

## CHAPTER XIV

### THE EYES OF BIRDS

A chapter on the anatomy of the eyes of birds at once suggests the name of CASEY ALBERT WOOD (1856-1942) (Fig. 482). Born of American parents in Canada, he graduated in medicine in Montreal in 1877, becoming one of the clinical clerks of the great physician, Osler, at McGill. After practising for some time in Montreal, he continued his studies in England and Europe, and in 1890 settled in Chicago where he occupied the Chair of Ophthalmology initially at the Northwestern University and eventually at the University of Illinois. He was successively president of the American Academy of Medicine and the American Academy of Ophthalmology, and a founder member of the American College of Surgeons. A man of extraordinarily wide interests and more than usual erudition, he is particularly remembered for his prolific writings, the most impressive of which is his editorship of the *American Encyclopedia and Dictionary of Ophthalmology* of 18 volumes, to which he contributed largely. He was also editor-in-chief of the *Annals of Ophthalmology* (1894-1901), the *Ophthalmic Record* (1902-8) and the *American Journal of Ophthalmology* (1908-14). His knowledge of the history of ophthalmology was most extensive, a subject on which he wrote an interesting manual; he also made scholarly translations of ancient works, studying for this purpose in the Vatican Library at Rome, and wrote a delightful book on his researches. The comparative anatomy of the eye interested him greatly, and within this sphere his passion for ornithology earned for him a world-wide reputation; in its pursuit he travelled widely to countries as far apart as British Guiana and the Far East to study the eyes of rare birds. These observations were collected in his classical book, *The Fundus Oculi of Birds* (Chicago, 1917), while his extraordinary erudition and painstaking thoroughness in literary research is nowhere better illustrated than in his elaborate and exhaustive *Introduction to the Literature of Vertebrate Zoology* (Oxon., 1931). A true scholar with an unusual and contagious enthusiasm, he was also one of the most delightful and gracious of men.

BIRDS, descendants of primitive Reptiles probably through the Dinosaurs,<sup>1</sup> are essentially adapted for the air for which purpose their forelegs are modified as wings. The extant species are divided into two main classes:

(a) PALEOGNATHÆ (OR RATITÆ), a relatively small class of running birds with degenerate wings and a flat breast-bone (the ostriches in Africa (*Struthio*) and America (*Rhea*), the emu (*Dromæus*) and the cassowaries (*Casuaris*) in Australia, the tinamous of Central and South America and the kiwi (*Apteryx*) in New Zealand, Fig. 484);

(b) NEOGNATHÆ (OR CARINATÆ), flying birds with well-developed wings and a keeled breast-bone, comprising the vast majority of birds of over 11,000 living species (Figs. 483, 485). The penguins (Impennes), however, have taken to the water and do not fly at all; they have hair-like feathers, a whale-like blubber



Emu



Tinamou



FIG. 482.—CASEY ALBERT WOOD (1856-1942).

## FIGS. 483 TO 486.—TYPICAL EXAMPLES OF BIRDS.



FIG. 483.—The Barbary turtle dove, *Streptopelia roseogrisea* (Zool. Soc., London).



FIG. 484.—The kiwi, *Apteryx* (Burton's *Story of Animal Life*, Elsevier Pub. Co.).



FIG. 485.—Chilean eagle, *Geranoaëtus* (photographed by Michael Soley).



FIG. 486.—The ringed penguin (Zool. Soc., London).

for heat-insulation and their eyes, highly myopic on land, are entirely adapted for aquatic vision (Fig. 486).<sup>1</sup>

Among the Vertebrates, Birds share with Mammals the distinction of having attained the highest degree of specialization, being inferior to them only in cerebral organization. With their intense activity and highly developed emotional life, it would be expected that the visual organs of the former would be very efficient; this is indeed the case and, in fact, the eyes of Birds are supreme amongst all

FIGS. 487 TO 491.—THE EYES OF TYPICAL BIRDS.

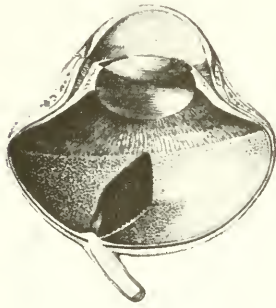


FIG. 487.—The falcon.

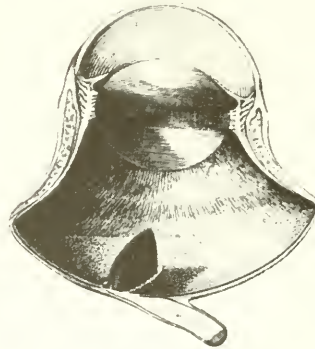


FIG. 488.—The owl.

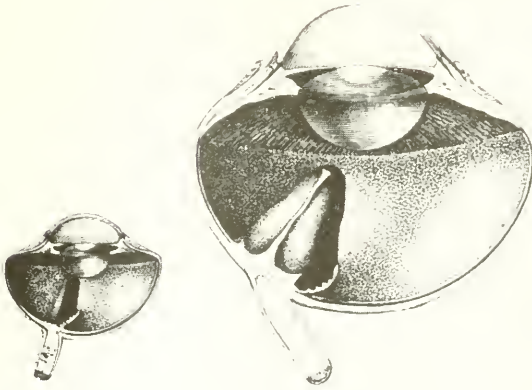


FIG. 489.—The parrot.

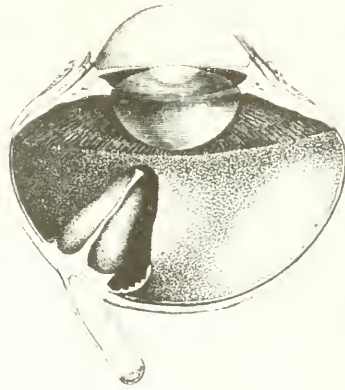


FIG. 490.—The ostrich.



FIG. 491.—The swan.

Some of Soemmerring's beautiful engravings. Natural size, showing the inferior half of a horizontal section of the left eye in each case.

<sup>1</sup> Other water-birds have eyes suited for aerial vision and have adopted devices for adaptation to aquatic vision, such as an exceptional range of accommodation (cormorant), a highly refractile nictitating membrane (ducks) or the use of a temporal fovea with a hypermetropic refraction (kingfishers); others have not done so and act blindly under water (tern) (compare p. 654).



## THE EYE IN EVOLUTION

FIGS. 492 AND 493.—THE AVIAN EYE.

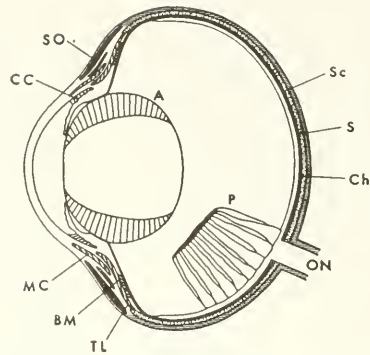


FIG. 492.—Diagram of the eye of a bird.

A, annular pad ; BM, Brücke's muscle ; CC, ciliary cleft ; Ch, choroid ; MC, muscle of Crampton ; ON, optic nerve ; P, pecten ; S, scleral cartilage ; Sc, sclera ; SO, scleral ossicles ; TL, tenacular ligament.



FIG. 493.—The eye of the domestic chicken (Norman Ashton).

living creatures. This somewhat sweeping statement applies to all birds with remarkably few exceptions, such as the shy, nocturnal kiwi, *Apteryx*, the eye of which, a small myopic organ, is the poorest among birds, for the dominant sense is smell rather than vision—a unique phenomenon in this class. Interestingly, its nostrils are placed near the tip instead of the base of its long, exploring beak (Fig. 484).

Built on the same general plan as the eyes of their ancestors, the Reptiles, the eyes of Birds are remarkably standardized throughout the entire class, showing few variations among themselves. The general features of the avian eye are as follows :

*The large size of the eye<sup>1</sup> and its flattened, globular or tubular shape with a nasal eccentricity of the cornea and lens to assist binocular vision.*

*The deep concavity in the ciliary region to maintain which the sclera is supported by scleral ossicles, the non-spherical shape of the globe being further supported by a posterior cartilaginous cup.*

*The presence of muscular elements in the choroid, ectodermal striated muscles in the iris, and a complex and well-developed ciliary musculature which bulges the lens forwards in accommodation.*

*A lens with a well-defined annular pad.*

*An elaborate vascularized glial pecten supplementing the choroid in supplying nourishment to the retina.*

*A thick and remarkably well-formed retina with precise layering and quite unusually dense packing of the visual elements, duplex in type with rods and single and double cones containing oil-droplets, and provided with one or sometimes two foveæ.*

THE GLOBE OF THE AVIAN EYE with few exceptions is relatively and absolutely large although, being entirely covered by the lids apart from the relatively small cornea, its external appearance gives the opposite impression (Fig. 494). The two eyes of a bird, however, often outweigh the brain, and some hawks or owls, despite their comparatively small size, have eyes larger than those of man. The shape is peculiar and distinctive : the cornea is small and globular, the posterior segment almost hemispherical with the horizontal diameter often slightly greater than the vertical, but the intermediate region between the two varies (Figs. 488 and 490). This is the region strengthened by the ring of scleral ossicles and its conformation determines the shape of the eye (Figs. 487 to 491). Most commonly it resembles a flat disc in which the cornea is set centrally while the peripheral border joins with the hemispherical posterior segment of the globe ; the result is a *flat eye* with a short antero-posterior axis, a

<sup>1</sup> The general rule (Haller's ratio, 1768) (p. 450) that the size of the eye is inversely proportional to the size of the body is here overshadowed by the complementary generalization (Leuckart's ratio, 1876) that the size of the eye varies directly with swiftness of movement.



