gull, the Yellow-legged Mediterranean Gull, and the Greater Black-headed Gull.

The *Herring Gull* has a perfectly round, easily contractile pupil; the iris is of a beautiful lemon or yellow-white color. This was one of the birds in which I felt certain that no such reflex as the "consensual" contraction of the pupil could be demonstrated. The gulls generally give some trouble with their nictitating membranes while using the ophthalmoscope upon them. In the examination of most other birds the third eyelid offered no obstruction to a fundus view.

The ocular backgrounds of all the gulls examined by me showed very little variation.

The Greater Black-backed Gull (*Larus Marinus*) has a background that, seen with the indirect image, appears dull-gray. A direct view shows it to be generally dull-brown, with reddish chorioidal vessels running in a vertical direction. The disc is a long, white, narrow oval, with a number of fine gray lines (opaque nerve fibers) radiating from its margin and extending toward the macula. The foveal region is an oval, reddish-brown area, surrounded by a gray-blue, iridescent reflex. The pecten seems to be in folds (about eight), the lower or broader portion extending toward the nasal half of the eyeball.

The Black Hornbill (*Sphagolobus Atratus*).—This curious member of the Coccygomorphæ has remarkably good sight for such a stupid-looking, top-heavy bird. In experimenting with his visual powers I found that he caught, with his enormous beak, grapes thrown into the air as quickly and as easily as a seal catches fish. Like the other hornbills, his lids are furnished with long, well-developed lashes. The specimen I examined had been in the London Zoo for years and did not present any disease of the fundus, although his refraction, determined at night by skiascopy, was about emmetropic. The background is of a drab or dull-gray color, and the retinal reflex is so marked that it is difficult to recognize the minute fundus details. The papilla is, as usual, on the nasal side of the eyeground, in the shape of a long, white oval about which opaque nerve fibers extend almost to the periphery. Toward the equator are seen faint red chorioidal vessels. The pecten is quite large and its antero-posterior view shows a saw-like contour (with about 20 plications or teeth on each edge), except at its distal extremity, which is more club-shaped. The pectinate body in this bird can readily be seen to expand and contract, apparently with the movements of the pupil. The foveal region is a red-brown, disk-shaped area with a dark-red spot in its center. The retinal reflexes are very noticeable, and give the impression of an iridescent, bluish-green sheen, so much so that it reminds one of a dull mirror reflecting colored light thrown upon it.

In a future paper I hope to furnish a description of a still larger series of avian fundi.

From the foregoing I believe we are justified in drawing the following conclusions:

1. The highest expression of vision, including the most varied and widest range of accommodation, is found in bird life.

2. The owls possess binocular sight, and their eyes in many other respects resemble those of man.

3. Probably every bird—carinate and acarinate—possesses a pecten. This is quite as true of the Apteryx (long thought to be without one) as it is of our common wild birds. The size, shape and relations of the pectinate body to the other ocular structures are so varied, and their appearances, as determined by the ophthalmoscope during life are so constant in each wild species, that the background picture of a particular wild bird furnishes certain data for a classification of quite as much value as the variations in any other organ.

4. The refraction of most wild birds is simple hypermetropia; of domestic species, hypermetropia, or myopia, with astigmatism.

5. The postmortem appearances of birds' eyes are decidedly misleading, especially as to the shape and size of the eyeball and the relations of the parts in the interior of the globe.

6. The range and rapidity of accommodation in birds far exceed that of man or other animals, and the accommodative and refractive apparatus is much more complex than in other sub-kingdoms.

7. The areas of distinct vision in birds are peculiar to them. In a single fundus may be present one or two foveæ, or one, two or three visual areas, thus enabling the bird to obtain the sort of vision most suited to its needs.

8. The color sense in birds is very acute, as shown by the great preponderance of cones in the retinal elements.

9. A number of congenital anomalies in man are but the evolutionary remains of birds' organs. For example, the posterior lenticulo-capsular opacities, described by Mittendorf, and the human persistent hyaloid artery are undoubtedly unabsorbed pectinate tissues.

10. An extended study of the ocular fundi of birds may not only throw light upon the classification of doubtful species and so prove useful to the zoologist, but may possibly illuminate some of the problems of human ophthalmology.