Grouse

conformation characteristic of diurnal birds with narrow heads, such as the Columbidae (doves, pigeons) or the Galliformes (pheasants, grouse, fowls, etc.). Alternatively, in diurnal birds with broader heads, such as the Passeriformes (perching birds such as thrushes, sparrows, swallows and the Corvidae—crow, raven, magpie, jay, etc.) and diurnal birds of prey, such as the Falconiformes (eagle, hawk, falcon), the

FIG. 494.—THE HEAD OF THE OWL, *STRIX ALUCO*.

To show the enormous size of the eye in the orbit when the lids and skin are removed (Bárány *et al.*, *Brit. J. Ophthalm.*).



Thrush

intermediate segment is cone-shaped, sloping backwards at a varying angle to meet the posterior segment, giving the configuration of a *globular eye*. In nocturnal birds of prey, on the other hand, the intermediate segment runs directly backwards with a marked waist-like concavity before it runs outwards to meet the posterior segment at a sharply angulated junction, producing a *tubular eye* as is seen most typically in the Strigidae (owls); in this case, of course, the retina is comparatively much smaller. In each type in the interests of easy binocular vision there is a considerable nasal asymmetry whereby the lens and cornea are centred towards the mid-line, making the intermediate segment shorter on the nasal than the temporal side.



Raven

The maintenance of this non-spherical shape demands skeletal support (Figs. 495–98). The hemispherical posterior segment is therefore

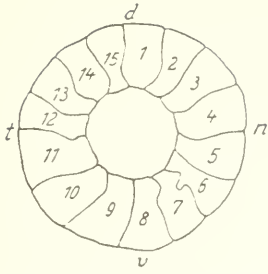


FIG. 495.—THE RING OF SCLERAL OSSICLES OF THE RIGHT EYE OF THE GOSHAWK, *ASTUR PALUMBARIUS*  
*d*, dorsal; *v*, ventral; *n*, nasal;  
*t*, temporal (after Franz).



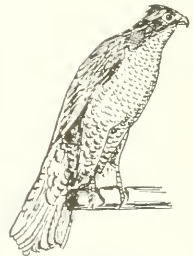
FIG. 496.—THE CARTILAGINOUS CUP IN THE POSTERIOR PART OF THE GLOBE OF THE HAWK.

strengthened by a firm *cartilaginous cup* which occupies the inner half of the thick fibrous sclera, while the waist-like constriction is maintained by a ring of imbricating *scleral ossicles* made up of membranous bones overlapping the anterior edge of the cartilaginous cup (Figs. 495 and 497). These ossicles, described by Malpighi (1697) in the eye of the eagle, vary in number from 10 to 18, the commonest being 15 (Dabelow, 1926-27), and while they are formed of compact bone in small eyes, in large and particularly in tubular eyes they contain air-spaces as do many of the bones of the bird's skeleton (Lemmrich, 1931); it is this ring of bone which essentially determines and maintains the configuration of the intermediate segment and therefore of the entire eye.

Incorporated in the posterior cartilaginous cup a ring- or horse-shoe-shaped bone may be found, the *OS OPTICUS* OR *OSSICLE OF GEMMINGER* (1852) surrounding the optic nerve-head in one or several pieces; like the anterior scleral ossicles it is highly cancellous in texture. Tiemeier (1950) found it present in 219 out of



Magpie



Goshawk  
*Astur*

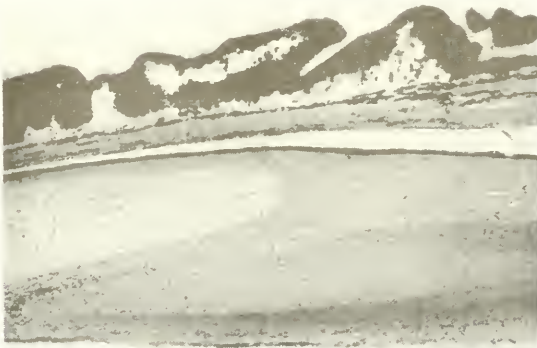


FIG. 497.—THE CILIARY REGION OF THE CHICKEN.  
 Showing the imbricated scleral ossicles beneath ( $\times 84$ ) (Norman Ashton).



532 species without any apparent logical distribution ; no satisfactory theory for its presence has been put forward.

The *cornea* is usually small, thin and highly arched but becomes large and prominently globular in predators, particularly those of nocturnal habit ; in diving birds it is relatively flat and thick. In these a zone around the limbus becomes thickened and opaque, resembling the sclera, while the scleral ossicles are particularly heavy to stiffen the globe against the shock of immersion (as in the cormorant, *Phalacrocorax*). In structure it conforms to the usual vertebrate plan.



The cormorant  
*Phalacrocorax*

The anterior chamber of certain owls (*Strix* (*Syrnium*) *aluco*) contains a slimy, highly viscous, mucinous substance of a mucopolysaccharide (hyaluronic

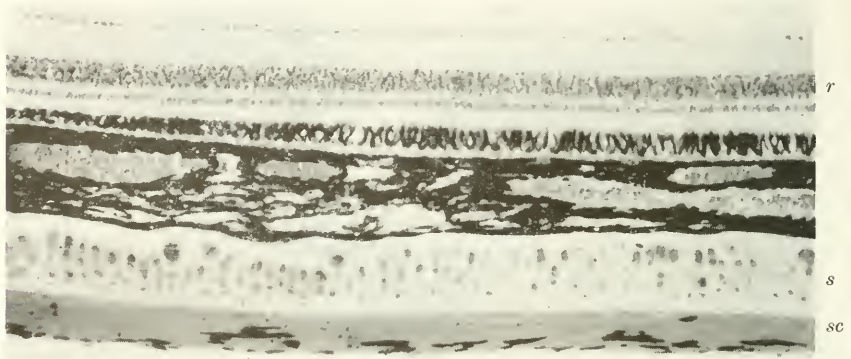


FIG. 498.—THE POSTERIOR SEGMENT OF THE GLOBE OF THE CHICKEN.  
*r*, retina ; *ch*, choroid ; *s*, scleral cartilage ; *sc*, sclera ( $\times 80$ ) (Norman Ashton).

acid) nature ; it is most concentrated (or more highly polymerized) close to the cornea and is perhaps secreted by the corneal endothelium (Abelsdorff and Wessely, 1909 ; Bárány *et al.*, 1957). It should be noted that the anterior chamber of the owl's eye is relatively enormous and it may be that this material allows the fluid in the anterior part to remain almost stagnant to decrease the turnover that would be necessary were the exceptionally large amount of aqueous to be renewed at the average rate.



The heron  
*Ardea*

The *uveal tract* has several peculiarities. The *choroid* is thick, particularly posteriorly, often especially so in the region of the macular area (Fig. 498). The lamina fusca lies directly on the scleral cartilage. Immediately external to the choriocapillaris there lies a stratum of feeding arteries, outside which is a thick layer of venous sinusoidal spaces traversed by radial cords of smooth (the heron, *Ardea*) or striated (the cross-bill, *Loxia*) muscle fibres and connective tissue of very variable distribution. These muscular cords, originally described by Wittich (1855), Pagenstecher (1860) and H. Müller (1861).

and most fully studied by Kajikawa (1923), are most marked near the fovea. It may be that they regulate the amount of blood in the choroid which in Birds is particularly distensible, swelling remarkably, for example, and becoming intensely engorged if the intra-ocular pressure is suddenly lowered by paracentesis of the anterior chamber (Abelsdorff and Wessely, 1909); others, again, consider that their contraction adjusts the position of the fovea in accommodation, acting after the manner of a fine adjustment of a microscope.

In the Picidae (woodpecker, *Colaptes*) the sinusoidal choroidal layer is filled with mucoid tissue, as if to provide a cushion against the repeated mechanical trauma of wood-pecking (Walls, 1942). Birds have no tapetum; the "eye-shine" seen in some species has been attributed to a reflex from Bruch's membrane (ostrich, *Struthio*).

The vascular layer of the choroid is continued forwards into the *ciliary region* without the intervention of an orbiculus, the whole zone being occupied by the numerous elongated ciliary processes; ventrally, in the region of the fœtal cleft, it is claimed that a particularly marked CILIARY CLEFT between the processes allows communication between the anterior and posterior chambers (Nüssbaum, 1901; Hess, 1912; Ischreyt, 1914). The ciliary processes and their associated uveal tissue angle sharply inwards to approach the lens, while the ciliary muscles cling closely to the sclera, thus separating the two components of the ciliary body and leaving a deep cleft-like space between the two layers traversed by the strands of the pectinate ligament (Fig. 499). The ciliary musculature, which is made up of striated fibres, resembles that of the lizard in its topography<sup>1</sup> (Fig. 500): both it and the muscles of the iris are supplied by a complicated plexus of motor and sensory nerves (Boeke, 1933). The meridional muscular bundle appears to be divided into two; anteriorly the MUSCLE OF CRAMPTON, a stout muscular band, arises from the inner surface of the cornea at its margin and is inserted into the sclera as it bulges axially in the ciliary region; more posteriorly BRÜCKE'S MUSCLE, arising from the inner aspect of the sheet of sclera which forms the anchorage of the pectinate ligament, is inserted into the posterior portion of the ciliary body, an insertion which is prolonged to the sclera by the TENACULAR LIGAMENT, thus relieving the choroid of mechanical strain. Accommodation, as in lizards, is mainly effected by the contraction of the meridional musculature forcing the ciliary body against the lens so as to deform it, tautening the fibres of the pectinate ligament meanwhile (Wychgram, 1913-14). Simultaneously the stout Crampton's muscle running from the cornea to the sclera like a bow-string, deforms the cornea and shortens its radius of curvature, an action much more pronounced in Birds than in lizards.



The ostrich  
*Struthio*

<sup>1</sup> p. 357.

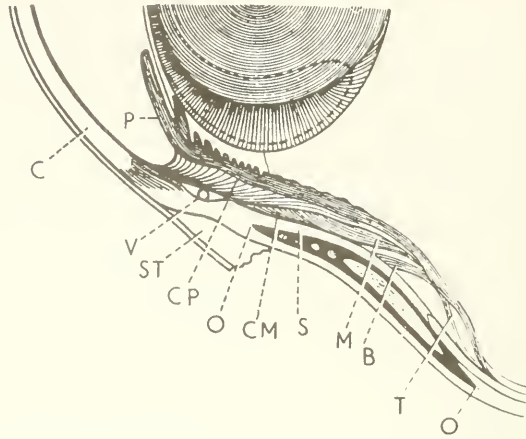


FIG. 499.—THE CILIARY REGION OF THE GOSHAWK, *ASTUR PALUMBARIUS*.

B, Brücke's muscle ; C, cornea ; CM, Crampton's muscle ; CP, ciliary processes ; M, Müller's muscle ; O—O, ring of ossicles ; P, ciliary process abutting the lens capsule ; S, fibrous sclera ; ST, subconjunctival tissue ; T, tenacular ligament ; V, ciliary venous sinus (after H. Müller, 1857).

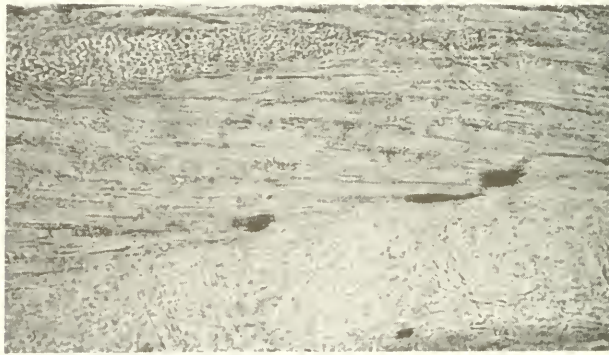


FIG. 500.—THE STRIATED FIBRES OF CRAMPTON'S MUSCLE IN THE CHICKEN ( $\times 240$ ) (Norman Ashton).



The cassowary  
*Casuaris*

These muscles are of considerable interest and have received much study. Crampton (1813) first described a muscle in this region in the ostrich, *Struthio*, and the anterior segment of the ciliary musculature has been called eponymously after him ; he termed it the *depressor corneæ*. Thirty-three years later, Brücke (1846) described a more posteriorly situated muscular zone in the eagle-owl, *Bubo orientalis*, and the cassowary, *Casuaris*, calling it the *tensor choroideæ*. Sometimes this latter muscle is divided into two—an anterior portion (*Müller's muscle*) which was first described by this author (1856) in the hawk, *Accipiter*, and a posterior, *Brücke's muscle*. There is probably little functional difference between these slips of muscles thus separated anatomically, nor is it easy to decide which is their fixed and which their mobile attachment ; connected as they are by aponeurotic membranes, they probably form a single functional system.





PLATE XI  
THE IRIDES OF BIRDS  
(Ida Mann)

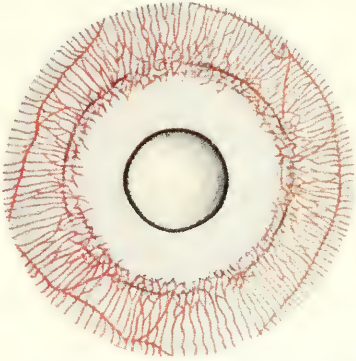


FIG. 1.—Jackdaw (albino), *Colaptes monedula*.



FIG. 2.—Pigeon, *Columba*.

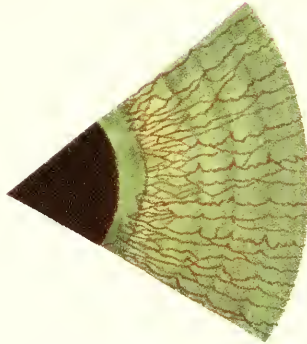


FIG. 3.—Duck, *Dendrocygna*.

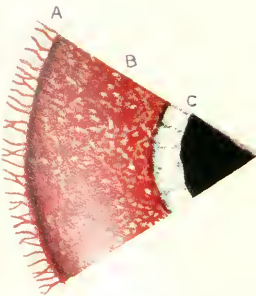


FIG. 4.—Rock-hopper penguin, *Eudyptes cecillius*.

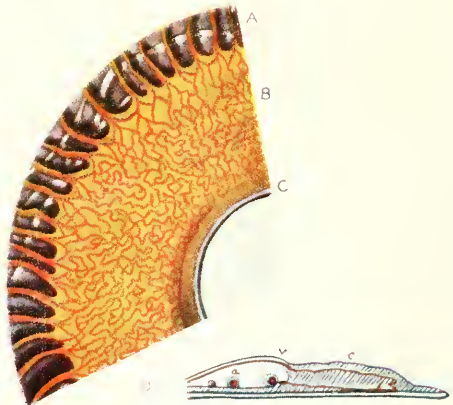


FIG. 5.—Scops owl, *Otus bakkamæna*.

A, zone of radial veins and deep circumferential arteries; B, sphincteric plexus; C, avascular circumpupillary zone; D, diagrammatic section through iris. a, artery; c, plexus; v, vein.

There are only incidental differences between these muscles in the various species of Birds. In diurnal predators they tend to amalgamate on the shortened nasal side and separate on the lengthened temporal side; in the swift, *Micropus*, the entire ring is symmetrical. In nocturnal predators Crampton's muscle is well-developed and Brücke's muscle is small and may be almost absent (most owls, Strigidae). Since deformation of the cornea is of no value in aquatic vision, Crampton's muscle is small in water-birds (as in diving ducks) or absent (as in the cormorant, *Phalacrocorax*), while in compensation and to attain the necessary accommodative range to change from aerial to aquatic vision, Brücke's meridional muscle is massive in these types and may even be supplemented by circular fibres as in the muscle of Müller in the human eye (cormorant; gannet, *Sula bassana*) (Ischreyt, 1914). A muscle homologous to the transversalis muscle of lizards has been described in the pigeon (Zalman, 1921).

The *iris* is remarkably thin at its ciliary attachment where it is reduced almost to the two ectodermal layers, thickens towards its mid-point and thins again at the pupillary margin. The ectodermal layers are both heavily pigmented and give rise to the striated sphincter and dilatator muscles. These are extremely active and unusually powerful, particularly the former which is richly vascularized; it braces the iris against the periphery of the lens thus assisting the ciliary musculature in the moulding of this tissue in the act of accommodation, at the same time confining the deformation to the axial region. The sphincter is particularly well developed in some amphibious birds (cormorant, *Phalacrocorax*; shearwater, *Puffinus*; gannet, *Sula*; and the sea-gulls, Laridae, etc.); in the cormorant, for example, it is able to force the axial portion of the soft lens as a conical protrusion through the pupillary aperture. The dilatator fibres form a complete layer behind the sphincter, running into the ciliary region, their unusually great development being perhaps due to the probability that they also play a part in compressing the lens on accommodation and provide a fixed anchorage for the sphincter (Grynfeltt, 1905; Hess, 1910; Zietzschmann, 1910; Wychgram, 1914; Zalman, 1921; Wehner, 1923; Anelli, 1934). In colour the iris is variegated. Most of the song-birds have a brown pigmentation resembling the mammalian type; but in other species brilliant lipochrome pigments are common, particularly yellow, bright blue and green, often giving the eye a bright colour-contrast with the rest of the body (Balducci, 1905) (Plate XI. Figs. 1 to 5).

This advertising habit is carried a stage further in the Peruvian guano cormorant, *Phalacrocorax bougainvillii*, the eye of which, with its dun-brown iris, is surrounded by a ring of naked skin coloured bright green. The colour of the iris is yellow in most owls, the pigeon, *Columba*, and the starling, *Lamprocolius chalybeus*; bright blue in the nocturnal oil-bird, *Steatornis*; sky-blue and chocolate in the yellow hang-nest, *Cacicus cela*; green in the cormorant and the duck, *Dendrocygna*, and the flamingo, *Phoenicopterus ruber*; white peripherally and chocolate with white concentric lines in the pupillary part in the budgerigar,



The swift  
*Micropus*



The gannet  
*Sula*



The shearwater  
*Puffinus*



The flamingo  
*Phoenicopterus*



The penguin  
*Eudyptes*

*Melopsittacus undulatus* ; white in the jackdaw, *Corvus*, and the crane, *Grus* ; and so on. In the rock-pigeon, *Columba livia*, it appears to be scarlet because of the richness of the superficial blood-vessels. In the honey-buzzard, *Pernis apivorus*, a layer of guanine-containing cells in the yellow iris makes the tissue opaque to transmitted light and a brilliant white to reflected light. Sexual differences occur in a few species ; thus the male breeding blackbird, *Euphagus cyanocephalus*, has a yellow, the female a brown iris ; again, in the rock-hopper penguin, *Eudyptes cristatus*, the colour of both the iris and the beak varies from red to yellow with the seasons (Mann, 1931 ; Lienhart, 1936 ; and others).

The *pupil* is always circular in Birds and very motile ; it responds relatively poorly, however, to changes in light-intensity, but actively to accommodation and, particularly in captive wild birds, so dramatically to emotional factors such as excitement or fear that it has been claimed to be under voluntary control. In domesticated birds, on the other hand, less alert and more placid on close examination, the ordinary response to light becomes relatively more conspicuous. There is sometimes an apparent consensual light reflex, slow in its onset and irregular in its degree ; Levine (1955) suggested that the reaction was due to light shining through the head to stimulate the retina of the other eye directly, and in birds such as the owl wherein the visual axes are parallel, no such reaction can be seen.

The vascular pattern of the iris is typical of the Sauropsida and conforms to the general plan seen in lizards (Mann, 1929-31) (Plate XI, Figs. 1 and 5). Several arteries enter at the periphery, run in a deep plane for some distance circumferentially and supply the rich capillary plexus associated with the sphincter muscle ; thence radial veins run superficially towards the periphery, sometimes raised up from the surface of the iris in high relief, sometimes largely obscured by pigment and sometimes completely so (the falcon, *Falco subbuteo*, or the shearwater, *Puffinus*). The sphincteric capillary plexus is usually prominent but is variable in extent ; it may be so broad as to occupy almost the entire surface of the iris (as in the oriental eagle-owl, *Bubo orientalis*, or the rock-hopper penguin, *Eudyptes cristatus*, or the pigeon, *Columba*) or may be reduced to a minimum so that the surface is largely occupied by the radial veins (as in the duck, *Dendrocygna*).



The house-sparrow  
*Passer domesticus*

At the angle of the anterior chamber the circumferential ciliary venous sinus forms a complex system lying in connective tissue close to the inner surface of the sclera, sometimes separated from it by the anterior end of Crampton's muscle. Two annular vessels encircle the eye associated with at least one large artery and sometimes with two (in the sparrow, *Passer domesticus*), and draining into the subconjunctival veins. Only occasionally, as in the kestrel, *Falco tinnunculus*, and the bull-finch, *Pyrrhula*, is the circle incomplete (Lauber, 1931).

The *lens* usually has a relatively flat anterior surface in diurnal t, almost plane in some species such as parrots (Psittaciformes),

but more spherical, although never completely so, in nocturnal and aquatic types (Figs. 501-3). It is always soft and readily deformed ; apart from its capsule it has no consistency (Rabl, 1898), and according to Kajikawa (1923), the soft mouldability is retained all through life into old age. In some aquatic species, particularly the cormorant, it compares in softness only with the lens of turtles. The system of sutures is simple, comprising a single line in some species, a star-shape

FIGS. 501 TO 503.—THE LENSES OF BIRDS.

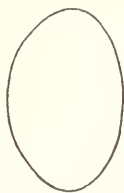


FIG. 501.—The pigeon.

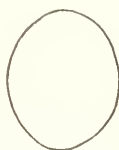


FIG. 502.—The owl.



FIG. 503.—The bullfinch.

Note the relatively flat anterior surface (to the right in each case).

in others. The ANNULAR PAD is usually well formed, sometimes enormous in diurnal predators with a high degree of accommodation, as in the hawk, wherein it occupies half the area of a cross-section of the lens (Fig. 504), smaller in nocturnal species (Fig. 505), still smaller in aquatic forms wherein the sphincter of the iris rather than the ciliary muscle is especially active in accommodation (as in the Anseriformes such as ducks, geese, swans, etc. ; the Ciconiiformes, such as herons, storks, spoonbills; and the cormorant), and very small indeed or even vestigial in running birds (Palæognathæ, particularly the kiwi, *Apteryx*) ; in the Australian goose, *Cereopsis*, a terrestrial bird which hardly ever leaves the ground, the pad is practically non-existent.

FIGS. 504 AND 505.—THE LENSES AND ANNULAR PADS OF BIRDS.

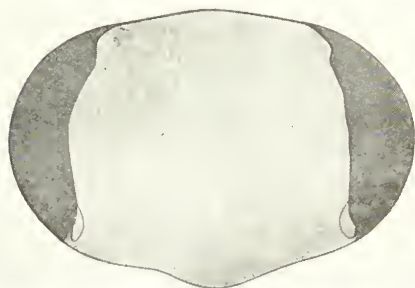


FIG. 504.—The lens of a diurnal predator (a hawk). Showing a very large annular pad.

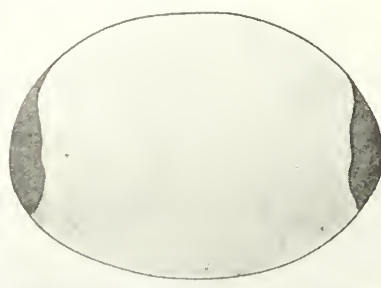


FIG. 505.—The lens of a nocturnal bird (an owl). Showing a small annular pad.



The zonular fibres arise over a wide area from and between the ciliary processes (Teulières and Beauvieux, 1931).

Between the annular pad and the main body of the lens a small vesicle filled with albuminous fluid remains as a remnant of the embryonic lens vesicle—the *CAVUM LENTICULI* of Franz (1934). To some extent this may be an artefact of preparation, but it probably aids the process of deformation when the lens is squeezed by the ciliary processes.

Ophthalmoscopically, the *fundus oculi* of Birds presents a remarkably constant picture which has been extensively studied and beautifully illustrated in a unique volume by Casey Wood (1917). The background of the fundus is usually fairly uniform and almost invariably besprinkled with pigmented dots of yellow or brown. Its colour varies from grey or a slate-colour to orange and red. In general, the fundi of diurnal birds are characterized by a grey or light brown background (such as the bluebird, *Sialia*) (Plate XII, Fig. 3); that of nocturnal birds tends to be yellow, orange or reddish (such as the kiwi, *Apteryx*, the tawny owl, *Strix aluco*, the European night-jar or goat-sucker, *Caprimulgus europaeus*) (Plate XII, Figs. 1, 2, 4); a multi-coloured background is more rare (buff and dull red in the American ostrich, *Rhea*; dark reddish-brown and grey in the bald eagle, *Haliaeetus leucocephalus*). Frequently choroidal vessels may be seen shining through, an appearance usually confined to a small segment of the fundus in its ventral part, as in the Australian pelican, *Pelecanus conspicillatus*, and the kestrel, *Falco tinnunculus* (Plate XII, Fig. 5); more rarely the vessels are generalized, as occurs in the tawny owl, *Strix aluco* (Plate XII, Fig. 2); as a rule these vessels are most apparent in nocturnal birds. Nerve fibres are usually not seen ophthalmoscopically; they are rarely visible in nocturnal birds, but in diurnal types they often radiate outwards from the disc, sometimes inconspicuously and running for a short distance only (Plate XII, Fig. 4) but occasionally covering a wide area (Plate XII, Fig. 3). The optic disc is invariably white and elongated into a long *CAUDA* (except in the kiwi, *Apteryx*) which runs ventrally along the line of the foetal fissure (v. Szily, 1922; Mann, 1924; Uyama, 1936); it is, however, almost entirely obscured by the pecten.

The *PECTEN*,<sup>1</sup> originally described by

<sup>1</sup> The name is derived from the French *peigne* (a comb), but in view of the fact there are no separate teeth in the structure, a more happily chosen name is the span *Fächer* (a fan). An early name was *Marsupium* (see Crampton, 1813).



The goat-sucker  
*Caprimulgus*



The ostrich  
*Rhea*



The bald eagle  
*Haliaeetus*



The pelican  
*Pelecanus*



FIG. 506.—VERTICAL SECTION OF THE RIGHT EYE OF A GOOSE.

Showing the temporal half of the globe. The pecten arising from the elongated optic disc is seen (Thomson).

PLATE XII  
THE FUNDI OF BIRDS

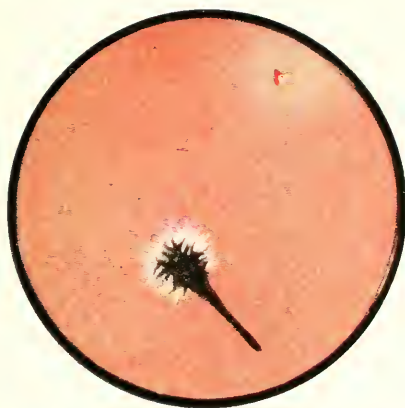


FIG. 1.—The kiwi, *Apteryx mantelli*.



FIG. 2.—The tawny owl, *Strix aluco*.



FIG. 3.—The bluebird, *Sialia sialis*.

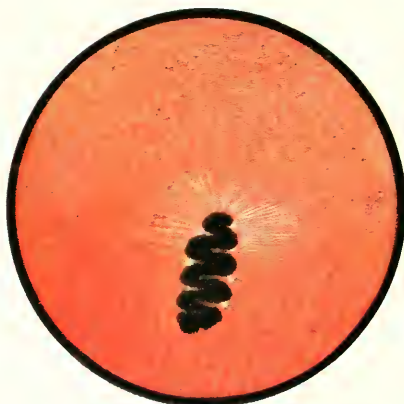


FIG. 4. The European nightjar, *Caprimulgus europaeus*.



FIG. 5.—The European kestrel, *Falco tinnunculus*.



FIG. 6. The albatross, *Diomedea*.

(Figs. 1-5, Casey Wood; Fig. 6, O'Day).

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Perrault (1676) whose observation was elaborated by Petit (1735), is a structure peculiar to Birds and forms the most dramatic feature of the fundus when viewed ophthalmoscopically. It appears in the ventral part of the fundus as a black velvety mass rising from the elongated optic disc, heavily pigmented particularly towards its apex. Beautifully and elaborately convoluted, it projects freely into the vitreous, usually moving undulantly with movements of the gel (Fig. 506). Morphologically two main types occur :

FIGS. 507 AND 508.—THE VANED TYPE OF PECTEN.

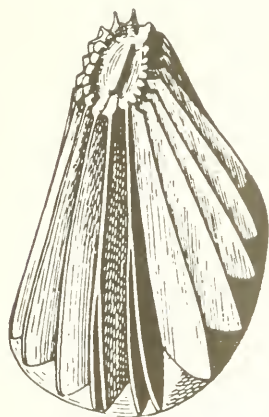


FIG. 507.—Diagram of the pecten of the ostrich, *Struthio* ( $\times 5$ ).

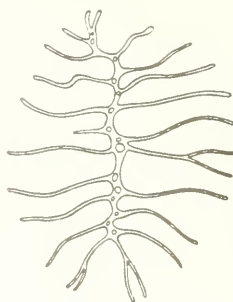


FIG. 508.—Section parallel to the base showing the central web and the lateral vanes (after Franz).

(1) *The vaned type.* In Palaeognathæ (except the cassowary and the kiwi) the organ is composed of a central vertical panel with laterally disposed vanes (Figs. 507–8). In the kiwi, *Apteryx*, it has a form resembling the conus of lizards (Fig. 512).

(2) *The pleated type.* In Neognathæ (and the cassowary) the whole organ is pleated upon itself like an accordion, the convolutions being held in place by a band-shaped apical BRIDGE running along the top (absent in the owl) ; if this is cut away, the pleats can be freely smoothed out (Fig. 509).

Although always built on much the same general plan, the pecten varies considerably in shape, size and the number of folds. To a certain extent its size and complexity vary with the visual acuity of the bird and its activity in daylight (Wagner, 1837 ; Virchow, 1901) ; active diurnal birds therefore tend to have a large and many-folded organ, nocturnal varieties a small and simpler structure.

The number of pleats varies between 5 and 30 (Wood, 1917 ; Kajikawa, 1923 ; Franz, 1934) (Figs. 510–11) ; 14 to 27 in the average ground-feeding or



The kiwi  
*Apteryx*



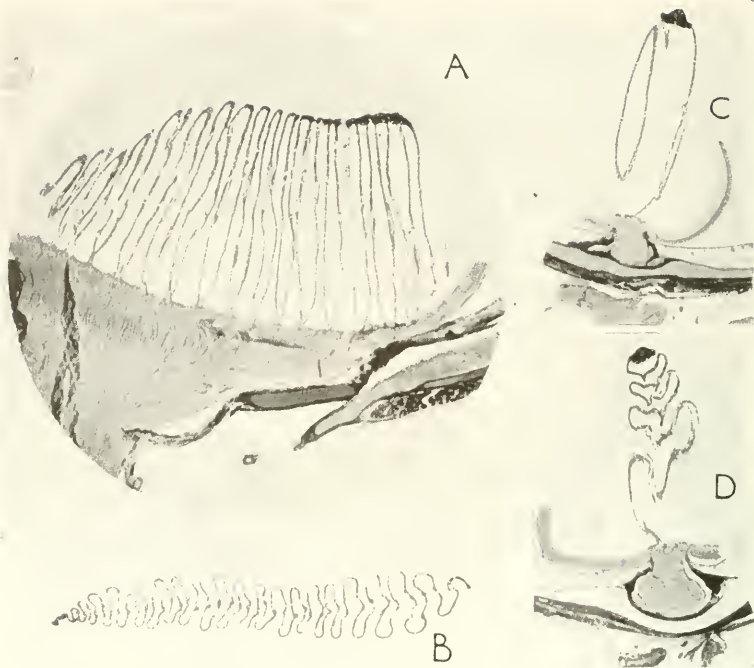


FIG. 509.—THE PLEATED TYPE OF PECTEN.

(A) vertical longitudinal section ; (B) transverse horizontal section ; (C) and (D) transverse vertical sections (Thomson).

perching (passerine) birds, 30 in the jay, *Garrulus* ; in predators the folds are thicker but fewer (13 to 17). Sea-birds and shore-birds tend to have fewer pleats, usually less than 12 ; Anseriformes (ducks and geese) average between 10 and 16 ; while the terrestrial Australian goose, *Cereopsis*, has only 6. Nocturnal sea-birds have very few (7 in the stone-curlew, *Edicnemus*). Other nocturnal forms have a similarly simple structure ; the swift, *Micropus*, has 11 pleats, the owl, *Bubo*, 5 to 8, and its relatives the European night-jar, *Caprimulgus*, 3 to 5, and the frog-mouth, *Podargus*, 3 to 4 ; none of these three members of the owl

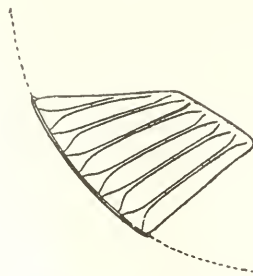


FIG. 510.—THE SIMPLE PLEATED PECTEN OF THE BARN OWL, *STRIX FLAM* (Casey Wood).

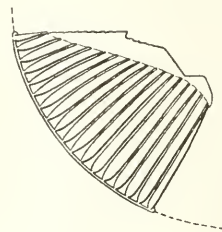


FIG. 511.—THE ELABORATE PLEATED PECTEN OF THE RED-HEADED WOODPECKER, *MELANERPES ERYTHROCEPHALUS*.

family possesses a bridge. The number of folds does not depend so much on the species of bird as on its habits. Thus among the Palæognathæ, the active diurnal ostriches, *Struthio* and *Rhea*, have 25 to 30 folds, the shy and crepuscular cassowary, *Casuarius*, 4 large and 2 small folds (almost a cone), and the nocturnal kiwi, *Apteryx*, none.

In its general form the pecten assumes a number of variations which have been classified into 4 types by Casey Wood (1917) (Figs. 512 to 520 ; Plate XII) :

(1) a stumpy structure projecting only a short distance into the vitreous, such as in the night heron, *Nycticorax*, and the secretary bird, *Serpentarius cristatus* (Figs. 513-4) :

(2) a curved structure sloping away from the visual axis ventrally,

FIGS. 512 TO 520.—TYPES OF PECTEN IN BIRDS  
(The fovea when present is shown) (after Casey Wood).

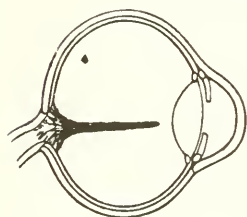


FIG. 512.—The kiwi,  
*Apteryx*.

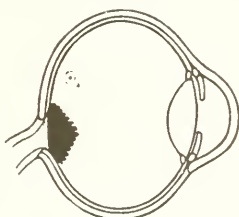


FIG. 513.—The common  
kestrel, *Falco tinnunculus*.

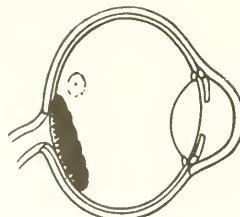


FIG. 514.—The secretary  
bird, *Serpentarius*.

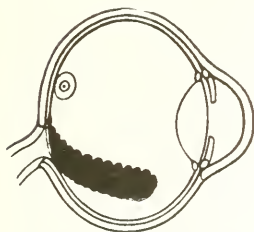


FIG. 515.—The herring-  
gull, *Larus argentatus*.

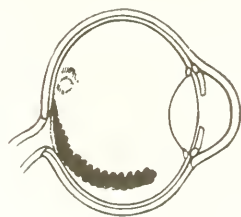


FIG. 516.—The wood-  
pigeon, *Columba  
palumbus*.

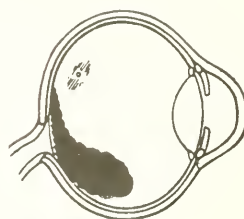


FIG. 517.—The American  
ostrich, *Rhea*.

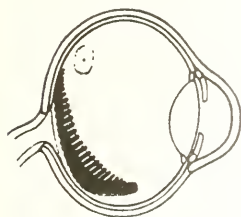


FIG. 518.—The laughing  
kingfisher, *Dacelo gigas*.

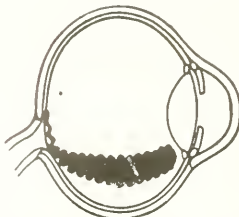


FIG. 519.—The chimney  
swallow, *Hirundo rustica*.

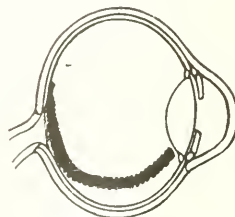


FIG. 520.—The blue jay,  
*Cyanocitta*.



The night heron  
*Nycticorax*



The secretary bird  
*Serpentarius*



The blue jay  
*Cyanocitta*

all the time, however, close to the bulbar wall and not penetrating far into the vitreous, such as in the pigeon, *Columba*, and the herring gull, *Larus argentatus* (Figs. 515-8) ;

(3) a slender sickle-shaped structure proceeding with a curved course from the disc towards the equator of the lens, such as in the blue jay, *Cyanocitta cristata*, and the chimney swallow, *Hirundo rustica* (Figs. 519-20), sometimes almost touching it, as in the Anseriform birds (goose, swan). Between these last two forms gradations occur, such as is seen in the great spotted woodpecker, *Dendrocopus major* ;

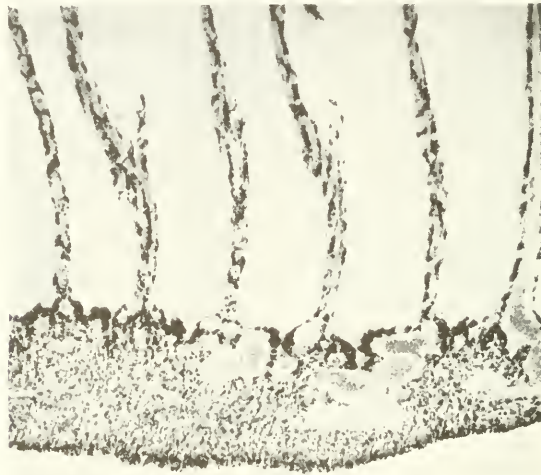


FIG. 521.—THE MICROSCOPIC STRUCTURE OF THE PECTEN OF THE CHICKEN  
( $\times 84$ ) (Norman Ashton).



The swallow  
*Hirundo*

(4) a cone-shaped structure without pleats, uniquely found in the kiwi, *Apteryx* (Plate XII, Fig. 1 : Fig. 512).

The histological structure of the pecten has received much attention (Fig. 521).<sup>1</sup> Essentially it is made up of a dense and elaborate capillary network associated with a comparatively small amount of supporting tissue ; this was originally (Mihalkovics, 1873 ; Leuckart, 1876 ; Kessler, 1877) and sometimes has subsequently (Bacsich and Gellért, 1935) been said to be mesodermal in origin, but following the work of Bernd (1905) and Franz (1908), has been generally accepted to be glial in nature. The glial tissue derived from the optic disc is more of the nature of a syncytium than cellular. The rich vascular plexus, which is composed of vessels of greater than capillary size, is supplied



The woodpecker  
*Dendrocopus*  
*major*

<sup>1</sup> Mihalkovics (1873), Denissenko (1881), Bernd (1905), Franz (1908-9), Blochmann (1910), v. Husen (1911), Ischreyt (1914), Kajikawa (1923), Mann (1924), Menner (1935), and others (1938).

by an artery derived from the hyaloid system emerging from the optic disc entirely separate from the choroidal circulation ; this artery runs along the base of the pecten and gives off ascending branches to each of the folds, whence the blood is gathered by large veins which combine to pierce the sclera and the cartilaginous cup at about the level of the middle of the pecten (Fig. 522). The walls of the capillaries contain no muscle or nerve fibres and between them lie epithelial pigment-containing cells ; the consensus of opinion is that there are no structures resembling sensory end-organs as was suggested by Franz (1908).

The function of the pecten has excited speculation ever since it was discovered ; this has, indeed, been one of the great puzzles in comparative ophthalmology and, based on the dramatic differences in its size and complexity in various species, more than thirty separate theories as to its possible use have been advanced. Unfortunately few of them are based on physiological experiment. It is to be remembered that the presence of the structures described by Franz (1908)—cilium-like hairs along the free edge of the bridge associated with bulbous cells with nerve fibrils running between the pecten and the nerve-fibre layer of the retina—has never been substantiated ; there is no evidence that the pecten is anything more than a complex capillary network or that it can be interpreted in any respect as a sense organ. Whatever accessory functions (if any) it may have, all authorities are agreed that its main role is *to assist in the nutrition of the retina* and the inner eye generally ; it is thus strictly comparable to the falciform process of teleostean fishes or the conus of lizards. The metabolism of birds runs at a high rate ; their normal temperature, for example, may be  $2^{\circ}$  to  $14^{\circ}$  F above that of Mammals. The metabolism of the cone-rich retina must be similarly high and, as we have seen, the size and the complexity of the pecten vary closely with the diurnal activity of the species concerned. Its nutritive function was proved by Abelsdorff and Wessely (1909) who showed the high permeability of the rich capillary system to the solutes of the blood, while its complex shape

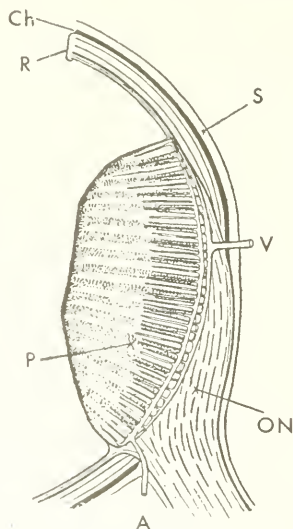


FIG. 522.—THE STRUCTURE OF THE PECTEN.

Showing its relations to the entrance of the optic nerve and its vascular connections. *A*, The supplying artery which sends a branch to each fold ; *Ch*, choroid ; *ON*, optic nerve ; *P*, pecten ; *R*, retina ; *S*, sclera ; *V*, efferent vein which receives a branch from each angle of the fold (Wood and Slonaker ; the illustration is inverted).



may be most simply interpreted partly as a mechanical expedient for buttressing the organ to give it rigidity but mainly as a means of increasing the available diffusing surface. From the optical point of view, there is little doubt that a pecten, occupying the space already taken up by the blind spot corresponding to the optic disc, is a more efficient method of nourishing the retina than the provision of a diffuse vascular system whether it be intra-retinal or supra-retinal. Indeed, the position of the pecten is such as to interfere as little as possible with the function of the retina (Petit, 1735), a point to be remembered when considering any possible optical function. In this respect the eyes of birds are optically superior to those of man.

The most popular subsidiary functions which have been ascribed to the pecten, four of them metabolic, four of them optical in purpose, may most conveniently be summarized as follows :

(1) An aid in the mechanism of accommodation (Beauregard, 1875 ; Rabl, 1900 ; Franz, 1909 ; Hess, 1910). It was suggested that an increase or decrease in turgidity makes the pecten act as an erectile organ capable of displacing the lens hydraulically. It is true that, in general, the size and complexity of the pecten vary with the accommodative capacity, but the accommodative capacity itself varies with the visual effectivity, that is, with the metabolic level of the retina. Any relationship between the two may therefore be parallel rather than causal and there is no evidence that the organ changes in volume with accommodative adjustments.

(2) A stabilizer of the intra-ocular pressure, acting as a large capillary-venous reservoir or as an organ of secretion or excretion to regularize the tension of the eye particularly during changes of altitude during flight (Franz, 1909).

(3) A means of smoothing out the considerable excursion in the ocular pulse-pressure.

(4) A means of maintaining a high temperature in the eye particularly at high altitudes in an animal with a metabolic rate as rapid as the bird (Kajikawa, 1923).

(5) To screen the retina from the sun's rays from above (Paul Bert, 1875) or, alternatively, to serve as a dark mirror, relaying images onto the retina, particularly from objects above. Thus it has been said to tone down excessive brightness from an image in the sky or, alternatively, to allow a ground-feeding bird to see a predator overhead (Thomson, 1928).

(6) To intercept rays reaching the eye simultaneously from in front and above (Beauregard, 1875). It is thus held to suppress binocular vision during monocular fixation or, alternatively, to suppress monocular diplopia during binocular vision.

(7) To aid the visual resolution of moving objects when in flight. Menner (1938) suggested that finger-like shadows were thrown upon the retina when the bird looked at the sun ; a moving object would thus be seen intermittently and therefore more clearly as are the spokes of a rotating wheel when viewed stroboscopically.

As an aid to navigation. This extraordinary faculty of birds has already been discussed.<sup>1</sup> We have seen that one of the necessities for orientation,

<sup>1</sup> p. 63.

in Wilkinson's (1949) view, is the observation of the sun's arc with great accuracy over a small excursion, and it is said that the pecten may play an important part in the visual analysis thus involved by acting as a fixed point when taking observations (Menner, 1938 ; Crozier and Wolf, 1943 ; Griffin, 1952).

*Areas subserving acute vision* are the rule in birds and are more elaborately constituted than in any other species.<sup>1</sup> An area centralis is almost invariably present, one fovea is the rule and two occur in many species.<sup>2</sup> The single fovea usually takes the character of a remarkably deep and well-formed pit, the depth varying with the excellence of vision ; it is thus deepest in swift-flying diurnal birds of prey. This central fovea subserves monocular vision. Only rarely does a single fovea occur in the temporal part of the fundus (owls). In bifoveate birds, usually diurnal birds of prey, the deep central fovea is associated with a temporal fovea which is shallow and less well formed, except in hawks and eagles, where it is deep ; the temporal fovea is used for seeing straight ahead and sometimes for binocular vision. The kingfisher, *Alcedo*, is unique in that it uses its central fovea for aerial vision, its temporal fovea for aquatic vision.<sup>3</sup> In addition to these macular areas with their foveæ, a ribbon-like band of specialized retina is sometimes associated (the *INFULA*),<sup>4</sup> running in the horizontal meridian through the fovea, particularly in birds that seek their food in the ground (*Struthio*, *Saxicola*) or in aquatic birds (Anseriformes: geese, swans, etc.). It would seem probable that this band subserving accurate vision may be designed for food-searching.

From the point of view of these areas for specialized vision, birds may be classified as follows, a classification which depends less on the type of bird than on its habits (Plate XII) :

(1) *Aforeal*. (a) Domesticated birds and some ground-feeders. There is a suggestion of an area centralis centrally but it is sometimes absent and at best is poorly defined, and a fovea is absent. Typical examples are the domestic fowl, *Gallus domesticus*, and the Californian valley quail, *Lophortyx californicus callicola*. In the turkey, *Meleagris gallopavo*, the guinea-hen, *Numida pucherani*, and the pigeon, *Columba*, there is an attempt at a shallow fovea. (b) Some sea-birds have a well-formed area centralis in which cones only are found but a fovea is absent—the shearwater, *Puffinus*, and the fulmar, *Fulmarus glacialis* (Lockie, 1952).

(2) *Central monofoveal*. This applies to the majority of birds in which a well-formed fovea situated centrally is surrounded by a large macular area.



Hawk,  
*Buteo*



Kingfisher,  
*Alcedo*



Winchat,  
*Saxicola*



Californian quail,  
*Lophortyx*

<sup>1</sup> Chievitz (1891), Slonaker (1897), Casey Wood (1917), Rochon-Duvigneaud (1919-23), Franz (1934), Walls (1942), Brückner (1949).

<sup>2</sup> Compare the lizard, *Anolis*, p. 365.

<sup>3</sup> p. 641.

<sup>4</sup> Lat. *infula*, a band (Casey Wood, 1917).



Owl-parrot,  
*Stringops*

(3) *Temporal monofoveal*. Owls (including the owl-parrot, *Stringops*) have a round macular area in the temporal quadrant with a shallow fovea (occasionally absent). The swift, *Micropus*, has in addition a trace of a central macula.

(4) *Infra-monofoveal*. Some ground-feeders and water-birds, including swimmers, divers and waders, have a central round macular area with a fovea of medium depth through which runs a horizontal band of acute vision. These include the albatross, *Diomedea cauta*, and the giant petrel, *Macromectes giganteus* (O'Day, 1940) (Plate XII, Fig. 6).

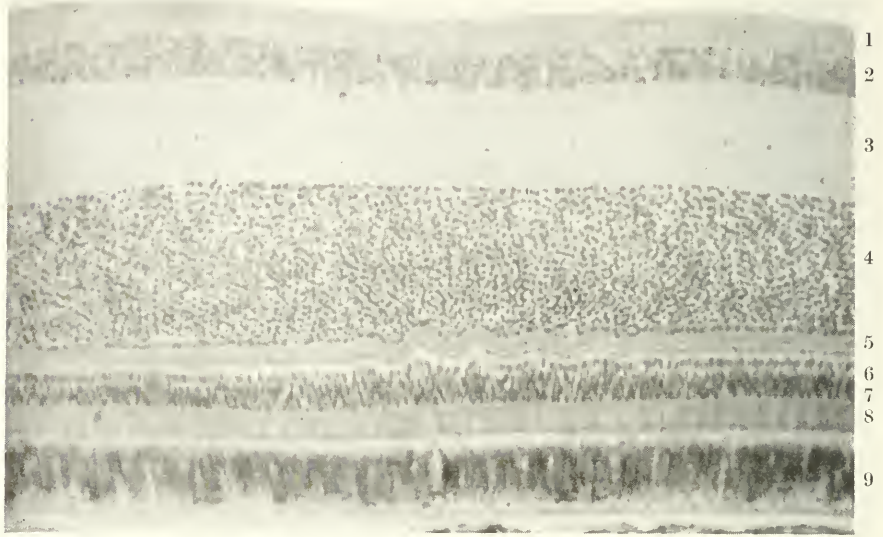


FIG. 523.—THE RETINA OF THE ALBATROSS, *DIOMEDEA*.

Section through the region of the central streak. 1, optic nerve fibre layer; 2, ganglion cells; 3, inner plexiform layer; 4, inner nuclear layer; 5, outer plexiform layer; 6, outer nuclear layer; 7, external limiting membrane; 8, visual cells; 9, pigment epithelium (O'Day).



Albatross,  
*Diomedea*

(5) *Bifoveal*. Many birds which seek their prey on the wing (passerines, kingfishers, bitterns, humming birds, *Calyptr*, and so on) are commonly provided with a deeply excavated principal central fovea and a subsidiary shallower temporal fovea surrounded by a smaller macular area lying about the same distance from the optic disc as the central fovea.

(6) *Infra-bifoveal*. Certain predators have two foveae associated with a band of clear vision. (a) The more common arrangement is two circular maculae connected by a band, as occurs in hawks, eagles and swallows; each macula has a fovea, the central being deepest. (b) Alternatively, as in the eagles wherein the temporal is deepest. (b) Alternatively,

the central fovea may be situated in a band but this does not include the temporal fovea which is situated above and separate from the former (the tern, *Sterna hirundo*).

(7) *Infular*. Some water-birds have a horizontal band only with no macular area and in it may be a linear trough-like fovea : gulls, flamingo.

Histologically the retina of birds is the most beautiful and elaborate in its architecture in the animal kingdom<sup>1</sup>; layers and sub-layers are clearly defined with each cell accurately in place (Fig. 523). As with other Sauropsida the pigmentary epithelial cells send slender processes containing fuscine granules extending inwards to the inner segments of the visual cells; their movements with variations of light and shade are rapid and extensive, possibly making up for the relative inertia of the pupil to light. In the visual retina the ganglion cells lie in 2 or 3 rows. The inner plexiform layer is unusually thick and stratified at the levels at which the arborizations of the amacrine cells deploy. The inner nuclear layer is expanded to have three strata—innermost the (integrative) amacrine cells which may even outnumber the bipolars, outermost the (conductive) bipolar elements, and in the middle a single compact row of Müller's fibres. This layer as a whole is thus very thick, and mainly because of the unusual development of this and the inner plexiform layer, the retina of Birds is some one-and-a-half times to twice as thick as that of the majority of Vertebrates, being approached in this respect only by a few Teleosteans.

The visual cells are slender and closely packed (Fig. 524). The retina is duplex in type, containing rods and single and double cones. The rods are slender with a long thin paraboloid and contain rhodopsin but have no oil-droplets, resembling in their general structure those of Chelonians or Crocodilians; in nocturnal birds they predominate while in diurnal types they may be very few and limited to



Tern,  
*Sterna*

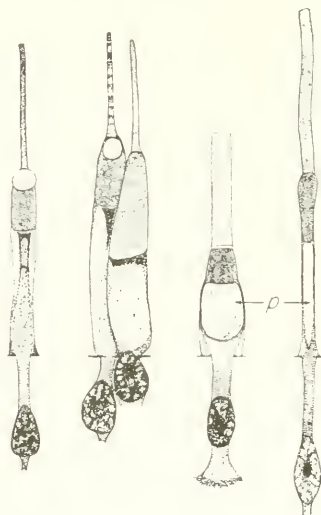


FIG. 524.—THE VISUAL CELLS OF BIRDS.

From the left, a single cone, a double cone, both from the periphery; a peripheral rod, and a central rod of the English sparrow, *Passer domesticus*. p, the paraboloid ( $\times 1,000$ ) (Gordon Walls).

<sup>1</sup> H. Müller (1856-63), Krause (1863-94), Merkel (1870), Dobrowolsky (1871), Schultze (1873), Waelchli (1881-83), Dogiel (1888-95), Cajal and Greeff (1894), Fritsch (1911), Rochon-Duvigneaud (1919-43), Kajikawa (1923), Kolmer (1924-36), Chard (1938), van Eck (1939), O'Day (1940), Walls (1942), Lockie (1952), Yamamoto (1954).



Kite, *Milvus*

the periphery. The cones, which in diurnal varieties greatly outnumber the rods, may be single or double. As in Chelonians, the single cones and the chief element in the double cones contain an oil-droplet, a prominent feature of the avian retina known to the early anatomists such as Treviranus (1837) and Hannover (1840). They are of various colours—red, orange, yellow—and colourless; they tend to be brightly coloured in diurnal types, particularly in small song-birds, but pallid

FIG. 525.—THE FOVEA OF THE ALBATROSS, *DIOMEDEA* (O'Day).Flicker, *Colaptes*

and almost colourless in nocturnal types. Green droplets are rare but have been described in a few species.<sup>1</sup>

At first supposed to be associated with colour vision (Krause, 1863), these oil droplets are now more generally considered to have a purely absorptive function, eliminating light-rays which are inconvenient qualitatively or quantitatively and aiding the acuity of vision.<sup>2</sup>

Stormy petrel,  
*Procellaria*

The fovea of Birds, particularly the central fovea, is remarkably deep with highly convex sides, resembling in its general shape the deep

<sup>1</sup> The domestic cock, *Gallus domesticus* (Waelchli, 1883), the kite, *Milvus*, and the parrot, *Chrysotis* (Kühne, 1882), the flicker, *Colaptes auratus* (Walls and Judd, 1906) and the stormy petrel, *Procellaria pelagica* (Rochon-Duvigneaud, 1943).  
p. 631.

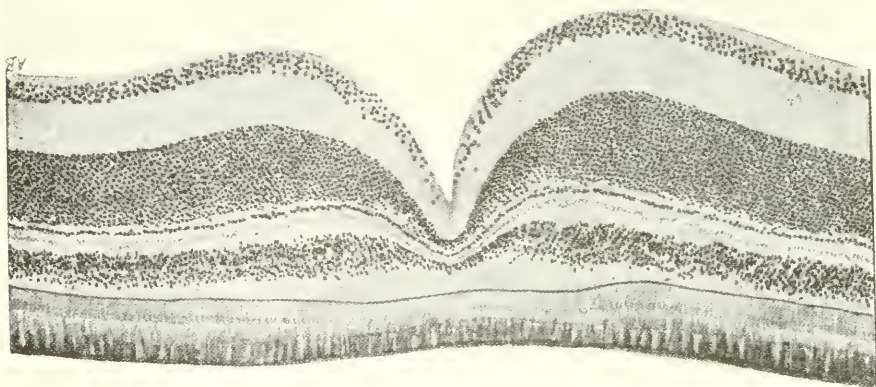


FIG. 526.—THE CENTRAL FOVEA OF THE SWALLOW, *HIRUNDO*.  
(Rochon-Duvigneaud).



FIG. 527.—THE LATERAL FOVEA OF THE SWALLOW, *HIRUNDO*.  
(Rochon-Duvigneaud).

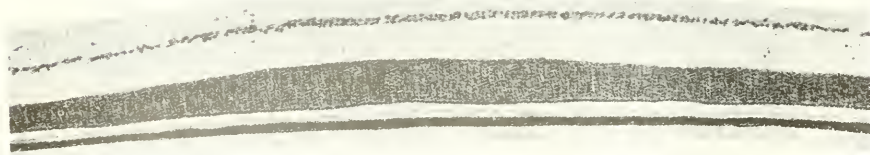


FIG. 528.—THE BAND-SHAPED AREA OF THE GANNET, *SULA*.  
(Rochon-Duvigneaud).

pit-like foveæ of lizards ; the temporal fovea is shallower and somewhat reminiscent of the human fovea (Figs. 525-7). In the central pit, single cones containing yellow oil-droplets predominate and rods are excluded. In the deep fovea of the Lacertilians and the shallow fovea

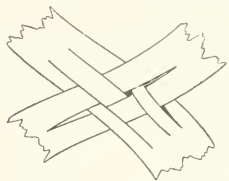


FIG. 529.—THE DECUS-  
SATION AT THE CHIASMA  
OF A BIRD.

of the Primates, the cones are slim and elongated, the nuclear layers are pushed away from the central area and the nerve fibres aggregated to form a layer of Henle ; in Birds, on the other hand, a considerable proportion of the nuclei is retained, a circumstance which would seem to support Walls's (1937) suggestion that the purpose of the fovea is not so much to remove cellular impediments to the incident light as to scatter it over a wider area.<sup>1</sup> In the band-

shaped areas of greater acuity the retina is thicker than usual so that it projects into the vitreous owing to an enormous increase in the number of nuclei in the bipolar layer, a considerable increase in the outer nuclei and a lengthening of the visual cells (Fig. 528). At the edge of the fovea this thickening of the retinal layers is further increased to form a definite ridge owing to the lateral displacement of cells from the foveal pit (O'Day, 1940).

The *optic nerve* is of the usual vertebrate type with a variable



FIG. 530.—THE MILKY EAGLE OWL, *BUBO LACTEUS*.

This bird is unusual ; showing the greater development of the upper lid which moves preferentially (photograph by Michael Soley).

<sup>1</sup> p. 658.



FIGS. 531 AND 532.—THE MECHANISM OF THE NICTITATING MEMBRANE IN BIRDS.

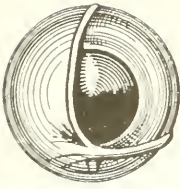


FIG. 531.—The anterior aspect of the eye of the turkey.

Showing the insertion of the pyramidalis tendon into the nictitans (Bland-Sutton).

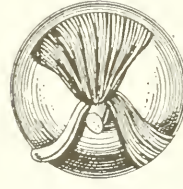


FIG. 532.—The posterior aspect of the eye of the turkey.

Showing the pyramidalis muscle continued as a tendon (below) looping through the sling formed by the quadratus muscle (above) (Bland-Sutton).

septal system : a single large septum may run to the axis where it subdivides ; the oligodendroglial cells are widely scattered and numerous, being thickly packed between the fascicules of nerve fibres (Prince, 1955). The decussation of fibres at the chiasma is complete with an elaborate interdigitation of fasciculi (Beauregard, 1875 ; Gudden, 1879 ; Gallerani, 1888 ; Faravelli and Fasola, 1889) (Fig. 529).

THE OCULAR ADNEXA. The *lids* almost cover the globe revealing only the small cornea through their (usually) circular aperture, deceptively hiding the relatively enormous eye (Fig. 530). In the

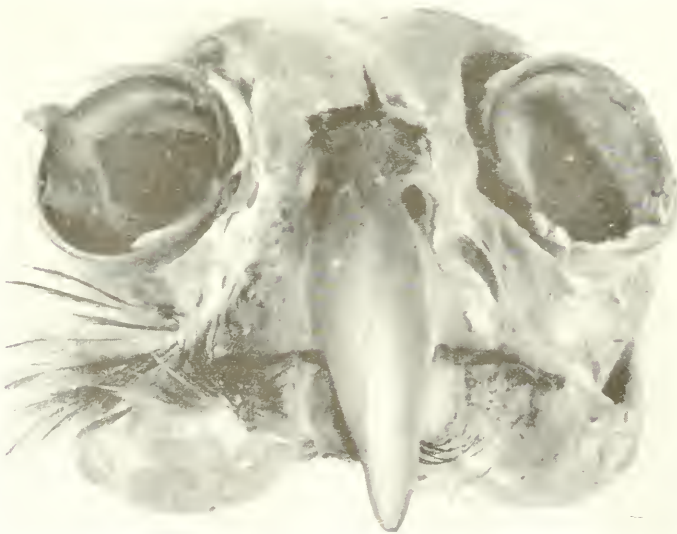


FIG. 533.—THE ORBITS OF THE SPARROWHAWK. *ACCIPITER*.



movements of the lids there is a more equable distribution of labour than is seen in Amphibians and other Sauropsidans (Bartels and Dennler, 1921): the lower is usually the more active of the two, but the upper lid also plays a considerable part. Except in parrots, the more active lower lid is provided with a fibrous tarsal plate composed of fibro-elastic tissue without cartilage (Naglieri, 1932). The nictitating membrane is well developed with a feather-like epithelium (Kajikawa, 1923, Kolmer, 1923-30; Anelli, 1935); it sweeps over the globe

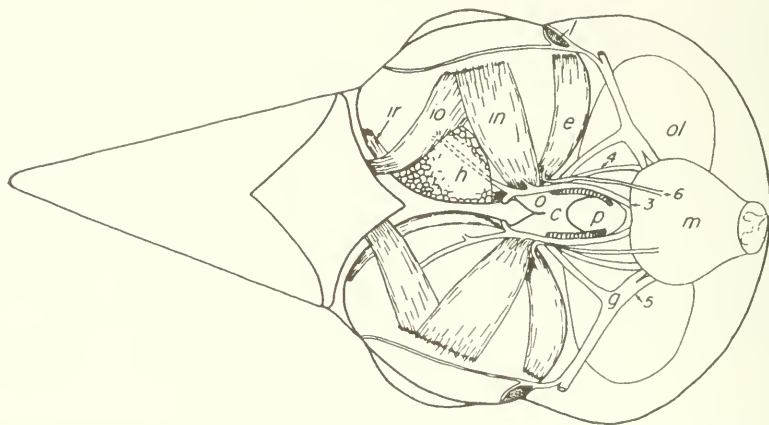


FIG. 534.—THE ORBITS AND BRAIN OF THE ENGLISH SPARROW, *PASSER DOMESTICUS*.

c, optic chiasma; e, external rectus; g, gasserian ganglion; h, harderian gland; in, inferior rectus; io, inferior oblique; ir, internal rectus; l, lacrimal gland; m, medulla; o, optic nerve; ol, optic lobe (midbrain); p, pituitary; 3, third cranial (oculomotor) nerve, supplying the superior, internal, and inferior recti and the inferior oblique; 4, fourth cranial (trochlear) nerve, supplying the superior oblique; 5, fifth cranial (trigeminal) nerve, several of the branches of which carry fibres to the eye and adnexa; 6, sixth cranial (abducens) nerve, supplying external rectus (Gordon Walls; drawn from Wood and Slonaker).

from the nasal canthus controlled by a pyramidalis muscle attached to the posterior surface of the sclera, the optic nerve being protected by lacing the tendon through the well-developed quadratus (bursalis) muscle (Figs. 531-2). It is probable that these two muscles are homologous with the retractor bulbi of Crocodilians (Wedin, 1953). The nictitans is very transparent and has no fibrous or cartilaginous basis; it is probable that it can cover the eye without affecting vision greatly, and in fact many believe that it is drawn over the cornea habitually as a protective goggle during rapid flight.

In diving birds (diving ducks; auks, Alcidae; and the loon, *Gavia*) the nictitating membrane has a central clear window which, being highly refractile,

adjusts the eye to under-water vision as it is drawn across immediately the head is immersed (Ischreyt, 1913-14) ; it thus acts as the lens of a diver's spectacle.<sup>1</sup>

The lacrimal gland with its single duct is ventro-temporal in location being associated, as is usual, with the more active lid ; although it is well developed in most water-birds, it is absent in the fully water-adapted penguins (Impennes) and also in the owl, *Bubo*. The harderian gland in its nasal position associated with the nictitating membrane, secretes a thick oily fluid ; in the cormorants it is exceptionally large and the secretion abundant, acting probably as a protection against sea-water. Meibomian glands are absent (Anelli, 1936). There are two slit-shaped lacrimal puncta, a larger upper and a smaller lower at the nasal canthus.

The orbits are very large to accommodate the enormous eyes and occupy a considerable proportion of the entire head (Fig. 533) ; as a rule they meet in the median plane, being separated from each other only by a thin bony interorbital septum (Bellairs, 1949).

The orbits are open in type <sup>2</sup> resembling in their general form those of Reptiles, particularly the tortoises ; it is to be remembered that the lack of protection to the anterior part of the globe that results from this configuration is to some extent compensated by the firm ring of imbricated scleral ossicles which encircles the sclera immediately behind the limbus.

Into this orbit the globe usually fits so snugly that the extra-ocular muscles must perforce be small (Fig. 534) ; a retractor bulbi is absent in Birds since the globe cannot be further retracted into a cavity which it already fills. In consequence, ocular movements are negligible or absent. As we shall see at a later stage,<sup>3</sup> this immobility of the eyes is compensated by the extreme mobility of the neck and the constant movements of the head. Nevertheless, although the muscles are tenuous, the four recti and the two obliques are normally represented, each being provided with the standard nerve supply characteristic of the vertebrate phylum.

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<sup>1</sup> p. 643.

<sup>2</sup> To this generalization there are exceptions, such as the Australian cockatoo, *Cacatua roseicapella* (Prince, 1956).

<sup>3</sup> p. 696.

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